FUNCTIONAL MORPHOLOGY AND EVOLUTIONARY BIOLOGY

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ABSTRACT

In this study the relationship between functional morpholoy and evolutionary biology is analysed by confronting the main concepts in both disciplines.

Rather than only discussing this connection theoretically, the analysis is carried out by introducing important practical and experimental studies, which use aspects from both disciplines. The mentioned investigations are methodologically analysed and the consequences for extensions of the relationship are worked out. It can be shown that both disciplines have a large domain of their own and also share a large common ground. Many disagreements among evolutionary biologists can be reduced to differences in general philosophy (idealism vs. realism), selection of phenomenona (structure vs. function), definition of concepts (natural selection) and the position of the concept theory as an explaining factor (neutralists vs. selectionists, random variation, determinate selection, etc.).

The significance of functional morphology for evolutionary biology, and vice versa depends on these differences. For a neo-Darwinian evolutionary theory, contributions from functional and ecological morphology are indispensable. Of ultimate importance are the notions of internal selection and constraints in the constructions determining further development. In this context the concepts of random variation and natural selection need more detailed definition.

The study ends with a recommendation for future research founded in a system-theoretical or structuralistic conception.

I. INTRODUCTION

The relationship between functional morphology and evolutionary biology is very differently assessed by various authors (see Hecht *et al.*, 1976). Opinions of evolutionary biologists range from considering morphology as practically useless in the study of evolution, to regarding it as the primary source of information, whilst those of the functional morphologists vary correspondingly from regarding functional morphology as a separate discipline to regarding it as a discipline which owes its existence to evolutionary biology. Why is there such controversy, why these wide differences of opinion?

In order to get some insight into these controversies an analysis with some knowledge of the structure of both functional morphology and evolutionary biology is needed.

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Two approaches seem possible: one, in which the structure of one discipline is compared with that of the other, and subsequently bringing both together in one structure, and the other, in which the significance of the concepts of one discipline for the other discipline are considered. The first approach lies almost completely in the field of philosophy of science; the relationship between the corresponding concepts will constitute a new disciplinary structure on a higher level. In general, we cannot expect that this structure will contribute much to the theory of biology as such, but rather show the philosophical basis of the latter. The second approach suggests a connection or synthesis with a mutual beneficial effect to both disciplines within the boundaries of biology. Since in the present exposition the interest focuses on biology itself, rather than on its philosophical basis, I have chosen the latter approach.

A pragmatic, and hopefully fruitful, approach seems to be to start with a clear example of an investigation in which both disciplines are connected. Liem's study (1973) was chosen. After the description I shall attempt to summarize the successive methodological procedures in this study. From this list of methodological steps I shall develop a strategy including the selection of the concepts in both disciplines which have to be confronted. With the confrontation of the concepts I intend to analyse a number of investigations of suitably high standard: a basic requirement since only studies of good quality can be expected to treat the concepts properly and to show the unsolved problems most clearly. They can be used as show pieces or the type specimens in the fields.

II. AN EXAMPLE

II.1. Liem's study of cichlid fishes

In a stimulating article, Liem (1973) presents his general ideas about the fascinating development of the trophic types of cichlid fishes. His study is an appropriate example wherein the relationship between functional morphology and evolutionary biology is used to reveal the kind of problems arising from a confrontation of both disciplines.

Cichlids are percoid teleosts of which certain genera contain numerous species[1] (Greenwood, 1951-1979). The species are clearly distinguishable by such features as the structures of the head region, which are adapted to various kinds of feeding habits (trophic types) (cf. Barel *et al.*, 1977). Cichlids possess pharyngeal jaws with teeth. These jaws are movably suspended from the skull base (fig. 1) in contrast to most other groups which possess freely floating pharyngeal jaws. The pharyngeal jaws are derived from branchial skeletal elements. The upper jaw is homologous to the pharyngealia 2, 3 and

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[1] Recently Greenwood (1979) proposed a splitting of the genus *Haplochromis* into several genera, so that in this proposal the cichlids are divided into many genera with few species. The new classification does not affect the present discussion.

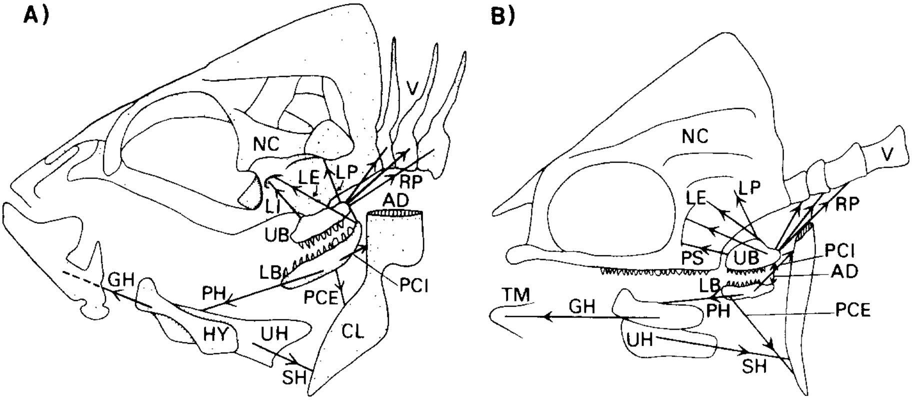

Fig. 1. (a) Position and direction of some major branchial muscles in a generalized cichlid fish. AD, adductor; CL, cleithrum; GH, geniohyoideus; HY, hyoid; LB, lower pharyngeal jaw; LE, fourth levator externus; LI, levator internus; LP, levator posterior; NC, neurocranium; PCE, pharyngocleithralis externus; PCI, ph. internus; PH, phar. hyoideus; RP, retractor pharyngeus superior; SH, sternohyoideus; UB, upper pharyngeal bone; UH, urohyal; V, vertebrae. (b) Similarly for *Pristolepis fasciatus*. PS, parasphenoid; TM, tip of mandible. From Liem (1973).

4 of which 3 and 4 are fused and form the main part of the jaw. The lower jaw is the ceratobranchial 5. The branchial musculature is well developed. There are levator, retractor and obliquus muscles, running from the upper jaw to the skull and the vertebrae, and retractor and protractor muscles connecting the lower jaw with the cleithrum and the hyoid respectively (fig. 2). The adductor muscle runs between the jaws. The various species differ widely in the size and the structure of their jaws, the muscles and the dentition. The teeth vary from pointed to blunt and flat in assorted shapes. These shapes suggest as many trophic adaptations. Cichlids occupy many ecological niches in all the great African lakes; every lake reveals a parallel series of adaptations (Greenwood and Barel, 1978).

In Liem's study, the pharyngeal jaws stand centrally. Liem's questions are: how did the 'free' suspended jaws change into articulating ones? what is the biological meaning of the new situation and what is the potential for adaptive radiation?

The 'free' suspension is found in *Pristolepis fasciatus*. Liem considers this the generalized percoid. He describes the topography of the pharyngeal jaws, their general outer shape, the position of the muscles and their movement, analysed by radiography and myography. This generalized percoid is compared with a generalized African cichlid, *Haplochromis burtoni*, and is analysed in the same way. The two species differ in their above-mentioned suspension of the pharyngeal jaws and in the places of attachment of the levator externus muscle. The latter is attached to the caudal aspect of the lower jaw in *H. burtoni* and to the upper aspect of the upper jaw in *Pristolepis fasciatus*. Moreover, in *H. burtoni* the lower jaw halves are united.

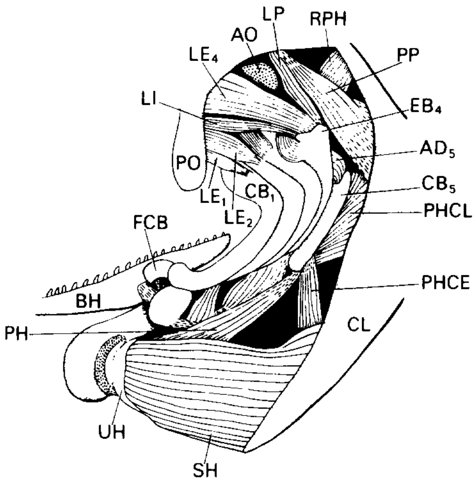

Fig. 2. Lateral aspect of the muscles of the pharyngeal jaw apparatus. AO, adductor operculi; BH, basihyal; CBI, first ceratobranchial; EB4, fourth epibranchial; FCB, fossa for hyoid ramus; PHCH, pharyngocleithralis externus; PHCI, pharyngocleithralis internus; PO, postorbital process; PP, protractor pectoralis; RPH, retractor pharyngeus superior. Other abbreviations in fig. 1. From Liem (1973).

The myogram is also different (fig. 3). In *Pristolepis* a clear two-phase activity can be observed. In phase 1 the jaw apparatus is levated and the jaws are opened; simultaneously activity of the levator posterior and the retractor muscles can be observed. In the second phase the jaws are closed simultaneously with activity of the levator and adductor muscles and the muscles between the hyoid and the buccal jaws.

In *H. burtoni* Liem distinguishes three phases: 1a, 1b and 2. Two muscles are active during all phases: the levator externus and the levator posterior muscle. In phase 1b the pharyngo-cleithralis internus is active and in phase 2 the hyoid muscles, the pharnygo-cleithralis externus and the adductor muscles.

According to Liem, the function of the jaw apparatus is different in the species insofar that in *Pristolepis* they serve for food transportation wheras in *Haplochromis* processing also takes place. The latter function can only be carried out when all the parts form a totality and the apparatus is well integrated in the entire head region. The use and development of this construction of the pharyngeal jaws Liem calls a *key-innovation*, because the construction gives rise to an astonishing radiation of adaptations. The various adaptive variations can be explained by the theory of natural selection. According to Liem there are only minor structural changes necessary for the large functional changes. However, Liem apparently does not exclude sudden saltatorial changes and says that in the process of evolution a kind of

