Chapter 5
Adaptation

Philippe Grandcolas

Abstract Adaptation is a concept central to evolutionary biology that explains why organisms fit their environment according to natural selection. An adaptation can be defined as a novel character appearing in an organism and maintained by natural selection. This concept must therefore be studied at two different levels, within a phylogenetic analysis for inferring relative novelty and within a populational analysis to assess the role of natural selection. By addition of these two study levels, ad hoc or tautological proposals of adaptive characters may be avoided. The related concepts of preadaptation or exaptation feature the importance of considering both a structure and its function to better understand the evolution of a character. The structure can remain stable and the function can change, subsequently contributing to an evolutionary innovation.

Living organisms inherit their characteristics by descent with modification. This general and basic process assumption explains the diverse range of situations observed with regard to biological evolution. Therefore, biological diversity is inferred to result from species divergence after successive modifications that occurred during the course of evolution. If the process of descent with modification explains the diversity of organisms well, it does not, however, explain the fit of organisms to their life conditions. Why species divergence does not occur by diversification in every phenotypic direction and why it often produces a better fit of species to their environment. For example, why a species of insect that shelters on trees shows the detailed aspect of a leaf not only to our eye but also to that of the predator. Why the different biological parameters involved in life histories and population dynamics are arithmetically adjusted to each other? To explain all these fits, one assumption more than descent with modification must be included in the process assumption, the one about the particular case of adaptation. Adaptations are inherited modifications of organisms, which are not maintained stochastically or independently of the environmental influence. These modifications that we know to

---

P. Grandcolas (✉)
UMR 7205 CNRS, Institut de Systématique, Evolution et Biodiversité,
Muséum National d'Histoire Naturelle, 45, rue Buffon, 75005 Paris, France
e-mail: pg@mnhn.fr; http://isyeb.mnhn.fr/

T. Heams et al. (eds.), *Handbook of Evolutionary Thinking in the Sciences*,
DOI 10.1007/978-94-017-9014-7_5

be heritable have been assumed to be maintained by natural selection since Darwin (1859). Darwin and Wallace established the theory of natural selection in a scientific context where the notion of biological evolution itself was largely recognised (cf. Perrier 1886; Mathews 1958). Since that time, scientists have searched for an understanding of the role of natural selection in the construction and maintenance of extremely diverse adaptations. These research projects have often been very successful but they have also led to some exaggerations or ad hoc explanations followed by controversies. The succession of achievements and controversies during 150 years has sometimes cast doubts on the heuristic value of the adaptation concept. Some biologists were afraid that this concept could be detrimental to the whole theory of evolution, by favouring narrative and inductivist over hypothesis-testing approaches. However, to explain the fit of organisms, the concept of adaptation remained unavoidable and it was to Darwin's (1859) great merit that he understood it and carefully exposed it.

1 The Concept, Its Definition and Its Implications

An adaptation can be defined as a novel character appearing in an organism and maintained by natural selection.[1] There are many subtle and somewhat confused variants of this definition, each of them linked to different uses in varied scientific domains.[2] In the present definition, the adaptation is the character itself but the term is also used to name the process by which this so-called adaptive character has been acquired by the organism. In all cases, this definition clearly refers to two important aspects of the concept of adaptation.

Adaptation should be worked out at two different observation levels. The first level allows one to detect if the character is an evolutionary novelty (*a new character appeared in an organism* and was maintained by natural selection), by the way of phylogenetic analysis relating species according to their shared original characters, the apomorphies.[3] By definition, an apomorphic character, original and shared by several species, is an evolutionary novelty, and therefore only a possible adaptation of these species. Conversely, every adaptation of one or several species is, by definition, a novelty at this level, thus an apomorphy.[4] To detect an evolutionary novelty and therefore to bring the first corroboration for the occurrence of an adaptation, a phylogenetic analysis must be carried out to check if the putative adaptation is actually an apomorphy of the taxon considered (Fig. 5.1). The second level of observation deals with the role of natural selection (a new character appeared in an organism and was *maintained by nat-*

---

[1] Antonovics (1987), Coddington (1988), Brooks and McLennan (1991), Leroi et al. (1994), Grandcolas and D'Haese (2003).

[2] For example, Sober (1984), Rose and Lauder (1996), Mahner and Bunge (1997).

[3] See Hennig (1965, 1966), Wiley (1981), Farris (1983).

[4] See Coddington (1988), Grandcolas et al. (1994), Deleporte (2002), Grandcolas and D'Haese (2003).

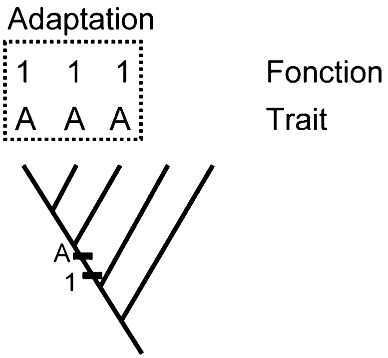

Fig. 5.1 An adaptation is, by definition, an evolutionary novelty. In this simple theoretical example, the three more nested taxa acquired the trait "A" with the function "1." From the phylogenetic point of view, the trait "A" can be an adaptation

ural selection). This role can only be studied with respect to processes of differential survival and reproduction in populations. Natural selection refers to the better survival and reproduction of some individuals, therefore more efficiently transmitting their genetically determined characters, in given environmental conditions (Darwin 1859). Environmental conditions are meant to include everything outside the organism: the physical environment, the conspecifics, the hetero-specifics, etc.

