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Darwin and barnacles

Darwin et les cirripèdes

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ABSTRACT

In this essay, I discuss the origin of Charles Darwin's interest in cirripedes (barnacles). Indeed, he worked intensively on cirripedes during the years in which he was developing the theory that eventually led to the publication of *The Origin of Species*. In the light of our present knowledge, I present Darwin's achievements in the morphology, systematics and biology of these small marine invertebrates, and also his mistakes. I suggest that the word that sheds the most light here is *homology*, and that his mistakes were due to following Richard Owen's method of determining homologies by reference to an ideal archetype. I discuss the ways in which his studies on cirripedes influenced the writing of *The Origin*.

RÉSUMÉ

Dans cet article, je discute de l'intérêt de Charles Darwin pour les cirripèdes. Il a travaillé intensivement sur ces petits invertébrés marins pendant la période de maturation de sa théorie, dans les années qui précèdent la publication de l'*Origine des espèces*. Je retrace les découvertes de Darwin dans la classification et la biologie des cirripèdes et aussi ses erreurs, à la lumière des connaissances actuelles. Je suggère que le maître mot pour suivre ces questions est le terme « homologie » et que les erreurs de Darwin dans l'interprétation de certains aspects de la morphologie des larves de cirripèdes sont dues au fait qu'il partageait à l'époque la démarche de Richard Owen de construction d'un « archétype » idéal. Je recherche les aspects de ses études sur les cirripèdes qui ont pu avoir des conséquences sur sa théorie.

1. Introduction

One might think that Darwin's favourite animals were the so-called 'Darwin's finches'. In my view, Darwin's favourites were without doubt the cirripedes (barnacles). Indeed, Charles Darwin spent as many as 8 years (1846 to 1854) studying barnacles, eventually writing two monographs on extant cirripedes, and two shorter ones on fossil cirripedes [1–4]. He was so involved in this work that, concerning a gentleman neighbour, one of his sons asked: "where does he do his barnacles?", as if studying barnacles were every father's main occupation. [5], p. 43.

In his autobiography, Darwin is rather ambivalent about his own work on barnacles, saying that it "possesses considerable value" and a few lines below, "I doubt whether the work was worth the consumption of so much time" [6]. In this essay, I will discuss Darwin's achievements in the classification and in the biology of the Cirripedia, as well as his *dreadful blunders* [6], in light of present knowledge. I suggest that the word that sheds the most light on both his achievements and his mistakes is *homology*. I will propose that his mistakes were due to following Richard Owen's method of determining homologies by reference to an ideal

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archetype. I will then discuss what impact Darwin's cirripede studies might have had on his thinking about and writing of *The Origin*.

2. Why – and why not – the cirripedes?

At first glance, the period of barnacle studies appears as an interruption in Darwin's reflections between the first drafts of *The Origin of Species* (1842 and 1844) [7] and the publication of the first edition (1859) [8]. Indeed, the monographs on the Cirripedia appear quite different from Darwin's more famous books, including *The Origin*, *The Descent of Man* and others. The monographs follow the typical harsh style of systematics. Each genus/species name is first given and discussed, with all its synonymous names; this nomenclature is followed by a short description in Latin and then by a more detailed description in English, with remarks on noteworthy peculiarities. Each of Darwin's two volumes on extant cirripedes includes a series of plates showing anatomical details. Actually, Darwin provided an exhaustive catalogue of all free-living cirripede species known at his time. Many of these were first described by him. Some historians have speculated that Darwin produced his highly systematic cirripede monographs with the aim of being acknowledged as a 'true' zoologist before launching his controversial theory of evolution. However, Charles Darwin was already famous and recognised as a major naturalist long before publishing his cirripede studies. Indeed, he was well known in the scientific community even before his return to England in 1836, his letters from the Beagle having been read by his correspondents at sessions of prestigious scientific societies. Furthermore, he was elected Fellow of the Royal Society as early as 1839, upon launching the first volumes of the *Zoology of the Voyage of HMS Beagle*.

Most probably, Darwin's interest in the cirripedes was in line with his previous work on and interest in the marine invertebrate animals collected during the voyage [9,10]. He was strongly motivated by his discovery of a peculiar barnacle, as he relates in his autobiography: "When on the coast of Chile, I found a most curious form, which burrowed into the shells of *Concholepas* [a sea snail], and which differed so much from all other Cirripedes that I had to form a new sub-order for its sole reception. Lately, an allied burrowing genus has been found on the shores of Portugal. To understand the structure of my new Cirripede, I had to examine and dissect many of the common forms: and this gradually led me on to take up the whole group." It often takes more time to complete a scientific project than one expects upon launching it. This event is not so surprising here, because, as Darwin pointed out, "The Cirripedes form a highly varying and difficult group of species to class" [6]. To me, this illustrates well the way in which Darwin practiced science; he undertook much work and made many precise observations in order to nourish large speculations.

3. Darwin's achievements in the biology of barnacles

Because of their calcareous shell, Cirripedes were long thought to be molluscs. In his *Règne animal* (1817) [11], Cuvier classified them as the 6th class of molluscs, yet stressed that "they present, by several respects, a kind of intermediary between this embranchment and that of the Articulates". We can imagine how difficult classifying the Cirripedia must have been in Darwin's time, if we recall the great 1830 dispute between E. Geoffroy Saint-Hilaire and Georges Cuvier. At the core of that debate lay the issue of whether all animals share a single body plan, or whether the body plans within each *embranchement* are distinct [12].