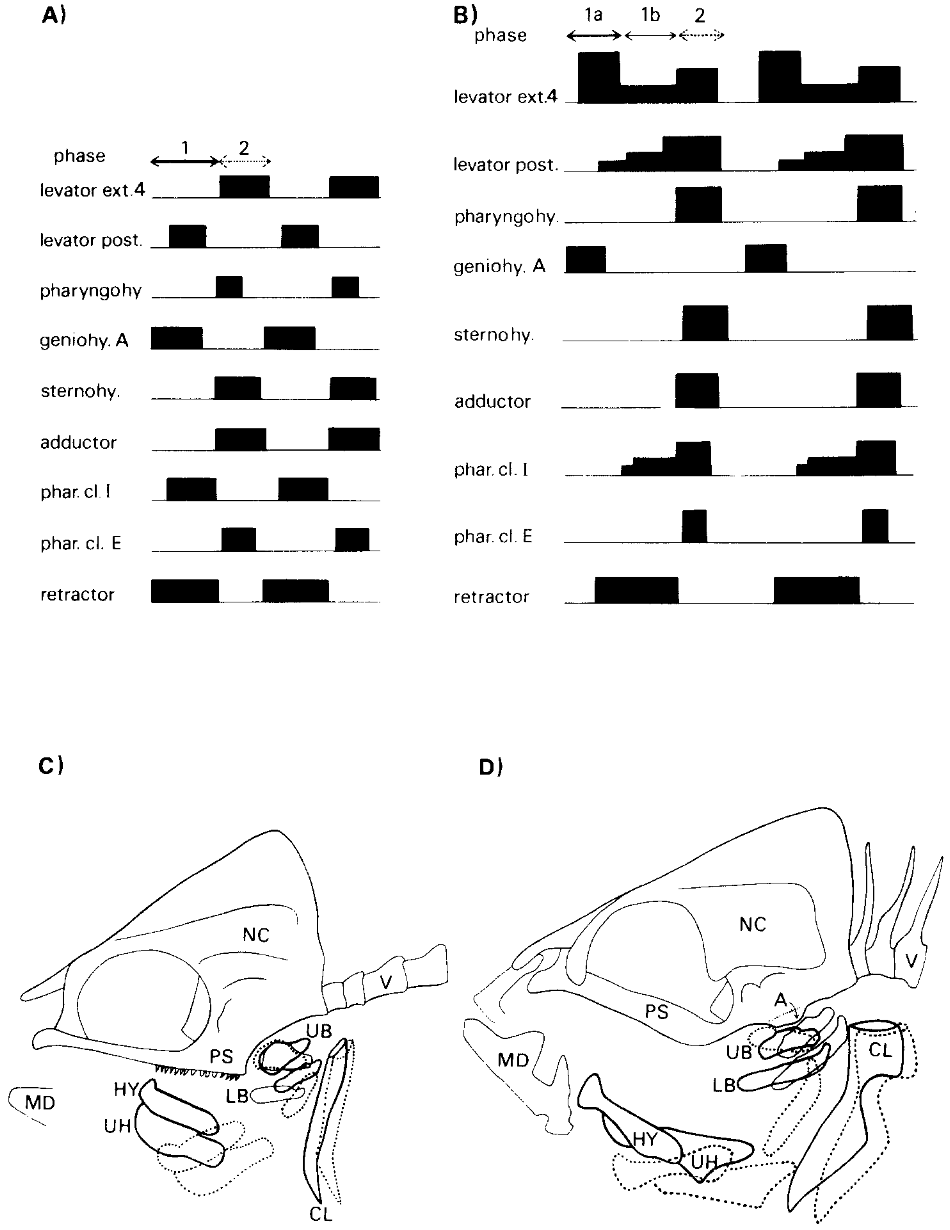

Fig. 3. (a) Active periods of branchial and hyoid musculature of unanaesthetized and unrestrained *Pristolepis fasciatus*, feeding on live crickets. (b) Similarly for *Haplochromis burtoni* feeding on *Gammarus* sp. (c). Movements of pharyngeal jaws as revealed by sequence of successive X-ray pictures in *Pristolepis fasciatus*. (d) Similarly for *Haplochromis burtoni*. Bold lines: phase 1, broken lines: phase 2. A, apophysis; H, hyoid; MD, mandible, other abbreviations in fig. 1. From Liem (1973).

opportunism can be discerned. The adaptation to the generalized cichlid comprises two major structural changes: the formation of a joint between the upper jaw and the skull base, and the shifting of the levator externus muscle from the upper to the lower jaw. The series consists of *Pristolepis* and partly *Badis* and *Cichla ocellaris* and *Haplochromis burtoni*. A characteristic of the former two species is the existence of an articulation disc between the upper jaw and the skull and also that the levator posterior changes its course. Liem supposes that the fusion of the lower jaw halves is not typical for this transition; it occurred frequently in the cyprinoid and percoid groups.

After this key-innovation, the cichlids were able to develop a broad spectrum of adaptations. Liem concludes from material of various *Haplochromis* species, not specifically mentioned, that in detail many structures show a certain degree of individuality of freedom. This makes the sudden change or the opportunism possible. The evolutionary patterns exhibited by the pharyngeal jaw apparatus illustrate most convincingly the ever-ready opportunism of evolution.

Considering such details in the structures separately, he calls their changes 'evolutionary strategies', implying that various groups of structures have different potentialities to find solutions to various environmental problems. Some of these 'strategies' involve the dentition, the course of the muscles, the size of the jaw and the shape of the joints.

It is suggested that the fundamental processes in evolution, described by the concepts of natural selection and adaptive radiation, can explain the structures in fish.

II.2. The evaluation of Liem's study

Liem's study is a good example of how we can obtain an insight into adaptation, into phylogenesis and into evolution by means of functional morphology.

There are also many questions and gaps in the information affecting our insight into the relationship between evolutionary biology and functional morphology. It is both necessary and opportune to ask whether this is due to the methodology or that we simply have to collect more information: sufficient reason to begin an analysis of the procedures with the above-mentioned knowledge.

What kind of study is Liem's? Did he aim at presenting a functional morphological investigation or an evolutionary study? The answer depends on what kind of questions he asked and how he selected the material. The way the study is presented gives the impression that Liem was not searching to find the proof of the validity of the concept key-innovation, but rather that he asked the question about the evolution of the Cichlidae. Being familiar with this group he assumed that the pharyngeal jaws were typical for the group.[2] Thus, the goal of the investigation was evolution-biological and not functional-morphological, although functional-morphological research procedures were used, and morphological features were used as objects for research, instead of phenomena or concepts of evolution. Yet, the study does not aim at answering such a functional-morphological problem as to how to explain the structure or the shape of the pharyngeal jaw apparatus from the function, or the kind of adaptation. In the course of the discussion, however, the goal seems to shift somewhat such that morphological features are explained by means of the theory of evolution, making the study a functional-morphological study with an evolutionary explanation. Thus, Liem's study seems to be a complicated mixture in which functional morphology and evolutionary biology are closely interwoven.

Such mixtures and changes of research aims, changes of theories, methods and sometimes phenomena to be explained occur frequently in the literature. They have great dangers of logic, because the author has to change the concepts and terms along with it, a rule which generally is violated. And, even worse, there is constantly the danger of circular reasoning behind it.

The choice of the pharyngeal jaws is a very good one, a choice that can only be made by someone who knows his material. Of course, this does not preclude the possibility that other structures are as important for an understanding of the evolution of the species and the group. In fact, recent research has shown that similar adaptations can be found in other parts of the cichlid body (Barel *et al.*, 1976, 1977; Hoogerhoud and Barel, 1978). The next step in the procedure is the choice of the species which are considered representative. Liem considers *Pristolepis* and *Haplochromis* to be representatives for percoids and cichlids. Actually, a comparative investigation is required to justify this choice. We must trust that the author has such a broad knowledge of the groups that he can make this choice without further argument: a procedure that is not uncommon. However, we must be aware that another choice may lead to other conclusions. Many disputes about interpretations are actually due to differences in choice of material.

In the case of Liem's choice, it is quite conceivable that the evolutionary series must not be read beginning with *Pristolepis*, but that *Pristolepis* is one of the many derived species among the Percoids. In fact the presence of an articulation disc is reason to doubt the primitive status.

Although Liem stresses the point that the apparatus has to be regarded as a totality, for the decision on the afore-said problem the analysis should be extended to more species and into more details of the structure. Unfortunately Liem does not give exact courses of muscles, no ligaments and no

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[2] Pharyngeal jaws occur in various fish families. The Cichlidae are in fact characterized by a combination of features amongst which are the pharyngeal jaws.

precise information about the shape of the jaws and their articulation. The interpretation of the movement and particularly the change from *Pristolepis* to *Badis* to *Haplochromis* remains therefore open to discussion. Also the myographic and movement analysis by lateral radiographs, although well carried out, need to be extended for the same reason.

According to Liem, in *Pristolepis* the movement and muscle output indicate transportation of the food only, whereas *Pristolepis* also has teeth on the skull base and the hyoid in contrast to *Haplochromis*. It therefore seems likely that *Pristolepis* cannot be considered a morphological forerunner of *Haplochromis*, neither in the phylogenetic nor methodological sense. It seems to have a completely different way of feeding. The biological meaning is still partly guesswork so long as we do not know exactly the natural kind of food and the ecological conditions. Now supposing the guess is not too bad, then it means that we know the kind of adaptation, but that we have to extend the analysis to other parts in order to find the morphological extension of the adaptation. Such a procedure and this kind of conclusion would be sufficient within the frame of functional morphological thinking. The structures are explained by their functions from the theory of kinematics and dynamics and the difference between the species are understood with the same theory. For this explanation evolutionary aspects are not needed yet.

However, Liem apparently has another aim. He attempts to explain the structure and its changes with the theory of evolution rather than to understand it logically with the theory of mechanics. This aim necessitates arranging the species in a phylogenetic order and showing the factors which caused the change. The series consists only of the two mentioned species with some additional information about two others. Many questions then arise: Is *Pristolepis* or *Cichla* indeed the primitive species? Is the change saltatorial or continuous? Is the indicated direction of evolution correct? Obviously, to answer these questions a broader comparison and a longer series is required.

After the comparison in a series of selected and abstracted structures (generalized!) related to their observed activity and suggested function the general conclusion amounts to the concept: key-innovation. The key-innovation consists of two steps: the origin of the pharyngeal jaws and the articulation of these jaws with the base of the skull.

The first step is difficult to prove, although everybody would agree that pharyngeal jaws are new and give the opportunity of a completely new function, thus constituting a key-innovation in terms of an apparatus not used for such functions before. Certainly it is true that these jaws can be used in feeding in a specific way. This truism, however, does not exclude the possibility that other systems could achieve the same end by other means, e.g. the buccal jaws (Barel *et al*., 1977, 1978). It would be a true innovation if certain food sources could not be obtained in another way. Or in other words, the advantage of the pharyngeal jaws can be seen, although difficult with respect to the common jaws, but a proof of the advantage over the common jaws can hardly be given. In this respect any structure which opens new ways of life is therefore an innovation, and thus, every structure is an innovation (cf. Mayr, 1960).

Such a conclusion, of course, does no justice to Liem's idea. Liem's concept implies more, viz. there is no other structure which can do the same and, most important, the structure has an enormous potential to develop easily into a large number of (closely related) adaptations (the difference between the concepts innovation and key-innovation).

As we have seen, the former implication is hard to prove. It seems that the common jaws can do the same. The fact that hardly any examples are available is probably due to our familiarity with the variety of structures of the common jaws and the specific ecological conditions in the tropical lakes. However, something completely different can be important. As Liem rightly remarks, with the presence of pharyngeal jaws the common jaws can be used for other functions, although the buccal jaws show a similar adaptive radiation. The mouth cavity and the surrounding elements can be adapted for an important part to, for example, mouth breeding. The relation between the functional components of respiration, feeding and mouth breeding is scarcely analysed; it promises to be a most interesting field of research.

The second implication of the key-innovation is clearly indicated by Liem and is well born out by pointing to the almost unlimited number of trophic types in cichlids. This goes along with differences in dentition, courses of muscles and structures of the jaws (*evolutionary strategies*). It becomes an interesting question as to whether we are dealing here in essence with *one* evolutionary strategy or with individual, free morphological changes of the parts.

In summary: the cichlid type of the pharyngeal jaws is derived from the percoid type, being, in fact, a specialization because a cichlid is a percoid. The origin of the pharyngeal jaws is open to investigation. The series, consisting of two types, is read in one direction which means an explanation of the second type from the first. The direction of the transformation is logical but hardly evolutionary, unless the taxonomic groups can be placed at the same level in this time order. The former is not supported by taxonomic arguments; the latter is very unlikely. Yet we follow the next step in the procedure, viz. to ask the question of the cause of the transformation. Liem accepts the neo-Darwinian theory of evolution. The research is not meant to challenge this theory, but rather to add new concepts. He accepts that random variation has occurred, containing the origin of the pharyngeal jaws and the articulation with the skull. This variation was subject to natural selection resulting in a 'better' adaptation and in adaptive radiation. In the investigation there is no observation or indirect indication that variation and natural selection indeed occurred. It is typical that the theory of evolution is taken as the most likely explanation without a proof of the 'better' adaptation. Here lies a large, open field for ecologic-morphological investigations. We can now conclude that the study is in fact a morphological investigation, because certain morphological features are questioned and explained, although a new concept was introduced which belongs to the theory of evolution.

The explained structures are called adaptive, the non-explained given structures preadaptive. Neither for the entire study nor for the theory has the latter concept much meaning, because it belongs still to the unexplained and unplaced concepts.

The analysis of this interesting study shows the rather complicated relationship between functional morphology and evolutionary biology. In order to obtain some grip on the relationship we can list the following steps which serve as a guideline for further exploration.

1. Typlogy of structures and functions.
2. Comparison and connection of structures and functions into functional components.
3. Transformation of functional components and the forming of series.
4. Analysis of the degree of adaptations, fitness.
5. Causal evolutionary explanation of the transformations and the freshly obtained new adaptations.

There are many intermediate steps or steps which only partly give an answer, e.g. comparison of structures only.