To document the role of natural selection and to validate the adaptive value of a character are often considered as difficult subjects of study, especially in natural conditions (Endler 1986). It necessitates documenting the survival and the reproductive success of different individuals differing by different states of the putatively adaptive character. The effect of natural selection is however inescapable, even if it is difficult to study and if its importance cannot be known conclusively in advance. A simple metaphor may help to understand the situation: individuals can be considered as objects of different size and shape put within different sieves with varying degrees of coarseness. Passing (by survival and reproduction) through the sieve (the environmental conditions) will have varying degrees of difficulty. At one extreme, if the objects are much smaller than the sieve, there will be no filtering. A naïve observer could claim that natural selection is not an explanatory concept. At the other extreme, where objects are the same size as the holes in the sieve, filtering will be of significant importance and the value of the concept will be obvious to any observer. Thus, the occurrence of this sieve (the selective environmental conditions) will be easier or harder to perceive depending on the intensity or the variance of its effect. This does not mean that it is impossible to find some cases where characters evolved without high direct selection (e.g., by neutral drift or by correlation/constraint with another character). It means rather that selection always acts fundamentally and potentially. In other terms, for not validating adaptive assumptions which are poorly documented or erroneous (type II errors, false positive), we must carefully avoid Type I errors (false negative) by refusing some correct adaptive assumptions too readily.

Based on all these considerations, it clearly appears that the complete study of adaptation is a tough job, demanding studies pertaining to several scientific disciplines (basically, phylogenetics and population biology) conducted at several observational levels (clades and populations). In addition, the population studies often do not consider the high diversity of possible situations in the field and generalise the results obtained in a particular population to the clade[5] or the species.

Another important property of the concept of adaptation is to be relative to the phylogenetic level of a given organism for which it is an evolutionary novelty. Adaptation must be defined with strict reference to a species or a group of species. If we ever refer to a group smaller than the one showing the apomorphy, we are no longer dealing with an evolutionary novelty at this level. For example, vertebrae are not an adaptation sensu stricto of mammals because they are a novelty for the ancestor of vertebrates, much anteriorly to the ancestor of mammals. They can still be maintained by natural selection in mammals, but they are not their exclusive adaptive peculiarity. It can be said, rather, that mammals show an adaptation of vertebrates.

Though operationally difficult to study, adaptation remains a concept central to evolutionary biology because it is the sole explanation for the fit of organisms to their environment. Organisms can evolve, change, but there are no reasons that can explain a better functional fit except an adaptive process involving natural selection. Neither neutral drift[6] nor developmental constraints[7] (Hall 1999), nor genetic assimilation[8] (Waddington 1953), nor more generally phenotypic plasticity[9] can explain, in isolation, why most organisms show features that look to be shaped directly by the environmental mould and adjusted to a better survival. All these kinds of process have often been misleadingly considered as valid alternatives to the presumptive action of natural selection. But all these processes are subordinated to the filter of natural selection, the action of which is ultimate and unavoidable, even if potentially variable in terms of intensity and variance. To sum up the situation, all organisms are genetically variable, and individuals with different genetic features will be confronted by different situations of survival and reproduction.

---

[5] A clade is a group of taxa including a common ancestor and all its descendants. This is a monophyletic group.

[6] Process of genetic drift, when variation in frequencies and fixation of alleles are made by random walk.

[7] They are effects of the organisms' structure in a developmental perspective (such as, amongst others, the *Bauplan*, or organisation levels, inherited from a deep ancestor, for example the organisational level of "vertebrates").

[8] Processes by which a phenotype initially produced in response to an environmental stimulus is finally expressed genetically, independently of the stimulus action.

[9] Variation of a trait caused by environmental changes.

2 The History of the Concept

Darwin formulated the theory of natural selection and he therefore determined the importance of the concept of adaptation (Darwin 1859). The theory and that concept have long been very popular: they are attractive and catchy. Etymologically, the word "adaptation" clearly specifies a change – "*ad*" – toward a higher ability – "*aptus*" and can only be confused with the reversible accommodation and phenotypic plasticity of organisms. It must be mentioned that the success of the concept is partly due to the very misleading notion of evolutionary progress with which it has been associated by some authors. According to this notion, life would "progress" during the course of evolution, from most simple organisms toward more advanced ones, on a ladder – a grade[10] – of life where the species supposedly most evolved and advanced would have accumulated more adaptations (unsurprisingly, *Homo sapiens* is considered the most advanced!) It must be noted that Darwin himself was clearly opposed to this gradist conception (Barrett 1960; O'Hara 1992) and that he considered adaptation an explanation for the diversifying fit of the organisms to their environment and not for a cumulative sophistication or advancement of organisms.

The concept of adaptation, already much employed at the beginning of the twentieth century, culminated in the 1960s, with general and famous presentations such as Williams (1966). Such studies and theories were referred as to "adaptationism" because they gave a central place to the concept of adaptation in evolutionary biology. This term "adaptationism" sometimes became pejorative because some of these adaptationist studies considered that showing characters were functional "proved" that they were adaptive, without checking within the organisms or the populations. Already at the beginning of the twentieth century, Morgan (1909) criticised Darwinists who believed in defending the concept of adaptation by employing it repeatedly as an ad hoc explanation in the case of characters that were simply documented as fully functional. This "naïvely" adaptationist trend was still widely found in recent studies that put an emphasis on the design or the optimality of the traits (e.g., Thornhill 1990). Adaptationism was also accused of proceeding by tautology according to the confusing locution of "*survival of the fittest*" put forward by Spencer (cf. Krimbas 1984). This tautology was actually linked to a bad use of the concepts of natural selection and adaptation. If organisms are considered globally, without the details of their characters' evolutionary histories, this principle is actually a tautology: if an organism is adjusted to its life conditions, its survival is generally better, and vice versa, building the tautology. In another way, if we consider a specific phenotypic adaptation and its genetic heritability (which is, by definition,

---

[10] A grade is a paraphyletic group (i.e. including an ancestor and some of its descendants only), an invalid group in evolutionary biology and phylogenetic systematics. This kind of group is built on the basis of a misleading assumption of evolutionary progress, together including taxa supposedly primitive and evolved with regard to characters on which a focus is put.

neither nil nor maximum), considering a “fit” to environmental conditions does not imply survival in any case but a contribution to the fitness[11] (Endler 1986).

