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Comparability in evolutionary biology: The case of Darwin's barnacles

<https://doi.org/10.1515/lingty-2020-2056>

Abstract: Language change and biological evolution are sufficiently similar that biologists and linguists often face similar challenges in reconstructing paths of historical change connecting different species or languages. Tracing evolutionary change over time requires us to consider how shared features have been modified in different lineages since they shared a common ancestor, and this means we have to be able to establish meaningful comparability between traits. In some cases, we may wish to understand how the same ancestral trait has been modified in each lineage in response to different pressures. But in other cases, we may wish to ask whether particular traits often arise in response to certain circumstances. Biologists must therefore consider different reasons for similarities between species, and choose to compare those traits that are relevant to the story they want to tell. To reconstruct histories of change, we need to compare homologous traits (those similar due to shared ancestry). But comparing analogous traits (independently derived but similar traits) highlights how separate evolutionary lineages can find similar solutions to common problems. I will illustrate the importance of comparability in constructing evolutionary explanations using one of the more obscure yet fascinating examples of Charles Darwin's scientific researches, his multi-volume taxonomic treatise on barnacles. Darwin faced the challenge of how to explain the evolutionary trajectory of unique and highly modified traits that appear to have no equivalents in related taxa. He did this by tracing the development of unique traits within growing individuals, looking for variation in these strange adaptations between individuals, and comparing them across species that varied in their degree of modification from their ancestor. Using meticulous observations to establish comparability, even in such an incomparable animal as the barnacle, he could reconstruct plausible evolutionary explanations for even the most bizarrely modified traits, such as the presence of parasitic males and the invention of the cement

Invited contribution to a Special Issue on Comparability for Linguistic Typology Eds. **Nicholas Evans & Maria Koptjevskaja Tamm**

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that sticks barnacles to rocks, boats and whales. Nowadays, scientists increasingly rely on DNA evidence to trace evolutionary paths, which brings both advantages and challenges in establishing comparability. Even if you, like most people, are not particularly interested in barnacles, Darwin's underappreciated taxonomic work is a surprisingly good place to go to if you want to think about the issue of comparability and why it matters to understanding evolution.

Keywords: analogy, cognate, evolution, functional category, hermaphrodite, homology

1 Comparing comparability between disciplines

What on Earth is a paper on a 160-year-old taxonomic treatise of a peculiar group of aquatic invertebrates doing in a Linguistic Typology journal? Well may you ask! The closest I can come to a reasonable explanation is this: I was asked to contribute to a cross-disciplinary panel on comparability for the 12th Conference of the Association for Linguistic Typology (ALT), held in Canberra, Australia in December 2017. But I was strictly instructed that I was not to talk about any work I had done in language evolution – I was there as the token biologist, and I must stick to biology. The problem is, though, that there is an awful lot of biology. What particular area of biology should I talk about? I avoided the issue by submitting an abstract that used only the vaguest of terms to allude to the topic of the talk. Nice, I was told, but not good enough: you must tell us more specifically what you will talk about.

As it happens, I was on leave at the time, and as part of my relaxing holiday reading, I had just finished reading one of Charles Darwin's more obscure works. Darwin wrote over 20 books in his lifetime, on topics ranging from the formation of coral reefs to the power of movement in plants to the action of earthworms. But perhaps the books of Darwin's that are the least read today are those he spent a substantial period of his research career working on: his four-volume taxonomic treatise on barnacles published between 1851 and 1854 (two volumes describing living barnacles, two volumes on fossils). These books are largely taken up by detailed species descriptions, painstakingly wrought by eight years of careful observations and dissections, written in the arcane language of formal taxonomy. These descriptions are, I think all would admit, tedious to read. But front and back of the hard-nosed taxonomic work, and scattered throughout, are Darwin's observations and thoughts, hypotheses and explanations. These are seams of gold running through the solid rock. So, in a kind of bold experiment in interdisciplinarity, I somewhat rashly amended my vague abstract to say that I would illustrate the problem of comparability in evolutionary biology using Darwin's barnacles. I sent it off, went back to my holiday and forgot all about it.

Until I was faced with having to give an actual talk on Darwin's barnacles at an actual Linguistic Typology conference, which, I think I can safely say, is one of the more surreal experiences of my academic life to date. What could be stranger than a talk on Darwin's barnacles at a Linguistic Typology conference? A paper on Darwin's barnacles in a Linguistic Typology journal. Here we go anyway.

2 Why did Darwin work on barnacles?

Charles Darwin had been a keen amateur naturalist as an undergraduate at both Edinburgh and Cambridge, but it was his five-year voyage on HMS *Beagle* (1831-1836) that set his reputation as an able and original researcher. His correspondence during the voyage had been published in learned journals, and when he returned he superintended the publication of various taxonomic works on the specimens he had collected on his global adventure. His account of the *Beagle* voyage, published in 1839, was highly successful and set his reputation in the scientific community, and gained him a certain amount of fame (Darwin 1839). The journey also led to several other publications, including his work on the formation of coral reefs (Darwin 1842). Darwin began working on his "species theory" not long after the return of the *Beagle*, and had a full essay of his theory written out by 1844 (with instructions that it should be published in the event of his death). Yet he did not publish his theory of evolution until 1859, at least 20 years after he had the essential components of the theory worked out (Darwin 1859).

"Darwin's delay" in publishing his evolutionary theory has generated a whole raft of conspiracy theories – was he afraid of public reaction, did he wish to avoid upsetting his wife, was he nervous that the case was not compelling enough? (see Van Wyhe 2007). The answer may be more prosaic, and entirely understandable to today's over-stretched academics: Darwin was busy working on other things. These other things provided important evidence to back up his ideas, and helped to build an invincible case for his theory of descent with modification. But these other projects were also valuable contributions to biology in their own right. And one of these other projects was barnacle taxonomy.

Darwin had collected barnacle specimens on the *Beagle* voyage, including some perplexing burrowing barnacles he discovered in a sea shell in Chile, which he carefully preserved for later decryption (Castilla 2009). While his other zoological and botanical specimens were distributed among leading systematicists to be described and published, he kept the barnacles for himself. Barnacles were an enduring zoological mystery, and lacked a comprehensive taxonomic treatment. A taxonomy is a detailed description of a group of species, setting out both their shared features (the traits that group them together as relatives) and their

diagnostic characters (the traits that allow each species to be unambiguously defined and identified). A taxonomy makes sense of the variation and commonality in a group of related species, assigning each species an official scientific name, providing a formal description of its characteristics, and classifying those species into hierarchical relationships. In his address to the British Association for the Advancement of Science in 1847, the eminent natural historian Louis Agassiz declared a taxonomic treatise on barnacles to be sorely needed (Mannouris 2011). Someone had to do the barnacles. Why not Darwin?

Darwin spent eight years dissecting and describing barnacles, not only his own specimens, but also those sent to him by a worldwide network of correspondents. To produce a taxonomic description requires a heroic attention to detail, and Darwin's barnacle work was all-consuming. His study at Down House became a shrine to barnacles, with boxes of borrowed specimens, pages of notes and detailed sketches, and the finest microscope a man of his comfortable means could acquire (Stott 2003). The degree to which the barnacles dominated his working life at the time is perhaps best illustrated by the oft-repeated story that one of his children asked a friend "but where does your father do his barnacles?", on the assumption that it was perfectly normal for one's father to dedicate his waking hours to dissecting marine invertebrates (e.g. Deutsch 2009). Darwin's children, who were in and out of his study and were often co-opted as assistants in his investigations, likened Darwin's descriptions of his "beloved barnacles" to the words of an advertisement. Yet, by the end of the project after dissecting hundreds upon hundreds of barnacles, Darwin declared "I hate a Barnacle as no man ever did before, not even a Sailor in a slow-sailing ship" (Darwin 1887).

Why should one of the greatest scientists of all time spend eight years recording minutiae about barnacles? I am guessing you could ask similar questions of many great linguists. Why would someone like Nick Evans spend years studying an Arnhem land language which is now spoken by less than half a dozen people (Evans et al. 2004)? If you want to learn about how language varies, and gain insight into processes of language change, then close study of particular examples is one of the most valuable ways to learn. Darwin's four volumes on the Cirripedia (the formal taxonomic label for the 'curl-footed' barnacles) are testament to his "unwearied patience as an experimenter and observer" (Lyell 1864).

Why barnacles? Why not. In Darwin's day, barnacles were an unsolved problem, unconquered taxonomic territory. And, like most problems in biology, the closer you look, the more interesting they get. I did not plan to write a paper on barnacles, and before I started I knew no more about barnacles than the average biologist (i.e. not very much at all). Yet the more I read, the more I discovered that barnacles provide an ideal case study for illustrating both the need for, and challenges of, establishing comparability in biology – among individuals, between

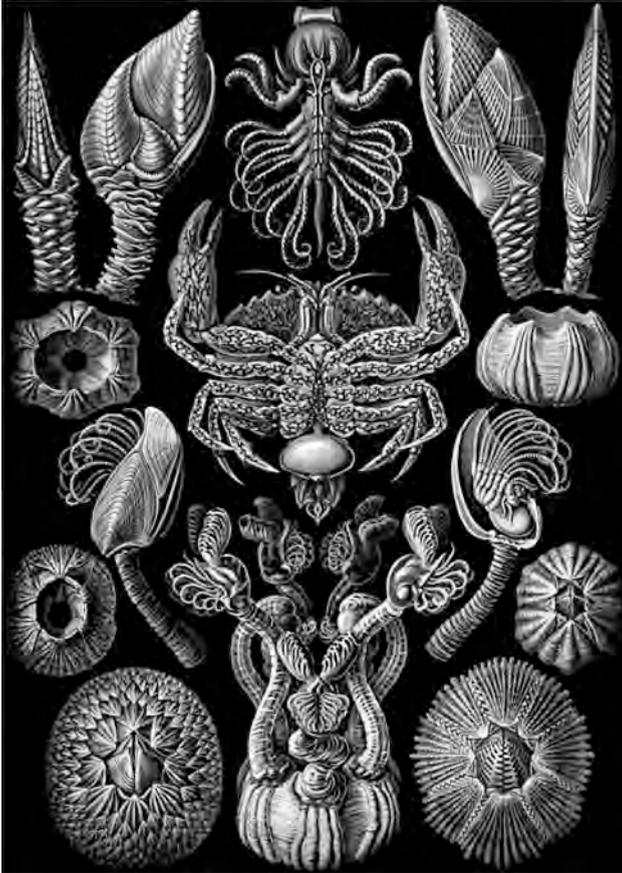


Figure 1: Barnacle diversity, as drawn by one of Darwin's enthusiastic followers, Ernst Haeckel (Haeckel 1904). The animal with jointed legs in the middle is not a barnacle, it's a crab, but it has a parasitic barnacle *Sacculina* growing out of its bottom.

species and across lineages. Darwin's barnacle taxonomy is a *tour de force* from a gifted and insightful scientist. No doubt he would have produced the same bright illumination of whichever taxonomic group he settled on. Yet the barnacles, so strange and dissembling, proved fertile ground for Darwin's bold and multifaceted approach of combining fine-scaled description of individual developmental trajectories, detailed examination of variation between individuals, and the differences in structures between lineages. It was this multifaceted approach that allowed him to generate convincing evolutionary narratives for the origin of the incomparable barnacles, a brilliant work of intellectual stealth years before his revolutionary theories were published.

