

## NATURAL SELECTION, ADAPTATION AND TELEOLOGY

(Naturlig utvalg, adaptasjon og teleologi)

Offentlig prøveforelesning over oppgitt emne

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There are at least two ways to account for the occurrence and diversity of life on our planet. It may be seen as the creation of God or some other supernatural power, or as having arisen spontaneously in some relatively simple form of matter and subsequently unfolded in a process of organic evolution.

This is not the time and place for a discussion of what I see as the fact of evolution, neither its relation to creationism. Rather I would like to explore the concept of Natural Selection, Darwin's unique contribution to evolutionary theory, and today the central explanatory principle of the neo-Darwinian theory of evolution. It has been the object of increasing criticisms in recent years from a number of quarters.

Time will not permit all aspects of this concept to be discussed (1). I will mainly explore to what extent it is infused with purposeful or teleological (2) thinking, an error usually ascribed to theologians or Lamarck.

The problem of teleology and evolutionary biology is apparently of very profound nature. The molecular biologist Jacob (3) suggested that there are two major questions to be asked in evolution concerning attributes of organisms. The first is "Where did this come from?" and the second is "What does this do?". He asserted that the second question (about function) was more important than the first (about origination) because it contained the answer of the first question within it. Thus function is seen to answer the problem of why a feature arose. As we shall see this way of thinking - which we will call functionalist - has its roots far back in history.

### Functionalism and structuralism - Aristotle and Empedocles

Let us look upon a case treated by Empedocles (492-432 B.C.) and Aristotle (384-322 B.C.) (4) more than 2000 years ago. The subject is the form of our teeth (5). Empedocles, the structuralist, argues:

Why not say, that Nature acts as Zeus drops the rain, not to make the corn grow, but of necessity (for the rising vapour must be condensed into water by the cold, and must then descend, and incidentally, when this happens, the corn grows), just as ... it did not rain on purpose to destroy the crop, but the result was merely incidental to the raining? So why should it not be the same with natural organs like the teeth? Why should it not be a coincidence that the front teeth come up with an edge suited to dividing the food, and the back ones flat and good for grinding it, without there being any design in the matter? And so with all organs that seem to embody a purpose. In cases where a coincidence brought about such a combination as might have been arranged on purpose, the creatures .... having been suitably formed by the operation of chance, survived; otherwise they perished, and still perish".

Aristotle, the functionalist, disagrees:

It is impossible that this should really be the way of it. For all these phenomena and all natural things are either constant or normal, and this is contrary to the very meaning of luck and chance. No one assigns it to chance or to a remarkable coincidence if there is abundant rain in the winter, though he would if there were in the dog-days; and the other way around, if there were parching heat. Accordingly, if the only choice is to assign these occurrences either to coincidence or to purpose, and if in these cases coincidence is out of the question, then, it must be purpose. But, as our opponents themselves would admit, these occurrences are natural. There is purpose, then, in what is, and in what

happens in Nature.

Aristotle urges that natural events are subservient to laws, and that Empedocles' argument in favour of coincidence moulding out natural events must be false. Aristotle assigns purpose to what is natural and introduces teleology as an explanatory principle.

Empedocles enquires why the parts and organs of the body should not be what they are, without there being any particular intention on the part of the Gods or Nature. Since there is no design, just fact, on the part of rain naturally falling because of basic laws of condensation, gravity etc. - thereby causing a grain of wheat to sprout that happens to be where the rain falls, whether sown by man or by chance - why should there be a design in shaping incisors unlike molars? Empedocles does not reject natural law in the name of blind chance, but he rejects teleology as the proper explanation of what takes place in nature.

To summarise: On the one hand structures may be viewed to develop because of some intrinsic properties or laws of the system itself. Function then becomes a secondary phenomenon, emerging from the relations between the organism and the environment. This is the structuralist approach to biology, and it is essentially causal. On the other hand, structures may be viewed to arise because there is purpose in their being in the relations of the organism with the external world. This is the functionalist approach and is essentially teleological.

Let this be our starting point for an evaluation of the concept of natural selection. Is Darwin an ally of Empedocles or Aristotle? Is he a structuralist or a functionalist (6)?

#### Darwin as a functionalist or adaptational teleologist

Darwin's book "The Origin of Species by Means of Natural Selection or the Preservation of Favoured Races in the Struggle for Life" from 1859 presents a world populated by organisms endowed with a sufficiency of independently occurring individual variations of varying number, direction and kind, but usually of infinitesimal extent, tending to be increased under changing conditions of life. Among these nature selects, in a manner analogous with the planning and intelligent human breeder, certain ones equipped more usefully - however slightly - than others for a perceived struggle for life. This process of gradual accumulation of very small changes goes on for ever, creating adaptations and diversity in step with the environmental changes to which the organisms are subjected.

Disregarding the anthropomorphic overtones in the description of nature, in some sense it seems, nevertheless, justified to regard Darwin's approach to be functionalist and teleological: e.g. the fangs of the adder and the ovipositor of the ichneumon flies are presented to be formed by natural selection as structures intended to cause harm and to aid in the struggle for existence. Organisms are pictured by descent to have acquired and preserved certain characters because these characters are useful to them.

Some biologists maintain that Darwin's Natural selection eliminated purpose and guidance from evolutionary thinking and likened natural selection to nature's blind watchmaker (7). They may find support for this in Darwin's own words:

"There seems to be no more design in the variability of organic beings and in the action of natural selection, than in the course in which the wind blows." (8)

However, it appears that Darwin was not trying to remove all teleology from explanations of natural process. Notable are these words of Asa Gray - the New York botanist friend of Darwin:

"let us recognize Darwin's great service to Natural Science in bringing back to it Teleology: so that, instead of morphology versus Teleology, we shall have Morphology wedded to Teleology."