The same criticisms that Morgan (1909) had about “naïve” adaptationism have been formulated more recently in a famous paper by Gould and Lewontin (1979). These latter authors argued in favour of a less teleological perspective in evolutionary biology, where the characters of the organism are not considered as necessarily built “for” the adaptive value that can be guessed from a priori functional conceptions. In their famous metaphor, the spandrels of the San Marco Basilica were not conceived by the architects for harbouring large paintings. On the contrary, the arches of the church were conceived from the beginning as a support to the building and they later provided an opportunity of ornamentation on their spandrels. This less teleological conception of adaptation is reasonable, in that it has made more clear for many that organisms, even if they look adjusted to their life conditions, have inherited many characteristics (arches and spandrels), the function of which has later been modified (from support to ornamentation). The organism is not “reinvented” with each generation but inherits many ancestral characteristics (the arches), the use of which can be sometimes modified (ornamentation). This conception is also involved in the term “evolutionary tinkering” used by some other authors (Jacob 1977) and that means that organisms employ old things (characters) they already have for building new functions.

Much older conceptions already followed the same rationale. Darwin (1859) himself envisaged these kind of difficulties with the validation of his theory, and he especially developed some thoughts in this respect in response to contradictors such as Mivart. How to explain that complex organs – for example, vertebrates’ eyes – could appear as very simple structures but are already adaptive enough to be maintained by natural selection and to allow subsequent complications. Darwin brought the answer from the very first versions of the Origin of species (Tort 1997): structures can appear, therefore already exist and then only change for their function, then complicate again, and change again with respect to their function, and also possibly regress, etc. This question, and this answer, have even been commented on and featured by fervent Darwinists such as Dohrn (1875), who saw them as one more good reason to adopt the Darwinian theory of natural selection. Later, some other authors again formulated the question and the answer, such as Davenport (1903) or especially Cuénot (1909, 1914), who coined the term “preadaptation.”

3 Adaptation or Preadaptation and Exaptation?

Cuénot (1909, 1914) considered the difficulty mentioned by Darwin himself – the origin of adaptations – and he concluded that the change of function could explain that some structures are “preadapted”, facilitating subsequent evolution. According

---

[11] Ability of a given phenotype to reproduce and transmit its genes, in given conditions.

to his papers, the conceptual difficulty is removed when the changes of function are considered in the context of vacant niches ("les places vides dans la nature").

However, the term of preadaptation has never been accepted unanimously. Fisher and Stock (1915) strongly criticised it from the beginning, also accusing the "mutationnist Cuénot" (!) to have a poor understanding of Darwin's theory. It is true that Cuénot's contribution was made in the particular context of strong antagonism between mutationnists and orthodox Darwinists. It is true also that Darwin (1859) already mentioned function changes and vacant niches (see, for example, Lawton, 1982 for a modern formulation of this latter concept), as explanations useful for understanding the origin of adaptations. The merit of Cuénot, if not of the more orthodox Davenport (1903) sometimes cited as a promoter of that concept, is to have coined a new term – preadaptation – that helps to take into account the functional changes in an adaptive context. This term, even if it is always used one century later, has never pleased the community, because its looks teleological, as if a species was "fated" to be (pre)adapted.

This was probably the reason why Gould and Vrba (1982), following the rationale of Gould and Lewontin (1979) and Lewontin (1969, 1978), proposed the concept of exaptation. They argued that this new concept valuably replaced the preadaptation concept formulated in a teleological way. Gould and Vrba (1982) did not cite, however, most of the literature on that question, eluding the contributions of Cuénot (1909, 1914). They followed the same and very old tradition of the adaptive explanation by functional change. They took the birds' feathers as an example, which functioned ancestrally as a thermoregulatory device, before playing a role of support and lift during flight. Gould and Vrba (1982) argued that characters could acquire new functions that were added or substituted to previous ones, or even occurred on a totally new basis. From this point of view, Arnold (1994) later created a terminology relative to the functions of a trait, distinguishing between first use exaptation, addition exaptation, and substitution exaptation. This concept of exaptation has been more successful than preadaptation, probably because of it has been elegantly formulated and it better fitted the political standards of the twentieth century (Pigliucci and Kaplan 2000; Andrews et al. 2002). It has even been used outside biology, in studies of cultural evolution, by linguistics or sociology (for example, Botha 2002; Delius and Siemann 1998), as Gould (1991) himself suggested. Even if the original formulation of exaptation implied that the concept was aimed at replacing preadaptation, it is actually complementary, as shown by the comparative analysis of Cuénot's and Gould & Vrba's works. Futuyma (1998) clearly explained that preadaptation concerns the character with the original function, while exaptation concerns the character with its derived function (Fig. 5.2). In the first case, the adaptation is seen as becoming, whilst in the second case, it is considered in respect to its origin. In both cases, the emphasis is put on the history of adaptation, with the need to consider adaptation as a modification of an ancestral legacy and not only as a simple evolutionary novelty. This conception is more in accordance with the nature of biological evolution, given that species inherit most of their characteristics from their ancestors and only evolve a few.