III. THE MAIN APPROACH

An analysis of the relationship between functional morphology and evolutionary biology involves an investigation into the relationship of the formal descriptions of the disciplines, or can be an investigation into the relation between the essential concepts in the discipline. The former approach would lead us into the philosophy of science and confront us with problems of classification and delimitation of disciplines. In a structuralistic synthesis we should try to replace the structures of both disciplines by one synthetic one, in which procedure the concepts have a very specific relation to each other. A requirement for such a procedure is that the structures of both disciplines are comparable and that the concepts can be described in a similarly ordered and structured way. This approach is hardly possible immediately. It presupposes an already well-established known structure of each discipline, which, as we shall see, is very difficult to obtain. Secondly, for the benefit of the practice of biology the following alternative approach promises to be more fruitful.

Each discipline contains a set of indispensable concepts. These concepts are used to describe phenomena, their analysis and synthesis, and to formulate the conclusions and the theory. To understand the relationship between disciplines, each of the concepts of one discipline can now be related to each of the concepts in the other. In this way, we not only obtain a connection of both disciplines, but we also get an insight into the eventual change and difference in meaning when similar terms in both disciplines are used. It provides also a means to estimate the mutual 'value' or significance of the terms so that indirectly the meaning for or the contribution of one discipline to the other can be shown. Moreover, such a procedure gives us, at least in part, a synthetic explanation, because each relationship can be written in the general formula of an explanation: $y = f(x)$ (Hempel and Oppenheim, 1953; Dullemeijer, 1974; Dullemeijer and Barel, 1976). Here, x is the variable to be explained, y the known variable and f the theory describing the relationship, or in other words, the factor providing the explanation. We can now take the concepts of either discipline and give them the position of y and the concepts of the other discipline the position of x. The problem is then to find f. Or in other words, x is the concept of one discipline, f a known theory, and the problem is to find the proper concept y of the other discipline. There are more alternatives; the choice for one of them will depend on the interest of the investigator or the discipline he wants to explain.

As the number of relations and alternatives increases exponentially with the number of concepts, it seems appropriate to start with a minimum for each discipline, thus clustering the concepts as much as possible. We shall call these the main concepts of the discipline and take the concepts which we found in Liem's study, generally found in studies dealing with functional morphology (Dullemeijer, 1974) and evolutionary biology (Maynard Smith, 1958; Simpson, 1949, 1961; Mayr, 1963, 1969) (fig. 4).

The main concepts in functional morphology are:

1. Form, which includes any form feature at any level of organization of animals.
2. Function, here primarily and preliminarily taken as activities at any level performed or shown by animals. Biological role will be discussed at various places, however, mainly with this concept.
3. Functional component, the connection of form and function. Concepts as compromise and integration will be discussed in connection with this concept.
4. Pattern, comprising the concepts construction, dominance, plasticity and hierarchy.

For definitions of the concepts and descriptions of related concepts I refer to Dullemeijer (1974) and Dullemeijer and Barel (1976).

Main concepts in evolutionary biology are:

1. Series or sequences, including concepts as morphocline and chronocline.
2. Phylogeny, including cladogram.
3. Adaptation as the state of being adapted, as well as the process of adapt-

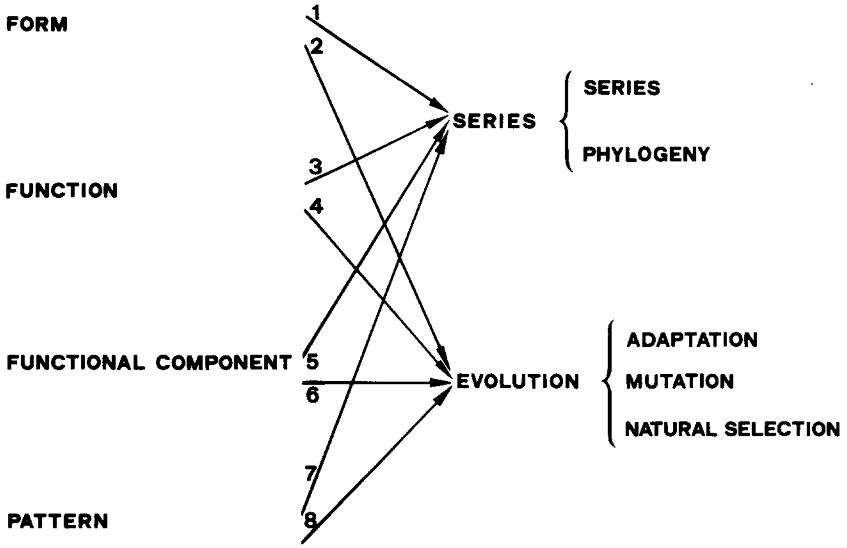

Fig. 4. Relationships between concepts in functional morphology and evolutionary biology. The numbers refer to the various paragraphs in section IV.

ing. In this connection the concepts adaptive radiation, preadaptation and key-innovation will be discussed.

4. Evolution, in a limited sense, as any change of taxa over historical time (actually phenotypic). In this connection the term evolutionary strategy will be considered. The latter concept is presented by Liem (1973) as a main concept, but it seems to be more the description of a phenomenon rather than an indispensable concept in evolutionary biology.
5. Mutation as any spontaneous or undirected change, including variation and variability (mainly genotypic).
6. Natural selection, in which we include external and internal selection and canalization.

For definitions of the concepts and description of related concepts Mayr (1963), Simpson (1961), Bock (1976) and Hennig (1966) are referred to.

It must be realized that this linear grouping does not do justice to the correct mutual positions of the concepts in the theories. These six sets of concepts in evolutionary biology can be combined in two main groups, viz. series of adapted statusses, and the causes or processes of the changes in the series. In the following section we shall analyse the relationship according to fig. 4.

IV. THE METHODOLOGY

IV.1 Forms and series

If the concept structure (x) is related to series (y) (of structures) the relating factor or theory (f) is that of comparative anatomy with two well-known differences in basic philosophy, viz. *idealism* and *realism*. The former is generally thought to be pre-Darwinian, but persists in many investigations in recent times. The latter is generally held to be immediately connected with evolutionary biology. The problems which have to be solved are comparability (homology), ordering (morphoclines) and time direction and time spacing (chronoclines). The structure can be considered without any nexus to function which makes these problems fall outside functional morphology. The reason for still devoting considerable attention to it is because of the tremendous impact the methodology and terminology still have on functional morphology. If, moreover, an adaptive feature is ascribed to the structures, then some functional morphological aspect is introduced. However, in the majority of comparative anatomical literature the adaptations are hardly ever properly analysed and are set aside as quickly as possible.

As formulated above, the series can be read as a changing structure, which is almost a tautology. In practice it leads to the explanation of one structure (x) (in Liem's study the pharyngeal jaws in *Haplochromis*) with the other structure as the known element (in Liem's study the pharyngeal arches in *Pristolepis*) by means of the theory (f). As already mentioned, the theory is not challenged, it is accepted and so is the original structure.

There are of course many extensively elaborated examples. All information in the textbooks of comparative anatomy can be used. It makes no difference whether rather simple structures, complexes of structures or features of structures are taken. Actually, all structures are described by a limited number of features (cf. Froebe, 1973). In Hennig's cladistic approach these features are character states if it concerns the various 'expressions' of the same character or feature. Hecht and Edwards (1976) define a character as a set of homologous features, occurring within two or more taxa. This shows immediately the tautology of the concept character states. For the determination of the character a feature (or features) of a character must be used and to determine whether we are dealing with the same character in another species, population or individual we must use similar features. Although these features can vary quantitatively, and in some respect even qualitatively, it does not exclude the preconception of the knowledge of similarity. How we obtain knowledge of similarity ought to be the problem. We shall return to this *inductive tautology* later on.

The determination of similarity, which we shall equate with the determination of homology, has exactly the character of typology as it was profoundly exposed and analysed in comparative anatomy by such authors as Goethe, Owen and Geoffrey St. Hilaire (see Lubosch, 1931).

In 1973 Froebe again consistently and clearly described the procedure in typology. For the application the reader is referred to Remane (1956). After determining the similarity, or rather, the degree of similarity, of characters, character states and character complexes, the sequence must be established. Convergencies and parallelisms cannot be discovered in advance. The sequence can be read in any direction, and any branching pattern can be postulated. Most authors apply the principles of the continuity and of the most likelihood. Only when other information is added, such as other characters, fossil evidence or genetic change, is there a possibility to reduce the number of branching patterns and the directions. Parsimonious criteria do not help, as will be shown further on. The only rather safe statement which can be made is that organisms with homologous structures were somewhere derived from a common ancestor. Some authors therefore define homology as including common ancestry. This is a very unfortunate combining of a concept with analytic methodological significance and a concept describing the conclusions. It leads to circular reasoning such that the term homology becomes an empty concept and can only be saved by adding qualifiers (Bock, 1973). The logical fallacy lies thus in the combining of the logical positions. Sometimes it is used as a method, sometimes as a description or conclusion in idealistic morphology and sometimes as a previously defined concept in evolutionary biology. In practice it means that on the one hand homology cannot be established before the ancestry is known, but that for the determination of the ancestry, homology criteria must be used. Restricting the term homology to comparability or similarity avoids the use of qualifiers (Bock, 1973; Peters, 1973) and the use of the term homoplasy (Simpson, 1961; Hecht and Edwards, 1976) but necessitates a reinterpretation of homology in terms of groups compared and for establishing phylogenetic relationships. Various authors have already stressed the logical derivation that homology as such cannot be used for describing the phylogeny immediately without additional arguments (Gutmann and Peters, 1973; Franzen *et al.*, 1976).

IV.1.a. An example. As an example showing the procedures in forming series of structures, the explanation of structure and the application of the theory connecting structure and series, I shall analyse a study by Patterson (1976). I shall proceed by discussing the methodologies put forward by Hecht and Edwards (1976), include an example of a study on the molecular level (Romero-Herrera *et al.*, 1978) and statements by Szalay (1976), and successively confront these with the formation of series in functional morphology (Gutmann, 1976; Bock, 1976). Such considerations can lead us to our following goal: the relation between the concept of functional components and concepts in evolutionary biology.

Although Patterson's study aims at showing the significance of palaeontology for the study of phylogeny, and connected with it, the change in opinion on the role of palaeontology under the influence of the theory of evolution, this clever and subtle analysis shows clearly the procedure in constructing series from structural data. Patterson's study concerns the classification of fishes in higher taxa. He makes his point by a historical analysis of the procedures in the construction of phylogenies and by giving a new analysis of teleost classification.

The classification of Agassiz is the first which is pictured in a time-order diagram (fig. 5). In this figure the number of fossils is indicated by the thickness of the lines. The classification is based on information about the structure of the scutes. Agassiz's classification contains neontological as well as palaeontological material and it is non-evolutionary. It is designed according to the principles of *idealistic comparative anatomy*. Nowhere in his diagram is there a connection between the groups, except for classification in groups. The slight convergence in the lines is an indication of greater similarity rather than phylogenetic connection. Yet Patterson writes that Agassiz's concept of relationship is such that the word 'classification' in his works can usually be replaced by phylogeny without altering the sense. This could never have been the opinion of Agassiz (Mayr, 1969; Ghiselin, 1969; Reed, 1978) and if a modern evolutionary biologist had this opinion, he would make a very inconsiderate philosophical and biological remark. Agassiz's system is consistent and correct within the framework of comparative anatomy given the choice of the structural characters. Transposed to the scheme of phylogeny there arises justified doubt about his system. In fact, Patterson proves this by pointing to various other classifications based on other characters and to the problems various authors met in their striving to a real phylogeny, viz. the problems of weighing of characters and of the proof of recency of relationships. Thus Müller used internal organs and soft tissue parts of extant fishes and Haeckel introduced the character states of the vertebral column and caudal skeleton of fossils as well as recent forms. It is almost a truism that many species and higher taxa had to be classified at variance.

