Chapter 2
The Problem of Macroevolutionary Trends

Our general view of the large-scale evolutionary process reveals prokaryotes as the earliest forms of life, followed by the first eukaryotic cells that formed multicellular organisms. The Cambrian "explosion" added new forms of life with hard skeletons, completely changing the fauna of the world. Within the then-existing phyla, a great variety of changes led to our present-day animals, including bees, squid, frogs, crocodiles, and horses. Every evolutionary biologist thinks that there were profound changes and innovations during this process that need to be described. Traditionally, these changes have been termed *evolutionary progress*. In recent years, this term has been criticized, and some authors claim that it has now been successfully eliminated from evolutionary biology. Nonetheless, on closer examination this seems not to be the case. There are hardly any textbooks that avoid using the terms *lower* and *higher* when referring to organisms. Furthermore, many phylogenetic reconstructions, especially at the level of phyla, include sequences that lead to "advanced" forms in the traditional sense, and in zoology or paleontology textbooks organisms are usually arranged according to this sequence. The criticism of this notion in recent decades has had the effect that scientists try to avoid using terms that refer to evolutionary progress, or they explicitly distance themselves from it, although nearly everyone still thinks of evolution in the sense of overall progression.

Ruse (1996) came to the same conclusion. His question is: Why do evolutionists continue to use such unscientific terms? However, my thesis is different from his: The term *progress* carries some historical burden, as it is problematic within the modern view of evolution; but, at its core, it expresses a central aspect of evolution that cannot be ignored if it is intended to build a fairly complete view of the evolutionary process that comes close to reality. If evolutionists cannot avoid the term, what do they see in their daily work, and how could they express their observations in a scientific manner?

The term *progress* has three predominant historical roots. One is the concept of the *scala naturae*, which until the nineteenth century was the most widely prevalent view of the general order of the world. It saw the world arranged in a linear hierarchy and was originally a static concept, but during the late eighteenth and early

B. Rosslenbroich, *On the Origin of Autonomy: A New Look at the Major Transitions in Evolution*, History, Philosophy and Theory of the Life Sciences 5,
DOI 10.1007/978-3-319-04141-4_2, © Springer International Publishing Switzerland 2014

nineteenth centuries, it was "temporalized" (Lovejoy 1982) so that its elements would appear in succession. The second root lies in the notion of *social and cultural progress*, which developed during the Enlightenment and gradually replaced the notion of the invariability of human affairs. During the late eighteenth century, this idea expressed the emerging consciousness of the capability of humankind to improve its circumstances and abilities. In these early considerations, progress included the aim of an achievable perfection, which introduced a strong teleological element. Critical reflection on the questions of change, development, and progress in human history, including its problems of linearity and teleology, took place in France and Germany during the eighteenth and early nineteenth centuries. This is the true origin of evolutionary thinking on which Darwin later could build his theory. During the nineteenth century, the general progress of society, science, technology, and industry was taken for granted, especially in England (Bowler 1983, 1989a, b).

The third root is the *theory of recapitulation*, the analogy that was drawn between embryogenesis and phylogeny. Knowledge of the embryo's development from a simple to a complex structure was intellectual help for initial ideas about the changeability of organisms (Richards 1992).

For a clear picture of the notion of progress in evolutionary biology, it is necessary to reflect on the different components and connotations that may be involved in varying combinations and derive from this historical background. At least five components must be distinguished:

1. Modifications in the living world generate increasingly higher organisms (however they are characterized).
2. These higher organisms are in certain ways better than lower ones (= "improvement").
3. This progression is essentially linear.
4. Evolution has an intrinsic force that drives this progress.
5. Progressive evolution leads eventually to some sort of perfection (end stage, culmination point, goal).

In the critical literature of recent decades, these components are often mixed together, contributing to the confusion. For example, it is often assumed that the notion of progress is always looking for related driving forces in evolution (component 4). Or, it is supposed that the view of evolution as progressive implies a goal toward which the process is moving, thus making evolution a teleological concept. This supposition would be a combination of components 4 and 5. However, these components are not necessarily involved. It is true that most biological thinking before Darwin's theory was introduced into science included these components, but afterward the picture became more varied.