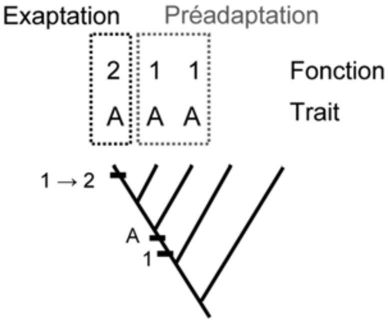

Fig. 5.2 The trait "A" can be considered as either a preadaptation or as an exaptation with the plesiomorphic function "1" or with the apomorphic function "2" respectively, provided that the selective value of the trait is measured in each situation

An adaptive character appearing in the ancestor of a very speciose group may be supposed to have strongly contributed to the evolutionary success of this group – the radiation – especially if its sister-group[12] lacking this adaptive character is much less diversified: this is the concept of adaptive radiation. A hypothesis of adaptive radiation is obviously highly speculative, depending on many auxiliary assumptions, including comparable extinction rates and sampling accuracy in both sister-groups and the focus on one supposedly influential adaptation.

4 One Example and an Insightful Discussion: The Adaptive Nature of Leaf Retention in Oaks

The literature is replete with examples of adaptive assumptions. However, few have been studied in every phylogenetic or populational context or have been insightfully discussed. One example is especially interesting from this point of view and concerns leaf retention in deciduous trees in temperate areas, this phenomenon during which most dead leaves remain on the tree after autumn and fall much later. In temperate areas, everyone can see oaks covered with dead leaves in winter, long after other forest trees have totally lost their leaves. Otto and Nilsson (1981) have proposed a possible function for this retention in the family Fagaceae. The leaves of oaks have a petiole lacking an abscission mechanism[13] and they fall only after the mechanical break of the dead petiole, therefore very late in the season. This delayed fall of leaves allows the soil at the tree base to be enriched with nutrients very early in spring at the time of tree regrowth. In the "usual" case of deciduous trees with leaf abscission mechanism, the soil is enriched earlier in autumn and nutrients can be lost because of weathering. This explanation based on experiments in oak populations referred to an adaptive context. The function of the trait – supposedly adaptive – was documented in a population, even if the selective value was not measured, strictly speaking. Wanntorp (1983) strongly opposed the interpretation within this study,

---

[12] Sister-groups are closer relatives to each other and they constitute an entire monophyletic group.

[13] Cut of the petiole owing to a particular structure in the tissue, allowing the fall of leaves.

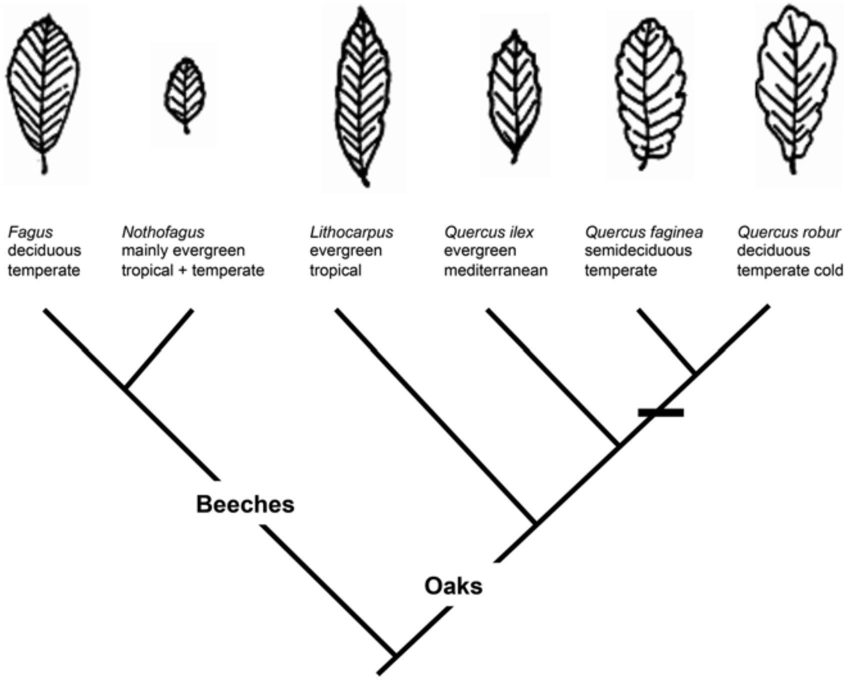

Fig. 5.3 The ancestor of the Fagacae was evergreen and the deciduous habit subsequently appeared in species from temperate areas. Leaf retention (dead leaves remaining attached to the tree during the cold season) may be considered an exaptation because the lack of petiole abscission involved in leaf retention in deciduous oak species is inherited from an evergreen ancestor (Modified from Wanntorp 1983)

putting forward that leaf retention is not an innovation in oaks (Fig. 5.3) but a plesiomorphy[14] inherited from a deep and evergreen[15] ancestor in Fagaceae, probably living in a tropical climate as are most present-day species of the same large family. For example, this evergreen habit occurred in several Mediterranean oak species. According to Wanntorp (1983), this phylogenetic context is contradictory with the assumption of adaptation made by Otto and Nilsson (1981), because the non-abscission of petioles is a plesiomorphic absence rather that an evolutionary novelty per se in oaks. These two opposite conceptions, Otto and Nilsson (1981) versus Wanntorp (1983), illustrate the necessary confrontation of both observation levels needed for the study of adaptation. In this case, the confrontation between these two conceptions was perceived as antagonistic. Actually, a synthesis between these two studies is still compatible with an adaptive hypothesis sensu lato (Grandcolas et al. 1994). In this way, the ancestral non-abscission may be considered as exaptive

---

[14] Ancestral trait or character, not modified.