To which Darwin responded:

" What you say about teleology pleases me especially, and I do not think any one else has ever noticed the point. I have always said you were the man to hit the nail on the head." (9)

To understand the extent of teleological thinking in Darwin's concept of natural selection let us consider some examples from his book. First on the possible transformation of the bear:

"In North America the black bear was seen ... swimming for hours with widely open mouth, thus catching, like a whale, insects in the water. Even in so extreme case as this, if the supply of insects was constant, and if better adapted competitors did not already exist in the country, I can see no difficulty in a race of bears being rendered, by natural selection, more and more aquatic in their structure and habits, with larger and larger mouths, till a creature was produced as monstrous as a whale." (10).

In later editions of the Origin this illustration of the presumed power of natural selection was deleted. Here is why, as Darwin explained in a letter:

"The bear case has been well laughed at, and disingenuously distorted by some into saying that a bear could be transformed into a whale. As I offended persons, I struck it out in the second edition: but I still maintain that there is no special difficulty in a bear's mouth being enlarged to any degree useful to its changing habits." (11)

Darwin's contemporary, the comparative anatomist Richard Owen, in his review of the Origin, remarked dryly that

we look ... in vain for any instance of hypothetical transmutation in Lamarck as gross as the one above cited (12)

It seems that the concept of usefulness in changing habits is the key to understanding Darwin's position. If something is thought to be useful in some hypothesized situation, it will be realised, or at least not offer difficulties for a first step in the transformation.

Darwin's belief in the extensive powers of Natural Selection was not shared by his friends. The views of Asa Gray is especially interesting for us:

Well, what seems to be the weakest point in the book is the attempt to account for the formation of organs, the making of eyes etc by natural selection. Some of this reads quite Lamarckian. (13)

Darwin himself often alluded to difficulties for his theory.

"If it could be demonstrated that any complex organ existed, which could not possibly have been formed by numerous, successive, slight modifications, my theory [of Natural Selection] would absolutely break down.(14)

The likely uselessness of the so-called "incipient stages of useful structures" was one of several objections critics raised against his theory. It was put forth with considerable force by St George Jackson Mivart. Let us look upon this problem as relating to the flatfishes (15). Darwin said:

The Flat-Fish, are remarkable for their asymmetrical bodies ... But the eyes offer the most remarkable peculiarity; for they are both placed on the upper side of the head. During early youth, however, they stand opposite to each other, and the whole body is then symmetrical... Soon the eye proper to the lower side begins to glide slowly round the head to the upper side ...

Mivart said, concerning the problem involved for Darwin's theory:

If the condition had appeared once, if in the hypothetically fortunate common ancestor of these fishes an eye had suddenly become thus transferred, then the perpetuation of such a transformation by the action of 'Natural selection' is conceivable enough. Such sudden changes, however, are not those favoured by the Darwinian theory, and indeed the incidental occurrence of such a spontaneous transformation is far from probable. But if the transit was gradual, then how such a transit of one eye a minute fraction of the journey towards the other side of the head could benefit the individual is, indeed, far from clear. It seems, even that such an incipient transformation must rather have been injurious'.

The extent to which Darwin believes in the functionalist and utilitarian approach to biology is revealed by the following reply to Mivart. The flatfishes

... whilst very young and still symmetrical ... cannot long retain a vertical position, owing to the excessive depth of their bodies, the small size of their lateral fins, and to their being destitute of a swimbladder. Hence soon growing tired, they fall to the bottom to one side. Whilst thus at rest they often twist ... the lower eye upwards, to see above them; and they do this so vigorously that the eye is pressed hard against the upper part of the orbit. The forehead between the eyes consequently becomes, as could plainly be seen, temporarily contracted in breadth .... We thus see that the first stages of the transit of the eye from one side to the other, which Mr. Mivart considers to be injurious, may be attributed to the habit, no doubt beneficial to the individual and to the species, of endeavouring to look upwards with both eyes, whilst resting on one side at the bottom. (16)

Let us be honest: it would be an error to attribute to Lamarck alone the notion of habits inducing changes (17).

It is quite clear from the citations we have made that Darwin's concept of natural selection was infused by teleological thinking to a very important degree in the form a utilitarian doctrine (18). To our question whether Darwin was an ally of Aristotle or Empedocles, we must reply that he was an ally of Aristotle. He was what we may call an adaptational teleologist to employ a term recently introduced by O'Grady.

### Neo-Darwinism and adaptational teleology

Historians of biology seem to agree that the theory of natural selection, as opposed to the idea of evolution, met with little success among Darwin's contemporaries and by the 1920-ies it was regarded as "long ago abandoned" (19). However, with the resurrection of Mendelian genetics, with the study of mutations in the genetic material and the mathematics of population genetics, all unknown to Darwin, the traditional Darwinism was transformed into the modern version - Neo-Darwinism or Neo-Mendelism. In this theory the genetic system is visualised as a system of independent genes positioned along the chromosomes. Morphology and morphogenesis is viewed as uniquely determined by these atomic units. Their distribution in populations may be treated mathematically. The genotype has a large amount of hidden diversity, imagined to be sufficient to respond to any selection pressures. Indeed as stated by Dobzhansky

If the appropriate genetic variants to face an environmental challenge are not already present in the population, they are likely to arise soon by mutation (20)

Concepts such as selection pressures, evolutionary needs (21) and random mutation won its way (22). With this theory came notions of fitness as differential reproduction, niche as a part of the environment, selection pressures adapting the organism to the niche, and notions of the niche as the causal agent which stimulates the adaptation (23).