It is obvious that a *realistic* interpretation can only be approached if as many characters as possible are applied. This was done by Woodward although the weighing of the characters was unclear. It remains a decision by the individual investigator (in the literary sense, subjective) and the classification cannot be tested due to the *inductive* way it is obtained. Woodward's schemes, presented and improved by Boulenger, have been followed for a long period and can still be found in Romer's books (fig. 6). In 1907 Gregory expounded very clearly on which a classification should rest 'in principium'. His paper includes an important exposition of the principles of classification. According to Patterson: 'blood relationship' (i.e. recency of common ancestry, which Gregory equates with genetic relationship) is distinguished from 'homological resemblance' (i.e. phenetic similarity) and Gregory wrote 'in

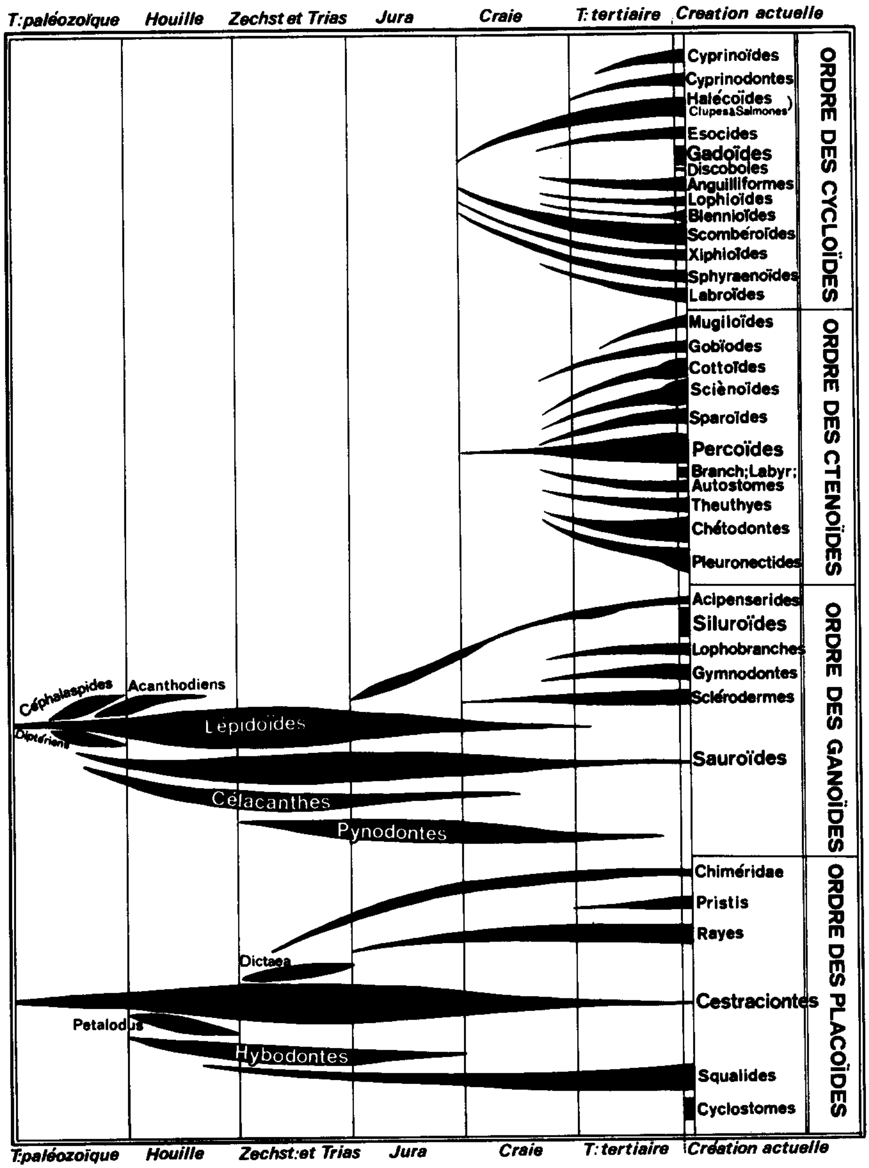

Fig. 5. Agassiz's classification of teleosts. From Patterson (1976).

order to make classification correspond even roughly to degrees of blood relationship, i.e. to phylogeny, we must assign varying systematic values to different characters in proportion to their inferred relative phylogenetic age!' Thus Gregory makes a clear procedural step from the idealistic system to the realistic phylogeny, in which the weighing of characters is indispensable. The inquiry into the ordering centres then on the weighing of characters

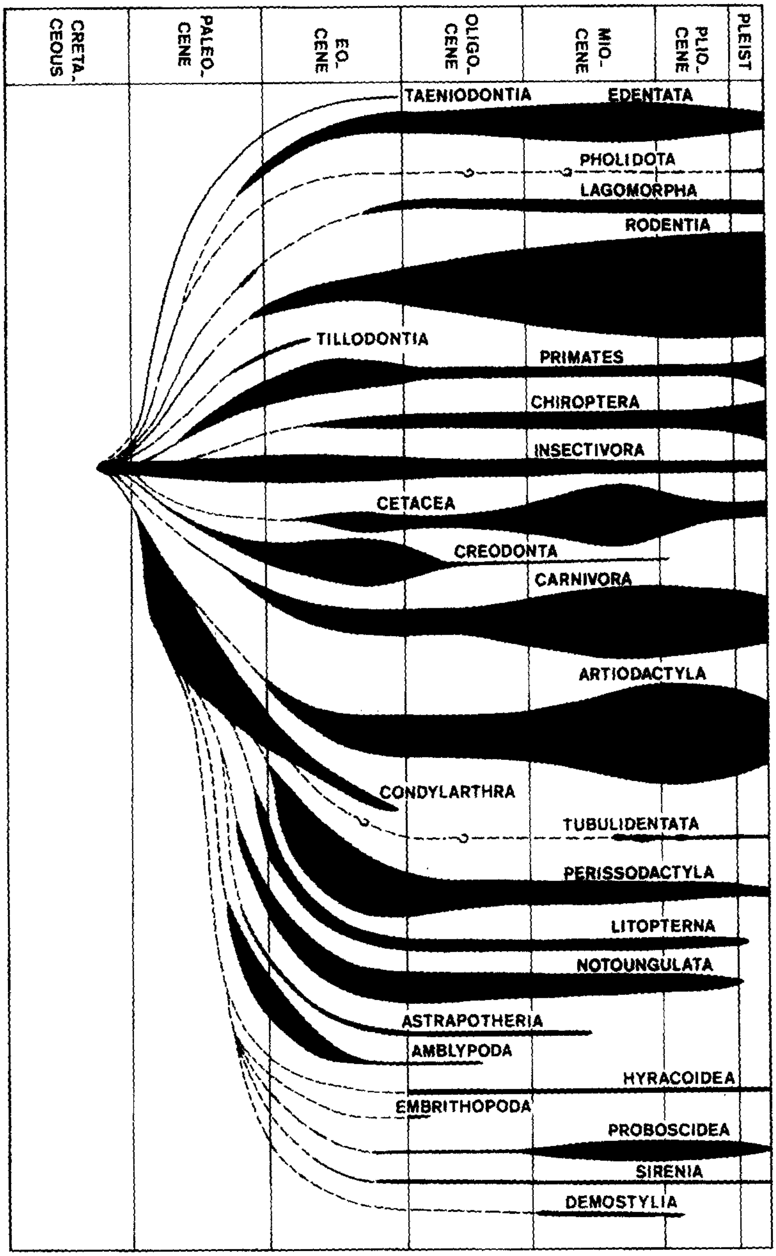

Fig. 6. Romer's phylogenetic classification of mammals. From Patterson (1976).

and the evaluation of the weighing for different phylogenetic systems and of the actual historical palaeontological data (Regan, 1923; Gardner, 1960). The discussion by Patterson continues in a direction, viz. which taxa have originated poly- or monophyletic, which is too specialized for our analysis. The recent important change in the system is that of Greenwood *et al.* (1966). They distinguish by means of many characters, which are weighed subjectively, four main groups, originated from the Pholidophoridae (fig. 7): the Clupeomorpha, the Elopomorpha, the Osteoglossomorpha and the Protacanthopterygii. The latter group gives rise to the Paracanthopterygii, the Atherinomorpha, the Acanthopterygii and the Ostariophysii.

According to Patterson the first group is well established and defined, but the others are described and delimited less distinctly. I doubt this; the Clupeomorph group is smaller and can be described probably in fewer characteristics than the others. More important, Patterson writes, that Greenwood

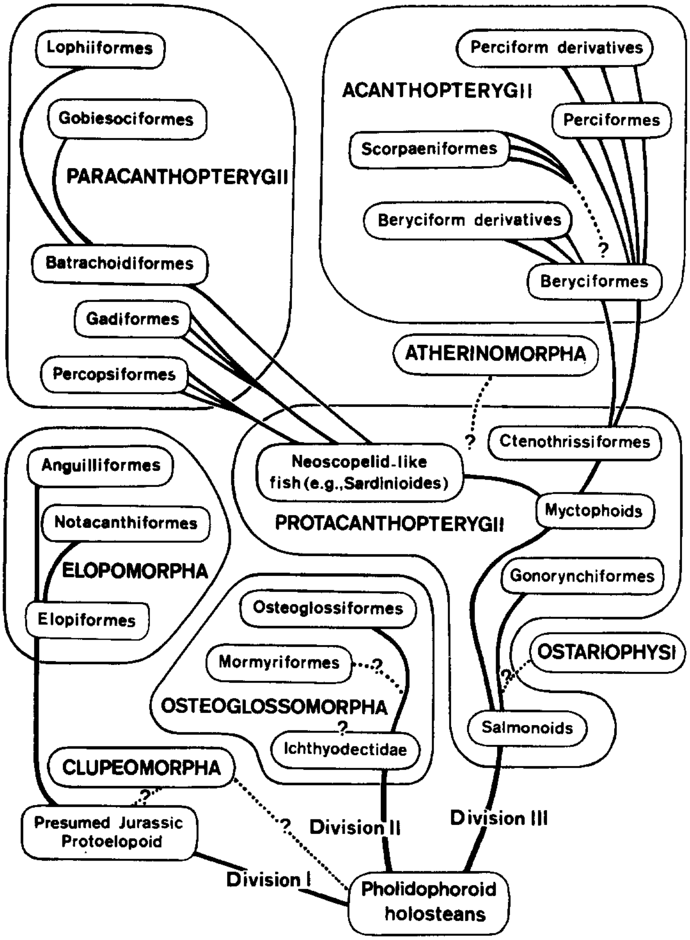

Fig. 7. Evolutionary relationships of the principal groups of teleostean fishes after Greenwood *et al.* (1966). From Patterson (1976).

et al. 'pointing out that none of the specializations of recent clupeomorphs had been demonstrated in the supposed ancestral forms' means, that 'their criticism was based on parsimony'. This is a peculiar conclusion, which may be true, but cannot be exclusively derived from this quotation. First, parsimony did not necessarily play a part. Secondly, it is quite possible that 'demonstrated' means 'present rudimentarily' or 'present potentially'. Thirdly, this statement does not apply to the *recognition* of other clupeomorph fossils, but is related to the better diagnosis Greenwood *et al.* could make of the clupeomorphs. Of course, by the more adequately described, larger number of fossil clupeomorphs the derivation could be improved. However, what appears more important to me is that Greenwood *et al.* called their classification real phylogenetic, an evolutionary relationship. The basis is not only the great similarity (which would be as such insufficient) but the possibility to derive the groups biotechnically and to establish the chronology (chronocline) by means of occurrence of an excellent series in the fossil record. For the most part they had to make intelligent guesswork, however, based on biological probability.

The guesswork was supported by Hennig's system, which was welcomed enthusiastically by many evolutionary biologists. It seemed that most of the problems could be solved, particularly the ordering and the direction of the evolution.

Patterson writes: 'Hennig's major contributions are, in my view, an unambiguous definition of relationship, in terms of recency of common ancestry, an unambiguous method of recognizing relationship by means of synapomorphies, and an unambiguous method of expressing such relationship diagrammatically in dichotomous cladograms'! These statements are certainly correct, but whether they are true is very doubtful. And they are false in terms of evolutionary theory, as will be shown further on. In the final part of his article Patterson presents his analysis of teleost classification (fig. 8). In this diagram thick lines represent the extant large taxonomic taxa, the thin lines a variety of lower fossil ones. The lines are drawn parallel and the taxa are placed at the same level, according to Hennigean rules. The numbers represent characters or character states of apomorphies. Extant forms are indicated with an upward arrow.