[15] Trees whose leaves do not fall together seasonally.

in the context of a seasonal temperate climate for these deciduous species of Fagaceae. Non-abscission was perhaps even without any function at the origin and it has later acquired an adaptive value in this new and particular context. This hypothesis still depends on a real measure of the selective value of this trait in oak populations, which is difficult to obtain and which is still lacking today.

This case study exemplifies how misleading it is to oppose the two observation levels of clades and populations, both are necessary to carry out a powerful scientific analysis. It also helps to understand how the traits of organisms need to be studied within a historical perspective. This avoids considering that every trait is an adaptation as soon as it looks functional.

5 A Few Conceptual Problems

Such a historical framework decoupling structure and function can look a priori attractive because it allows one to get rid of naïve adaptationist conceptions where organisms directly "solve" all of their problems under the action of natural selection. This framework has, however, a conceptual limitation, sometimes mentioned but rarely discussed. Probably representing a large majority of researchers, Coddington (1988 and pers. comm.) and Dennett (1998) argued that all innovations are based on an ancestral legacy, even partial, and then concluded that there is no reason for distinguishing amongst adaptation and exaptation. All adaptations would actually be potential exaptations.

Several comments can be made in this respect. Firstly, this is difficult to affirm that there is no true innovation that appears in the course of organism evolution when a particular level of phenotypic integration is considered, for example, morphology or behaviour (Müller and Wagner 1991). The genome may not show true novelties, except with horizontal transfers,[16] but some phenotypic characters may a priori be considered true novelties (even if their genetic determinism has been modified from an ancestral legacy). If we then admit that some true innovations actually occurred, this will bring a conceptual paradox in which adaptations sensu stricto – representing indeed the original concept – would be most uncommon and exaptations – a more specific and derived concept – much more frequent.

Secondly, as already emphasised, the concept of exaptation and its less appreciated companion – the preadaptation – allow one to consider adaptation sensu lato in a historical framework that is still underemphasised. From this point of view, both concepts need to be employed. If we share the opinion of Coddington (1988) or Dennett (1998), why not simply consider exaptation and preadaptation as particular cases of adaptation (aptation sensu Gould and Vrba 1982)?

---

[16] Transfer of genetic material by other means that specific reproduction mechanisms and by capture of genetic material present in the environment (possibly interspecific); to be distinguished from vertical transfers (sexual reproduction, pathenogenesis, scissiparity).

A much more important problem concerns the gap that remains unravelled between the phylogenetic reconstruction documenting the origin of the presumptively adaptive trait, and the populational study documenting the selective value of the trait in a population at the present time. Even if the presumptive adaptation is actually an apomorphy in the taxon considered, even if this trait actually confers high fitness in one or two present populations, it will still remain unknown whether this trait has, strictly speaking, been adaptive from the time of its origin to the present-day populations (Grandcolas and D'Haese 2003). Some authors focused on this gap and argued that history does not matter and that we should redirect all our attention to study the present populations (Reeve and Sherman 1993). With such an opinion, they overlook the fact that phylogenetic analysis allows one to ask the right questions by setting the evolutionary study's background.[17] Very often, the question asked at the beginning of such a study is not appropriate: for example, to study how parental investment can explain the extreme sexual dimorphism by the decrease of the body size – presumptively adaptive – of males of Nephile spiders is nonsensical since phylogeny shows us that females have increased their size and that males did not actually increase in size (Coddington et al. 1997).

To fill the gap between phylogeny and population studies, some authors have searched to take the effect of natural selection at the level of phylogenetic analysis into account (Baum and Larson 1991). On this scale, a "selective regime" would be substituted to the real measure of the natural selection in populations. According to the examples cited by these authors, this regime corresponds to using presumptively adaptive characters, the history of which would also be reconstructed onto the phylogenetic tree. Tarsal structures in lizards have been considered this way, by putting them into relationships with the kind of movement performed by the animals and the kind of substratum on which the animals move. The use of such attributes on a phylogenetic tree represents a very poor surrogate for measuring the selective value. This value is not measured in terms of differential survival and reproduction but in terms of use or performance with a trait. In addition, this method is supposed to reconstruct the phylogeny of this approximated selective value. The main problem there is that natural selection is an environmental context, not an organismic character, and therefore it is not heritable. To analyse its evolution on a phylogenetic tree is thus nonsensical (Grandcolas and D'Haese 2003). In addition, a character, even very functional, does not necessarily have a high selective value. This is the problem of optimality studies (Thornhill 1990) that consider that a good design and a perfect optimality are strong indications of adaptation. This is the teleonomic domain of the study of adaptation that claims philosophical legitimacy: every function is assumed to necessarily have a purpose as indicated by the quality of its design or it efficiency (for example, Griffiths 1993; Crespi 2000).

In this context, the study of the purpose of the adaptive fit of a trait comes to guess which function has been the target of the natural selection. The problem is that this guess, especially when it is made without a phylogenetic context, is nothing other than an ad hoc history (the "*just so stories*" after S.J. Gould, borrowing from

---

[17] Wanntorp (1983), Coddington (1988), Carpenter (1989), Grandcolas et al. (1994).

Rudyard Kipling). This is just the modern and sophisticated continuation of the adaptationist tradition from the early twentieth century. From this point of view, evolutionary biology should learn how to characterise the uses of a trait without assuming a function as essential from ethology: ethologists have long understood that a morphological structure can be used in several ways by an organism in a behavioural context, without considering that one amongst these uses is purposely functional.