According to O'Grady (24), one may legitimately claim that Neo-Darwinism like the classical Darwinism implies the view that whether or not evolutionary change will occur is determined by the functional efficiency or adaptedness of an organism in its interactions with the external world. The intrinsic factors which control the ontogeny and structural integrity of the organism are not considered capable of spontaneously changing in an orderly manner. Biological order is seen as consisting of functional levels - niches - into which organisms evolve, rather than coherent functional capacities emerging from structural change. It thus becomes quite legitimate to answer the question "why did this structure evolve?" with "in order to adapt to ...". The neo-Darwinist position is therefore also an expression of the functionalist approach to evolutionary change and allows questions like "what does this do?" to be connected with the evolutionary question "how did this thing get there?" Biological order is seen as a functionally imposed order and not a structurally emergent order.

Adaptational teleology therefore appears not to have been weeded out of traditional Darwinism by its merger with population genetics. It may therefore be of some interest to examine a few examples of teleological language prevalent in neo-Darwinian literature.

### Teleological language

The following is offered by Stenseth by way of "evolutionary explanation" of the migratory habits of some birds (25). Note the inverted causal statements.

Birds must, e.g. fly south in order to increase their survival as much as possible: Presumably the mortality resulting from flying from Scandinavia to Africa to survive through the winter there, is less than it would have been during an harsh winter in Scandinavia. Correspondingly, it is conceivable that birds finding themselves in Africa in the spring, will be able to produce more off-spring that each survive better by moving north to an area with less competition for limited resources.

Here the purpose is again regarded as the evolutionary reason. Migratory birds became so from non-migratory ancestors because they increase their survival, maximize or optimize fitness, etc. by migration.

The same author also claims that

"Natural selection must all the time select forth ("selektere fram") new variants so that the species shall not become extinct." (26)

If one assumes animals not to be aware of their need not to become extinct, it is not obvious what the phrase "must ... select forth new variants" means. Even Darwin guarded against a view of natural selection creating variants.

Price (27) considered thysanopteran males to lack wings so that they may remain on the host-plant for mating, not that they might stay there because they lacked wings.

Fitch writes that

"the organism might be better off if it could vary its mutation rate upwards in stressful times and downwards in favorable times. If that would be beneficial, then surely organisms [would] have found a way to do it."

Weisman stated that variation occurred so that natural selection could act upon it, and that death occurred so that there would be room for newly evolving organisms.

Dobzhansky considered entire species to fulfil a purpose:

"species are not accidents but adaptive devices through which the living world has deployed itself to master a progressively greater range of environments and ways of living."

In most of these statements the teleology is recognisable by inverted causal statements, by the replacement of the causal "because" with the teleological "so that" or "in order to". Purpose can be found in every modification. After all if organisms are "problem-solvers" (28) or "exploiters", "calculators" and "anticipators" of evolutionary fitness (29), then biological structures and habits can be seen as the result of these premeditated, teleological actions.

All the writers we have cited seem to make little distinction between the purposeful actions of a human being and the properties of biological systems. These concepts are being used to explain evolution, but exactly what type of evolutionary forces the authors have in mind is not specified. One author said of Dobzhansky's statement:

"I confess to experiencing a feeling of shock when I realised that Darwin's great achievement of freeing biology of teleology and the supernatural, had been surreptitiously supplanted by the old theological concept deceptively clad in new clothes." (30)

Here is a widely accepted view of the evolution of primates:

All these changes - development of a grasping hand or foot, conversion of claws to nails and friction pads, the increasing role of the sense of sight at the expense of the sense of smell with concomitant flattening of the face - are being explained as ever more perfect adaptations to life in trees. The selection mechanism is obvious. Individuals that were clumsy or less able to climb fell down and killed themselves and their hereditary matter did not further take part in the evolutionary process ... Life in trees demands instantaneous ability of perception and quick reactions; all apes are therefore brisk and agile animals. (31)

The claims as to the demands of life in trees are surprising. We all know that sloths - the most phlegmatic and sluggish mammals known, progressing upside down along branches at the maximal rate of about 4.5 meters pr hour

(in a female hurrying towards her baby) and spending about 18 of the days 24 hours dozing and sleeping (32) - also pass their whole lives in trees. According to the author's argument certain traits are assumed to have developed teleologically as adaptive responses to ecological opportunities or demands, all of which are left unspecified (33). The opposite view, that various evolutionary changes in the primates' body enabled them to exploit the environment in a novel fashion seems not acceptable, as it leaves the structural changes unexplainable in terms of the functional adaptationist framework. We have before us Darwin's utilitarian doctrine in a somewhat camouflaged form: hypothetical usefulness in a particular environment is the cause of the evolutionary origin of the characters. It is far from "obvious" why the ancestor of the primates should climb into the trees in the first place, considering that many of them - according to the author - would fall down and die. Deprived of its neo-darwinist idiom the argument is indistinguishable from the putative lamarckian mechanism: the organisms develop abilities and various traits because they have got a certain habit (climbing into trees).

To return to our question whether Empedocles or Aristotle is the ally of the modern Neo-Darwinist, the answer is clearly Aristotle.

### Why the teleological language? (34)

It ought to be of some concern that it seems impossible to root out teleological language which imply that structures and habits evolved in order for the organism to take advantage of their function, since those employing the language probably do not consciously believe in teleology. Why then do biologists so often give functional or purposive explanations of the state of certain traits, rather than causal ones relating to changes of states, which after all is what evolution is all about?