In fact, cirripedes have articulated limbs; in that respect they deserve the term 'Arthropods'. It was only after John Vaughan Thompson's [13] "capital discovery" [1], p. 8, of cirripede nauplii, a larval form typical of crustaceans, that the scientific community of the time recognized them as belonging to the Crustacea. When Darwin undertook his studies on cirripedes, there were still some uncertainties about this, and he dedicates the first pages of his book to refuting certain authors' claims for including Cirripedia in other groups, not only molluscs but also annelids (!) [1].

Darwin's main purpose for this work was to provide a comprehensive systematic review of the species belonging to the Cirripedia. He based his classification on descriptions of adult morphology. Mainly, he attended to the number and forms of the plaques (which he called "valves") composing the calcareous shell, and to the muscles attached to them. At his time, each author used his own nomenclature in describing barnacles' shells and shell parts, thus generating great confusion [3], p. 3. Darwin coined a specific name for each valve according to its relative position (Fig. 1). This precise nomenclature allowed him to compare shell morphology across species. In a sense, he thus applied Geoffroy Saint-Hilaire's "*principle of connections*" [14] to derive homology from comparative anatomy. The terms coined by Darwin are still used by cirripede specialists today [15].

He provided a detailed account of various biologically significant traits, such as larval development and metamorphosis, nervous system and sense organs, feeding and growth, and geographical habitats. These traits are shared by most species, so he grouped his observations on them into introductory chapters at the beginning of each volume, probably to avoid repetitions.

These introductory chapters comprise a large part of each monograph (66 out of 400 pages in the first volume, and 175 out of 600 pages in the second one). In my view, these chapters are not the least interesting parts of the books. In them, Darwin accurately described cirripede larval development. Within this development, he distinguished two main steps: the naupliar step; and the step in which the larva becomes what we now call a cypris, but which he called a "*pupa*", likening it to the pupa of holometabolous insects. Indeed, the metamorphosis of the cypris into the juvenile cirripede is as profound as that of a caterpillar into a butterfly. Similarly, but convergently, it involves a lot of cell and tissue lysis. He was right to homologise the natatory (thoracic) limbs of the cypris to the cirri of the adult. Countering the previous belief that cirripedes were always hermaphrodites, he described males as epizootic creatures living in close relation with females or with hermaphrodite adults. He called them

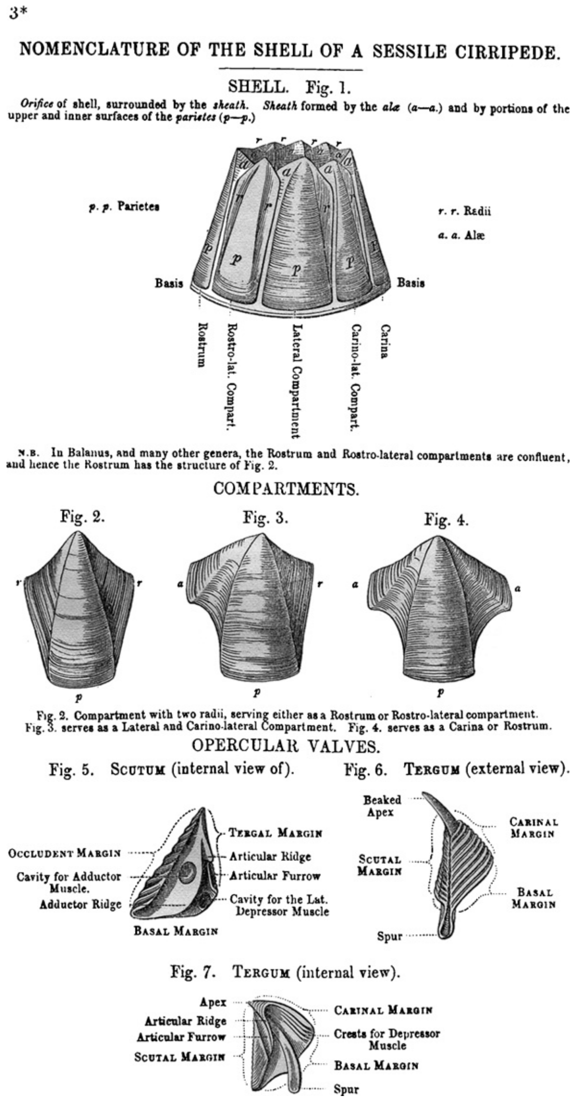

Fig. 1. Darwin's nomenclature for the valves of sessile barnacles. From [3], p. 3.

"complemental males" [1,3]. Darwin was rightfully proud of this finding, writing in his autobiography: "This latter discovery has at last been fully confirmed; though at one time a German writer was pleased to attribute the whole account to my fertile imagination" [6].