How did Darwin himself deal with these components in *On the Origin of Species* (Darwin 1872)? Darwin unequivocally disapproved of any idea of an inherent force that was supposed to be driving evolution. That the process should have a goal was also incompatible with his theory and was explicitly refuted, as was the idea of linearity in evolution. He argued repeatedly throughout the book against contemporary advocates of such views, and their refutation was one of his main concerns. This was an important achievement in his time.

The problem of whether the evolutionary process might generate higher organisms is nonetheless complex in Darwin's thinking, and it hides a dichotomy. His theory is mainly an explanation of how populations adapt to their changing environments and to their biotic factors. The theory of natural selection maintains that in the struggle for existence, those individuals who best adapt to new conditions will survive and reproduce, whereas others less well adapted will become extinct. Over many generations, positive adaptive characteristics are enhanced until eventually the population becomes a new species, incapable of interbreeding with the parent form. Neither the variations in features from which an adaptive characteristic is selected nor the environmental changes include directionality. Therefore, this process can deliver only a set of meandering responses in the adaptive adjustments of organisms to local environments (Gould 2002; Bowler 1989a). Depending on the respective selection factors, this process would lead to an ever-increasing divergence of forms independently of one another and result in a network of adaptations to the respective vicissitudes of the struggle for life. According to the traditional understanding of progress, this process does not include any directionality. In addition, it does not seem to make sense to compare different "levels of organization" when the main reality is branching evolution.

Through competition between individuals and victory of some creatures over others in the struggle for limited resources, direction might be involved (Gould 2002) after all. Darwin expected an accumulation of "improvements" from the struggle, which would make organisms fitter and thus generate progress. "Now species triumph because, in some sense admittedly difficult to define, winners are 'better' than the forms they vanquish. And the more uniformitarian the larger picture – the more that macroevolutionary pattern arises as a simple summation of immediate struggles – so do we gain increasing confidence that replacement and extinction must record the differential success of globally improved species" (Gould 2002, p. 475).

In a paragraph, "On the Degree to which Organisation tends to advance," Darwin (1872, pp. 127, 228) writes:

> "Natural Selection acts exclusively by the preservation and accumulation of variations, which are beneficial under the organic and inorganic conditions to which each creature is exposed at all periods of life. The ultimate result is that each creature tends to become more and more improved in relation to its conditions. This improvement inevitably leads to the gradual advancement of the organisation of the greater number of living beings throughout the world. … Although we have no good evidence of the existence in organic beings of an innate tendency towards progressive development, yet this necessarily follows … through the continued action of natural selection. For the best definition which has ever been given of a high standard of organisation, is the degree to which the parts have been specialized or differentiated; and natural selection tends towards this end, inasmuch as the parts are thus enabled to perform their functions more efficiently."

Thus, increased specialization and differentiation of parts make their bearers superior to other ones in the struggle for life.

> If we take as the standard of high organisation, the amount of differentiation and specialization of the several organs in each being when adult (and this will include the advancement of the brain for intellectual purposes), natural selection clearly leads towards this standard: for all physiologists admit that the specialization of organs, inasmuch as in this state they perform their functions better, is an advantage to each being; and hence the accumulation of variations tending towards specialization is within the scope of natural selection. (Darwin 1872, p. 128)

Hence, by means of the selection process Darwin intends to explain not only adaptation to the immediate environment but also gradual progress.

> "Thus, from the war of nature, from famine and death, the most exalted object which we are capable of conceiving, namely, the production of the higher animals, directly follows" (Darwin 1872, p. 560).

How Darwin envisaged large-scale "improvements" of organs and higher animals corresponding with increasing fitness for survival is shown, for example, in his paragraph on eyes (Darwin 1872, p. 188).