One reason may be that the preevolutionary naturalists still exert their powerful influence. These, like William Paley in the book "Natural Theology" (35) from 1802 (36), explain properties of organisms by reference to their divine and eternal design and purposiveness and the usefulness of their structures. They could not do otherwise, because at their time the species were timeless and placed in a non-evolving world by a divine being, and there were no specific events to be explained where characters changed from other character-states or arose anew.

In fact, Ole Heie (37) considers teleological "in order to" or "so that" explanations with associated reference to design and purpose not only legitimate, but true causal explanations in camouflaged form. According to Heie all "in order to" statements in evolutionary biology are of the following general 2-step form when formulated completely :

- (1) It [a feature or habit] is like this or that or happens in this or that way, so that the organism obtain this or that advantage,
- (2) because the ancestors of the organism obtained this advantage on the basis of genes that arose from fortuitous changes in other genes, and this advantage revealed itself through the fact that the carriers of the new genes left a higher number of offspring than the carriers of the unchanged gene, with the result that the unchanged genes in the end disappeared from the population (gene-pool).

And Heie finds it understandable that one in the daily work omits the "because" term since

"We have to do with a generalisation of high rank (wide applicability) and of advanced nature".

Such a view suggests that natural selection has become axiomatic in the neo-Darwinian theory and that the latter properly should be treated as a widely distributed belief system (38). From within the theory it is no longer deemed necessary to demonstrate empirically several implicit assumptions, among which we may now mention only three: first that a particular phenotypic variant really exists, secondly that it consistently leaves more offspring than others, and thirdly that the higher fitness is the direct result of the presence of the particular trait itself (39). At the same time, however, the neo-Darwinian explanation is revealed as the product of the application of a standard algorithm to a simple teleological statement. Any natural theologians' or lamarckian type of explanation can be processed by it and the correct Darwinian one is produced. In some sense God is removed and replaced with Natural Selection. Neo-Darwinists seem to know that natural selection and adaptation is the way of nature.

Another reason may be that many biologists seem not to demand strict causal explanations in terms of knowledge of initial conditions and action of universal laws, but on the whole are satisfied with non-causal more pragmatic

explanations. These are deemed good if they clear away real or imagined preconceptions rather than demonstrate empirically the truthfulness of one's own position by subjecting it to rigorous tests.

This may account for the popularity of the how-possibly type of explanation. Rather than explaining why necessarily or how actually a particular evolutionary event occurred, an how-possibly type of explanation merely removes objections the questioner might have to the event's possible occurrence. This is quite typical of the language in which e.g. Darwin's book is framed. He uses the very phrase "remove difficulties" several times, and statements like "can it be thought unreasonable", "can we doubt", and "... may well..." are frequent. This aspect of Darwin's language was criticised by his contemporaries, especially Fleeming Jenkin (40), who stated in 1867:

The general form of his argument is as follows: - All these things may have been, therefore my theory is possible, and since my theory is a possible one, all those hypotheses which it requires are rendered probable. There is little direct evidence that any of these maybe's actually have been.

Up to this day there has of course been no lack in the evolutionary literature of this type of biological tales, termed "just-so-stories" by Macbeth (41).

### Melanism of moths

After this examination of functionalist and teleological language widespread in current biological literature, I would like to examine a case where a functional explanation appears not to be in doubt. It concerns industrial melanism in moths, as exemplified by the Peppered Moth Biston betularia, widely published as an example of natural selection in action (42).

Melanism in moths seem to offer protection to the melanic forms from predatory birds, which thus may be compared to Darwin's breeder or Hand of Nature. As a result of birds picking out a proportionally large part of the light variants on the sooted tree trunks or tree-trunks without lichens, as in the upper section of the slide, the population has apparently changed in the last hundred years in gene frequencies and the dark or melanic forms, which also are present in the upper part of the slide, have become very common. The formerly most frequent variant of the moth is the light form, which is almost invisible on the lichened bark of an oak tree, as shown in the lower section of this slide.

However, the matter appears not be so simple as the text-book writers believe. Lepidopterists practically never find the Peppered Moth resting on tree-trunks like in this photograph (same SLIDE), and the Finnish entomologist Kauri Mikkola suggests that it is artificial. In Kettlewell's experiments the moths were released in an illumination bright enough for the human eye, and, being night-active, the Peppered Moths may therefore have chosen their resting sites as quickly as possible and probably atypically. Mikkola, has since established (43) that the Peppered Moth normally rests beneath small horizontal branches, probably high in the canopies. Others (44) do not accept even this, and maintain that the resting site of Biston betularia during daytime still is unknown. Quote:

"In 25 years we have only found two betularia moths on the tree trunks or walls adjacent to our traps (one on an appropriate background and one not) and none elsewhere."

That Kettlewell's moths thus were not free to take up their normal resting site for the first day seems to be of special importance. On the basis of published release and recapture data Mikkola suggested selection to be weaker or absent during the days succeeding the first, thus when the moths were able freely to determine their site of rest. Mikkola also claimed that the results of Kettlewell fail to demonstrate the qualitative predation of the different morphs of the Peppered Moth by birds or other predators in natural conditions. He thus called for new experiments of this type. Another reviewer (44) concluded that the development of industrial melanism in Biston betularia must depend on gene flow and on powerful non-visual selective forces whose nature is as yet unknown, and claimed that there were

"more to melanism than meets the eye."

In short, the problem of melanism is still a mystery.

Thus, neo-Darwinists appear to be far from having made such a clear case for functional selection that it seems warranted to trust or extrapolate from functionalist explanations in general (46).