4. Darwin's blunder about the cement gland

What were Darwin's blunders? In his autobiography, Darwin wrote: "I discovered the cementing apparatus, though I blundered dreadfully about the cement glands" [6]. First, Darwin described how the cypris larva settles: "In the larva, the cement escapes through the prehensile antennae" [he meant the first antennae, also called antennulae]. Immediately following a lengthy discussion of how this occurs in the larvae of a number of pedunculate cirripedes, Darwin turned to the cement apparatus in adults. Regarding this, he surprisingly assumed, "how extremely improbable it must appear" (his own words), that the cement gland is formed from a part of the ovarian tube! [1], pp. 36–38. Why did he do so? He could not find any trace of antennae at the base of the peduncle, and as the peduncle is full of ova, he thought that the peduncle itself was an ovarian tube. He made good observations of the larvae: the cement glands are actually located within the antennulae. He based his hypothesis about the cement gland in the adult only on the gland's location, although he was perfectly aware of the huge modifications that occur during the metamorphosis of the cypris to the juvenile cirripede, during which the anterior end becomes basal [16,17].

However, this is not the only blunder that Darwin made during his studies on cirripedes, and I will now review some of his other mistakes.

5. Darwin's blunders about homology of naupliar limbs

Darwin made mistakes in the interpretation of the limbs of the nauplius larva (Fig. 2). Cirripede nauplii bear two curious pairs of 'appendages' in the front of their heads. The more anterior ones are the so-called 'frontal filaments'. Such frontal filaments are not observed in any other crustacean species, except in remipedes. Remipedes are very peculiar crustaceans, living in marine caves, and have only recently been discovered [18,19]. Darwin erroneously thought the cirripedes' frontal filaments were articulated [20] (Fig. 2, b). Their position and their supposedly articulated morphology led Darwin to interpret them as the first pair of antennae [1]. This homology has now been refuted, because in crustaceans, the first antennae are connected to the deutocerebrum, or the second part of the arthropod brain, whereas the frontal filaments are connected to the protocerebrum [20–22]. The second curious pair of appendages present in cirripede nauplii comprises the so-called 'horns' (Fig. 2, c). These horns are specific to cirripedes. They are found in nauplii belonging to all three cirripede orders, but are absent in all other crustacean nauplii, including those of the ascothoracids, the cirripedes' sister-group. The horns are hollow tubes, and Darwin interpreted them as "cases including the second pair of antennae". However, they do not contain any appendage. Rather, they are likely chemosensory organs, as suggested by the presence of pairs of characteristic neurons (Blin, Mouchel-Vielh and JD, unpublished observations). As a consequence of his misinterpretation of the anterior appendages, Darwin mistakenly took the other three pairs of appendages (Fig. 2 e, f, g) to be thoracic appendages. These three pairs of appendages are actually those usually found in all nauplii: the first and second antennae and the mandibles. He might have mistaken them for thoracic appendages because they are used not for sensation or feeding, but

[1] Contrary to the other mandibulate arthropods, i.e. hexapods and myriapods, crustaceans bear two pairs of antennae. The anterior-most antenna, also called antennula, is homologous to the single antenna of hexapods and myriapods.

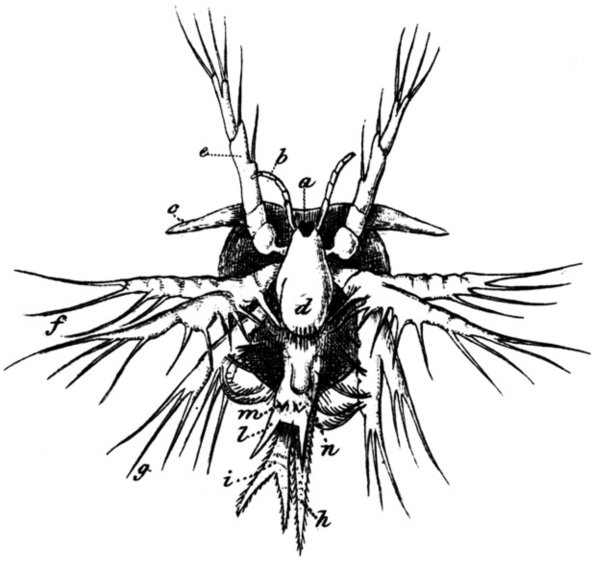

Fig. 2. Darwin's interpretation of naupliar appendages. Nauplius larva of *Chtamalus stellatus* (a sessile barnacle). Darwin's legend: a: eye; b: first pair of antennae; c: horns, including the second pair of antennae; d: mouth; e: first, uniramous natatory leg (homologically the second thoracic limb); f: second, biramous natatory leg (homologically the third thoracic limb); g: third, biramous natatory leg (homologically the fourth thoracic limb). Modern interpretation: a: eye; b: frontal filaments; c: horns, sensory organs; d: labrum; e: first uniramous antenna (antennula) (used as a natatory appendage); f: second, biramous antenna (used as a natatory appendage); g: third, biramous mandible (used as a natatory appendage).
From [3], plate XXIX, Fig. 10.

for swimming. In fact, this is their function for all crustacean nauplii. [2]

To me, this mistake of Darwin's is more surprising than his mistake about the foremost 'appendages,' for two reasons. First, he rightly noticed that what he homologized to the second thoracic limb was actually uniramous, i.e. composed of a single branch, whereas the next two appendages were biramous, or composed of two branches. This might have attracted his attention, as uniramy is characteristic of the antennula, whereas the other naupliar limbs are biramous. Second, he should have been aware that shared function, whether it be natatory, sensory or alimentary, is not a good criterion for homology. He underscores this several times in *The Origin*, clearly establishing "the very important distinction between real affinities and analogical or adaptive resemblances" emphasizing that "analogical or adaptive characters, although of the utmost importance to the welfare of the being, are almost valueless for the systematist" [8]. Thus, Darwin himself critiques the reasoning behind his own mistake about the naupliar appendages, which are cephalic and not thoracic.