Another abuse of the adaptation concept concerns the so-called "comparative method", a very specific term for a particular branch of comparative biology that pretends to detect adaptation by the study of convergence.[18] The "adaptationist wager", according to Pagel (1994) and borrowing from Pascal, acknowledges adaptation by assessing a recurrent association between a character and a role in varied taxa (for example, warning coloration, gregariousness and aposematic defence[19] in butterflies – cf. Sillén-Tullberg 1988). This association will be statistically evaluated on phylogenetic trees. This adaptationist bet does not take into account the populational dimension of the study of adaptation. It also misunderstands that a functional character and efficiently functional is not necessarily a novelty at the considered taxonomic level, nor does it favour the fitness of the organism. Leroi et al. (1994) have presented a complete list of criticisms of this adaptationist bet, showing that convergence can be caused by many confounding factors, such as genetic linkages or trait architectures. In addition, a fundamental problem of the comparative method (and especially of the "phylogenetic correction" method) is that it considers phylogeny as a source of statistical error because of non-independence among the compared species (Coddington 1994). This method limits itself to evaluating the real size of samples in terms of independent taxa used in species comparisons. To compare several groups of closely related taxa would only compare their common ancestors, significantly less than the number of taxa, and therefore decreasing the number of degrees of freedom (Clutton-Brock and Harvey 1979). The so-called "phylogenetic correction" also ignores the many different and detailed evolutionary histories that allow for a better understanding of the context of adaptation evolution (Wenzel and Carpenter 1994). This is the reason that it has become less and less employed by comparison with detailed phylogenetic analysis.

As a matter of statistical analysis of data and generalisation of results, for the test of adaptational hypotheses it would be much more interesting to control the biases occurring according to the selection of phylogenetic case studies. Do the clades studied until now correctly sample the Tree of Life (Guyer and Slowinski 1995; Grandcolas et al. 1997)? This question can be answered by looking at the topologies of the groups studied. For example, the study of small clades will prevent taking the possibility of radiations that can be detected only by considering large clades into account.

---

[18] Adaptive convergence means that unrelated species present adaptations functionally similar but that appeared independently during evolution (for example, the wings in bats and in birds). See Clutton-Brock and Harvey (1979), Felsenstein (1985), Harvey and Pagel (1991).

[19] It is said from the appearance of animals advertising a potential predator that it is dangerous to eat them (e.g., toxicity).

6 When There Is no More Adaptation: Maladaptation or Desaptation

The notion of maladaptation or desaptation (Baum and Larson 1991; Crespi 2000) is not often employed. It probably suffers from the difficulty of qualifying negatively and of being characterised by a lack or an absence. Indeed, an organism is said to be maladapted or desadapted with respect to a specific trait if it decreases the fitness of, but is maintained, in that organism. The novelty of that trait or its function is not a defining criterion as in the case of adaptation. On the contrary, a desaptation is diagnosed by reference to a previous state in the course of evolution, in which the trait and its function already existed and increased the fitness. To demonstrate this, a quantitative genetic study should be performed on the supposedly maladapted species and on a related species showing the ancestral state still "adaptive", thus within a phylogenetic framework. This way, a hypothesis of maladaptation could be validated by showing the contribution of a trait to the fitness which apparently becomes negative in the course of evolution.

Some other less complete and more disputable approaches have also been presented. According to Baum and Larson (1991), the present sub-optimality of the supposedly maladaptive trait is a hypothesis corroborated by its lower performance compared to the ancestral state. This again relies on the notion of the performance/selective regime, as a misleading approximation of the selective value. Many authors have also proposed some teleological approaches that basically assume that all selected traits are a priori optimised and that maladaptation can therefore be diagnosed as an exception to these optimal situations. In that context, a theoretical functional study allows one to assess that the trait is not optimised, on the basis of an optimality criterion referring to energy, metabolism, functional morphology, etc.

A maladaptation or a desaptation is not necessarily a vestige or a regression, contrary to a common misunderstanding (concerning vestigial traits, cf. Griffiths 1992). A trait can be lost or have regressed in the course of evolution, specifically under the effect of natural selection: in this case, the trait optimally fits because setting up a non-functional trait saved some energy (or any other functioning cost) when the function was no longer essential to the survival or the reproduction, at least with the same development or intensity of functioning. On the other hand, if the function of the vestigial trait has not changed, the same true adaptation may still be at work even with a vestige, contrary to any other a priori assumption. If the function has been lost with that regression, the trait can be said to be non-functional and thus *ipso facto* a non-aptation. To actually be maladaptive, a vestige issued from a regression should negatively contribute to the fitness.

Another notion often related to maladaptation is the "constraint." It has, however, become a vague term (Antonovics and van Tienderen 1991), to the extent that many authors refuse to employ it (for example, Crespi 2000). Concerning the specific case of maladaptation, the notion of constraint can be employed if we consider an organism maladapted, for example, because of an inherited ancestral character contributing negatively to the fitness. The maladaptive trait is hence considered to constrain the organism.

7 Conclusion

> Unlike Gould and Lewontin (1979), we do not hypothesize that many traits are not adaptive. Rather, we are making the case that adaptive (or nonadaptive) nature of traits cannot be determined from most comparative data (Leroi et al. 1994: 397).

If the debate concerning the use of the concept of adaptation has to be summarised in one sentence, it can be said that it is invaluable to evolutionary biology but difficult to study in practice. As showed by the epigraph above, discussions about adaptation are often marked by strong opinions a priori: *I am* or *I am not adaptationist*, *I believe* or *I do not believe* that comparative biology brings decisive information in this respect. Rather than making such strong a priori arguments, we would do better to analyse the data in the strictly defined and well-made methodological framework of recent decades. This appropriate methodological framework allows us to carry out the scientific study of adaptation by putting several different disciplinary fields, phylogenetics and population biology, in conjunction. Some see it as an operational difficulty but instead this is a great opportunity to carry out a very heuristic scientific approach and an interdisciplinary synthesis. The phylogenetic analysis of the presumptively adaptive traits is a remarkable opportunity to set up the historical background knowledge for the adaptational study and to understand what a case study can actually teach us. That way, the polarity and the number of changes can be inferred for the considered trait, allowing an understanding of why functional or populational studies sometimes totally fail to reach their aim (Grandcolas et al. 1994; Coddington et al. 1997). The theoretical justification of this methodology, considering both phylogenetic and populational evidence, also shows how useless it is to employ shortcuts. Some authors have attempted to get rid of phylogenetic studies (Reeve and Sherman 1993) or from populational studies, either with the comparative method that disputably equates convergence and adaptation (Harvey and Pagel 1991), or with methods aimed at detecting a supposedly adaptive optimality.