3 Modification challenges comparability

You will have seen barnacles stuck to tidal rocks, the pillars of jetties, the underside of boats and even clinging to other marine creatures (Figure 1). Many earlier naturalists, including the great systematist Carolus Linnaeus, had thought that barnacles must be molluscs, as they look rather similar, being soft squishy animals, protected by hard shells, stuck to rocks. But Darwin, building on the works of other naturalists (e.g. Thompson 1835), confirmed that they are, without a doubt, crustaceans, belonging in the group that includes crabs, lobsters and shrimp (see Winsor 1969). So the closest relatives of the barnacles are groovy little animals with lots of cool animal equipment – like legs, claws, feelers, eyes and tails – that zip about doing groovy animal things like swimming and fighting and attracting mates and hiding and catching things to eat and so on. The contrast to unmoving, unseeing barnacles, curled inside a shell with no face, no legs and no heart, could hardly be more striking.

But the early stages of the barnacle lifecycle betray their crustacean affinities (Winsor 1969). All barnacles have at least two free-swimming larval stages, which are similar in form to the larvae of other crustaceans. The final larval stage does not feed, because it is focussed on the job of finding somewhere to settle. When it finds a suitable surface, it glues its head to the substrate and undergoes metamorphosis. Now the body is completely remodelled: the larval features dissolve, the body rotates, the antennae retract, and a hard-plated shell forms around the body (Maruzzo et al. 2012). The adult barnacle lives squished inside this shell, with its modified feathery limbs, useless for walking or grabbing, poking out of the shell to filter microscopic morsels from the seawater.

And this is where the challenge of comparability in evolutionary biology comes into the story. Darwin's evolutionary theory demanded that, however different two living species are, there must be a chain of intermediates linking them, each of which is a slight modification of its immediate ancestor. "... Looking not to any one time, but to all time, if my theory be true, numberless intermediate varieties, linking most closely all the species of the same group together, must assuredly have existed; but the very process of natural selection constantly tends, as has been so often remarked, to exterminate the parent forms and the intermediate links. Consequently evidence of their former existence could be found only amongst fossil remains, which are preserved ... in an extremely imperfect and intermittent record." (Darwin 1859: 179).

There are no living intermediates between barnacles and other crustaceans, no species that represents a "missing link" that illustrates the process of change from mobile, legged animals to sessile, shell-encased animals. Can fossils fill the gap?

Barnacles are exactly the kind of organisms that fossilize well: they are marine (so they often live where sediments form) and they have taxonomically distinctive hard parts (so they can make informative fossils). But the fossil record is still unavoidably patchy, some barnacle groups have no fossils at all, and many of the most interesting features of barnacles do not tend to leave a trace in fossils, such as their delicate appendages or internal organs (Schram 1982). Darwin described the available fossils for barnacles (Darwin 1851a, 1854b), but this evidence is fragmentary and incomplete, and provides only irregular glimpses of the geological past. Just as having fragments of a few ancient religious texts will not give you a complete picture of the development of a modern spoken language, the fossil record is an informative but incomplete record of the evolutionary history of the barnacles. “Lyell’s excellent view of geology of each formation being merely a page torn out of a history & the geologist being obliged to fill up the gaps, — is possibly the same with the philosopher who has traced the structure of animals & plants. — He get[s] merely a few pages.” (Darwin 1838: 60)

In spite of the incomplete fossil record, and the lack of living intermediates between barnacles and other crustaceans, Darwin sought to piece together an evolutionary trajectory of stepwise changes from an ancestral crustacean, equipped with legs, eyes, a heart and all the rest, to the faceless shell-encased barnacle. Describing the paths of evolutionary change from shared ancestors to living species (or extinct forms) relies upon comparing the end results of that process, features modified from a single original ancestral form. In evolutionary biology, there are two broad classes of comparable traits: homology and analogy. Homologous traits are comparable because, however similar or different they are now, they are derived from the same ancestral trait. A classic example is the hands of apes, the flippers of whales and the wings of bats: different in form, different in function, but clearly all modifications of the same five-fingered ancestral limb (Figure 2). In contrast, analogous traits may serve the same function, but all represent independent “inventions”, so that any similarity between them is not due to shared descent but shared purpose. A classic example is the wings of birds, bats, and pterosaurs. Any similarities are due to the design necessities of flight organs, not because they are modifications of the same ancestral structure (because the last shared ancestor of birds, bats and pterodactyls was a wingless animal that lived hundreds of millions of years ago). We even refer to completely unrelated and dissimilar flight organs as “wings”, such as the wings of a dragonfly or sycamore seeds, even though they share no common origins. Analogous traits are brilliant for comparing how evolution can modify existing forms to suit new purposes, and they allow us to consider how different species become adapted to similar environments or ways of life. But only

homologous traits, carried by the tide of history even if modified on the journey, can be used to trace a shared ancestry.

Given how different barnacles are from their closest known relatives, how could Darwin establish the comparability of traits? How could he identify homologies, connecting the highly modified traits of barnacles to shared crustacean features from which they must be derived? He used three broad strategies to leverage comparability in his study of barnacle evolution: development (change within an individual), variation (differences among individuals), and comparison (differences between species). Perhaps the analogy of these levels of analysis in language change would be combining evidence from language acquisition studies, sociolinguistic studies of variation in populations, and comparative historical linguistics. In other words, in true Darwinian spirit, he conducted his study of barnacles across the individual, population and lineage levels, connecting micro-level processes to macro-level change.

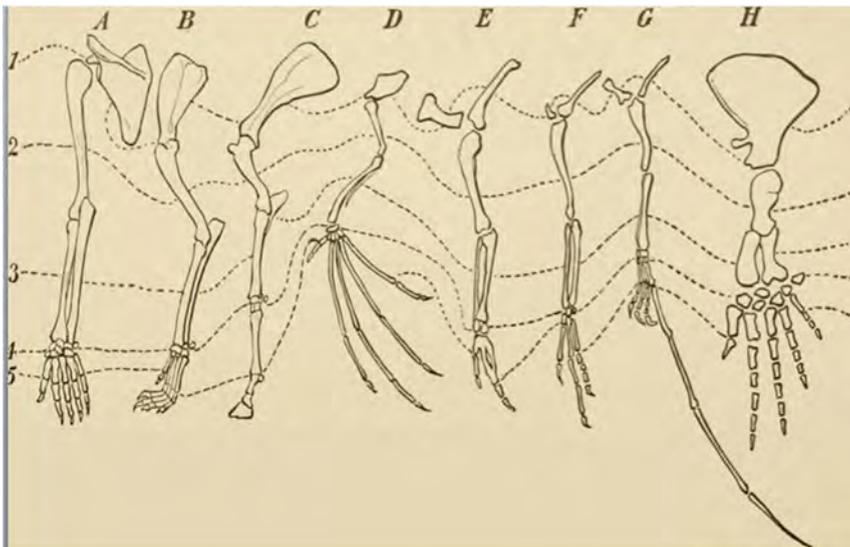


Figure 2: A classic comparison of the bones in tetrapod limbs reveals homology of the underlying bone structure. Here the homologous parts of limbs are identified (though not to scale) from a human (A), dog (B), horse (C), bat (D), bird (E), “dinobird” (*Archaeopteryx*): F), pterosaur (G), and whale (H).

3.1 Establishing homology

Having confirmed that barnacles were crustaceans, Darwin had to construct an evolutionary path that would connect a crustacean ancestor to a barnacle descendant. His attempts to do this illustrate the central role that the concept of homology plays in evolutionary biology. Homology is at the same time one of the most straightforward concepts in evolutionary biology, yet also one of the most difficult. It is something that many biologists feel they intuitively understand, yet the concept is a bit more slippery than most would usually like to admit. A homologous character is one shared by common descent, even if its current form and function is very different from its ancestor or relatives, just as a cognate set like English *town*, Dutch *tuin* ‘garden’ and German *Zaun* ‘fence’ derive from a shared ancestral form referring to enclosure, despite the shifts in sound and meaning they have undergone. The classic example in evolutionary biology is the bones of the limbs in tetrapods (four-limbed vertebrate animals): although they vary in size and shape, they are clearly all modifications of an ancestral form (Figure 2). When you compare the bones in a bat’s wing, a pterosaur’s wing, and a bird’s wing, you can identify a shared underlying bone structure, so we can see that these wings are homologous at the level of the skeleton. Yet the actual wings themselves are not homologous, because they do not represent modifications of an ancestral wing. The last common ancestor of pterosaurs, bats and birds was a four-legged reptile (who must have had the same set of bones in its limbs shared by all its descendants, including you). So while the wings of birds, bats and pterosaurs are analogous (independently derived solutions to a common need), the bones from which the wings are made are homologous (modified from a common ancestral form). Tracing homology is easy in some cases, difficult in others, but always essential to reconstructing meaningful evolutionary paths. We would be led astray if we considered the wings of birds, bats and pterosaurs to be homologous and therefore inferred a winged ancestor of all mammals, birds and reptiles.