6. Darwin and the abdomen of thoracican cirripedes

In his drawing of the internal anatomy of the sessile barnacle *Balanus tintinnabulum* [3], (plate XXV, Fig. 1, here shown as Fig. 3), Darwin clearly represents the six thoracic segments, each bearing biramous cirri (a single pair is drawn in the figure). These segments are not followed by any abdomen (arrow in Fig. 3). The presence of an abdomen has long been a contentious issue in cirripede biology; some adhere to the view of a complete absence of the abdomen [23], and others to the view that a vestigial abdomen is still present [16]. Studies conducted by my colleagues and I have revealed the presence of a vestigial abdomen consisting of three to four segments in the nauplius larva [24,25]. This larval abdomen disappears during the metamorphosis of the nauplius to the cypris stage [25], except perhaps in some acrothoracican species where it remains in the cypris as four tiny segments intercalated between the thorax and the non-segmented posterior end of the body, which is called the 'telson' [26].

What does Darwin say about the abdomen? He based his description of the abdomen of the "larva, last stage", i.e. the cypris, on his observation of the cypris of *Lepas australis*, [1] p. 14, which he harvested on the coasts of Patagonia during his voyage on the Beagle. These larvae "are of unusual size, namely from 0.065 to even almost 0.1 of an inch in length", that is, about 3 mm, or 10 times as long as that of the cypris of European *Lepas* species. Indeed, this exceptional size greatly facilitated observations and dissections. In the cypris, he described a small abdomen, consisting of three segments. In my opinion, what he calls 'abdomen' is actually the telson, the non-segmented posterior end of the arthropod body. Indeed, Darwin's

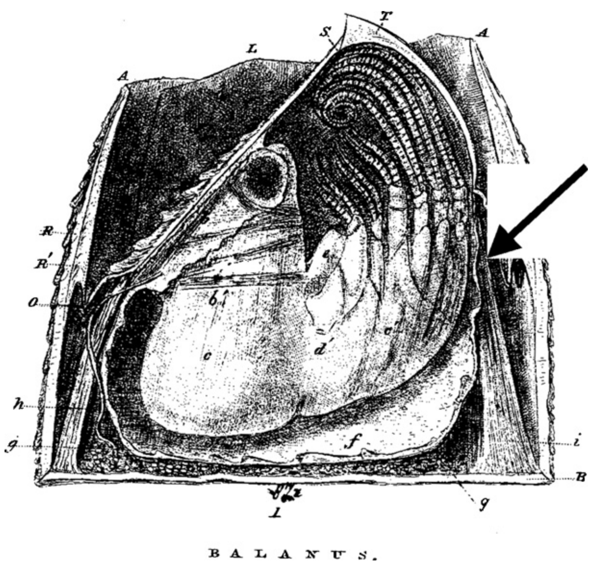

Fig. 3. Darwin's internal anatomy of an adult sessile barnacle. Darwin's legend: *Balanus tintinnabulum*; an enlarged longitudinal section through the shell and sack, with the right-hand scutum and tergum and the right-hand half of the shell and basis removed, exhibiting the body of the animal not in section. The cirri are exhibited only on one side. Arrow is mine.
From [3], plate XXV, Fig. 1

[2] In that respect, Darwin did not follow John Vaughan Thomson, who correctly interpreted cirripede nauplii as bearing "*three pairs of members, the most anterior of which are simple, the others bifid, having his back covered by an ample shield, terminating anteriorly in two extended horns, and posteriorly in a single elongated process*" [21b].

description of "caudal appendages" exhibited by the so-called 'abdomen' precisely corresponds to the furca, which is the usual appendage of the telson. In addition, he states: "the abdomen contains only the rectum and two delicate muscles running into the two appendages, between the bases of which the anus is seated". Actually, the anus opens into the telson in all arthropods.

In another instance [1], p. 28, he wrote: "the abdomen, which we know becomes in cirripedes after the metamorphosis, rudimentary". Thus, Darwin was taking the stand that an abdomen, albeit a reduced one, is present in both the larval and adult stages of thoracican cirripedes. Yet, he created the order 'Thoracica', which he described as "body formed of six thoracic segments, generally furnished with six pairs of cirri, abdomen rudimentary" [3], p. 30. The very name he gave to this order accentuates the fact that the trunk of these cirripedes is mostly composed of a thorax.

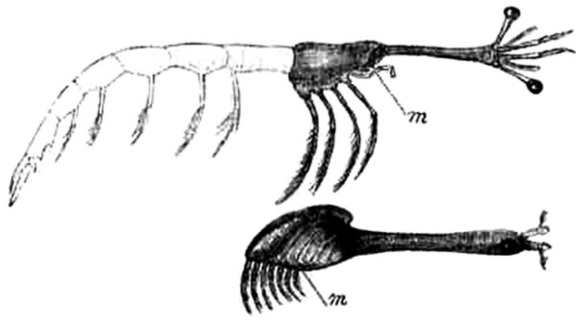

Fig. 4. Darwin's comparison between a decapod crustacean and a cirripede. See text for comments.
From [1], p. 28.