The absence of one of those two kinds of study – phylogenetic or populational – makes the adaptive assumptions less corroborated and brings about some doubts as to the general value of the concept in the long term. In this context, it really is inappropriate to claim to be for or against adaptationism a priori, which can only bring about important biases in case studies.

References

Andrews, P. W., Gangestad, S. W., & Matthews, D. (2002). Adaptationism – How to carry out an exaptationist program. *Behavioral and Brain Sciences, 25*, 489–553.

Antonovics, J. (1987). The evolutionary dis-synthesis: Which bottles for which wine? *American Naturalist, 129*, 321–331.

Antonovics, J., & van Tienderen, P. H. (1991). Ontoecogenophyloconstraints? The chaos of constraint terminology. *Trends in Ecology & Evolution, 6*, 166–168.

Arnold, E. N. (1994). Investigating the origins of performance advantage: Adaptation, exaptation and lineage effects. In P. Eggleton & R. I. Vane-Wright (Eds.), *Phylogenetics and ecology* (Linnean Society symposium series, no 17, pp. 123–168). London: Academic.

Barrett, P. H. (1960). A transcription of Darwin's first notebook on 'transmutation of species'. *Bulletin of the Museum of Comparative Zoology, 122*, 245–296.

Baum, D. A., & Larson, A. (1991). Adaptation reviewed: A phylogenetic methodology for studying character macroevolution. *Systematic Zoology, 40*, 1–18.

Botha, R. P. (2002). Are these features of language that arose like birds' feathers. *Language & Communication, 22*, 17–35.

Brooks, D. R., & McLennan, D. A. (1991). *Phylogeny, ecology, and behavior: A research program in comparative biology*. Chicago: The University of Chicago Press.

Carpenter, J. M. (1989). Testing scenarios: Wasp social behavior. *Cladistics, 5*, 131–144.

Clutton-Brock, T. H., & Harvey, P. H. (1979). Comparison and adaptation. *Proceedings of the Royal Society of London, B, 205*, 547–565.

Coddington, J. A. (1988). Cladistic tests of adaptational hypotheses. *Cladistics, 4*, 3–22.

Coddington, J. A. (1994). The roles of homology and convergence in studies of adaptation. In P. Eggleton & R. Vane-Wright (Eds.), *Phylogenetics and ecology* (Linnean Society symposium series, no 17, pp. 53–78). London: Academic.

Coddington, J. A., Hormiga, G., & Scharff, N. (1997). Giant female or dwarf male spiders? *Nature, 385*, 687–688.

Crespi, B. J. (2000). The evolution of maladaptation. *Heredity, 84*, 623–629.

Cuénot, L. (1909). Le peuplement des places vides dans la nature et l'origine des adaptations. *Revue générale des sciences, 20*, 8–14.

Cuénot, L. (1914). Théorie de la préadaptation. *Scientia, 16*, 60–73.

Darwin, C. (1859). *On the origin of species by means of natural selection*. London: John Murray.

Davenport, C. B. (1903). *The animal ecology of the Cold Spring sand spit, with remarks on the theory of adaptation* (10, pp. 157–176). Chicago: The Decennial Publications, University of Chicago.

Deleporte, P. (2002). Phylogenetics and the aptationist program. *Behavioral and Brain Sciences, 25*, 514–515.

Delius, J. D., & Siemann, M. (1998). Transitive responding in animals and humans: Exaptation rather than adaptation? *Behavioural Processes, 42*, 103–137.

Dennett, D. C. (1998). Preston on exaptation: Herons, apples, and eggs. *Journal of Philosophy, 95*, 576–580.

Dohrn, A. (1875). *Der Ursprung der Wirbelthiere und das Princip des Functionswechsels: genealogische Skizzen*. Leipzig: W. Engelmann.

Endler, J. A. (1986). *Natural selection in the wild*. Princeton: Princeton University Press.

Farris, J. S. (1983). The logical basis of phylogenetic analysis. In N. Platnick & V. A. Funk (Eds.), *Advances in cladistics: Proceedings of the second meeting of the Willi Hennig Society* (Vol. 2, pp. 7–36). New York: Columbia University Press.

Felsenstein, J. (1985). Phylogenies and the comparative method. *American Naturalist, 125*, 1–15.

Fisher, R. A., & Stock, C. S. (1915). Cuénot on preadaptation: a criticism. *Eugenics Review, 7*, 46–61.

Futuyma, D. J. (1998). *Evolutionary biology*. Sunderland: Sinauer Associates.

Gould, S. J. (1991). Exaptation: a crucial tool for evolutionary psychology. *Journal of Social Issues, 47*, 43–65.

Gould, S. J., & Lewontin, R. C. (1979). The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. *Proceedings of the Royal Society of London B, 205*, 581–598.

Gould, S. J., & Vrba, E. S. (1982). Exaptation – A missing term in the science of form. *Paleobiology, 8*, 4–15.

Grandcolas, P., & D'Haese, C. (2003). Testing adaptation with phylogeny: How to account for phylogenetic pattern and selective value together? *Zoologica Scripta, 32*, 483–490.