Historical linguists may face similar challenges of defining homology when they seek to identify cognate forms, or correspondence sets in language structural change. At first glance, there may be little obvious similarity between the English form *tree* and the Greek *dendro* (*δέντρο*). But if we consider other contemporary forms, such as the Russian *derevo*, and archaic forms, such as the Old English *trēow*, we can construct trajectories of change connecting all to a common ancestral term (Figure 3). In cases such as these, we may have “fossils” of the language in the form of ancient texts. But the reconstruction of a protolanguage can occur without any historical samples at all, using only information from living languages, even in the absence of any written record (Durie and Ross 1996; Rankin

2017). However, care must be taken to identify true homologues (cognates derived from a protolanguage), rather than incidental similarities (for examples see Evans 2011). If two words in the same lexical category are independently derived but happen to have a similar form, their similarity could be mistaken as a sign of shared origin. While chance similarity may be unlikely for complex or lengthy words, it becomes more likely for language features that have a restricted “design space”: if a given feature can only occupy a small number of states, it increases the chance of independently deriving the same feature in separate languages. For example, word order is evolutionarily labile but restricted to a relatively small number of possible states, so two languages might be SVO by analogy (they independently evolved that word order) rather than by homology (both inherited word order from a common SVO ancestor). Similarities by analogy may also arise when there is a non-arbitrary relationship between word and meaning, as in the case of onomatopoeia, or shared iconicity, as may occur in signed languages (Zeshan and Palfreyman 2017).

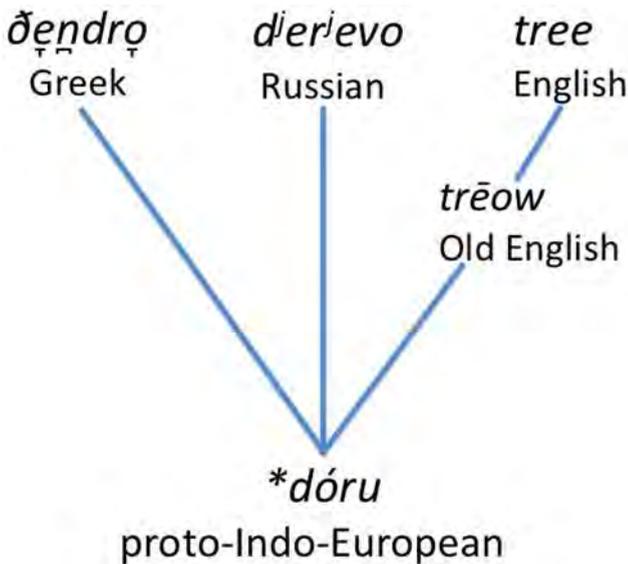


Figure 3: Homology can be recognized by comparison with contemporary cognates (such as the Greek and Russian terms for “tree”) or by comparing contemporary and past forms (such as the modern English and Old English forms) (Greenhill et al. 2018). Homology can be used to reconstruct an inferred ancestral form (proto-Indo-European). The analogies to evolutionary biology are constructing homologies by comparing traits in living species, or to fossil species, and reconstructing putative ancestral states.

Importantly, identification of cognates is generally not based on similarity alone. While there have been statistical approaches to cognate detection (e.g. Ellison 2007; Rama et al. 2018), cognacy is typically determined through expert consideration of word similarities across a related group of languages. Expert attention is generally needed because simply measuring similarity may not be fully informative of descent, both for lexicon (e.g. Greenhill 2011) and for grammar (e.g. Dahl 2008), particularly given the restricted options in “design space” for some grammatical features. But experts also make use of background knowledge in identifying cognates, particularly making use of assumptions about patterns of systematic sound change that may affect many words (though this will not be useful for all aspects of language, nor for all languages). The key role that systematic sound change plays in the identification of homology in language has no obviously useful analogy in biology. Changes in one character of a species may influence another character, creating sets of intertwined changes, and predictable patterns of change may arise from allometry (the physical consequences of changes in size and shape). For example, the larger a mammalian species is, the lower its surface-area-to-volume ratio, and its mass specific metabolic rate will get lower, and its limbs must become comparatively thicker relative to its size to support the extra weight (Haldane 1927). But allometric changes are more likely to reflect analogy – similar trajectories taken independently by different lineages – than to be a guide to identifying homology. At the molecular level, genome-wide changes can affect multiple genes, such as shifts in base composition (relatively how many Gs and Cs there are compared to Ts and As), but these rarely give the biologist the kind of information on descent with modification that systematic sound changes provide for linguists.

How could Darwin map homology between crustaceans and their profoundly modified barnacle relatives? First, Darwin had to formalize the comparison of different parts of the barnacles by developing a standard terminology, giving specific names to each part of the barnacle, from the hard valves of the “shell” to the soft appendages within (Deutsch 2009). The tendency of each naturalist to develop their own specialist terminology to describe the parts of barnacles had made direct comparisons across different specimens, or different studies, difficult. Giving consistent names to homologous parts is a practical necessity for comparability. While this may be akin to the establishment of comparative linguistic concepts to allow cross-linguistic comparison, there is an important difference. A morpheme such as a dative, might be doing the same “work” in two different languages, but it does not necessarily imply that they are derived from the same ancestral source (Haspelmath 2010). It is a functional category, not a marker of descent. We can refer to the wing of a pterodactyl, the wing of a bat, or the wing of a dragonfly, using “wing” as a functional category to describe an

appendage used for active flight, not as a class of structures that are similar by descent.

In other cases, to make clear the difference between functional categories and homologies, biologists invent new terms for similar structures in order to emphasize that they are analogies not homologies. Consider another comparable feature of these winged tetrapods: hairiness. Birds, bats and pterosaurs are all, at some stage of their life, “hairy”: think of the fur of a fruitbat or the fluffy down of a duckling – and beautifully preserved specimens show at least some pterosaurs were hairy too (McKellar et al. 2011). The primary reason for having hair is thermoregulation: homoeothermic (“warm-blooded”) animals use hairiness as insulation. It is generally assumed that the last common ancestor of birds, bats and pterosaurs was likely to have been a poikilothermic (“cold-blooded”) reptile, and therefore unlikely to need a warm pelage. In this case, birds, mammals and pterosaurs would have “invented” hair separately, presumably because each of them also evolved homeothermy (warm-bloodedness) independently. If this is true, then the fluffy down of chicks, the simple filaments covering many dinosaurs, the soft fur of a possum, and the hairy belly of baby pterodactyl are all analogous structures: hair is a functional category of structures that fulfil a particular role, and in each case it evolved in response to the acquisition of another trait, homeothermy. This view is supported by the different developmental paths: for example, mammalian hairs are extruded from different cells in the skin than feathers are.

Because biologists need to distinguish homologies from analogies in order to construct evolutionary narratives, they may mark the difference by using non-identical terms for independently derived structures. For example, biologists generally reserve the word “hair” only for the structure that mammals grow, and refer to “hair” of birds and dinosaurs as down or feathers, and pterosaur “hair” as pycnofibres (Kellner et al. 2009). But there is dissent: as new discoveries push the evolutionary origin of feathers back deeper into the early dinosaur lineage, as more hairy pterosaur fossils are discovered and described, and as aspects of the shared genetic architecture of the different forms of skin outgrowths are uncovered, it becomes increasingly plausible to say that all of these structures share a common evolutionary basis (Benton et al. 2019). Once considered a clear case of analogy, now hairiness illustrates how uncertain issues of comparability in evolutionary biology can be: when we compare hair, feathers and pycnofibres, are we telling a story of repeated origin of the same useful structure (analogy), or a tale of an array of possible modifications of an ancestral trait (homology)?

This example also illustrates another use of terminology in regulating comparisons: functional equivalence. Biologists avoid using the terms warm-blooded and cold-blooded because these general terms fail to distinguish two key features

of interest: the temperature at which species operate, and the mechanism of thermoregulation. Birds and mammals use a substantial amount of metabolic energy to generate and maintain a constant body temperature, so they are homeothermic (maintain a constant temperature) and endothermic (use metabolic energy to do so). Most reptiles also need a warm body temperature for optimal function, but they modulate this temperature through behaviour, such as basking, so they are poikilothermic (able to operate at a range of temperatures) and ectothermic (they rely on environmental energy to moderate their body temperature). This is why lizards and snakes are sluggish when cold but move fast when they warm up. Both homeotherms and poikilotherms may have “warm blood” but they achieve it in different ways. The discovery of “hair” on pterosaur fossils and feathers on non-flying dinosaurs suggests they needed to insulate their “warm blood” against heat loss (homeothermy), although this doesn’t necessarily tell us whether they warmed their blood by endothermy (like mammals and birds) or ectothermy (like lizards and snakes – though the fact that no living ectotherms are hairy is strongly suggestive). It is possible, for example, that larger dinosaurs were effectively “warm-blooded” not through endothermy but through gigantothermy - large bodies generate a lot of metabolic heat but lose less due to a low surface-area to volume ratio.

The separation of traits similar by descent (homology) from traits similar as independently derived solutions to fulfil the same need (analogy) has an important role to play in generating and testing hypotheses about functional connections between traits. That is because we seek different kinds of explanations for the two categories of similarity. Repeated evolution of a similar analogous trait in many different lineages tells us about evolutionary change in response to similar challenges: for example, if we discover another hairy lineage, we can make inferences about its metabolism, because we have observed that hairiness tends to evolve in endothermic (“warm-blooded”) lineages. On the other hand, erroneously treating shared homologous characters, which are similar by common ancestry, as if they were all independently derived solutions to the same problem could lead us to false conclusions about the functional connection between traits. This problem – referred to as Galton’s problem or phylogenetic non-independence – is just as pernicious in evolutionary biology as in comparative linguistics (Bromham 2017). The co-occurrence of two linguistic structures or features in many different languages cannot be used as evidence that the two have a functional connection if they all inherited those two features from a common ancestor: the two may be associated by historical inertia and not due to functional constraint. In the words of Francis Galton, if co-occurring features are derived from a common source, then they are duplicate copies of the same original, not independent datapoints that can be included in a statistical analysis (Galton 1889). Happily, we can prevent ourselves being led astray

by similarity by descent by incorporating information on relatedness into any analysis looking for functional associations between language features, as well as between aspects of language and the population or environment in which they arise (Bromham et al. 2015; Bromham et al. 2018; Hua et al. 2018).