However, there exists a gap in this extrapolation from microevolutionary adaptive processes to large-scale macroevolutionary progress: Those species, which are supposedly more advanced, do not necessarily have an enhanced capacity for survival. If continuous improvements accumulate toward progressive forms (e.g., through the generation of complex organs as Darwin expected), the bearers of these improvements must finally be the fittest organisms, which is not the case in nature. Bacteria as well as protists had enough fitness to survive for a longer time than even vertebrates. The accumulation of complex organs and functions from single cells to vertebrates (which is usually referred to as progress, also by Darwin) delivers anything but enhanced survival capacity. For this reason, there is on one hand incongruence between the microevolutionary adaptation process that leads to fitness and on the other hand what is traditionally called progress in the large-scale, macroevolutionary outcome of evolution. However, this does not question the validity of either of the two principles but only states that their relationship is not clear within the original Darwinian scenario. It also does not mean that there might not be a resolution of the incongruence, but one has not yet been definitively established as differing views prevail.

It is hard to judge how clearly Darwin saw the incongruence, but his ambivalence concerning the term *progress* may hint at his struggle with it. When Darwin's theory is read as it was presented in his "ambiguous book" (Ruse 1996, p. 172), it includes a dualistic tension between populational thinking and progressive thinking, two not necessarily irreconcilable but instead complementary perspectives of a complicated matter. In one respect, Darwin wrestled with the notions of directionality and progress, and in another respect, he wrestled with his principle of an ever-branching and diverging evolution. Darwin's theory abandons elements of linearity, an intrinsic force, and a goal of evolution, but still makes an attempt at explaining "organisational advance," as he formulated it. I maintain that Darwin saw this tension and attempted to deal with the observable differences between organisms rather than focus on a more radical and reductionistic theory, which would ignore a significant part of reality.

The view that progress might be a simple accumulation of fitness is not necessarily an element of modern Darwinian thinking, but the relationship between fitness and progress has remained unresolved since the days of Darwin (Saunders and Ho 1981; Wicken 1979; Nitecki 1988; Calcott and Sterelny 2011; McShea 1991, 1998; Jablonski 2007). Gould (1996, p. 199) points out this relationship: "I have long been entirely underwhelmed by the standard arguments for general advantages of increasing complexity in the Darwinian game – adaptive benefit of more elaborate bodily form in competition for limited resources, for example. Why should more complex conformations generally prevail? … I can envisage just as many situations where more elaborate forms might be a hindrance – more parts to fail, less flexibility because all parts must interact with precision." Remember that Darwin expected functional improvements through the building of organs that were more complex, and today complexity is often equated with progressiveness.

Darwin's ambivalence and the inconsistencies in his theory led to diverging attitudes among many scientists, thus establishing at least two fundamentally different views of evolution, which have remained relatively divergent at all times. This schism pervades all evolutionary biology with a spectrum of opinion ranging from the presupposition that evolution generated progress in some form, to a complete denial of any sort of progress in it whatsoever. The history of ideas after Darwin shows how these different perspectives and their dualistic tension have always been at work (for more details, see Rosslenbroich 2006).

2.1 The Epistemological Problem

During the twentieth century, the term *progress* came under pressure from two different directions: One is that it transports some historical baggage that was not compatible with modern knowledge of evolution. The other is the dominance of thinking in adaptation and population dynamics, as it was strongly favored by the synthetic theory. Scientists expected the solution of evolutionary questions exclusively from this perspective. Also, major transitions seemed to be explainable through accumulated microevolutionary events. Against this backdrop, there was no interest in general macroevolutionary questions. There were even strong attempts to discuss any general qualitative changes away or to dismiss them as epiphenomena in a world that consisted exclusively of adaptation and fitness. Good examples for this are many depictions of brain organization in vertebrates (see Chap. 10). However, this is changing dramatically today, as is discussed in Chap. 12 (McShea and Simpson 2011).

At its core, the term *progress* expresses, nonetheless, the observable qualitative differences between organisms of different evolutionary levels. However, because of the dominance of thinking in terms of adaptation, not enough thought has been put into the question of these qualitative differences. There is an aspect of organic evolution to which the term has been applied and for which it is necessary to develop an epistemologically satisfying approach. The persistence in the use of the term and of related terms proves this.