IV.1.b. Evaluation of the procedure. How did Patterson obtain this diagram? He separated the *Halecomorphi* (*Amia*) from the teleosts by states of 52 characters, considering *Amia* as original and the other teleosts as advanced. Although we all would agree with the statement that *Amia* is more primitive, the logical argument is still valid that the order can be reversed. All 52 characters mentioned by Patterson can be read in reverse. The evidence is not better than the old idealistic comparative anatomical. Patterson denies data from palaeontology giving time order on the argument that ancestral species

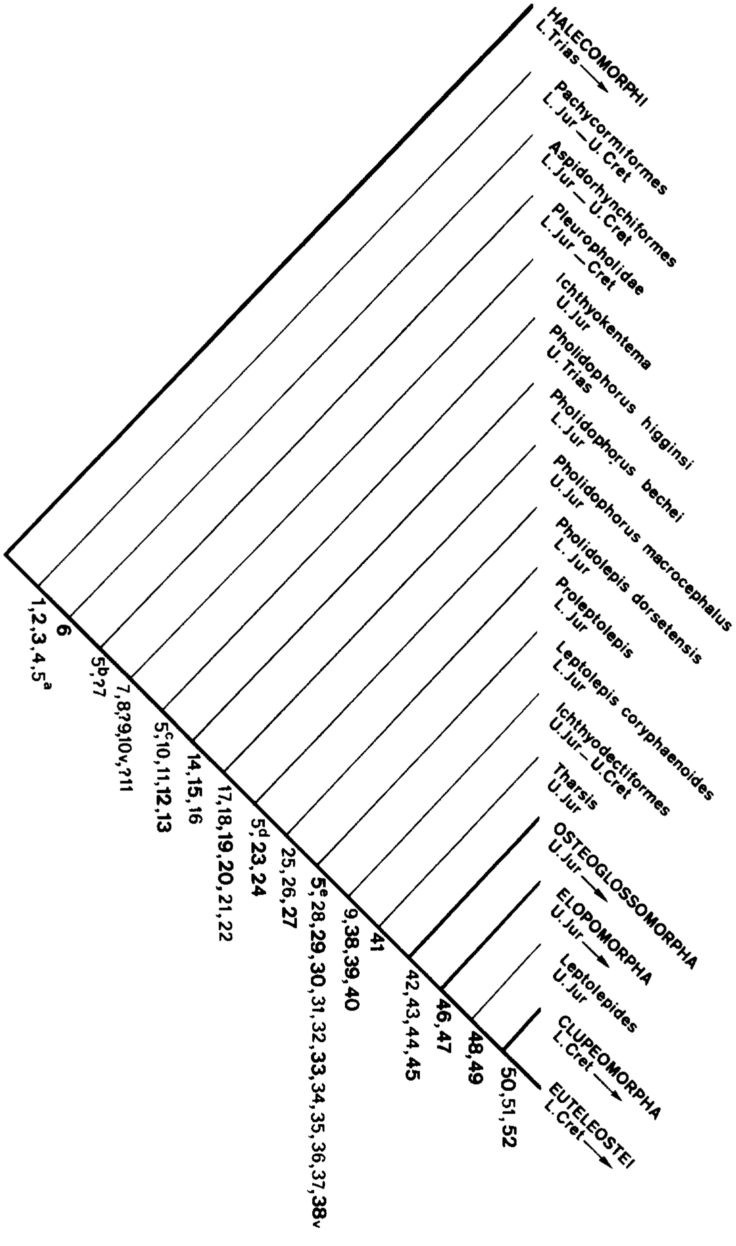

Fig. 8. Patterson's classification of teleostean fishes according to Hennigean principles. From Patterson (1976).

occur simultaneously with derived ones. However, the argument of the evolutionary biologist is that the first appearance of these species goes back much farther and that this appearance is what makes them 'ancestral'. Moreover there are plenty of examples in which stratigraphically ordered species are found.

The second step in the procedure is more questionable, viz. the order of the characters. Patterson applies parsimony here, which probably points to the number of dichotomies. However, parsimony would also be present when the dichotomies are larger, but show less splittings on the base line. There is no way to decide this point. If Patterson wants to present this as a real evolution he must conclude that evolution occurs parsimoniously. Unless parsimony is equivalent to efficiency, constraint or survival chance, such a concept is very unlikely.

Patterson writes: 'When phylogenies are viewed as schemes of relationship in which the distribution of synapomorphies is explained parsimoniously, their empirical basis is clearly and concisely shown, so that they are open to criticism. Traditional phylogenies, expressed as ancestor-descendent sequences which include some hypothetical ancestors and some named ancestral groups or species, are not open to criticism in the same way. . . . They are therefore not subject to the parsimony criterion, the only test of a phylogeny that is available to us.' Indeed the possible criticism is different for both systems but this does not mean that therefore one is better than the other. They are so different that one is an arrangement of chosen and preconceivedly ordered characters and the other an arrangement of biologically-genetically hypothesized connections. If we suppose now that Patterson is correct in his view, what then can be this test? Suppose we find an unknown fossil or recent form with the mentioned characters in a specific state. Would such a form probably disprove the diagram? No, because it can always be inserted somewhere without disproving the model, since Hennigean cladograms are presentations of an *inductive system*.

The only real criticism is to suggest a most likely scheme of relationship (see the cichlid fish investigations of Greenwood) from completely different information e.g. geographical or likely geological occurrences. But this proves that cladograms are *idealistic* and belong to the pre-evolutionary theory. The new information has to include information about direction and time of the sequence before it can disprove or assert the cladogram. The conclusion must be that the cladogram is a good tool as a preliminary simple arrangement to which new findings can be added easily, but which does not represent in any way the real course of evolution, so cannot be called a phylogeny.

Apart from the mildly presented axiomatic critique by Løvtrup (1976) it is easy to prove methodologically that the theoretical contributions of Hennig are dubious and full of tautologies in an inductive system (cf. Gutmann and Peters, 1973; Bock, 1976). Such a pertinent disapproval needs of course further argument, which I shall present in the following discussion.

Let us therefore first follow Hecht and Edwards's (1976) exposition on the methods to be applied. According to these authors, 'the goal of phylogenetic inference is to produce a scheme or construct which depicts the genealogical relationships of the taxa under consideration'. They consider only intrinsic data as relevant and from this group only the shared derived character state (the synapomorphy of the cladist). Shared primitive character states (= samplesiomorphies) cannot be used to indicate monophyletic groups (Hennig, 1966) or lineages.

The first problem Hecht and Edwards bring to our attention is the definition of a character. At the start of the analysis of any unknown group the choice of the character and its delimitation are the choice of the investigator. By going back and forth over his material he obtains a feeling of the importance of the various possibilities, but he has no way of ascertaining this except for the consensus of his colleagues. Because of its inductive character this procedure cannot meet the test of a critical logic. This is not the fault of the investigator, but rather it is due to the necessary steps in the procedure (cf. Froebe, 1973). It implies, however, that agreement can only be obtained on the basis of a common feeling about the material (he has to know his material) and that somebody else could arrange it differently. When new data become available then the arrangement will also change. This is what happened in Patterson's story. By using different characters, adding new information and evaluating the importance of the characters over the years, systematicists arrived at different classifications. And the more information is *added* the more likely a common opinion will be reached. What holds for a 'separate' character, holds in the same way for character complexes and for character states.

The next question concerns the apomorphy or plesiomorphy of the character state. Hecht and Edwards rightly remark that there must be at least three groups, an ancestor and two sistergroups, to start with before anything can be decided about this matter. However, the definition of apomorphy relies on this distinction (Løvtrup, 1976) and the distinction is made on the apomorphy (Hennig, 1966; Patterson, 1976). A more disastrous circular reasoning cannot be thought of. Here again the prepresent subjective knowledge of the investigator plays a dominant part. It makes this kind of procedure tolerable and artistic, but not science. Art can be highly appreciated, in biology also, and in a way it is the beginning of all science. However, to become science it must not be presented as science but rules of correspondence from this art to science should be formulated. These rules are completely lacking in Hennig's system.

From this point on, the procedures become more scientific. The next step is to connect those taxa which have a very close recency in relationship. Therefore there must be something specialized in common, the synapomorphy. By definition now all other connections by common features are excluded. However, at the start these groups were already placed together on the basis of common features. The cladist seems to work already in a framework of large group relationships in which this problem is embedded. This is denying an important source of information, a feature which will be discussed later on.

The determination of the recency is a problem in itself which is not clearly stated in Hennig's theory, because a similar tautology occurs. With extant forms it again becomes an evaluation on artistic, and at best on common-sense, probabilities. True, certain groups are difficult to *think* to be ancestors, but the final proof is lacking. This becomes clearly apparent when we list the criteria for the determination of the primitive state by Kluge and Farris (1969).

1) The primitive state of a character for a particular group is likely to be present in many of the representatives of closely related groups.
2) A primitive state is more likely to be widespread within a group than in any one advanced state.
3) The primitive state is likely to be associated with states of other characters known from other evidence to be primitive.

It needs no further discussion to see that these so-called criteria are mainly tautological as Rieppel (1978) also has shown when confronted with the definition of apomorphy, and that they are largely redundant. They do not provide any criterion for distinguishing the primitive state except for what the investigator calls already primitive. This again does not need to be disastrous or unacceptable so long as the diagram is not intended to be a presentation of the real evolution. The system shows here again its subjective idealistic character. Hecht and Edwards came via a less compelling discussion to the same conclusion and in their practical example they followed their own method (Hecht, 1976). Hecht and Edwards point to another difficulty: the recognition of parallelism. The demand of the system for dichotomous splitting and the monophyly in the morphocline must lead to many parallelisms, almost proportional to the number of subgroups. It is not my intention to discuss parallelism any further. The reader is referred to Hecht and Edwards (1976).

The placing of the groups in dichotomies follows the principle of parsimony. Hecht and Edwards rightly stress the point that here is a logical procedure but that the real evolution need not be parsimonious. Parsimony in empirical sciences is known as Occam's razor and is applied in case many possibilities cannot be distinguished on other grounds, or that no more concepts or factors should be introduced than are absolutely necessary. It means 'try to keep your logics as simple as possible'. Occam's razor has frequently been challenged on logical grounds. And nobody ever believed that nature behaves (or evolution occurs) parsimoniously in changing the taxa. At best it behaves economically or efficiently, which is something completely different.

The result of the application of the parsimonious criterion is always preliminary; any additional information can change the results. Also, the necessity of the application of a specific type of parsimony should be tested in relation to the system involved. For this testing we need a criterion, or a logical derivation. Two questions concern us with respect to the parsimonious criterion for the construction of phylogeny. First, what kind of parsimony can be applied and second, what is the status of the concept, is it indeed only a logical tool or does it describe the empirical phenomena adequately?

Before going further I shall first make some short remarks about an elegant study on the molecular level. Romero-Herrera *et al.* (1978) studied the evolution of myoglobin in representatives of the major mammalian orders. They analvsed the amino acid sequences in the myoglobin. On the basis of differences in kind, and position, in the sequence of the 153 amino acids, they constructed cladograms according to Hennig's principles. The smallest change is the difference of one acid and with this knowledge it is possible to apply parsimony and construct dichotomous cladograms. We note that the first procedure is to cluster those organisms which have the most amino acids in common on the same location.

The authors then had to introduce a number of limiting conditions to avoid a result with an almost infinite number of cladograms. 'Thus we constrained the parsimony method within the limits of what we regarded as acceptable on the criteria of comparative anatomy and the fossil record'. And further 'we have drawn on the evidence of comparative anatomy and the fossil record to provide possible dates of divergence between the ancestors of the living species in order to investigate the relationship between the number of fixed mutations and time'.