7. Darwin and the Cirripede archetype

Without any doubt, Darwin was convinced by Vaughan Thompson's evidence from larval morphology that the Cirripedia actually belong to the Crustacea. Still, he tried to find additional evidence for this in the body plan of the adult. His approach was explicitly to construct the cirripede 'archetype' and to compare it to the crustacean 'archetype'. The archetype concept had been proposed by Richard Owen a few years before Darwin's cirripede monographs [27]. In Owen's thinking, the archetype is an ideal model to which the anatomist can refer in order to draw homologies between species, despite those species' anatomical differences. At the time, Owen was the leading British comparative anatomist. Because of his expertise, Darwin gave him the vertebrate fossils he had collected in South America during the Voyage for description and analysis. Indeed, Owen was the first contributor to *The Zoology of the Voyage of HMS Beagle* (1838), a publication devoted to Darwin's observations and collected material. Owen later became a fierce opponent of Darwin's theory. As evidence of this, he acted as an advisor to Bishop Wilberforce for the famous Oxford lecture in which the Bishop was opposed by Thomas Henry Huxley.

On p. 28 of the first volume of his *Monograph on the Cirripedia* [1], Darwin presents a very curious figure (Fig. 4), which "gives at a glance the homologies of the external parts" between a pedunculate barnacle, *Lepas*, and another crustacean, *Leucifer*. The latter, now called *Lucifer*, is a decapod malacostracan. It is a relative of the peneids, the large prawns more commonly known as *gambas*. Why did he choose this species? First, it is a malacostracan. Indeed, Darwin wrote [3], p. 562: "The archetype crustacean consists of twenty-one segments". This fits well with the body plan of malacostracan crustaceans, which is composed of six cephalic, eight pereionic (thoracic) and six (seven in Leptostraca) pleionic (abdominal) segments. Thus, although Darwin was well aware of the diversity in morphology and body plans among the Crustacea, he took the Malacostraca as representatives of the "true crustaceans" [1], p. 28. In this respect, Darwin followed Milne-Edwards [28], to whom he dedicated his monographs on the Cirripedia. Second, like some but not all other crustaceans, *Lucifer* has a long rostrum and pedunculated eyes, which the figure demonstrates. I wonder whether he chose these characteristics to enforce the overall similarity of shape between the two crustaceans. The pleion (abdomen) of *Lucifer* "is given only in faint lines [because] the abdomen, which we know becomes in cirripedes after the metamorphosis, rudimentary, does not fairly enter into the comparison". Curiously, the sketch of *Lucifer* is so inaccurate that it is hard to reconstitute the malacostracan body plan from it.

Even more curious is the drawing of the cirripede species. Seven pairs of cirri are drawn, suggesting seven thoracic segments, instead of six (see above). The anterior end is more surprising still. Darwin wrote: "the lower figure is a mature *Lepas*, with antennae and eyes, which are actually present in the larva, retained". Thus, the picture does not show a real animal, but a chimera, with mixed characteristics, some belonging to the adult, but some found only in the larva. Darwin did not find antennae at the base of the peduncle in the adult (see above). What he actually found is that, *in the larva*, the cement gland is located within the antennulae. While this is correct, it does not imply that the antennulae are located at the tip of the peduncle *in the adult*. Conversely, the adult cement glands, which derive from the larval ones, are in fact located at the base of the peduncle [15]. Furthermore, both naupliar and compound eyes degenerate during the post-settlement metamorphosis of the cypris into the juvenile [16]. Yet Darwin put them near the tip of the peduncle, because he thought that this represents the anterior of the animal, where the eyes *would* be, if they were maintained.

We can take for granted the homology of the six cephalic segments between Cirripedia and Malacostraca. Cirripedes have six thoracic segments, while malacostracans have eight. To homologize the body plans of these two different crustaceans segment by segment, Darwin hypothesized that in the thoracican cirripedes "there must be two segments missing between the outer maxillae and the first thoracic pair of legs" [1], p. 27. Darwin found these two lacking segments in a curious cirripede he called *Proteolepas bivincta*, for which he created a special order, the 'Apoda' [3], pp. 587–605. The order comprises only this species, which was described by Darwin alone from a single specimen. It is no longer found. Re-examining

Darwin's specimen, Bocquet-Védrine showed that it was not a cirripede [29–30], but actually an isopod crustacean that parasitizes cirripedes. Adding its two additional 'thoracic' segments and three abdominal ones (see above), Darwin brought the number of segments in the cirripede archetype up to 17, as compared with the 21 of the 'archetypal crustacean', "the four missing being abdominal, and, I presume, the four terminal segments".

This exemplifies well the drawback of the 'archetype' approach. The archetype is an ideal model. It does not represent any real animal, extant or fossil. In order to construct the 'archetype', the naturalist adds his own prejudices to his observations. This allowed Darwin to depict an imagined cirripede as the illustration of the archetype!