In the first place, the five components in the previous list require further explication. It should be clear that accepting the notion that large-scale trends reveal increasingly higher organisms (1) does not necessarily include an agreement with the other components. Thus, the process does not need to be linear (3). Equally, it presupposes neither some sort of inherent force (4) nor a final stage, or goal even, that supposedly drives the whole process (5). Furthermore, it does not necessarily include the idea that new forms are in some sense “improved” or “better” (2); they may just have a different lifestyle, a different adaptation strategy, or a different type of general morphological and physiological organization. This much can be definitively stated, leaving open for the moment the question of the evolutionary forces that generated such differences.

In today’s use of the term *progress*, when we are simply looking into the history of organisms, reconstructing and describing the sequence of basic changes, components 2 to 5 are not necessarily taken into account. In the history of theory building, these components have been abandoned. However, component 1 is still relevant. Thus, a modern interpretation of the term *progress* would accept only that macroevolution generates forms that increasingly differ from earlier forms in such a basic way that it is necessary to provide a description and analysis of the general patterns involved. For this, the terms *higher* or *lower*, and even the term *progress* itself, have until now served as metaphors.

Another basis for my further discussion comes from a proposal by Rapp (1992) in a study of the term *progress* (including social progress), who distinguishes a *genetic* (in the philosophical sense) from a *normative* form of progress. Genetic progress is a sequence of steps in time: the succession of changes and the valueless generation of the new. In addition to this, normative progress makes value judgments in the sense that every progressive step achieves an improvement with respect to a higher goal toward which it is worth striving morally. The genetic term is the prerequisite of the normative term, but the positive value judgment of the normative term can be transferred to the genetic one, either tacitly or explicitly. However, it is not certain that genetic progress always leads to improvement. This confusion stems from the historical link between the terms when they were first used.

The historical overview shows how closely the use of the term in biology has been connected with the development of social thought and theories. The notion of normative progress helped to start thinking in terms of developments, including those in the organic world. However, the normative aspect, in the sense of moral appraisal, cannot be introduced into a scientific context. Nonetheless, even the genetic aspect may contain several different elements that at the same time are possible elements of the term *evolution*. This is summarized in Table 2.1, which is compiled from considerations by Rapp (1992), Lewontin (1968), and Simpson (1973).

Change is the basic feature of the evolutionary process: The current state of a system is the result of one or more changes from a former state. Pure change can be the raw material of evolution, but for most evolutionists, the term *change* does not describe evolution sufficiently, as change can also be, for example, reshuffling playing cards. Thus, a different *order* can be generated by a rearrangement of elements.

Table 2.1 Possible elements of "progress"

Genetic:	- Change	Progression	Progress
	- Order		
	- Direction		
	- General patterns		
Normative:			

Using the same basic elements, it leads to the appearance of a new state in a system that was not present in the system in its former condition. The generation of a new species from an earlier one might be the generation of a new state, a new order.

The generation of a new order and properties can shift irregularly or can change in a certain *direction*, perhaps over a long time, by one or more sequences of transformations. However, these changes need not be linear. Directionality, revealed by the fossil record, for example, is usually described as an "evolutionary trend." Thus, the evolution of early mammals from mammal-like reptiles is described in paleontology as a sequence of trends that led to mammalian characters.

These trends can be described and followed throughout evolution, but often, especially in large-scale macroevolutionary trends, more basic questions can be addressed: Did a general difference evolve? Are organisms in later periods different in some general aspect of their individual characteristics from those in earlier times (McShea 1998)? The evolution from reptiles to mammals, for example, involved the generation of a largely different physiology, allowing for a completely changed lifestyle. The two classes reveal different sets of characteristics with respect to morphology, physiology, behavior, and relation to the environment. These basic differences of systems are described here as *general patterns*, expressing integrative features of large-scale macroevolutionary trends.

Evolutionary theories can be distinguished by how many of the elements (see Table 2.1) are included (Lewontin 1968). Some evolutionists only include change and order; others add directionality. Although large-scale patterns are rarely addressed explicitly (e.g., Bonner 1988; McShea 1996, 2002; Vermeij 1999; Calcott and Sterelny 2011; Jablonski 2007), they are often embedded in general discussions and in textbooks. This clearly shows that the understanding of the term *evolution* to a large extent depends on the perspective on evolution and the paradigmatic background of the respective researcher. Much of the controversy concerning the term *progress* has its origin in these different views. In today's evolutionary biology, large-scale changes of general patterns are the heart of what is usually called progress. Because a term for this is needed, it will not be possible to eliminate it in the future, just as it has not been possible to avoid it in the past.