## Natural selection - inability to account for transformation of form

In fact it is also far from evident that stories like the one about the Peppered moth - granted them to be true - have anything to do with evolution above the species level. Put otherwise, it can be questioned whether small random changes in a population are really the building blocks of evolution. It is far from evident that population genetic theory - being mostly a theory of the distribution and change in frequency of genes in equilibrium (47) situations - is able to explain the diversity of life - being a problem of transformation of form and origin of evolutionary novelties.

According to Waddington, transformation of form is clearly out of the grasp of the mathematical approach of the population geneticists. During a symposium on Neo-Darwinism in 1966 (48) he said:

... "the survival of the fittest" ... is a very elementary old-fashioned concept; but of course that was what Darwin is talking about. By "fittest" he meant best able to carry out the functions of life, best adapted to some environmental situation and some way of life. ... What has happened to it since, in the process of turning this into a lot of mathematics, is that "fitness" has been redefined, leaving out anything to do with way of life, simply in terms of leaving offspring. So the theory of neo-Darwinism is a theory of the evolution of the changing population in respect to leaving off-spring and not in respect to anything else. It is smuggled in and everybody has in the back of his mind that the animals that leave the largest number of offspring are going to be those best adapted for eating peculiar vegetation, or something of this sort; but this is not explicit in the theory. All that is explicit in the theory is that they will leave more offspring.

There... is in fact a vacuous statement: Natural selection is that some leave more offspring than others; and you ask, which leave more offspring than others; and it is those that leave most offspring; and it is nothing more to it than that.

The whole real guts of evolution - which is, how do you come to have horses and tigers, and things - is outside the mathematical theory ... The sheer mathematical language is largely vacuous.

## Non-adaptive traits

I will now consider the concept of natural selection in relation to actual cases of evolutionary events as these are available to taxonomists through character analysis according to the principles of phylogenetic systematics.

Among higher flies there is a genus named Pollenia often known as clusterflies. Among them is a particular group of about 20 species variously distributed in the Old and New World. The adults are extremely similar in external appearance. One species is shown here. All males of these species have a peculiar midventral projection on the copulatory organ. No other flies whatsoever have this structure and it is reasonable to assume that those having it form a natural group which originated at the time far back in history when a species - which we can term the stem species - acquired this evolutionary novelty. By successive speciation events we have got the group of 20 species we have today. These species also have a peculiar strengthening of the hypophallic lobes of the male copulatory organ, also not found in other insects. Under the neo-Darwinian theory these characters should be thought of as being formed in the stem species by gradual accumulation of small "advantageous" modifications. I find it difficult to accept that the features should be advantageous at all compared to its untransformed ancestor lacking these features, since the 80 other Pollenia species in the world today thrive and reproduce excellently without them. It also seems dubious that these characters should confer some advantage to their bearers in an assumed struggle for life, or confer a greater reproductive success as the theory of natural selection demands, or that they have been formed in response to some selective pressure or demand from the environment. In fact it appears quite far fetched to assign the feature "adaptive significance" and ascribe its origin to the agency of natural selection. Nevertheless, in retrospect its acquisition seem to reflect an event of considerable evolutionary significance (49).

Zoologists have through time been struck by and discussed the problem of the apparent unadaptedness of several taxonomic features of organisms. As a solution is usually invoked correlation with other features, identified or unidentified, assumed to be adaptive (50). As empirical support is not produced, the assumption of correlation is clearly ad hoc, invoked to protect the utilitarian doctrine from falsification by non-adaptiveness. Unfortunately, one



can hardly argue with a theory which portrays attributes to be either adaptive or non-adaptive without giving criteria on how to distinguish between the two.

Various authors have emphasized the facts that ecological changes do not precede or accompany speciation very often, that speciation does not result in ecological changes very often, that species differences are rarely correlated with any independent ecological variable (51). One author (52) estimates that ecological shifts occurred approximately once in every thirty speciation events in various insect groups. Boucot (53) suggests that evolution occurs in an ecological vacuum, quite the opposite of the idea that natural selection, competition (54) and dispersal drive the evolution. Brundin and Sæther (55) found that ecological changes lag far behind morphological changes in the evolution of chironomid midges. On this background it is difficult to see how ecological factors drive evolution, as the current wisdom will have us to believe.

### Natural selection - creating noise obscuring true relationship

However, from detailed studies of natural groups I am sure every systematist has discovered some general pattern of correlation between traits exhibited by unrelated species and their environment (56). Such patterns seemingly demonstrate that natural selection, conceived of as a determinate relation between the environment and the organism (57), of some kind operates.

From this type of experience a systematist with good knowledge of his groups may be able to predict with considerable confidence some features of the environment of a particular species previously unknown to him.

Such examples are of special interest since they seem to demonstrate that natural selection operates with a measure of testability only in cases where features are formed which have little or nothing to do with the genealogical relationship of their bearers. As far as evolution is concerned, natural selection then possibly mostly creates "noise" obscuring true relationship.

### Conclusion

It may be impossible to avoid the teleological trap as long as functionalist theories prevail in biology. It also appears that the peculiar "Darwinian" vocabulary - adaptation, selection regimes, natural selection, usefulness, need, gradualism - with its emphasis on utility and advantage is singularly conducive to entering the trap. Today there exist comprehensive structuralist theories which seem to be able to avoid these shortcomings of both Darwinism and neo-Darwinism (58). They deserve careful study.

### Notes

1. For an in-depth discussion of the concept from philosophical angles including a clarification of the various charges of tautology and untestability and defenses against them, the following papers by Ronald Brady are recommended:

Natural selection and the criteria by which a theory is judged. *Syst.Zool.* 28: 600-621 (1979)

Dogma and doubt. *Biological Journal of the Linnean Society* 17: 79-96 (1982).