3.2 Development: Change within an individual

To construct a trajectory for descent by gradual modification, Darwin had to connect the highly modified parts of the barnacle to common features of the crustacean body plan. Darwin was strongly influenced by naturalists who encouraged the use of embryology to uncover natural affinities. He drew on the concept of the “archetypal crustacean”, an inferred ancestral form (akin to the inference of a protolanguage), but most of the archetypal features could not be identified in the highly modified barnacle by inspection of the adult form (Richmond 2007). For example, the “archetypal crustacean” had been predicted to have 21 body segments, but adult barnacles have no obvious segments at all (Figure 4). How can you study the evolution of the barnacle from a crustacean ancestor, when all the classic crustacean features have changed so much there is nothing left to compare?

For Darwin, tracking traits as they developed from the embryo to the adult was an important platform for establishing homology. He was committed to the principle that it's not sufficient to point out the similarities in different structures, you have to show that they are derived from the same source. As an individual animal develops from a single fertilized egg cell, the early stages of development may point to the shared ancestral origin of a trait. After all, it was the similarities of the larval stages that revealed barnacles' crustacean affinities. More specifically, the origins of highly modified parts might be revealed if they originated from shared features of the embryo. If one end of the barnacle develops from the part of the embryo that in all other crustaceans would go on to form the head, then that is evidence that the part is homologous to the head of other crustaceans, however highly modified and un-head-like the end product of that developmental process is.

Darwin used developmental pathways to work out which barnacle structures are directly comparable to parts found in other crustaceans – which parts of the adult barnacle are homologous to the head of the lobster? Which appendages are equivalent to the first set of legs? By tracking development from egg to larva to juvenile to adult, he identified many of the classic crustacean segments in the adult barnacle, though some appeared to have been lost altogether. The loss of unneeded anatomical features became a key part of Darwin's theory of descent with

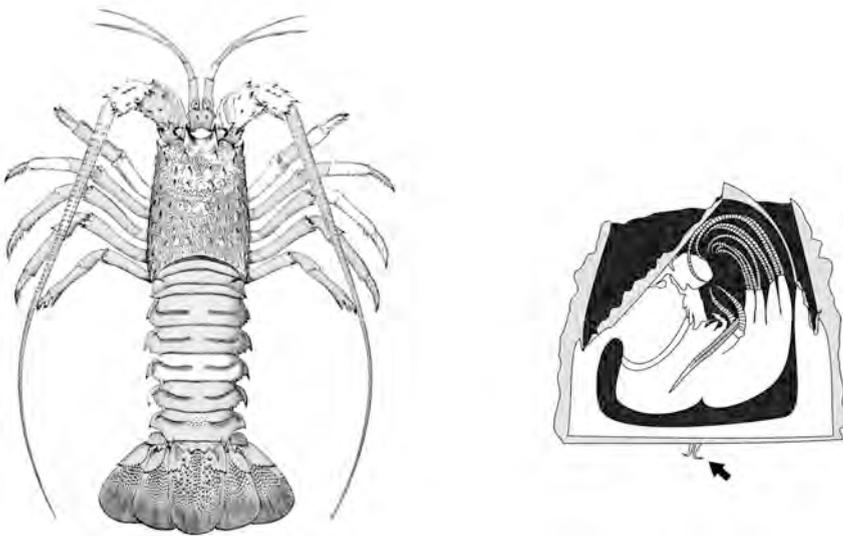


Figure 4: The body of a typical crustacean, like this handsome rock lobster, is made up of clearly defined segments, some of which bear a pair of appendages, such as antennae, mouthparts or legs. In barnacles, there is no clear distinction between body segments, which are essentially all fused into one body mass. In the adult barnacle, the antennae have been repurposed as attachment organs (see arrow), and the six pairs of “limbs” are reduced to feathery appendages for filter feeding. (Lobster diagram by H. L. Todd, CC0; Barnacle diagram by M. A. Broussard; CC4.0).

modification. If an organ is not needed for survival, any variation that arises in it will not be checked by natural selection. If the economy of the organism is improved by reduction in that unnecessary organ, selection will favour a reduction in size. Vestigial traces may persist, revealing the history of change and loss over time. Darwin drew a linguistic analogy: “Rudimentary organs may be compared with the letters in a word, still retained in the spelling, but become useless in the pronunciation, but which serve as a clue in seeking for its derivation” (Darwin 1859: 455).

In addition to explaining the loss of characters as barnacles evolved from a more morphologically complex ancestor, Darwin also had to explain how novel structures arose. Barnacles have unique features that have no equivalent in other crustaceans. One of the most characteristic features of barnacles is that they make a wickedly tough cement to glue themselves to the substrate. No other crustacean makes cement. Although there are other cement-making organisms in different animal groups, like tube worms (Annelida), mussels (Mollusca) and ticks

(Arthropoda), these are not closely related to barnacles. Each has independently invented cement as an aid to their sessile lifestyle. The cement has exactly the same function in each case – gluing an animal to the spot and making it damned difficult to remove - and looks the same to the casual observer (or the annoyed sailor). But differences at the molecular level give away the independent derivations (Kamino 2010; Suppan et al. 2018). So, cement in barnacles, tube worms, mussels and ticks are analogies, not homologies, representing separate inventions, not shared inheritance.

If not inherited from a stuckfast ancestor, where did the barnacle’s ability to make cement come from? Unlike language, where it is at least technically possible to invent something completely *de novo* (even if it is more common to adapt an existing linguistic feature), all biological traits must have evolved from pre-existing features. Nothing can evolve from nothing. From his dissections, Darwin could see that the cement travels down structures derived from the antennae. An adult barnacle, glued to one spot its entire life, does not need to feel its way in the world, so the antennae have been repurposed for cement delivery. Because the cement glands occur in close association with ovarian tissue (Kamino 2010; Walker 1970), Darwin’s dissections led him to believe that the cement glands were derived from egg producing tissues (something that he later reluctantly admitted was a blunder: Richmond 2007). Darwin refers to a comment by the great comparative anatomist, Richard Owen, with whom Darwin corresponded on this point:

“I have entered on this subject at some length, (and I wish I had space for more illustrations,) from its offering, perhaps, the most curious point in the natural history of the Cirripedia. It is the one chief character of the Sub-class. I am well aware how extremely improbable it must appear, that part of an ovarian tube should be converted into a gland, in which cellular matter is modified, so that instead of aiding in the development of new beings, it forms itself into a tissue or substance, which leaves the body in order to fasten it to a foreign support. But on no other view can the structure, clearly seen by me both in the mature Cirripede and in the larva, be explained, and I feel no hesitation in advancing it. I may here venture to quote the substance of a remark made by Professor Owen, when I communicated to him the foregoing facts, namely, that there was a new problem to solve, – new work to perform, – to attach permanently a crustacean to a foreign body; and that hence no one could, *a priori*, tell by what singular and novel means this would be effected.” (Darwin 1851b: 38)

On the one hand all novel traits must be derived from some pre-existing trait. On the other hand, the same problem may be solved in different ways, using different raw materials. Bat wings might superficially resemble pterosaur wings, but they represent different solutions to the same problems – the bat wing membrane is connected across all digits of the “hand”, whereas the pterosaur wing membrane is stretched out along only the outstretched fourth “finger” (Figure 2).

3.3 The complexities of establishing homology

Studies of development, from embryo to adult, continue to challenge the concepts of homology by highlighting the difficulties of separating functional equivalence and shared ancestry. It may seem obvious that the great diversity of eyes in the animal kingdom are not homologous, but instead represent repeated acquisition of a particularly useful functional category – vision – in multiple different lineages. Specialized organs for vision have evolved dozens of times in different lineages, with an array of different forms covering a wide range of structural complexity (Land and Nilsson 2002). Eyes vary from simple light-sensitive spots, to camera eyes that use a transparent lens to focus a detailed image (like the human eye), to compound “flies eyes” that form a single image with many fixed lenses. Even within the Crustaceans, the eyes are so morphologically diverse that it is difficult to establish homology with any great certainty (Oakley 2003), and there may be at least four evolutionary origins even of the simplest eye forms (Elofsson 2006). It gets even more complicated: a single species may have more than one kind of eye, and those different eyes might not necessarily share the same evolutionary origin. Barnacle final-stage (cyprid) larvae, whose sole purpose is to find a nice place to settle, have compound eyes, made up of multiple lenses that work together to form a detailed image (not unlike the kind of eyes found in crabs and flies). These complex eyes allow the larvae to see other barnacles (most prefer to settle near other barnacles, for reasons that will become obvious later), and have sufficient colour vision to discriminate good substrate choices (Cronin et al. 2017). But, once the larva has glued itself to a rock, the adult barnacle does not need visual acuity, so it only has simple eyespots (ocelli) that can discern light or shadow, which is sufficient to detect a looming predator and pull your soft parts into your shell. So the presence and complexity of different kinds of eyes represents different levels of need for visual acuity, according to life style. But does this mean that we can suppose that they are all independent solutions to a shared need? Or might there be some shared ancestral architecture on which all these different kinds of eyes are built? To answer this question requires a great deal of evolutionary detective work, conducted at the level of individual development.