Simpson (1973) differentiates the term *progress*, which might include a normative undertone, from *progression*, which avoids assumptions about any kind of changes for the better (Table 2.1). I argue here that today the term is used in the sense of progression because no modern scientist would include a normative judgment.

A common criticism of the term *progress* is that it could be anthropocentric. However, a scientific description of large-scale patterns in the evolutionary process need not focus a priori on the characters of man. A large portion of the organic world went through an evolution that does not contain elements of the line toward human beings and so cannot be judged according to criteria generated from this line. Here, the perspective determines the traits observed as well as the systematic level chosen. With this prerequisite, the term *progress* is not necessarily anthropocentric. It just tries to describe large-scale patterns.

2.2 The Ontological Problem

The course of evolution, therefore, is not characterized by a process directed toward the generation of vertebrates and mammals. Instead, early forms of organisms were joined by forms with different general patterns. This is the case among not only vertebrates but also invertebrates and plants. What are the characteristics, then, of these lineages? What is the essential difference between a bacterium and a mammal or a squid? This is the question that remains at the center of this topic. In any case, the obstinacy, with which progress has remained, shows that a term is needed for referring to the underlying phenomena. Eliminating the term from the vocabulary of evolutionary biology is not the solution but rather a moratorium.

From the middle of the nineteenth century, there have been repeated attempts to establish standards, the first attempts stemming from Meckel (1821) and Bronn (1853, 1858). Most authors compiled lists of the patterns that should be considered valid (Rensch 1959; Remane 1967; Kämpfe 1985), but opinions diverged. Several attempts to operationalize patterns scientifically have been published, but they did not generate much interest from the scientific community (Dobzhansky et al. 1977; Kämpfe 1985; Rensch 1959; Simpson 1971, 1973; Storch and Welsch 1989; Wake 1986). On the other hand, there was always a certain general consensus regarding which organisms should be considered lower and which higher. McShea (1998) published one of the most thoughtful considerations about what might constitute “largest-scale trends.”

Among the patterns mentioned most often is that of “increasing complexity,” not always distinguished from “increasing differentiation.” In recent decades, when the term *progress* has become the subject of criticism, the term *complexity* has often been used as a substitute. McShea (1991, 1996), however, shows that the definition of “*what everybody knows*” is unsatisfactory and predominantly based on general impressions rather than on scientific data.

Some authors just took it for granted that evolution generates complexity and saw it as a product of selective processes. Bonner (1988) and Rensch (1959), for example, argue that complexity should be favored by natural selection because organisms that are more complex are mechanically more efficient, having more parts and greater division of labor among different cell types. Others claim that relating complexity to fitness is problematic, and that it is not clear whether and how complexity contributes to fitness (Wicken 1979). Further skeptical discussions are provided by Williams (1966), Lewontin (1968), McCoy (1977), Gould (1985), and Hinegardner and Engelberg (1983). Other authors make attempts at defining complexity and making it measurable (McShea 1991, 1996; Saunders and Ho 1976, 1981; Papentin 1980; Thomas and Reif 1993; Finlay and Esteban 2009). McShea (1996) developed a conceptual basis for objective investigations and found trends of increasing complexity in some measurements but not in others. McShea and Brandon (2010) propose a concept concerning increasing complexity as a constant background condition of evolution.

Many authors see "increasing differentiation" as overlapping with complexity and use the phrase in the sense of division of labor. Formulated as "increase in the number of cell types" or "increasing specialization of cells," it may provide a measurable variable (Valentine et al. 1993; Bonner 1988). The number of cell types increased with the generation of multicellularity, but a count of cell types does not seem to be able to describe the difference between an amphibian and a mammal. Also, it is difficult to distinguish cell types using a standard for comparison. Increasing "differentiation and centralization of nervous systems" has always been a widely recognized pattern. Rensch (1959), for example, sees it as a typical characteristic of his "anagenesis" and analyzes it within mollusks, arthropods, annelids, vertebrates, and others.