8. Darwin's Abdominalia

Besides the Apoda, devoted to the single '*Proteolepas*', and the Thoracica, comprising the large majority of the other cirripedes he described, Darwin created a third order within the Cirripedia: the 'Abdominalia' [3], pp. 563–586. This order includes a single species, specifically the "most curious form" that Darwin found on the coast of Chile within the shell of a marine gastropod, and for which he undertook the whole systematic work on the Cirripedia. I wish to emphasize the meaning of this discovery. First, it was not so easy to discover such an animal in the shell of a gastropod. Indeed, *Cryptophialus minutus* is not like a hermit crab that you might see inhabiting an empty gastropod shell. Rather, it lives in a hole it has drilled within the shell of a living sea snail. Moreover, it is very tiny. Hence, its species name is *minutus*. So, you cannot find it without cautiously dissecting the snail's shell. Second, Darwin rightly recognized it as a cirripede, which clearly shows the degree of his knowledge and interest in marine invertebrates at the time of his trip on the Beagle, long before he started his very tedious cirripede studies.

This is the first peculiar trait of *Cryptophialus*. The most common cirripedes, sessile or pedunculated, are all fixed animals as adults, but they live on the outside of the substrate to which they are fixed. In contrast, this species lives *inside*. Actually, after Darwin had discovered *Cryptophialus*, but before he described it, another burrowing barnacle was discovered, namely *Alcippe* (now called *Trypetesa*) *lampas* (Fig. 5). A. Hancock [31], cited in [3], found it burrowing in the shells of large sea snails, such as *Buccinum*, on the eastern English coasts. These two species are indeed very similar. Thinking that *Alcippe* should be included in another order, likely the Abdominalia [3], Darwin did not include it within the Thoracica in the first volume of his *Monograph*. Yet, at the end of his second volume, devoted to the sessile barnacles, he returns to the Lepadidae (the pedunculate barnacles) to give a description of *Alcippe* [3], pp. 526–563, before describing

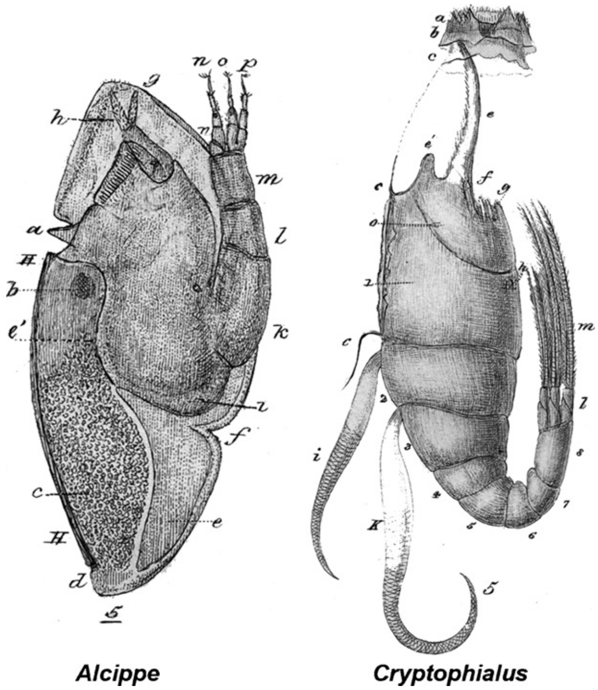

Fig. 5. Alcippe and Cryptophialus.
From [3]. *Alcippe lampas*, plate XXII, Fig. 5; *Cryptophialus minutus*, plate XXIII, Fig. 5.

Cryptophialus and the Abdominalia order. In 1854, Darwin quite frankly gave an account of his hesitations, saying "I almost wish I could persuade myself that I had taken an erroneous view of the thoracic segments, and therefore that the three pairs of terminal appendages were all abdominal, for then *Alcippe* would come into much closer relationship with *Cryptophialus*" [3, p. 546].

Finally, Darwin made the reverse error: he rightly homologized the posterior-most appendages of *Alcippe* with the cirri-bearing thoracic appendages of the Thoracica, but he erroneously mistook the posterior appendages of *Cryptophialus* as abdominal. This mistake was later corrected by A. Gruvel [32], who grouped together *Alcippe* and *Cryptophialus*, denied the presence of an abdomen in adult burrowing cirripedes, and according to the new (and still valid) homology of the posterior limbs and segments as both thoracic, changed the name of the order from 'Abdominalia' to 'Acrothoracica', which means "thorax at the extremity".

Darwin's mistake is understandable, due to the curious shape of the acrothoracican adult. Indeed, in order to fit in the narrow burrow drilled into the mollusc's shell, the animal takes the form of a hairpin; the posterior end comes close to the anterior one. The bent thorax is elongated, and several thoracic segments are depleted of limbs. The trunk, which like that of thoracican cirripedes is actually made of a single thorax, thus seems to be cleaved into two different parts: an anterior thorax and a posterior abdomen.

However, this curved shape is common to both *Alcippe* and *Cryptophialus* (Fig. 5). Why then did Darwin interpret the morphology of these two species so differently? They both burrow in gastropods. The question then arises

[3] Indeed, he changed his mind between 1851 and 1854. In the first volume (1851, p. 27) he wrote "*In another order, including, probably Alcippe of Mr Hancock, the cirri, of which there are only three pairs, are abdominal*".

whether their morphological similarity is due to ''true affinities'' or to analogy due to convergent adaptation to a similar way of living.

Are there important differences between them? Darwin convinced himself that there is no rectum or anus in *Alcippe* (= *Trypetesa*), the digestive tube being blind. He wrote: ''I am prepared to assert positively that this is the case'' [3], p. 546. This observation has been fully vindicated by modern authors [33]. On the contrary, he could observe a large anus in his tiny *Cryptophialus* [3], p. 578. I assume that this is the reason why he homologized the hind end of *Cryptophialus'* body as abdominal, and that of *Alcippe* as thoracic, in spite of their morphological similarities (see also the above discussion about the distinction between the telson and the abdomen).