Barnacle eyes challenged Darwin’s program to identify the embryological and evolutionary sources of unique barnacle traits:

“The eyes of Cirripedes certainly undergo a remarkable series of changes: in the larvæ in the first stage, there is a single eye, perhaps formed by the confluence of two eyes, occupying the normal position in the front of the head: in the second stage, ... the eye has become double, but the two are as yet simple; they are now situated posteriorly to the second pair of antennæ: in the third or pupal stage, they remain in the same situation, but have become compound, of

great size, and are attached to the apodemes of the antennæ: in the mature and fourth stage, they have moved somewhat posteriorly, and again have become simple, of minute size, and are either confluent, as in the Lepadidæ, or tolerably far apart, as in the Balanidæ. It must not be supposed that the eye of the mature Cirripede is metamorphosed from the eye of the pupa, for such is not the case; the new eyes and old eyes being formed somewhat apart, and frequently both can be seen within the pupa ... at the same time. It is scarcely possible that the eye of the larva in the first stage, can be changed into the double eyes of the second stage; though these latter may possibly be multiplied into the eyes of the pupa, as both continue to occupy nearly the same position" (Darwin 1854a: 120)

Darwin's dissections suggested to him that the compound eye of the cyprid larva was "cast off" with the larval cuticle at metamorphosis (Darwin 1851b: 22). So where did the adult barnacle's ocelli (eye spots) come from? Were they homologues of the larval eyes (modification of the same structure) or were they analogies (independent derivation of an organ with the same function)? The question is still not entirely settled, but perhaps there is a halfway-between explanation. In at least one species of barnacle, components of the early larval eye separate, migrate across the body, and are remodelled into two separate visual structures in the adults (Takenaka et al. 1993). So if some parts of the old structure are re-used to rebuild several new structures, do we call that homology? If you aren't confused at this point, you probably haven't been concentrating.

It gets worse. You might think that a study of the genetic architecture underlying development of the eyes would clear this up: if two different eye structures were specified by the same set of genes, then they would clearly be derived from the same ancestral eye, right? Yet studies of the genetic determination of eye development in animals have generated perhaps the biggest challenges to the concept of homology since Darwin's day (Wray and Abouheif 1998). Scientists were flabbergasted to discover that the formation of the great diversity of eyes in the animal kingdom, from the simple eyespots of flatworms to the intricate compound eyes of flies to the camera-type eyes of octopuses, is controlled by the same "master regulator" gene, generally referred to as *pax6*. Not only that, but the developmental genetic switch is so universal that you could take the *pax6* gene of a mouse and put it in a fly and it would still turn on eye development – wherever it was switched on, leading to unfortunate flies with eyes growing on their elbows and backs. This is because the *pax6* gene activates the 'make-an-eye' genetic program, present in all cells but usually only expressed in the appropriate place on the head. When *pax6* is activated, it tells those cells to make an eye, no matter what kind of animal, or what kind of eye, or where in the body it is expressed. Are master regulatory genes the "universal grammar" of animal evolution, the shared structure underlying the development of all the anatomical diversity?

The presence of a shared genetic architecture underlying very different anatomical structures challenges the way we interpret and define homology. The gene *pax6* itself is definitely homologous between animal species. Some sections of the gene are so similar between widely separated species that they could not represent independent inventions, but must have all been copied from the same gene in the ancestral animal (Figure 5). But the eyes themselves have evolved independently in many different animal lineages. It is clear that complex compound eyes, where many independent lenses must co-operate to produce a single image, have been independently “invented” in many different lineages (Nilsson and Osorio 1998; Oakley and Cunningham 2002), and even within the crustaceans there may have been many independent origins of visual systems of varying degrees of complexity (Elofsson 2006).

There are two broad explanations for the same genes controlling the development of different kinds of eyes. One is that despite their differences, the broad diversity of eyes are all modifications of an eye in the ancestor of all animals, that lived over half a billion years ago (e.g. Gehring and Ikeo 1999; Gilbert 2003). In this scenario, the many kinds of animals with no eyes, such as sponges, sea urchins and corals, represent losses of the ancestral state. The other possible explanation is that many animal lineages have independently evolved visual organs, and when they did so, they co-opted the same pre-existing gene into their regulation (e.g. Oakley and Cunningham 2002).

So how are we to interpret homology of eyes in animals? Do we say that animal eyes are like the tetrapod limb (Figure 2): despite great differences in outward morphology, the underlying structure betrays a common heritage, and that therefore all eyes are homologous? Or do we say that animal eyes are like the wings of bats, birds and pterosaurs, where a similar structural solution has been derived multiple times independently using common base materials, so that the genes may be homologous but the eyes themselves are analogous? Not surprisingly, different researchers strongly favour one view or the other, demonstrating that even concepts as apparently instinctive and essential to evolutionary biology as homology and analogy are surprisingly difficult to pin down.

Perhaps the barnacle eye gives a model on how to use comparability of parts to establish a less black-and-white view of homologous structures and analogous functions. The simple ocelli (eye-spots) of the adult barnacle do not develop directly from the larval eye, nor are they directly homologous to ocelli in all other crustaceans. The adult barnacle’s ocelli represent a solution to a problem: they need to be able to detect an incoming threat and behave appropriately. In evolution, solutions to problems must come from modification of existing structures, or repurposing of components already present in the system. A lineage can “invent” an eye anew, incorporating existing tools such as a light-sensitive protein

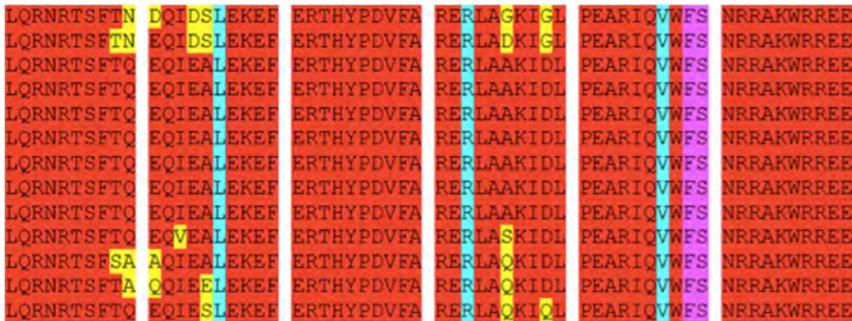


Figure 5: An alignment of homologous proteins from different arthropod species. Each letter represents one of 22 amino acids that make up proteins (in this case, part of the Pax6 regulatory protein which, amongst other functions, plays a key role in switching on eye development in embryos). These protein sequences are from species that last shared a common ancestor hundreds of millions of years ago, yet the sequences are still recognizably similar (the species are not unambiguously identified in the source (Kleinjan et al. 2008) but appear to include a fruitfly, lancelet, cavefish, chicken, human, quail, toad, zebrafish, squid, sea urchin and flatworm). Reproduced under Creative Commons licence from *PLoS Genetics* 2008 4:e29.

(Rhodopsin) and a handy regulatory system for neural development (Pax6). We can view the existence of shared features, such as the Pax6 regulatory switch and the light-sensitive pigment Rhodopsin, as homologous parts that have been brought together in different ways in a wide range of animal lineages to create new eye forms (Arendt 2003). But if we want to consider homology as an all-or-nothing phenomenon – either two structures are homologous or they are not – then we might find it difficult to make clear distinctions or unambiguous definitions in many cases (Lewin 1987). Luckily, most biologists are inured to mess and confusion. We have to be: evolution is not usually simple and neat.

3.4 Variation: Differences among individuals

We have seen that Darwin used comparability across life stages, from embryo to larva to juvenile to adult, to trace the formation of distinct barnacle characters. He used these observations to explain how features present in the ancestral crustacean could have been modified over time to produce the unique barnacle physiology and form. As well as looking at changes occurring within an individual during its lifetime, Darwin also used comparability between individuals to explain how the change took place. Here, the difficulties of comparability that made taxonomy troublesome provided essential support for Darwin's developing evolutionary theory.

One key purpose of a taxonomic treatise is to identify the distinctive characteristics that define a species: features, or combinations of traits, shared by all members of the species and no members of any other species, so that they may serve as diagnostic characters (Dubois 2017). Darwin's frustration as a taxonomist is palpable as he tries, and fails, to find invariant diagnostic characters for barnacle species: "there is scarcely a single external character which is not highly variable in most of the species" (Darwin 1854a: 3). The problem got worse the more specimens he examined: "it is hopeless to find in any species, which has a wide range, and of which numerous specimens from different districts are presented for examination, any one part or organ, – which from differing in the different species is fitted for offering specific characters, – absolutely invariable in form or structure" (Darwin 1854a: 155). The lack of invariant diagnostic characters made it difficult to make a clear distinction between varieties and species, similar in many ways to debates over whether a particular population speaks a dialect or a distinct language. In biology, as in linguistics, the process of descent with modification produces a continuum of variation between different populations that may confound clear categorical distinctions. In fact, some of the populations of barnacles that Darwin combined together because they lacked diagnostic differences have been shown by DNA analysis to be separate species (Southward 1983).

But the variation that frustrated taxonomy was fine fuel for the evolutionary fire: "Systematic work would be easy if it were not for this confounded variation, which however is pleasant to me as a speculatist though odious to me as a systematist" (Darwin 1849: 37). Here is what Darwin saw in his beloved barnacles. There was no character that did not vary between individuals of a species. Any part that varied between species also varied within species, but the characters that defined species were more variable than the characters that defined genera (groups of related species). If any species had a very distinctly modified trait, then that trait would be found to be highly variable. Just as sociolinguistic variation attests the continuous process of language change, so individual variation in biological populations forms the foundation of ongoing genetic change.

Darwin didn't just see variation, he saw hierarchies of differences: not simply taxonomic structure, but the telltale signs of evolution in action. The implications of these observations speak to the heart of the Darwinian explanation for diversity, because it is the variation between individuals that is fuel for the formation of distinct traits in different species. Any heritable variation that made an individual more likely to successfully reproduce would be present in greater frequency in subsequent generations. If this advantage was sustained over time, and given that more individuals are born than can possibly survive, eventually individuals with the advantageous trait would replace the others. In this way, the

individual differences generated every generation could be amplified by natural selection.