Unfortunately none of these papers are cited or discussed in "Evolusjonsteorien" the Norwegian book pretending to present to the Norwegian public the status of the current status of the evolutionary theory.

2. I use the word "teleology" in the trivial sense, i.e. "the use of design, purpose, or utility as an explanation of any natural phenomenon". The definition is taken from Løvtrup, *Phylogeny of the Vertebrata*, p. 4 (foot-note), who cites Webster's Third New International Dictionary.

3. Cf. Brooks, D. R. What's going on in evolution? A brief guide to some new ideas in evolutionary theory. *Can. J.*

Zool. 61: 2637-2645, (1983), p. 2644; O'Grady, R. T. Evolutionary Theory and Teleology. *J.Theor.Biol.* 107: 563-578 (1984).

4. Dates are taken from Rancke-Madsen, E. (1987) *Kemiens Fødsel*. Gad, Copenhagen, 92pp.

5. The discussion of Empedocles and Aristotle's views are taken from Croizat, L. (1962-64). *Space, time and form*. Caracas. 881pp. (pp. 495-496). See also Løvtrup, S. (1977) *The Phylogeny of Vertebrata*. Wiley & Sons, 1977. 330pp. (p.284, pointing to 213).

6. The distinction between functionalist and structuralist approaches is taken from O'Grady (see above) and Brooks, D. R. & Wiley, E. O. (1986) *Evolution as Entropy. Toward a Unified Theory of Evolution*. The University of Chicago Press, Chicago and London, 335pp.

7. See e.g. Tjønneland, A. (1986) Review of Richard Dawkins: *The blind Watchmaker*, Longman, 1986. *Naturen*, no. 6, 1986: 238-9)

8. Darwin, Løvtrup, p. 232-33

9. O'Grady, p. 568.

10. In a review of the "Origin..." by Owen in 1860; Løvtrup, p. 86. Se også Owen i Hull: *Darwin and his Critics*.

11. Løvtrup s. 87, see also Darwin's letter to Lyell on this transformation: "Observe, that in my wretched Polar Bear [sic] case, I do show the first step by which conversion into a whale 'would be easy', 'would offer no difficulty'!!" (ibid.).

12. See note 22.

13. Løvtrup, p. 230.

14. Gould SZ 32(4):444; *ArtOpr* 5, p. 208.

15. The discussion is taken from Løvtrup, pp. 243-267. See also Mivart's contribution in Hull: *Darwin and his Critics*.

16. Løvtrup, *Darwinism. The refutation ...*, p. 255.

17. See e.g. Løvtrup p. 54 and p. 251 to appreciate the similarity between Lamarck and Darwin's views of the neck of the giraffe.

It may not be historically correct to attribute to Lamarck the notion "that desires and efforts can engender organs". Possibly this can be traced to Cuvier "Éloge de M. Lamarck (1835). Hull remarks (in SZ 27(2):248-250) that "Cuvier writing Lamarck's eulogy is comparable to G.G.Simpson or Ernst Mayr writing a scientific obituary for Willi Hennig today. If this be so, then Darwin may be the originator of the notion of habits inducing traits and abilities.

18. Se Young, *Darwin's Metaphor*, p. 468

19. E. Nordenskiöld, *The History of Biology (1920-1924, New York: Tudor, 1928)*, p. 476 - cited from R.M.Young, *Darwin's metaphor: Does nature select?* *The Monist* 55: 442-503, p. 497: "To raise the theory of selection, as has often been done, to the rank of a 'natural law' comparable in value with the law of gravity established by Newton is, of course, quite irrational, as time has already shown; Darwin's theory of the origin of species was long ago abandoned." As to the reception of the theory of natural selection by Darwin's contemporaries, see Løvtrup, *Darwinism. The refutation of a myth*.

In Young's paper (p. 500) we can also read: "It is clear that Darwin's putative mechanism of natural selection suffered grievously for philosophical, theological, and scientific reasons - and often for all three - at the hands of the critics who combined their reservations and/or enthusiasms. But, as they concentrated on skirmishes the main issue was settled. Putting the matter another way, Darwin's mechanism - in its nineteenth century form and in its

nineteenth century context - turned out to be a very frail reed, but in bending with the winds it allowed his real commitment to the uniformity of nature to contribute to the general movement of nineteenth-century naturalism. It we notice the extent to which the special status of natural selection was weakened by scientists, theologians, and philosophers, Darwin's achievement turns out to be much more like that of Lyell and the other evolutionists: together, by a rather confused mixture of metaphysical, methodological, and scientific arguments which depended heavily on analogical and metaphorical expressions, they brought the earth, life, and man into the domain of natural laws.

20. Dobzhansky et al, 1977, cited from Saunders and Ho, in *Evolutionary theory. Paths into the future*, p. 125.

21. See e.g. Mayr (1988) *Toward a new philosophy*, p. 108 in chapter on natural selection as far as "evolutionary needs" are concerned.

22. See Løvtrup, pp. 337ff.

23. See Mayr's view as cited by Wiley, *Phylogenetics*, p. 254.

"On the other hand workers such as Mayr (1969: 593-595) conceive of the niche as the causal agent which stimulates the adaptation."

To what extent is the concept of niche operationally distinct from the species occupying the niche? Cfr. note 34, below.

24. I am basing this on O'Grady's discussion in his "Evolutionary Theory and Teleology" in *J.theor.biol.*

25. Stenseth, N.Chr. (1984) *Den darwinistiske teori for mikroevolusjon*. Pp. 97-113, in "Evolusjonsteorien".

26. Stenseth, *ibid.* s. 117.

27. The following examples have been taken from O'Grady, *op.cit.*

28. Lewontin, *Adaptation*, *Scientific American*, September 1978.

"The modern view of adaptation is that the external world sets certain "problems" that organisms need to "solve", and that evolution by means of natural selection is the mechanism for creating these solutions. Adaptation is the process of evolutionary change by which the organism provides a better and better "solution" to the "problem", and the end result is the state of being adapted."