Notwithstanding these restrictions the authors concluded that many relations are uncertain and that many solutions are imaginable. To get some feeling of the kind of problems they met, we shall mention one small characteristic example. The hominids have a common ancestor; the hominids are characterized by 110 Cys, 140 Lys, 144 Ser and 145 Asn. Man, gorilla and chimpanzee are distinguished by 22 Pro and 116 Gln for *Homo*, 22 Ser and 116 Gln for gorilla and 22 Pro and 116 His for chimpanzee. Each species has one common and one different amino acid with the other two species. We thus have a kind of triangular relationship in which the direction of evolution cannot be determined. Other characters on the same (molecular) level do not differentiate, e.g. the fibrino-peptides A and B are all identical. But they write: 'One might expect that comparison of the adult haemoglobins could help. Man and chimpanzee have identical α- and β-chains (Dayhoff, 1972), and differ from the gorilla by one residue on both chains. This could be interpreted as indicating common ancestry for chimpanzee and man, after the divergence of the gorilla lineage. However, this situation could also have arisen if a common ancestor of chimpanzee and gorilla diverged from the stem leading to man and the haemoglobin mutations became fixed in the gorilla lineage after this common pongid stock split further into the branches leading to the living forms. Thus, the haemoglobin evidence does not refute the hypothesis that the phylogenetic distance is the same from man to either of the two pongids. As is well recognized by comparative anatomists, such problems can only be resolved when the ancestral and derived states have been distinguished.' This remark points to the crucial problematic step in the procedure, viz. how to connect the morphocline to the chronocline.

Analogous situations occur frequently in the other data. They all lead to the same conclusion.

1. Hennig's system only says what idealistic comparative anatomy has done for ages (only the words are different and thus superfluous).
2. The parsimonious criterion can only be used in an idealistic system and even then it does not give a unique and correct answer in most cases.
3. The transformation from comparative anatomy to real evolutionary biology always demands additional information, or in other words, we need independent new information to make the inference from morphocline to chronocline.
4. This transformation necessitates a change in philosophy; there is a paradigmatic change in the sense of Kuhn.

The question remains, how can the ancestral and derived states be distinguished? Here I cite Romero-Herrera *et al.* again. 'The observations indicate that there are a limited number of ways of remaining a functional myoglobin molecule. Functional morphology is paramount, whether we are considering the anatomical or the molecular level. The limitations of mechanics at the anatomical level, and chemical limitations at the molecular level, place constraints on the pattern of evolution.' The thinking can hardly be more philosophically structural and Darwinistic (see also Reed (1958) and Ghiselin, 1969).

The difference between Hennig's system and the cladists on one hand, and the Darwinian evolutionary biologists and the functional morphologists on the other, is clear. Within the idealistic system, which Hennig's system is in principle, there is hardly any alternative other than parsimony in the sense of looking for the simplest branching pattern (which in itself should be defined). As we have seen, Hennig's system does not allow objective weighing of characters, it is axiomatically dichotomous and it is, by definition, focussed on apomorphies. These three conditions do not leave any alternative other than parsimony, if various investigators want to reach identical conclusions. This is nicely demonstrated by Hecht and Edwards (1976) and by Underwood (1976) on a critique on Hecht and Edwards. Their difference of opinion in salamander classification goes back to the difference in weighing. Denying the parsimony would probably lead to an almost infinite number of classifications. The consequence is also that a large number of parallelisms are likely to occur.

The question on the status of the parsimony concept is more difficult. Hecht and Edwards want to give the concept the status of a logical tool only. However, when they describe the classification, the concept almost automatically assumes the status of a real phenomenon, in the sense that evolution follows the most parsimonious way. The correctness of the statement cannot be proved immediately. In fact there are many indications that evolution follows a much more complicated course (see for examples, Simpson, 1961; Mayr, 1963; Bock, 1976). It is clear that in this way we cannot reach a solution to the dilemma of the status of the concept. The reason is that parsimony is an unavoidable part in the Hennigean system and that evolutionary parsimony is inacceptable in the neo-Darwinian theory of evolution. By considering the basic differences between the systems, this reason can put us on the track. The difference is actually very simple. It is the old one between idealism and realism. Hennig is thinking in the tradition of German idealism[3] but as many formal morphologists did before him (Gegenbaur,

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[3] Idealism goes back to Platonic philosophy, implying that all observable phenomena can be traced back to a number of general schemes. These schemes or ideas can be present in a heaven (Plato) or be real in this world (Aristotle) or only existing in our minds (Popper). The ideas can be connected and are thought to be transformable in each other (typological transformation) (Meyer, 1926; Van der Klaauw, 1966). Mathematics is for the greater part an expression of idealism.

Realism, on the other hand, principally tries to equate observation and objects including as much as is practically possible. The change from one object to the other must be assigned to a direct connection; in terms of forms by a direct material connection.

An unfortunate terminological confusion in the use of the terms idealism, essentialism, conceptualism and realism has occurred. As Plato considered the idea as the essence of all phenomena, and aimed at understanding this essence, the concept 'idea' has an ontological status. Practically and methodologically it readily leads to a static interpretation well known in describing forms only and in Linnean classifications.

Popper (1969) and many other English speaking authors call it essentialism (Reed, 1978), which is incorrect. Essentialism is also present in Aristotelian philosophy although the latter is realistic. For Aristotle the ideas were present in the real world. A subsequent position is taken by the 'hard' realists, who deny any other world than the directly touchable and empirically observable. Their position can be called ontological realism. In Aristotelian as well as in the latter realism, static as well as dynamic attitude are possible (in fact Aristotle is inclined to such a dynamic attitude).

Conceptualizing takes place in any scientific approach with any ontological position. Conceptualism is a methodological concept. It is present in Darwinism as in any other biological theory (pace Reed, 1978).

It is tempting to place phenotypes in idealism, and genotypes in realism, but this is not correct. It is merely a question of abstraction. As soon as phenomena are schematized and generalized they tend to become idealistic. In constructing phylogenies, which requires a direct real connection between the members, there is, of course, a greater chance to demonstrate this connection in the genotypes than in the phenotypes.

1870; Remane, 1956) he used incorrectly terms of Darwinian evolution theory, suggesting that the idealistic schemes (cladograms) can be transformed in realistic evolutionary schemes without transformation rules (see also Gutmann and Peters, 1973a, b, c).

Simple idealistic homology, which is what his synapomorphies in essence are, cannot be used to show a phylogenetic relationship without adding information about real blood relationship, genetic connection and time direction and time spacing (cf. Gutmann and Peters, 1973; Dullemeijer, 1976). On these latter aspects the discussion should focus and on these aspects the opponents of the system should meet instead of holding a fixed position (Bock, 1976; Patterson, 1976; Bonde, 1976, etc.). For idealism there is no reason to use a concept like Darwinian evolution. When it is still used it has the original Platonic meaning of a transformation. This sytem was already worked out extensively by Goethe, Geoffrey St. Hilaire, Vicq d'Azyr, Owen and many others. In fact the methods in comparative morphology have been worked out nicely (Nordenskiöld, 1926; Lubosch, 1931). It means that most of the quarrels could have been avoided by a better knowledge of the discussiants of the history of biology.

There is therefore nothing new in the three statements of Hennig which Patterson believes to be essential. These three statements read: an unambiguous definition of relationship, in terms of recency of common ancestry; an unambiguous method of recognizing relationship by means of synapomorphies; and an unambiguous method of expressing such relationships diagrammatically in dichotomous diagrams.

The first definition has been presented by former authors long ago and more unambiguously than Hennig did. They did not confuse relationship (*affinity*) and blood relationship (*consanguinity*) (Lubosch, 1931; Russell, 1916). The method has been discussed. Within comparative anatomy this method has been worked out almost completely. Recently it has become possible to describe the homologies and the degree of difference in more quantitative terms particularly on a molecular level (Fitch *et al.*, 1976). However, the system remains as idealistic as before and the real problem that remains is the bridging to the realistic system.

Concerning the third statement we have seen that it is practically the simplest method. Human thinking operates best in binary systems (see computer work) and any phenomenon can be described in such a binary system. But that does not mean that other systems are worse and it does not mean at all that the biological phenomena behave like that. Thus parsimony can only be given a logical status and as such it is rather trivial.

Considered idealistically Patterson's discussion is a fine and elegant example of consistent reasoning, but we must leave out Darwinian evolution and not include terms like ancestry. Fossil evidence is in fact stripped of its essentials, viz. time recording evidence, and fossils are given the same status as any extant organism.

IV.1.c. Idealism, realism or something else? The crucial question which remains: How do we bridge idealism with realism? Do we have to reduce one system into the other or does one system encompass or engulf the other? Or do we have to replace both systems by a third one? Although this is a matter of later concern some indication can be given already by reproducing here Hecht's weighing system (1976). It contains five categories (see Hecht and Edwards, 1976).

Character and character states of the lowest value are those involving loss of a structure. Character weighing group I has zero information (as to monophyly) because there is no way of determining whether the state has been derived by a single change or by two or more independent processes. Loss characters are here defined as characters which have no developmental information to indicate the pathway by which the loss occurred.

The second category, character weighing group II, has more informational content than the preceding, and includes simplification or reduction of complex characters. These are indicated by comparative or developmental anatomy. Lost characters, such as eyelessness in cave salamanders or fish, in which the developmental mechanism leading to the loss is known, should be included in this category. Independent reduction of the same characters by two closely related taxa may show a different developmental process in some minor detail.

The third category, character weighing group III, includes those character states that are the result of common growth processes for the taxa being compared. These similarities are due to growth and developmental processes dependent on size, age or hormonal and other physiological relationships, such as allometry or neoteny.

The fourth category of weighed characters includes all those states which are part of a highly integrated functional complex. It is not surprising that many characters that are closely integrated should change together in order to maintain biological efficiency or permit the organism to remain viable. Therefore, the separation of such a functional complex into more or less arbitrary components may result in undue weighing. The complexity of characters in this weighing state makes them important indicators of polarity and useful to distinguish parallelism, and their reliability is greater than any of the preceding types.

The fifth and more informative type of weighing group is that which is innovative and unique for the morphoclinal series, and, therefore, most useful as a shared and derived character state to distinguish a new lineage. The more complex the innovative character state, the more reliable an indicator of lineage it is. At the higher hierarchical levels, this character weighing group usually indicates new functional or adaptive trends. If the characters or character states are complex enough, they can preclude parallelism.

This weighing system is already an improvement. Although classical comparative anatomists have used weighing of characters (see Van der Klaauw, 1966) it has never been expressed so clearly before. The weighing provides a means to determine the polarity to a certain degree (compare Hecht and Edwards, 1976, and Underwood, 1976) but does not yet solve the time spacing and direction in the chronocline nor the question of dichotomy or pluritomy.

So much for the criteria by Hecht. I shall return to them later (p. 210), though it is apparent that Hecht considers separate morphological elements as rather insufficient. The functional complex, in our terminology the functional totality composed of functional components, is far more important than the character states of the apomorphies and plesiomorphies. Idealism fades.

Another good example is Szalay's study (1976) on phylogenetic relationships and a classification of the eutherian Mammalia.

After arguing that the postcranial evidence is generally neglected in classification, especially in palaeomammalogy, Szalay focuses on one structure, the astragalocalcaneal complex, including articulation facets and attached ligaments. Of particular interest in our discussions is the methodology presented by the author. He distinguishes five steps in the procedure which I shall cite here.