Darwin's explanation of evolution drew heavily on the concept of uniformitarianism, a principle established in geology and codified by the great geologist Charles Lyell. Lyell insisted that we should not invoke unknown mechanisms to explain past changes, but base our explanations only on processes we can witness in operation in the present day. This stricture reins in speculation and discourages hypotheses that rest on extraordinary mechanisms that cannot be directly investigated: "No unnecessary intervention of unknown or hypothetical agency" (Charles Lyell 1856, quoted in Burkhardt Smith 1991: 169). Darwin applied Lyell's doctrine to the living world, and used only observable mechanisms to explain biodiversity: individuals vary in ways that may be inherited by their offspring, competition for resources will tend to favour those individuals whose variations make them better suited to their environment, so any variations that increase the chance of reproduction will be more likely to be passed on to the next generation, and will thus rise in frequency over time. The uniformitarian doctrine is also widely accepted in linguistics, on the assumption that individual speech variants contribute to sociolinguistic change in language use, potentially contributing to the formation of dialects, which may eventually become distinct languages (Christy 1983). Indeed, Lyell himself drew this very analogy: "Languages are intensified by isolation & time – hybrid when they radiate & touch others – idioms & dialects which are contemporaneous resemble in space what the change of the same tongue does in time at two distant epochs" (Lyell 1860: 284). In fact, Lyell used the example of language change to convince himself of the reality of species evolution (see Bromham 2017).

Darwin's difficulties in classifying barnacles due to these hierarchical patterns of variation provided an important pillar for his developing evolutionary theory. He struggled to determine which forms should be designated as proper species in their own right, and which as mere varieties of other species (Southward 1983). Later, in the *Origin of Species*, Darwin would argue (as Lamarck 1809 had done before him) that the inability of naturalists to agree on clear distinctions between species, subspecies, varieties and races was evidence that species were formed by gradual descent with modification from a shared common ancestor: "Hereafter we shall be compelled to acknowledge that the only distinction between species and well-marked varieties is, that the latter are known, or believed, to be connected at the present day by intermediate gradations, whereas species were formerly thus connected" (Darwin 1859: 485). Linguists face the same challenges – while some may consider that a particular speech community speaks a dialect, others may consider it has a separate

language - though their categories may reflect socio-political settings as well as degree of measurable difference.

Interestingly, Darwin's wrestle with variation in his barnacle work also convinced him of the role of experience and wisdom in identifying species. It was not possible, he felt, to write an unambiguous list of characters that would allow any person to identify a barnacle species: "After considerable experience, when numerous varieties of a species have been carefully examined, the eye acquires a sort of instinctive knowledge, by which it can recognise the species, though the character cannot be defined by language" (Darwin 1854a: 155). This indefinable knowledge has been called "a feeling for the organism" (by the pioneering geneticist Barbara McClintock), and is still a strong thread running through biology today, even in the apparently objective and quantitative age of genomics (see Bromham 2016). Perhaps this feeling for the organism has a parallel in a linguist developing idiomatic competence in a language they are studying (e.g. Pawley 1993), or in being able to identify unusual features shared between languages (e.g. Evans 2011).

3.5 Comparative biology: Differences between species

Darwin used comparability between life stages to trace the origins of highly modified organs, and comparability between individuals to provide a mechanistic explanation for that change over time. Now we will consider how comparisons between different species allowed him to construct evolutionary narratives for some singular aspects of barnacle life. One of Darwin's most bizarre barnacle discoveries provides an excellent case study in the role of comparability in identifying highly modified organisms, and constructing narratives of evolutionary change for distinctive species characteristics.

The story begins on HMS Beagle, as Darwin discovers a strange parasite-like organism, embedded in tiny boreholes in a seashell. On close inspection, he recognized this tiny animal as having the anatomy of a barnacle, although no-one had ever described a burrowing barnacle before: "Who would recognize a young *Balanus* [barnacle] in this illformed little monster?" (Charles Darwin in 1834, quoted in Keynes 2000: 276). This was a puzzle to be solved later: he preserved the specimen (Castilla 2009). On his return to England, he once again turned his attention to this curious find. How could he explain this bizarre, simplified, shell-less barnacle? To answer this question, he needed to be able to compare its anatomy to other barnacles – and so was launched his epic eight-year journey with cirripede taxonomy. He did not solve the puzzle of the bizarre burrowing barnacle until a decade after its initial discovery, and the story behind this perplexing

specimen turned out to be more interesting, and more important, than he could have imagined (Buchanan 2017).

One of the unique features of barnacles that Darwin had to explain was that, unlike other crustaceans, they are hermaphrodites, with both male and female reproductive organs in the same individual.¹ Indeed, the hermaphroditism of barnacles, in stark contrast to the separate males and females in all other crustaceans, had been a sticking point for classifying the barnacles within the Crustacea (Buchanan 2017). Although individual barnacles typically produce both male and female gametes, they are generally not able to self-fertilize (Yusa et al. 2013). Furthermore, they do not broadcast gametes into the water, as some sessile marine animals do, but have internal fertilization and brood their offspring within their armour plating. How can a sessile animal with internal fertilization, but without the ability to self-fertilize, get gametes from one individual to another? The barnacles' solution to this paradox is to possess exceedingly long penises, up to eight times their body length, so that they can reach across to nearby mates. Being a hermaphrodite makes sense for such an animal, as the chances of mating with a nearby barnacle will be higher if you don't have to be picky about whether they are Arthur or Martha.

Darwin's mantra was that any comparable traits in different species must be linked by a series of intermediate steps, each just a slight modification from their immediate ancestor. So he needed a plausible set of steps connecting a species with two sexes to a hermaphrodite species. This was not just a peculiar barnacle problem: the evolution of separate sexes had long been a subject of fascination for Darwin in the formation of his species transmutation theory (Buchanan 2017). The challenge here is to provide a gradualist explanation for the transition between discrete states. A linguistic analogy might be change in distinct grammatical structures. If we see related languages with distinct syntax, such as subject-object-verb (SOV) or subject-verb-object (SVO), can we imagine a chain of intermediate steps that are neither wholly one word-order or the other but somewhere in between (Dunn et al. 2011; Maurits and Griffiths 2014)?

Two discoveries offered the delighted Darwin a possible solution. In examining some tiny parasites living within an adult hermaphrodite barnacle, he was astounded to find that these parasites were actually male barnacles, much reduced in morphological complexity: "there is no mouth, or stomach, or thorax, or limbs of any kind, or abdomen. It is obvious that these males must be very short-lived: they perform their masculine functions and then perish." (Darwin 1854a: 561). He joyfully reported his discovery in correspondence to his friend Joseph Hooker,

1 A century later, two other rare groups of hermaphrodite crustaceans were discovered: remipedes and horseshoe shrimps.

citing it as firm evidence for his species theory: “an hermaphrodite species must pass into a bisexual species by insensibly small stages, & here we have it, for the male organs in the hermaphrodite are beginning to fail, & independent males ready formed” (Darwin 1848). Male function was apparently being gradually transferred to separate individuals specialized for nothing but insemination, leaving individual hermaphrodites free to invest more in female function, and less in sperm production.

Furthermore, reinspection of the puzzling burrowing barnacle he had found in Chile showed that it was actually a female, hitherto unknown in barnacles. Now Darwin had a path to follow between hermaphrodites and bisexual species, passing through stages where one sex is reduced in size. The discovery of parasitic males was therefore not just a biological curiosity, but a triumph of Darwinian explanation: “we have one curious illustration more to the many already known, how gradually nature changes from one condition to the other, – in this case from bisexuality to unisexuality” (Darwin 1854a: 29). In fact, the transition from hermaphroditism to androdioecy (males and hermaphrodites) appears to have occurred at least four times in barnacles (Kelly and Sanford 2010), and these androdioecious lineages have given rise to at least four different species with separate males and females (Yusa et al. 2012), highlighting a surprising degree of evolutionary gender fluidity in these sessile invertebrates. So the barnacles provide an interesting case in how a character occurring in apparently distinct states, such as separate sexes, can be “diverse, continuous and plastic” (Yusa et al. 2013: 701).

In addition to providing an evolutionary bridge between different mating systems, Darwin’s discovery of dramatically reduced parasitic males and burrowing females demonstrated that simplification and loss are as much a part of evolution as complexification and gain. The living world had traditionally been arranged as a chain of simple to complex beings, with the more complex organisms near the top of the hierarchy. But Darwin’s work on barnacles suggested a more utility-focussed approach to species traits (Love 2002). A species may be simple in some characters but complex in others, as long as it was able to thrive in its environment: “all these facts proves perfection of organs have nothing to do with perfection of individual, ... but that perfection consists in being able to reproduce” (Darwin 1838: 55). The tiny “complemental males” of different barnacle species vary in their degree of morphological reduction, from relatively intact juvenile-like individuals to sac-like males that lack any features such as a mouth or appendages (Buhl-Mortensen and Hoeg 2006; Ozaki et al. 2008). The most highly modified males don’t eat or grow, they are “essentially just short-lived bags of sperm” (Kelly and Sanford 2010: 40). But if they successfully father offspring, then they have contributed as much to evolution as any other, more fully-formed, male.

These complementary males and burrowing female barnacles are so highly modified that their cirripede affinities were only obvious on close dissection and observation. In fact, Darwin failed to recognize an entire group of barnacles, the rhizocephalans, parasites so reduced in form that they have no discernible external barnacle features at all. The females are essentially just reproductive organs in a formless body, which grows inside their unfortunate arthropod host, replacing the host's own reproductive organs. For example, the barnacle *Sacculina* takes over its host crab's physiology, preventing it from growing and moulting, and uses mind-bending chemicals to convince the host crab that she is pregnant so that she will brood the barnacle's larvae as if they were her own (and if it has infected a male crab, it first convinces him he's a female and then makes him think he's pregnant). If you saw a female *Sacculina*, you might think it was a fungus, so devoid it is of crustacean features (Figure 1). The tiny male *Sacculina* is even more reduced: in its larval stage it enters the body of the parasitic female and then lives within her body as little more than a testis. How can we study the evolution of animals so dramatically simplified that they have lost all comparable traits?

3.6 Does DNA solve the problem of comparability?

We now have a new tool in our comparative toolkit that circumvents many of the problems of comparability that Darwin faced. Molecular evolutionary analysis allows us to look beyond the highly modified morphology and glimpse the genome within. This gives us universal comparability because all living species use the same basic language to store genetic information and translate that information into the working parts of a cell. All genes in all species are written in the same entirely comparable alphabet, the bases of DNA, which are represented as A, C, G and T. These genes are translated into linear strings of amino acids, which then fold into the active three-dimensional shape of working proteins. Not only is the language of molecular evolution essentially the same for all species, some of the actual genes are present in all living species, circumventing the problem of making comparisons between widely separated lineages that share few physical characteristics in common (Figure 5). Even highly modified species like *Sacculina*, devoid of most of the characteristic features that aid barnacle classification, have the same basic set of genes as all other animals, such as those involved in metabolism, gene regulation and DNA replication. This gives us a powerful new way to investigate even the most intractable taxonomic puzzles and evolutionary conundrums. However much the external morphology has been modified, the genes continue to record history and reveal species' origins.