Some authors observe "increasing efficiency" of tissues, organs, or the whole organism, citing examples such as performance capacities of nervous systems and sense organs, biomechanical changes in movement capacities, and enhancement of metabolic capacities. However, it may be argued that also in lower organisms tissues are structured to fulfill effectively the functions for which they have been adapted. A similar argument may be applied to an increase in the "effectiveness of adaptation," whereas efficient environmental adaptation has occurred within all different phyla and classes without providing the ability to describe their general differences.

Some authors hope that an increase in the "amount of genetic information" would be a measurable trait of progress, but correlation between the supposed level and genome size turned out to be poor. This first appeared as the "C-value paradox" and has become more complicated in recent years.

Body size, of undoubted importance for many physiological, ecological, and life-history traits, is one of the general features of organisms most often deliberated. Based on a rough scale from bacteria to whales, several authors consider that the "increase in maximal body sizes" during successive periods of life on Earth is a pattern of progress (Bonner 1988).

"Energy intensiveness" has been studied in greater detail, although not always in the context of progress (McCarthy and Enquist 2005; Milewski and Mills 2010). Vermeij (1999) proposes that interactions of individuals within the adaptation process can be expected to lead to increases in size, having a higher productivity or metabolism, engaging in a larger number of interactions, and performing more functions at a higher level. Overall, they may show a pervasive increase in energy flux.

Within these various considerations, the pattern of an increasing autonomy of organisms in the sense of an "emancipation from the environment" is often mentioned. Here, again, as with some of the other criteria, authors usually give some examples, but there is no single attempt to define the pattern more closely or to describe the phenomena systematically. More about this literature follows in Chap. 3.

2.3 A Biological Dilemma?

Greene (1986, 1991) states that evolutionary biologists can live neither with nor without the idea of progress, a situation he refers to as a "biological dilemma." Attempts have been made to ban the term from evolutionary biology, however, with limited success. On the other hand, there have recently been attempts to reexamine the question of a directional trend in macroevolution and its possible conditions (Calcott and Sterelny 2011; Conway Morris 2003). A recurring question is how it can be detoxified from the connotations the term *progress* carries and how the idea of progressive change can become empirically tractable. This has motivated attempts to decouple work on large-scale trends from directional and progressivist ideas of history. McShea and Simpson (2011) insist that the project to examine the sense in which living beings constitute a series from the simplest forms at one end to humans at the other is legitimate. And, books are still published with titles such as, *Life Ascending* (Lane 2009), in which some of the major innovations along the path are presented.

Sterelny (2011) essentially formulates the same point when he states that evolution is a history of extraordinarily fecund changes. He describes that many lineages have seen the evolution of complex morphological innovations in the macrobes (sensory systems, locomotion, internal structural systems for circulation and support) and metabolic innovations in the microbes (nitrogen fixation, photosynthesis). Other lineages have histories of extraordinary diversification. Perhaps most striking, there has been directionality in evolutionary history. There has been an evolutionary trend of a special kind: the evolution of new forms of organization, the eukaryotic cell, multicellularity, eusociality. These transitions expand the space of biological possibility. The upper bound on possibilities is not fixed; rather, it is moved by such key innovations.

Developing a way of describing general macroevolutionary changes within a sound epistemological framework should be valuable for understanding evolution. The study of large-scale general patterns is a necessary element of the new evolutionary biology presently under construction. The study of directional qualitative shifts in morphology, physiology, molecular biology, and other fields of interest contributes to a more complete view of evolution. Within such a program, the "biological dilemma" might rather be part of the fruitful tension as Darwin implemented it.

In such an approach, the old metaphor of "progress" may be modified or understood in a new empirical light. This is a third direction between using the term indiscriminately on one hand and on the other hand ignoring the general patterns that evolution has produced. For the rest of the book, I leave the whole topic of progress and concentrate on a contribution to the question of large-scale patterns in evolution.

http://www.springer.com/978-3-319-04140-7

On the Origin of Autonomy
A New Look at the Major Transitions in Evolution
Rosslenbroich, B.
2014, XII, 297 p. 61 illus., Hardcover
ISBN: 978-3-319-04140-7