29. For a source to the use of exactly these terms in authoritative texts, see O'Grady, p. 570.

30. See O'Grady, *Teleology ...*

31. Elgmork, K. (1984) *Menneskets utvikling*. Pp. 196-209, in: *Evolusjonsteorien*. KR's translation.

32. *Life nature Library*, *Mammals*, s.70-71; *Cappelens dyreleksikon*, vol. 1, s. 267ff.

33. How can we really study the notion of "adaptation" to life in trees, without specifying the exact niche to which the organism under study is postulated to be "adapted"? Can we ever hope to be able to specify the niche independent of the organism itself? How can we then avoid the circularity and avoid serving platitudes of the type "apes are adapted to apes' life"; or "hawks being perfectly adapted to hawks' way of life" (NRK, i program om flyging og rovfugl, kommentarer lest av H. Chr. Alsvik). In a Norwegian popular science magazine we are informed of the astonishing fact that "each animal species has eyes adapted to their needs" (PM - *Populærvitenskapelig magasin*, nr. 7, 1988, s. 3, s. 53. Tekst og foto ved Johan Christian Frøstrup, men utsagnet forekommer i en innholdsfortegnelse og en overskrift og er muligvis satt av redaktøren Georg Parmann). Lewontin and van Valen thinks otherwise:

Lewontin, *Adaptation*, *Scientific American*, September 1978:

"If ecological niches can be specified only by the organisms that occupy them, evolution cannot be described as a process of adaptation because all organisms are already adapted. Then what is

happening in evolution?"

However, rather than proving that all organisms are adapted, it only reveals the emptiness of the concept of adaptation. To say that organisms are adapted is identical to saying they are alive. No further information is conveyed by the term, which appears quite superfluous.

As to the use of the concept "teleology" here, see also the discussion in Greenwood, *Macroevolution - myth or reality?* *Biol.J.Linn.Soc.* 12: 293-304 (1979), p. 301.

As to this and similar "axiomatic verbiage" and the (im)possibility of testing entities such as "selective regimes" (Elgmork's "life in trees") etc, see Cracraft, J. (1978): *Comparative biology and brain evolution* [reviews]. *Systematic Zoology*, 27 (2): 260-264; especially pp. 262-263.

34. Much of what follows is inspired by Robert J. O'Hara (1988): *Homage to Clio, or, towards an historical philosophy for evolutionary biology*. *Systematic Zoology* 37(2): 142-155.

35. Paley was read by Darwin during his studies in Cambridge according to Himmelfarb, *Darwin and the Darwinian Revolution*, see index. On the similarity of views between Natural Theologians and Darwin, see Webster & Goodwin, *J.Social Biol. Struct.* (1982) 5: 15-47, *The origin of species: a structuralist approach*.

36. Young, *Darwin's Metaphor*, p. 488, gives exact references to Paley's book.

37. Ole E. Heie (1977): *Håndbog i biologi undervisning I. Biologiundervisningens mål og veie*. Gyldendal, København.; s. 68, 116. KR's translation.

38. On the axiomatisation of natural selection, see O'Grady, *Evolutionary theory and teleology*; also:

Cracraft, *SZ* 27(2): [in review article] (1978), p.261:

"Here and elsewhere in these books we read of "adaptive themes", "adaptive processes", "adaptive thresholds", and the like. Why? Perhaps these authors believe they are studying process, but how we are never told. In fact, is it possible to study process in any historical analysis? Perhaps statements about postulated sequences of change (inferred, not observed, patterns) being caused by selection or depicting adaptive modification are really only articles of faith and not subject to scientific analysis (hypothesis testing). How can we, for example, recover evidence pertaining to selection forces or fitness?"

ibid, p. 263:

And how can we ever study the "same selection regime"? What most workers - and presumably also Gould - mean is "living under similar environmental conditions." If these workers would admit that these discussions about "selection" and "adaptation" are axiomatic verbiage, I would have few complaints; my contention is, however, is that language captures people's thought processes and can impose a "world view" that precludes them from considering alternative viewpoints regarding the scientific analysis of nature. If natural selection is to be invoked, it seems essentially axiomatic; if it is to be defended, it is only because there is not yet a better alternative.

Cf. Cracraft, *American Zoologist*, 21: 21-36 (1981) "The use of functional and adaptive criteria in phylogenetic systematics", p. 31:

One implication of these adaptive stories is that survival, reproduction, and/or fecundity are non-random with respect to the variance of the phenotypic characteristic being studied. What is the evidence, derived from information about the population structure of the species, that these components of fitness are not simply random with respect to the pattern of phenotypic variation being studied? And if the correlation between phenotypic variation and fitness is nonrandom, what is the evidence that differences in fitness are a direct result of that particular phenotypic variation?

39. The genetic atomism, the fortuitous genetic changes affecting the particular trait under investigation, the simple relation between a gene and a specific morphology or behaviour, the existence of competition (cf. Brady,, Dogma and Doubt) in nature and its effect (cf. Simberloff, The status of competition theory in ecology), the higher number of offspring of the particular variants compared to other variants, the disappearance of the unchanged gene. Cf. also note 33, ref. to Cracraft's two papers. On the practical and theoretical difficulties in measuring fitness directly by measuring the reproduction of various genotypes, see Lewontin, The genetic basis of evolutionary change, pp. 235ff; pp. 242ff; pp. 317-318: who argues against genetic atomism, and in favour of context and interaction between genetic elements.