'1. Observations are made (as an indirect result of a host of unexpressed assumptions and hypotheses) and a particular set of circumstances is stated to be present in two or more taxa. In other words, characters are *recognized* and *delineated*. We can refer to this as data gathering.
2. If these similarities, as originally recognized, can also be recognized by others (i.e. if they are repeatable), then it may be said that we have an empirical data base.
3. The hypothesis may now be advanced that the similarity is either the result of homology and more specifically, that it is the sharing of an ancient (primitive, ancestral) or less ancient (advanced, derived) character, or, if not a homology, that it is convergence. This hypothesis is arrived at when *alternative* character states are compared by an examination of both *ontogenetic* and *adult states*, as well as by *mechanical* analysis of the character. This pivotal phase of analysis requires the use of the biologically most sophisticated methods, techniques and interpretive schemes. Decisions on this level profoundly affect what is commonly called 'testing' of phylogenetic hypotheses . . . Working hypotheses, which are based on biostratigraphic evidence are important starting points for the establishment of morphocline polarities.
4. 'Testing' of polarities should proceed beyond character analysis when possible, by comparing the hypothesized polarities of character clines to one another, a method referred by Hennig as 'reciprocal illumination'.
5. With the known or suspected polarities of as many character clines as

> possible, using shared and derived characters, and by weighing the phylogenetic valency of biologically *different kinds* of shared and derived characters, a phylogenetic hypothesis is constructed (using both 'sister group' and 'ancestor-descendant' concepts, depending on the temporal nature of the evidence) about taxa into which one should attempt to place the investigated homologies in a relative time frame work. When possible attempts should be made to arrange a phylogenetic hypothesis in an absolute time framework, using all the available rockstratigraphic and biostratigraphic evidence. It is desirable that this phylogenetic hypothesis should postulate the least number of possible derivatives for *unique* and *functionally highly integrated features*. That theory of relationships of taxa which accounts most parsimoniously for *all* the postulated polarities of the known and weighed characters (Hecht and Edwards, 1976) is to be preferred. Should this call for parsimony not be heeded then nothing prevents one from postulating any phylogenetic hypothesis, because without this methodological limitation independent evolution of characters may always be postulated.'

This methodology of Szalay's needs some comment.

As we have already seen, the remark between parentheses mentioned in the first step of the procedure is crucial. Opinions, and thus hypotheses about phylogeny and evolution, already diverge strongly at the choice of a, generally unexpressed, assumption (Dullemeijer, 1974). The basic philosophy is so different that many authors are not on speaking terms any more.

It is easy to see that even the description, i.e. the recognition and delineation of structure, differs; this philosophy has a consequence for the aim of the investigator and thus also influences all other operations in the procedure.

The second step is a common one in any inductive empirical data gathering. It is indeed surprising that Szalay and Hecht and Edwards needed to give these methodologies which have been known since the development of logic in Greek philosophy (see for comparative anatomy Goethe, Geoffrey St. Hilaire, Cuvier and many others).

The important question is, what to do if there is no agreement and how to answer the question: how many independent authorities have to agree to reach a valid conclusion?

With respect to step 3, it is important to note that Szalay, in contrast to Hecht and Edwards, also included external characters. It is also a new aspect that Szalay deviates at least in terminology from the cladists operation. I interpret his demand of modern methods as the need for information other than structural.

In step 4 Szalay apparently wants a weighing system, by comparing the clines. Here again Hennig's terminology can be omitted. Long ago various authors have tried to answer these questions (ref. Dullemeijer, 1974). The solution seems to be first to study the biological relationship between the characters as is also implicit in Hecht's recommendations, rather than to compare the clines.

It must be stipulated that the parsimony criterion in step 5 has hardly anything to do with the parsimony criterion of the cladists. First Szalay requires functionally integrated features, and in step 4 the integration of the characters. Then he demands external characters also. One short step further and he can omit the specific parsimony criterion altogether by showing a polarity on the basis of necessary functional development. The constraints from the construction in evolution have become almost compelling for the direction (see Romero-Herrera *et al.*, 1978).

Idealism fades, but strict realism does not appear. Structure is connected more to function and the whole organism is coming into the picture instead of just its parts. The chances that the postulated diagrams do indeed represent real evolutionary developments increase, although a real consanguinity is not yet adequately demonstrated.

Our problem remains the question of the relation between idealism and realism, or of their replacement by a modern, if possible synthetic, philosophy or paradigm. This becomes even more apparent from Szalay's last statement in the summary. 'Strictly cladistic classifications are based on incomplete evolutionary theory and subsequently peculiar operational criteria. Whereas evolutionary classifications will employ paraphyletic groupings as dictated by data and weighing of evolutionary changes, the 'logical' practice of subordinating taxa according to dichotomously resolved sister-group relationships require the use of taxonomic categories. Because the use of an inordinately large number of categories renders such a logical system useless, the necessary choices to limit the number of categories introduces 'art' or 'caprice'. The use of authority therefore, is potentially more rampant in a Hennigean classification than in an evolutionary one. Contrary to an evolutionary classification in which biological information may be gleaned from the arrangement of groups, a strictly cladistic classification offers no information beyond hypothesis of furcations. As hypotheses of minor branching relationships are falsified and new ones are posed, drastic alterations become necessary in a dichotomous system of classifications.'

In the last step of his procedure we see Szalay's argument against purely cladism and his plea for evolutionary classification based on functional integrated components. His classification of eutherian mammals based on the analysis of pedal structures does not yet fully use and expose these sources of information. His system is also rather limited to personal selection and evaluation of structural features but the general trend points to a real biological understanding.

This brings us to our next category of relations wherein x is the structure, y the process of change and f the neo-Darwinian theory, comprising mutation and natural selection.

IV.2. Form and evolution

As we already observed in Szalay's study, the construction of sequences and phylogenies cannot rely on abstract ideal constructions of the mind but have to consider the consanguinity by attempting to set up and test hypotheses about genetic relationships of the structures. The change of the structures is considered to be caused by mutation and natural selection.

The procedures in this category are basically the same as in the first category about structure and sequence, but the format of the phylogenies is not necessarily described in dichotomies (according to Szalay (1976) they are preferably not) and the polarity is measured directly by scaling the fossils in time order. When only extant forms are used this latter aspect poses a real problem, for by definition, it cannot be said which form is the older one. In such cases one makes a guess based on such principles as the simplest one is probably the oldest, the euryecological structure is the oldest, etc.

The simplicity of a feature seems so simple to describe, but in practice the reverse is true. Simplicity is always a relative concept, thus it finds its base in comparison which in its turn demands a certain ordering of the phenomena. One senses the dangerous air of the tautological monster. Simplicity can refer to geometric easily describable forms, it may also carry a functional connotation like an easy apparatus. Whatever this may be, the focus lies on the question, how did the change in structure occur? with the subordinate question: what is the direction of change – are there many directions, and thus many possible causes?

Practically all investigations constructing phylogenetic series can be used as an example. Evolutionary biologists almost unanimously declare natural selection and mutation as the causes of the change. Other possible explanations are hardly mentioned, or suggested, because they do not fit the Darwinian theory of evolution. Although it is hard to imagine such alternatives, it must be realized that we know only a few examples in which it is proved that natural selection operates. These examples are mainly concerned with skin coloration of animals which have many generations in a short time. This supports the argument that observing the operation of natural selection is greatly hampered by the relatively short time over which one can observe. However, since the victory of selection theory over creation, not many serious attempts have been made (see e.g. Goldschmidt, 1952, and the discussion in Maynard Smith, 1958).

The procedure can be illustrated with examples borrowed from Bock (1976). In discussing multiple pathways of evolution, Bock writes: 'The arrangement of a right dorsal aorta in birds and of a left dorsal aorta in mammals in comparison with the double aorta in their reptilian ancestors is a good example of multiple pathways. Evolution from a double to a single, dorsal aorta may be considered as an adaptive evolutionary change [although the details of this adaptive change are unknown to the writer], but the loss of the left aorta in birds and of the right aorta in mammals depended upon the exact morphology of the heart in the different reptilian ancestors of birds and of mammals. And these different heart morphologies (i.e. how the ventricle was subdivided) depended upon different historical patterns of genetical events in the reptilian lineages leading to birds and to mammals.'

Bock's argument of the origin of these adaptations is certainly that of natural selection. In fact he defined adaptation in connection with natural selection. Natural selection taken as one and the same selective factor can bring about different adaptations depending on the 'answer' of the organism: multiple pathways of evolution leading to paradaptation or convergence. I would say, analogous forms. Although I can agree with the general trend and purpose in this example and its explanations, a number of critical remarks should still be made to reveal the limitation of our knowledge and inight, and to see the weakness of the explanation.

Let us see what kind of data we have, and what kind of hypotheses we can formulate for an explanation and how these hypotheses can be tested. We have selected the dorsal aorta, in a generalized form, of birds and of mammals and regarded both as originating from reptiles, or more precisely each form from a different reptilian ancestor.

We can begin to ask, was the difference already recognizable in the different reptilian ancestor? If so, where can we find the ancestor that does not show the difference, and how accurately do we have to look at it?

If there is indeed a completely identical origin, then we can consider the possibility of different pathways with the same selection force. It is clear that we cannot be absolutely sure that the selection force was always the same for both lines, because the same outcome in a complicated structure does not automatically warrant the conclusion that the same factors have operated. Let us accept it, because somewhere there must be a common origin, and state that only the presence of the two types of aortae enables us to speak of multiple pathways (I prefer the concept analogy).

Before we can prove that one selection force has operated on the same original structure and has given two solutions, we must first be sure whether we are dealing with exactly analogous structures. This implies an interpretation of the activity and the function of the structures. Information about structures and series of structures only, is insufficient to understand the course and the cause of evolutionary change. It is absolutely necessary to understand the function. Thus, together with the shift from the relationship between structure and series to the relationship between structure and natural selection we are forced to make the change from structure to function and even to functional component. If it can be ascertained that the origin and the selection force are the same, then there remain two possibilities for the ultimate explanation of different pathways or analogies. One is that the relation between structure and activity and function changes due to an unknown cause. The other is that boundary conditions such as, for example, constructional conditions, cause the change to follow another path.

In the example of the aortae the analogy is not quite the same. Although in both cases we can say that the function is the transportation of the blood from the heart to the body, the difference is large – both sides of the body are considerably different and the exact course of the vessels shows pertinent differences. Embryological studies tell us that origin and position of the vessels are influenced by many surrounding constructions, although this influence is less apparent for the arterial vessels originating from the heart. These constructions in their turn are part of a larger system, which in one case has something to do with being an organism able to fly, in the other case to being a terrestrial quadruped. And these structures are not pertinently influenced by similar selection forces.

If we now suppose an identical origin and a selection force on the demand of the transportation as such, then we must suppose that constructional boundary conditions determined the different pathways. That is to say, that this selection force is not the only factor responsible for the differences, or that internal selection worked or that selection forces worked indirectly via the boundary conditions. The choice of these alternatives cannot be made on the known information. It is necessary to restate the hypotheses and to continue the investigations both in a more accurate and more detailed manner.

Another example, presented by Bock (1976), reveals the problems even better. The ungulates are divided into even and uneven ungulates. According to Bock, the foot is equally well adapted for 'ungulate' locomotion, especially when considering the broad and widely overlapping types of locomotion of these two groups of mammals (Hildebrand, 1963).

It is indeed most probable that locomotion is a crucial function in the origin and maintenance of these animals; it is, however, likely that not the method of locomotion but only the speed is of overall significance and that various other conditions ask for different types of locomotion. The difference in locomotion and with it the difference in structure seems to be determined by different selection forces. A type of hierarchy in selection forces does not seem to be improbable. Again we cannot decide whether indeed similar selection forces have worked, or constructional boundary conditions or internal selection mechanisms. The reason is that the analogy, the multiple pathways and the selection forces are not defined in 'comparable', proper accuracy in relation to the questions asked. To obtain a conclusive answer, it is absolutely necessary that the definitions of the concepts, the collected information and the formulated hypotheses are in logical concordance with the investigated problems; the information must be of a sufficient detail to meet the formulation of the hypothesis and precision of the definition of the explaining concept. This methodological demand is certainly difficult to determine beforehand and is almost never met sufficiently. In practice it is obtained by going back and forth between the information to the definition of the concepts and the hypotheses. Here it requires a better analysis of locomotion and an exact definition of the specific selection factor.

Another interesting study by Bock shows even more clearly the need of such a concordance. Bock writes (the study is by Bock and de Witt Miller, but Bock is the actual author): 'Morphological arrangements of the toes that would be favored by selection for a good perching foot [in birds] would be 1) elongation of the hallux (anisodactyl or syndactyl), 2) reversal of the fourth toe (outer anterior toe, zygodactyl foot) and 3) reversal of the second toe (inner anterior toe, heterodactyl foot). All of these arrangements have evolved in birds and the first two have evolved several times' (Bock and de Witt Miller, 1959) (fig. 9).