Grandcolas, P., Deleporte, P., & Desutter-Grandcolas, L. (1994). Why to use phylogeny in evolutionary ecology? *Acta Oecologica, 15*, 661–673.

Grandcolas, P., Deleporte, P., & Desutter-Grandcolas, L. (1997). Testing evolutionary processes with phylogenetic patterns: Test power and test limitations. In P. Grandcolas (Ed.), *The origin of biodiversity in insects: Phylogenetic tests of evolutionary scenarios* (Mémoires du Muséum national d'Histoire naturelle 173, pp. 53–71). Paris: Éditions du Muséum.

Griffiths, P. E. (1992). Adaptive explanation and the concept of a vestige. In P. E. Griffiths (Ed.), *Trees of life: Essays in philosophy of biology* (pp. 111–131). Kluwer: Dordrecht.

Griffiths, P. E. (1993). Functional analysis and proper functions. *British Journal for the Philosophy of Science, 44*, 409–422.

Guyer, C., & Slowinski, J. B. (1995). Reply to Cunningham. *Evolution, 49*, 1294–1295.

Hall, B. K. (1999). *Evolutionary developmental biology*. Dordrecht: Kluwer Academic Publishers.

Harvey, P. H., & Pagel, M. D. (1991). *The comparative method in evolutionary biology*. Oxford: Oxford University Press.

Hennig, W. (1965). Phylogenetic systematics. *Annual Review of Entomology, 10*, 97–116.

Hennig, W. (1966). *Phylogenetic systematics*. Urbana: University of Illinois Press.

Jacob, F. (1977). Evolution and tinkering. *Science, 196*, 1161–1166.

Krimbas, C. B. (1984). On adaptation, neo-Darwinian tautology, and population fitness. *Evolutionary Biology, 17*, 1–57.

Leroi, A. M., Rose, M. R., & Lauder, G. V. (1994). What does the comparative method reveal about adaptation? *American Naturalist, 143*, 381–402.

Lewontin, R. C. (1969). The bases of conflict in biological explanation. *Journal of the History of Biology, 2*, 35–45.

Lewontin, R. C. (1978). Adaptation. *Scientific American, 239*, 212–230.

Mahner, M., & Bunge, M. (1997). *Foundations of biophilosophy*. Berlin: Springer.

Mathews, H. (1958). Darwin, Wallace, and "pre-adaptation". *Journal of the Linnean Society of London, Zoology, 44*, 93–98.

Morgan, T. H. (1909). For Darwin. *Popular Science Monthly, 74*, 367–380.

Müller, G. B., & Wagner, G. P. (1991). Novelty in evolution: Restructuring the concept. *Annual Review of Ecology and Systematics, 22*, 229–256.

O'Hara, R. J. (1992). Telling the tree: Narrative representation and the study of evolutionary history. *Biology and Philosophy, 7*, 135–160.

Otto, C., & Nilsson, L. M. (1981). Why do beech and oak trees retain leaves until spring? *Oikos, 37*, 387–390.

Pagel, M. D. (1994). The adaptationist wager. In P. Eggleton & R. I. Vane-Wright (Eds.), *Phylogenetics and ecology* (Linnean Society symposium series. Number 17, pp. 29–51). London: Academic.

Perrier, E. (1886). *La philosophie zoologique avant Darwin*. Paris: Félix Alcan.

Pigliucci, M., & Kaplan, J. (2000). The fall and rise of Dr Pangloss: Adaptationism and the Spandrels paper 20 years later. *Trends in Ecology and Evolution, 15*, 66–70.

Reeve, H. K., & Sherman, P. W. (1993). Adaptation and the goals of evolutionary research. *Quarterly Review of Biology, 68*, 1–32.

Rose, M. R., & Lauder, G. V. (1996). *Adaptation*. New York: Academic.

Sillén-Tullberg, B. (1988). Evolution of gregariousness in aposematic butterfly larvae: A phylogenetic analysis. *Evolution, 42*, 293–305.

Sober, E. (1984). *The nature of selection. Evolutionary theory in philosophical focus*. Cambridge: MIT Press.

Thornhill, R. (1990). The study of adaptation. In M. Bekoff & D. Jamieson (Eds.), *Interpretation and explanation in the study of animal behavior* (pp. 31–62). Boulder: Westview Press.

Tort, P. (1997). Phylogénie du faillible. Notes introductives à la théorie de l'instinct chez Darwin (à propos de l'essai posthume sur l'instinct). In P. Tort (dir.), *Pour Darwin* (pp. 229–244). Paris: PUF.

Waddington, C. H. (1953). Genetic assimilation of an acquired character. *Evolution, 7*, 118–126.

Wanntorp, H. E. (1983). Historical constraints in adaptation theory: Traits and non-traits. *Oikos, 41*, 157–160.

Wenzel, J. W., & Carpenter, J. (1994). Comparing methods: Adaptive traits and tests of adaptation. In P. Eggleton & R. I. Vane-Wright (Eds.), *Phylogenetics and ecology* (Linnean Society symposium series, no 17, pp. 79–101). London: Academic.

Wiley, E. O. (1981). *Phylogenetics. The theory and practice of phylogenetic systematics*. New York: Wiley-Liss.

Williams, G. C. (1966). *Adaptation and natural selection*. Princeton: Princeton University Press.

Philippe Grandcolas Senior Scientist CNRS. Head of the CNRS laboratory "Institut de Systématique, Evolution et Biodiversité" that includes most of the systematists at the Muséum national d'Histoire naturelle of Paris. His studies focused on phylogenetic analysis of evolution, with a special concern for the origin of phenotypic traits and insular biota.