For example, Darwin had described a “very curious cirripede”, *Anelasma*, without a shell, and with only a simple mouth and reduced feeding appendages, which reportedly grew embedded in the flanks of deep-sea sharks (Darwin 1851b: 170). Parasitic species, with their simplified morphology lacking many of the features shared by other barnacles, were challenging to place in a taxonomic hierarchy, due to limitations on comparability with other species. Now we can simply sequence the DNA of such recalcitrant species, compare it to billions of sequences in the giant public databases, and find the closest matches. DNA analysis can even be used to identify barnacle larvae before they have developed their characteristic adult traits, which aids a range of investigations from detecting invasive species (Chen et al. 2013) to working out which marine creatures feed on barnacle larvae by analysing their stomach contents (Bowser et al. 2013). Not only does DNA allow species identification, we can use molecular phylogenetic analyses of DNA to reconstruct evolutionary narratives that took Darwin years of fine microscope work to uncover. Of course, there are limitations to historical information that can be derived from DNA phylogenies. All the DNA samples in the world couldn't tell you there were once pterodactyls with 10 m wingspans.

One of the advantages of DNA analysis is that it can reveal entirely unexpected relationships. Many species of barnacles are specialized to live on marine animals such as turtles and whales. These barnacles use their hosts as a home, piggy-backing on the larger animals but still filtering their own food from the water. While sometimes described as “commensals” (meaning a relationship that is beneficial to one partner and neither beneficial nor harmful to the other), there is some evidence that barnacle passengers are, at very least, very annoying to their vertebrate hosts, and might even be harmful (Fertl and Newman 2009). Some whale-riding barnacles attach deep within their host's tissues (Frick et al. 2011). It would not seem to require much of an evolutionary leap to go from burrowing into your host's body to actually drawing nutrition from their flesh, as does the shark-parasitic barnacle *Anelasma* (Ommundsen et al. 2016). But a recent DNA analysis of *Anelasma* revealed an unexpected story, suggesting that their closest relatives are not the ocean-going riders of turtles and whales, or the plateless form of goose barnacles they had previously been allied with (Figure 6). Instead, the DNA phylogeny groups *Anelasma* with stalked, shore-dwelling barnacles (Rees et al. 2014). On the basis of this molecular phylogeny, it was suggested that *Anelasma* might represent a unique snapshot of the evolutionary transition between a free-living filter-feeder and an obligate parasite.

While DNA solves some comparability problems, it creates new problems. In fact, it's the super-comparability of DNA that is the heart of the problem. The four bases of DNA – A, C, G and T – are interchangeable. A mutation could change an A at one place in the sequence to a G, and if individuals with that G mutation out-

reproduce those with the original A, then eventually the population may be full of individuals all carrying a G where their relatives have an A. If we compare the sequences from one population to another, we might detect this molecular evolutionary change as a difference in the DNA sequence. But, if that site undergoes another mutation, there is a one in three chance it will change back to an A. Now there will be no difference between that sequence and its relatives because the previous change has been entirely erased (Figure 7). A similar problem may occur in language change in cases where there are a limited number of states a feature can have and a relatively high rate of change, for example some grammatical features with a limited “design space” (Dunn et al. 2011; Greenhill et al. 2017). In this case, unrelated languages may end up with similar states by analogy, not homology (Dahl 2008).

Although DNA alignments may look superficially like the matrices of cognates used in language phylogenies (Figure 8), there is an important difference. When two languages share a similar form of the same word, we can be quite confident that those words are homologous (cognates ultimately derived from a common source, whether by descent or borrowing). We build on the assumption that the chance of two groups of people independently inventing the word “jama” for animal is low (though not impossible), and therefore the presence of similar forms in the same lexical category is convincing evidence of shared origin (whether by descent or borrowing). The same logic applies when we see the same gene sequence in different species (Figure 5): we conclude that the similarity between them is far greater than we would expect if they had been independently “invented” in different lineages.

But this confidence in homology cannot extend to the individual bases in the DNA sequence. When we see that two species share the same base in a DNA sequence, we might think that this is good evidence that they both copied that base from a recent common ancestor (Figure 8). But we can't rule out that they both independently changed from an A to a G at that position, because the end result would look exactly the same. A G is a G, and it looks just the same whether it is analogous (independently evolved) or homologous (shared descent). In fact, because there are only four possible states for any given position in a DNA sequence, as time goes on and more changes accumulate, the chances of analogous changes (incidentally matching bases) increases as the number of homologous matches (identical by descent) decreases. Eventually, the sequence is randomized, all historical signal is erased, and yet 25% of bases will be the same simply by chance.

The phenomenal comparability of DNA bases ironically leads us to be unable to make a definitive statement about homology. Instead, whether a shared base at any given position in the gene sequence represents a homology, and therefore holds the signal of the evolutionary past, or an analogy, that has been acquired

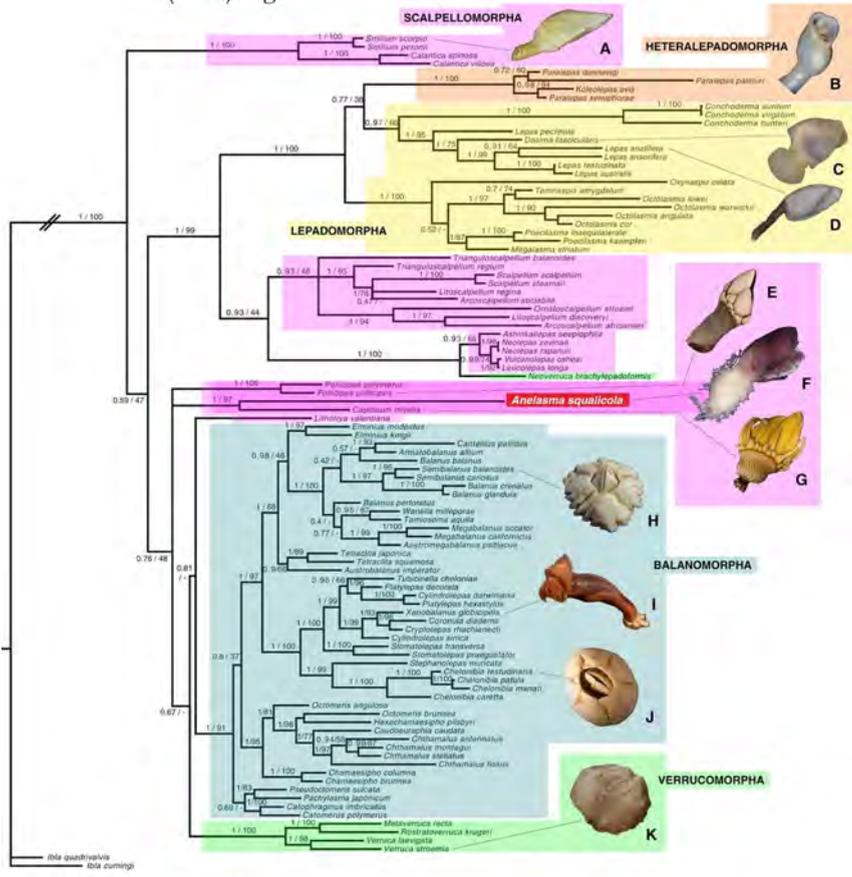


Figure 6: A molecular phylogeny of various barnacles of the Pedunculata (called Goose barnacles because of an early hypothesis that geese hatched from these barnacles, which conveniently allowed goose flesh to escape religious prohibitions on eating meat). This family tree was derived from computational analysis of DNA sequences from each of these living barnacle species (Rees et al. 2014). The numbers on the branches represent a statistical measure of support for that grouping from the data: the first number being a Bayesian posterior probability, and the second a bootstrap percentage. Many biologists follow the convention that bootstrap values less than 95% are not considered convincing evidence for a grouping (Felsenstein 1985). For example, in this tree, grouping the shark-parasitic barnacle *Anelasma* (labelled in red) with the rock-dwelling Japanese goose barnacle *Capitulum mitella* has high bootstrap support (97%), suggesting that these data support a relationship between these species, given the assumptions of the analysis. But the placement of this pair of species within the phylogeny is uncertain, as the nodes connecting it to the rest of the tree have less than 50% bootstrap support. Reprinted from *Current Biology* 24, Rees, David J., C. Noever, Jens T. Høeg, A. Ommundsen and H. Glenner, *On the Origin of a Novel Parasitic-Feeding Mode within Suspension-Feeding Barnacles*, 1249–1434, Copyright (2014), with permission from Elsevier.