Darwin found that both stages of the *Alcippe* larvae – the nauplius, previously described by Hancock, and the so-called 'pupa', i.e. cypris, described in detail by himself – [3], pp. 548–549 and Plate 23 – are very much like those of the common barnacles. Among the similarities is the existence of six pairs of natatory legs. On the contrary, in *Cryptophialus*, he found that the shape of ''the last larval, or pupal condition, before the final metamorphosis into the mature animal'' differed greatly from the usual cypris shape. It has prominent antennae like most cyprises, but is devoid of natatory limbs, and has an oval shape. This great dissimilarity between the 'pupae' of the two species was the main evidence that convinced Darwin to keep *Alcippe* within the Thoracica and to separate it from *Cryptophialus* [3], p. 566, although he did so only after wavering. In fact, Turquier [17], studying the very same *Alcippe* (now called *Trypetesa*) *lampas* species, showed that the cypris stage is followed by an additional moult and metamorphosis, leading to a novel larval stage. This new 'pupa' exhibits the oval shape and lack of thoracic limbs that Darwin found in the pupa of *Cryptophialus*. Indeed, the life cycles of both species are the same, differing by an additional larval stage from that of thoracican cirripedes. Most likely, Darwin missed this stage in *Alcippe*, and missed the cypris stage in *Cryptophialus*. Had he collected the various larval types corresponding to the complete life cycle of the two species, he would have joined them into a single order, called 'Cryptosomata', in keeping with Hancock's nomenclature, and he would not have created the new order 'Abdominalia'.

9. Cirripedes and ''The Origin of Species''

In ''The Origin of Species'', Darwin alluded to the cirripedes several times: in chapter IV, ''Natural selection''; in chapter VI, ''Difficulties of the theory''; in chapter IX, ''Imperfection of the geological record'' and in chapter XIII, ''Mutual affinities of organic beings''.

His work on the Cirripedia was clearly a source of the ideas expressed in the last chapter, which was mainly devoted to systematics. Darwin put systematics in an evolutionary context, the link between systematics and evolution being the principle of ''descent with modification''. He wrote: ''this element of descent is the hidden bond of connexion which naturalists have sought under the term of Natural System [of Classification]'' and ''the natural system is founded on descent with modification; the characters which naturalists consider as showing true affinity between any two or more species are those which have been inherited from a common parent, and, in so far, all true classification is genealogical'' (in modern words we say 'phylogenetic').

As evidence for descent being involved in systematics, he noted that the naturalist ''includes in his lower grade, that of a species, the two sexes; and how enormously these sometimes differ in the most important characters is known to every naturalist: scarcely a single fact can be predicated in common to the males and hermaphrodites of certain cirripedes, when adult, and yet no one dreams of separating them''.

I wish here to underscore the link Darwin made between systematics and development. A large part of the chapter is a plea to naturalists to take into account, not only the adult morphology, but also developmental traits. He wrote: ''the structure of the embryo should be more important for this purpose [systematics] than that of the adult''; and ''The embryos of distinct animals within the same class are often strikingly similar''; and ''certain organs in the individual, which when mature become widely different and serve for different purposes, are in the embryo exactly alike''. Turning to larvae, he wrote: ''In most cases, the larvae, though active, still obey more or less closely to the law of common resemblance. Cirripedes afford a good instance of this: 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. So again the two main division of cirripedes, the pedunculated and sessile, which differ widely in external appearance, have larvae in all their several stages barely indistinguishable.''

This emphasis on the link between evolution and development was pushed further by Darwin's German propagandist Ernst Haeckel, in his 'biogenetic law' claiming that ''Ontogeny recapitulates phylogeny'' [34]. The 'recapitulation theory' was eventually rejected, leading to a divorce of developmental from evolutionary sciences, which lasted until the resurrection of the link between the two disciplines as the 'new synthesis' of evolutionary developmental genetics, abbreviated as 'evo-devo' [35].

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References

[1] C. Darwin, A Monograph on the Subclass Cirripedia, with Figures of all the Species. The Lepadidae or Pedunculated Cirripedes, Ray Society, London, 1851.
[2] C. Darwin, A monograph on the fossil Lepadidae or pedunculated cirripedes of Great Britain, Palaeontol. Soc. 5 (1851) 1–88.