40. Hull, Darwin and his Critics, p. 339; Løvtrup, s240.

41. Norman Macbeth: Darwin retried.

Brady, Natural selection and the Criteria:

The representative power of a theory is its ability to represent, or to explain, the world in its terms - to form a picture of what the world would be like, if the theory were true. A theory that cannot represent all of the relevant information after its own model is a non-starter, for one could not, if the theory failed to do this, even imagine it to be true.

...

Could evolutionary biologists, for example ever lack for "just so stories" - narrative scenarios which explain how it all happened after the fact? No mythology, belief system, etc., has ever been found wanting on this requirement.

42. The discussion to follow is based on the following sources:

Kettlewell, H. B. D. (1955) Selection experiments on industrial melanism in the Lepidoptera. Heredity 9: 323-342;

- (1973) The evolution of melanism. The study of a recurring necessity. With special reference to industrial melanism in Lepidoptera. Clarendon Press, Oxford, 423pp.

Jones, J. S. (1982). More to melanism than meets the eye. Nature 300: 109-110.

Mikkola, K. (1984). On the selective forces acting in the industrial melanism of Biston and Oligia moths (Lepidoptera: Geometridae and Noctuidae). Biological Journal of the Linnean Society 21: 409-421.

Clarke, C., Mani, G. S. & Wynne, G (1985) Evolution in reverse: clean air and the peppered moth. Ibid 26: 189-199.

43. Mikkola, 1984

44. Clarke, Mani & Wynne (1985), p. 197.

45. Jones, 1982; Løvtrup, s. 319.

46. Paraphrase - with possible twist of meaning - of the final sentences of Lewontin, R. C. (1972) Testing the theory of Natural Selection. Nature 236: 181-182. Lewontin claims that selection of the character states themselves are the essence of darwinism and thus not some unknown entity correlated with them.

47. Maynard Smith, The Evolution of Sex, p.6-7:

So far I have discussed only the maintenance of sexual reproduction and genetic recombination. But what of their origins? Surely evolution theory should be concerned with the origin of adaptations, not

merely with their maintenance once they have arisen. There is much in this objection; indeed ... my own insight into the field may have been obscured by an obsession, which I share with most population biologists, with equilibrium situations.

Yet there is really little alternative. Recombination probably originated some three thousand million years ago, and eukaryotic sex one thousand million years ago. Each origin may have been a unique series of events. We can speculate about such events, but cannot test our speculations... We have to concentrate on maintenance rather than origins because only thus can we have any hope of testing our ideas.

48. Waddington, pp. 13-14, in: Moorhead, P. S. & Kaplan, M. M. (eds.) (1967) *Mathematical Challenges to the Neo-Darwinian interpretation of evolution*. A symposium held at The Wistar Institute of Anatomy and Biology April 25 and 26, 1966.

49. Note that "Natural selection of the character states themselves is the essence of Darwinism." as maintained by Lewontin (1972) *Testing the Theory of Natural Selection*, *Nature*, .... And he adds: "All else is molecular biology."

50. Darwin e.g. alluded to "mysterious forces of correlation"; e.g. Mayr i *Population, Species and Evolution*. The Belknap Press of the Harvard University Press, Cambridge, Massachusetts, 1971. I am leaving out of consideration the view of Simpson:

"The fallibility of personal judgement as to the adaptive value of particular characters, most especially when these occur in animals quite unlike any now living, is notorious"

or Dobzhansky

[no biologist] can judge reliably which 'characters' are neutral, useful or harmful in a given species

on the question of adaptiveness, cited by Brady, both op.cit. These remarks seem to shake the foundations of adaptationist literature.

Jenkin i Løvtrup, p. 239, kritiserer dette korrelasjonsargumentet sterkt.

51. Brooks and Wiley, *Evolution as Entropy*...

52. Ross (1972a), cited from Brooks and Wiley, *Evolution as Entropy*...

53. Ref. in Brooks & Wiley, *Evolution as entropy*, ...

54. Se Simberloff, Status of competition theory in ecology. *Ann.Zool.Fennici*. 19: 241-253. 1982.

"This theory has caused a generation of ecologists to waste a monumental amount of time."

55. See Sæther, Nye ideer innen evolusjonsteori. *Naturen* 1987 nr. 4, pp. 138-144.

56. Copulation on the ground in chironomids is correlated with a suite of similar features in unrelated species (Sæther, O. A., 1986: The myth of objectivity - post-Hennigian deviations. *Cladistics* 2: 1-13. High altitude calypterate flies within various monophyletic groups tend to have long dense hairing, dark colour, long subgenal edges, protruding mouthedges, small eyes, short arisal hairing, lost the prst ia, etc. Undoubtedly other specialists can tell about similar cases. Mayr cites an impressive case involving unrelated fleas modified similarly on similar hosts (p.154 i "Toward a new philosophy of biology. Observations of an evolutionist. The Belknap Press of the Harvard University Press, Cambridge, 564pp., 1988).

57. The basic postulate of the Darwinian theory of natural selection, according to Brady, op.cit. p. 604 is: There is a determinate relation between animal traits and the environment.

We could add "and this relation explain speciation and diversity".

58. E.g. the one put forth by Brooks & Wiley in *Evolution as entropy* ... (1986, 1988) based upon non-equilibrium

thermodynamics; see also G. Webster & B.C. Goodwin. The origin of species: a structuralist approach. *J.Social Biol.Struct.* (1982) 5: 15-47; and J. D. Murray: How the Leopard Gets its Spots, *Scientific American*, March 1988: 62-69.