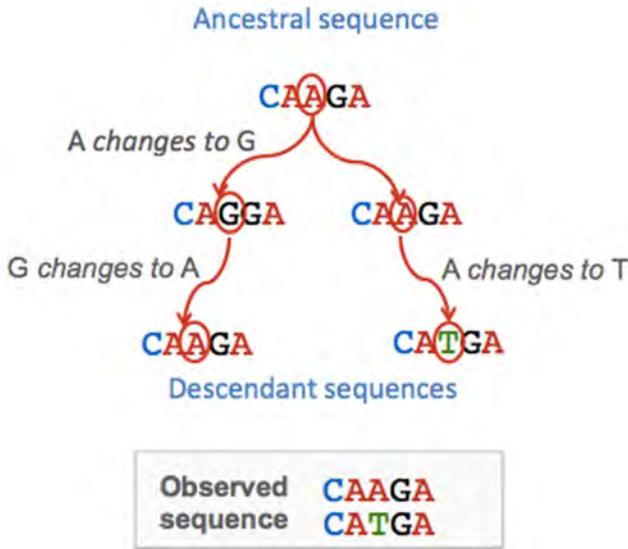


Figure 7: The problem of multiple hits in DNA sequences. If a position in a DNA sequence changes base more than once then it erases past historical signal. An alignment of DNA sequences (e.g. Figure 8) shows only the contemporary sequence and cannot directly reveal past changes, which must be inferred from a statistical model of DNA base substitutions. In this case, the alignment (observed sequences) shows only one difference although there have been three base substitutions since these sequences last shared a common ancestor. If you are interested in learning more about how the comparison of DNA sequences is used to reconstruct evolutionary past and processes, you can find an introduction to the data, methods and evolutionary inference in Bromham (2016).

separately in different lineages, can only be judged from context, and can only ever be a statement of probability. We can say that we think it is more likely that two sequences with a G in the 26th position in the alignment inherited the G from their common ancestor, and therefore it is a homology that carries with it historical signal, and that it is less likely that they both changed independently from an A to a G at that position (Figure 8). But, since a G looks the same whether its shared by homology or gained by analogy, we can never know for sure. So all inference of evolutionary narratives from DNA data must be expressed in term of statistical confidence, not as an error-free statement of the true history (Bromham 2016). A phylogeny is a hypothesis, not an observation, and we evaluate the level of support that our data brings to that hypothesis using a range of statistical tests (Bromham 2019). In fact, DNA analysis lends itself well to making formal statistical tests of support, a strength arising from the weakness of the uncertainty of comparability. In the case of the shark-parasitizing barnacles, the statistical support for the

A841_Badwe	ɔr	mɔb	ɛfi	ɔɔ	ɛdɔ	mɔ	ɛnɛ	mɛn	ɛwɔ/ɔ
A85b_Bekwɛl Makokou	ʔit	mɛɔ	ɛɔi	ɔɔi	ɔɔi	mɔ	na dʒɛndʒao	nɛn	ɛkɛwɛl
A85b_Bekwɛl Mɔ	ɔr	mɛɔ	ɛɔi	ɔɔi	ɔɔi	mɔ	ɛɔbɛ	mɛn	ɛlɔm
A86c_Mpiemo	ɔrɪ	mɛɔ	mɛɛɔi	ɔɔɔ	ɛwɔɔɔ	mɔ	ɔɔɔɔ	ɛnɛ	ɛkɔɔɔɔ
A87_Bomwali	ɛr	mɔ	mɛwɛɛi	ɔɔɔw	?	mɔ	ɛbɔbɔ	mɛnɪ	ɛtɔɔɔ
A91_Kwakum	bɔpɔ	mɛɔ	ɛbɔɔ	ɛp-ɔɔɔɔ	ɔɔɔ	ɛbɔm	?	ɛɔn	ɛwɔɔ
A93_Kako	mɛmɔ	ɔɔ	mɛmɛmɛ dɔɔ	ɔɔpɔ	ɛɔɔ	mɔ	ɛpɔpɔm	ɛnɛ	ɛwɔɔ
B11a_Mpongwe	nɛmɛ	ɔɔɔ	ɔɔmɔ	ɔɔmɔ	ɔɔɔ	ɛwɛmɛ	ɔɔɔ	ɛnɛ	ɛpɔmɔ
B11b_Orungu	nɛmɛ	ɔɔɔ	ɔɔmɔ	ɔɔɔ mɔ	ɔɔɔ	ɛwɛmɛ	ɔɔɔ	ɛnɛ	ɛnɔmɛ
B11c_Galwa	nɛmɛ	ɔɔɔ	ɔɔmɔ	ɔɔɔ mɔ	ɔɔɔ	ɛwɛmɛ	ɔɔɔ	ɛnɛ	ɛpɔmɔ
B11d_Dyumba	nɛ mɛ	ɔɔ ɔɔ	ɔɔmɔ	ɔɔɔ mɔ	ɔɔɔ	ɛwɛmɛ	ɛɔɔ	ɛnɛ	ɛd nɔ mɛ
B11f_Enenga	nɛmɛ	ɔɔɔ	ɔɔmɔ	ɔɔmɔ	ɔɔɔ	ɛwɛmɛ	ɔɔɔ	ɛnɛ	ɛnɔmɛ
B31_Tsogo	nɛmɛ	ɔɔɔɔ	mɔɔ	ɛwɛɔ	ɛkɔɔ	ɛbɔɔ	ɛɔɔ	ɛnɛ	ɛmɔɔɔ
B32_Kande	ɛnɛmɛ	ɔɔɔɔ	mɔɔmɛnɛ	nɔɔɔɔ	ɛnɛkɔ	ɛwɛmɛ	ɛɔɔ	ɛnɛ	ɛmɔmɔmɛ
B301_Viya	ɛbɔ	ɔɔɔ	mɔɔ	ɛwɛɔ	ɛkɔɔ	ɛbɔmɛ	ɛɔɔ	ɛnɛ	ɛmɔmɛ
B302_Himba	ɛnɛmɛ	ɔɔɔɔ	ɛmɔɔ	nɔɔɔɔ	ɛnɛkɔ	ɛbɔɔ	ɛwɛɔɔ	ɛnɛ	ɛmɔmɔmɛ
B304_Pɛzi	ɛnɛmɛ	ɔɔɔɔ	mɔɔmɔɔ	nɔmɔmɛ	ɛnɛkɔ	ɛbɔm	mɔɔɔɔɔɔ	ɛnɛ	ɛmɔmɔmɛ
B305_Vove	nɛmɛ	ɔɔɔɔ	mɔmɛ	ɛwɛɔ	ɛnɛkɔ	ɛbɔmɛ	ɛɔɔ	ɛnɛ	ɛkɔkɔ

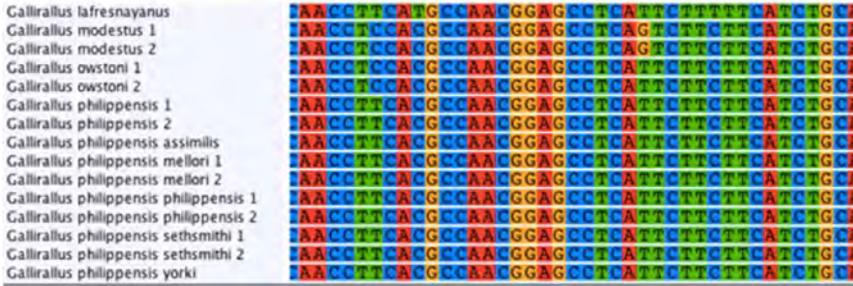


Figure 8: Raw data for phylogenetics may look superficially similar, whether from language data (here represented by a table of cognates for Bantu languages: Grollemund et al. 2015) or DNA phylogenetics (here represented by mitochondrial sequences for rails: Kirchman 2009). But a key difference in the way changes accumulate means that these data must be treated somewhat differently. Perhaps the appropriate analogy for a cognate set of a lexical category is not a position in a DNA alignment, but a whole gene. However, while cognate classes are recognized as discrete categories (like DNA bases), genes show continuous variation (varying at some percentage of positions in the alignment).

placement within the group of shore dwelling barnacles is not particularly strong. In fact, the DNA data is not entirely clear on which of several major clades they might belong to (Figure 6). So perhaps the puzzle of Darwin’s “very curious cirripede” has not been solved yet.

4 Conclusion

One of Darwin’s staunchest defenders, the zoologist Thomas Henry Huxley, said in a letter to Darwin’s son Francis: “in my opinion your sagacious father never did a wiser thing than when he devoted himself to the years of patient toil that the Cirripede book cost him” (Darwin 1887: 347). Darwin’s barnacle work was so admired that it earned him the Royal Medal of the Royal Society, even before all

four volumes had been published (Parsons 1853). Far from being wasted years, Darwin's barnacle work made important contributions to zoology and systematics, and built a rock-solid foundation for his evolutionary theorizing. In this way, Darwin's barnacle treatises ultimately contributed not only to the foundations of modern biology but also to historical linguistics, as Darwin's theories were co-opted into studies of language evolution (Schleicher 1869).

Darwin had to directly address challenges of comparability, in order to trace the ancestral source of barnacle features and construct a convincing narrative for how they had changed over time. In order to establish comparability among life stages, individuals and species, he had to come up with a standardized terminology. He used developmental processes to ensure that he compared not just traits that had the same appearance, but that were derived from the same fundamental structure. His comparisons between individuals revealed a surprising degree of variation within living populations, which made the task of description and classification difficult, but provided the fuel for evolutionary change, thus supporting Darwin's proposed mechanism for the origin of species. And comparisons between species revealed potential stepping-stones between apparently discontinuous traits. Different kinds of comparisons reveal different stories, whether seeking explanations for why the same function arises independently in multiple lineages (such as cement) or how a shared feature is modified in many varied descendants (like limbs) or cases where it is difficult to draw a line between shared inheritance and independent acquisition (such as eyes). We must choose the appropriate class of comparison for the question at hand.

The challenges that Darwin faced are still faced today, as we can appreciate when we consider the problem of inferring homology of eyes between life stages, and across different animal lineages. Darwin would have loved DNA because it would have made his life as a naturalist so much easier, solving many of his problems in comparability, providing a ready means of tracing evolutionary histories, and providing evidence for his grand theory linking change in individuals to population divergence to the generation of biodiversity (Bromham 2009). But while DNA solves some of the challenges of comparability, it generates more problems for us to solve, such as the analytical problems of tracing changes in sequences of only four different "letters", and the puzzle of reinterpreting homology in light of developmental genetics (Lewin 1987). As with most aspects of biology, the more we learn, the more complex, confusing and wonderful the story gets.

Acknowledgments: My heartfelt gratitude is due to Felicity Meakins, Hilde Schneemann, Kim Sterelny, Hedvig Skirgård, Simon Greenhill and Matt Spike for their insightful feedback. Thanks also to Nick Evans for inviting me to participate in ALT panel, and to Nick Evans, Ulrike Zeshan and an anonymous reviewer for

helpful comments on the manuscript. More broadly, I thank Nick, Felicity, Hedvig, Simon and all members of the Centre of Excellence for the Diversity of Language (COEDL) for welcoming me so warmly into the linguistics community.

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