[3] C. Darwin, A Monograph on the Subclass Cirripedia, with Figures of all the species. The Balanidae, the Verrucidae, etc., Ray Society, London, 1854.
[4] C Darwin, A Monograph on the Fossil Balanidae and Verrucidae of Great Britain, Palaeontol. Soc. 8 (1855) 1–44.
[5] J. van Wyhe, Darwin, The story of the man and his theories of evolution, Andre Deutsch (2008).
[6] C. Darwin, The Autobiography of Charles Darwin 1809–1882. With Original Omissions Restored. Edited With Appendix and Notes by Nora Barlow, Harcourt, Brace & Co., New York, 1959.
[7] C. Darwin, The Foundations of the Origin of Species. Two Essays Written in 1842 and 1844, New York University Press, New York, 1986.
[8] C. Darwin, The Origin of Species, Penguin Books (1968), London, 1859.
[9] A.C. Love, Darwin and Cirripedia prior to 1846: Exploring the origins of the barnacle research, J. Hist. Biol. 35 (2002) 251–289.
[10] J. van Wyhe, Mind the gap: did Darwin avoid publishing his theory for many years? Notes Rec. R. Soc. 61 (2007) 177–205.
[11] G. Cuvier, Le Règne animal, distribué d'après son organisation, pour servir de base à l'histoire naturelle et d'introduction à l'anatomie comparée, Deterville, Paris, 1817.
[12] E. Geoffroy Saint-Hilaire, G. Cuvier, La querelle des analogues, Éditions d'aujourd'hui (1983), Plan de la Tour, France, 1830.
[13] J.V. Thomson, On the cirripedes or barnacles and the class of animals to which they belong, Zool. Res. I (1830) 69–85.
[14] E. Geoffroy Saint-Hilaire, Des organes respiratoires, Philosophie anatomique, 1er Vol., Méquignon-Marvis, Paris, 1818.
[15] D.T. Anderson, Barnacles. Structure, Function, Development and Evolution, Chapman & Hall, London, 1994.
[16] L.J. Walley, Studies on the larval structure and metamorphosis of *Balanus balanoides* (L.), Phil. Trans. Roy. Soc. (London), B 256 (1969) 237–280.
[17] Y. Turquier, Recherches sur la biologie des Cirripèdes Acrothoraciques. III. La métamorphose des cypris femelles de *Trypetesa nassaroides* et de *T. lampas*, Arch. Zool. Exp. Gen. 111 (1970) 573–628.
[18] J. Yager, Remipedia, a new class of Crustacea from a marine cave in the Bahamas, J. Crust. Biol. 1 (1981) 328–333.
[19] S. Koenemann, F.R. Schram, A. Bloechl, T.M. Iliffe, M. Hoenemann, C. Held, Post-embryonic development of remipede crustaceans, Evol. Dev. 9 (2007) 117–121.
[20] G. Walker, The fine structure of the frontal filament complex of barnacle larvae (Crustacea: Cirripedia), Cell Tissue Res. 152 (1974) 449–465.
[21] G. Scholtz, G.D. Edgecombe, The evolution of arthropod heads: reconciling morphological, developmental and palaeontological evidence, Dev. Genes Evol. 216 (2006) 395–415.
[22] J.V. Thomson, 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. R. Soc 125 (1835) 355–358.
[23] L.A. Borradaile, F.A. Potts, G.A. Kerkut, The Invertebrata. A Manual for the Use of Students, Cambridge University Press, Cambridge, 1958.
[24] J.M. Gibert, E. Mouchel-Vielh, E. Quéinnec, J.S. Deutsch, Barnacle duplicate *engrailed* genes: divergent expression patterns and evidence for a vestigial abdomen, Evol. Dev. 2 (2000) 194–202.
[25] M. Blin, N. Rabet, J. Deutsch, E. Mouchel-Vielh, Possible implication of Hox genes *Abdominal-B* and *abdominal-A* in the specification of genital and abdominal segments in cirripedes, Dev. Genes Evol. 213 (2003) 90–96.
[26] G.A. Kolbasov, J.T. Hoeg, A.S. Elfimov, Scanning electron microscopy of acrothoracican cypris larvae (Crustacea, Cirripedia, Acrothoracica, Lithoglyptidae), Contrib. Zoology 68 (1999) 143–160.
[27] R. Owen, Report on the archetype and homologies of the vertebrate skeleton, Brit. Assoc. Rep. 1846 (1847) 169–340.
[28] H. Milne Edwards, Histoire naturelle des crustacés, Vol. 3, Librairie Encyclopédique de Roret, Paris, 1834–1840.
[29] J. Bocquet-Védrine, Suppression de l'ordre des Apodes (Crustacés Cirripèdes) et rattachement de son unique représentant, *Proteolepas bivincta*, à la famille des Crinoscidae (crustacés isopodes cryptonisciens), C.R. Acad. Sci. Paris, Sér. D. 275 (1976) 2145–2148.
[30] J. Bocquet-Védrine, Interprétation actuelle de la description de Proteolepas bivincta Darwin, 1854, représentant unique de l'ancien ordre des Cirripèdes Apodes, Crustaceana 37 (1979) 153–164.
[31] A. Hancock, Notice of the occurrence on the British coast of a burrowing barnacle belonging to a new order of the class Cirripedia, Ann. Mag. Nat. Hist. 2 (1849) 305–314.
[32] A. Gruvel, Monographie des cirrhipèdes ou thécostracés, Masson, Paris, 1905.
[33] J.T. Tomlinson, The burrowing barnacles (Acrothoracica), in : A.J. Southward (Ed.), Barnacle Biology, A.A. Balkema, Rotterdam, 1987, pp. 63–71.
[34] E. Haeckel, Generelle Morphologie der Organismen. Allgemeine Grundzüge der organishen Formen-Wissenschaft, mechanish begründet durch die von Charles Darwin reformiete Descendenztheorie, Reimer, Berlin, 1866.
[35] S.F. Gilbert, J.M. Opitz, R.A. Raff, Resynthesizing evolutionary and developmental biology, Dev. Biol. 173 (1996) 357–372.