We shall first record Bock's statement and carefully distinguish between data and interpretation. The author observed several types of toe arrangement in birds which are able to perch, and frequently do so. These arrangements, however, differ considerably and the detailed outer morphology does so even more. From the original paper it does not become clear why the author arranged the toe pattern in these lineages. Taking the toes separately various other lines could be drawn. We suspect that knowledge of the

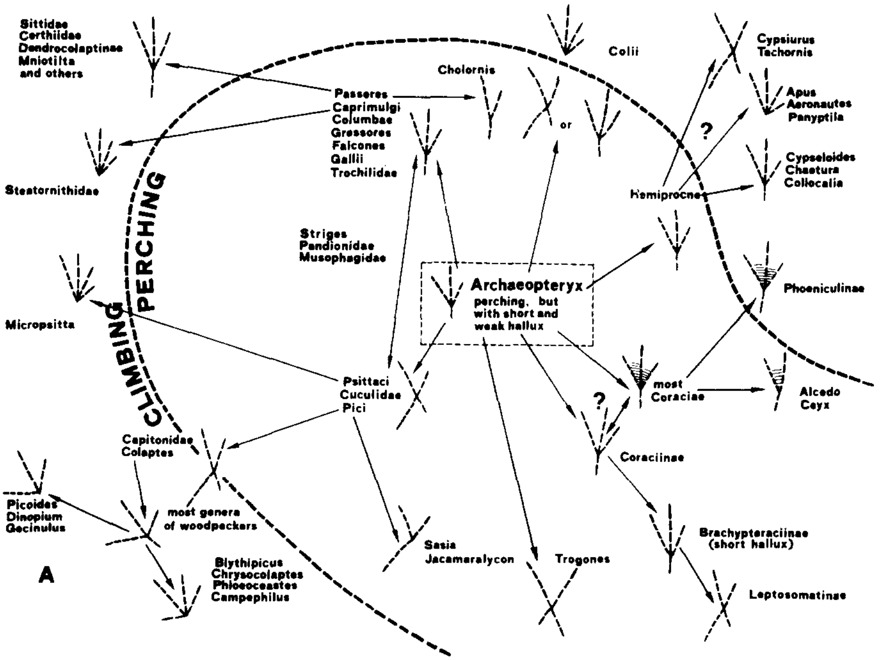

Fig. 9. (a) Dendrogram of birds derived from the information of toe arrangement. From Bock and de Witt Miller (1959).

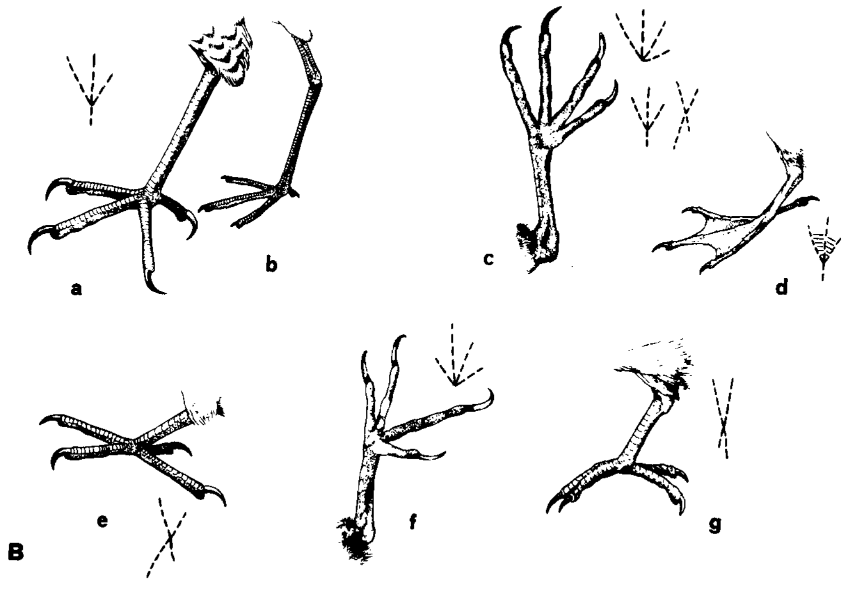

Fig. 9. (b) Various types of toe arrangement in birds.

taxonomy of birds has influenced the picture, which is valid information but should be mentioned in the construction of the dendrogram. The function of perching is likely to occur in these birds and is an important factor for bird life. However, many other functions are performed by these feet and it is very likely that these functions have played a dominant part in the evolution of the specific perching foot and its details in structure.

Notwithstanding the above mentioned objections we shall take, with Bock, perching as the main activity. A suggestion for the best toe arrangement for perching can then be made, probably the four toes arranged in opposing pairs. This arrangement need not always be present and thus it can be obtained in various ways for various occasions. Perching is not very specific. If this is so, then natural selection would probably hardly have any effect; it can be hypothesized that it is much more likely that entirely different selection factors were responsible for the toe arrangement. But proof of a selective force would be hard to give. Therefore, we need much more detailed information of the functional significance of the structure and its adaptation, not only to the environment, but also to the other parts of the body.

These examples show that for an evolutionary explanation structure alone does not give sufficient information. More structures and structural connections have to be added. Moreover, as many functional aspects as possible must be gradually introduced, although the determination of function is frequently restricted to speculation. The main reason for these requirements is that the

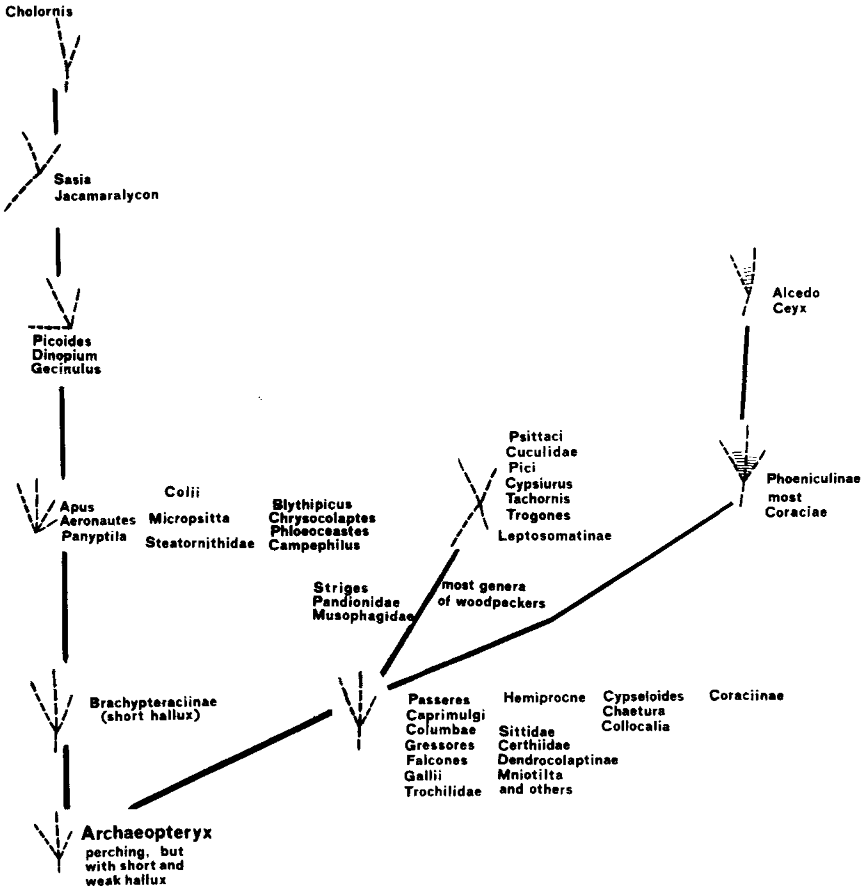

Fig. 9. (c) Alternative arrangement of birds in a dendrogram using only the toe arrangement.

mechanism of the change of the structure according to the neo-Darwinian theory of evolution involves three principles: 1) heritable variation, 2) mutation and 3) natural selection. The first two can be considered strictly morphologically or morphogenetically. However, the third can only be imagined to operate on the activity of the structure. This logical tension between structure and natural selection requires a number of other concepts, viz. adaptation, functional component and fitness. It means also that a number of the relationship arrows in our fig. 4 are not real or relevant.

IV.2.a. Adaptation and natural selection. Most likely there is no concept in biology which has so frequently been the focus of discussion and on which so many articles have been written as the concept of ‘adaptation’. This is due to the situation that almost any part of biology is in some way involved in using the concept (also before the origin of the evolution theory) and to the fact that the concept has many changing meanings. Besides its common general meaning, the concept of adaptation seems to carry specific characteristics in various subdisciplines in biology. Geneticists imply something other than physiologists (Van der Veen, 1978). Evolutionary biologists seem to adhere to slightly different meanings than functional morphologists (Lewontin, 1978; Bock, 1976). Given the overwhelming number of publications, it seems therefore carrying coals to Newcastle to add yet another discussion. There are, however, two reasons for remarks. There is hardly a strict methodological analysis available for the scheme we use here, and a choice from the various meanings of the concepts is unavoidable, even more so as these meanings and definitions contain controversial aspects. In the scope of this study, the concept of adaptation will be described according to functional morphological usage and then compared to the concept in evolutionary biology. The most thorough discussions have been presented by Bock and Von Wahlert (1965); Lewontin (1978), Maynard Smith (1958) and Van der Klaauw (1949). These articles and a few other important ones will be used as a basis for discussion.

Adaptation has a variety of meanings (Van der Klaauw, 1949; Maynard Smith, 1958; Bock and Von Wahlert, 1965) many of which have, what Maynard Smith calls an aprioristic status. 'Anybody, being a layman or a biologist, is immediately aware that plants or animals live in more or less specific surroundings and knows when this relation is broken down, the organism dies.' Or as Van der Klaauw says 'adaptation is a phenomenon, observed by our senses, and not a logically derived concept'. This implies many options to differences in definitions due to a philosophical point of view, discipline, observation of other phenomena and methodology. In pre-Darwinian idealistic periods adaptations were indeed recognized, but were considered of hardly any interest to scientific inquiry. Adaptation was defined as being adapted to, or fitted into, the environment. It was no problem because of the prevailing belief of the divine harmony in Nature and because of the fashionable interest in comparative anatomy, functional aspects and adaptations were considered a barrier to the understanding of structure (Russell, 1916; Lubosch, 1931; Dullemeijer, 1974).

With the change of philosophy, adaptation became the crucial concept in the understanding of the operation of natural selection in evolution. In its most propounded form we find it exposed by Bock and Von Wahlert (1965) and Bock (1976). Adaptation is defined by them as the process of becoming adapted. From an empirical point of view both definitions must be maintained, as most authors do (Van der Klaauw, 1949; Maynard Smith, 1958; Osse, 1978; Van der Veen, 1978) and they deserve further consideration.

The state of being adapted is generally accepted as self-evident. But as Maynard Smith clearly points out, it is difficult to prove; it relies mainly on an aprioristic method of recognition. 'We argue from the function to be performed to the kind of organ likely to perform it effectively or elsewhere. This is the kind of structure which, in view of what we know about how things work, we would expect to perform a useful function in these conditions.' We see here already a tendency to prove adaptation by means of model comparison, albeit a model vaguely present in our minds. (Note also the presence of the term 'useful'.) Maynard Smith is aware of this. He writes, when discussing the leg bones of horses: 'the argument is seldom really apriori, we know what the legs of horses are like before wondering why it is efficient for them to be like that. There is, therefore, a constant danger of being illogical or fanciful in our explanations.' We would say, there is a tautology which has to be broken up. The question then remains. Is there adaptedness? Or more specifically, is a certain structure, organ or feature adapted to any kind of environment? The general opinion is that any structure or organ is adapted, and thus it is a challenge to prove the kind of adaptedness of such an organ or structure, and the rules governing the fitting into the environment. Clearly this question belongs to the domain of functional morphology and can be answered without any reference to evolutionary biology. The simple reasoning comes from the observation that structures, organs and organisms maintain (Maynard Smith's apriorism) themselves and if not adapted they would be eliminated by the environment through natural selection. Thus, as Bock deduces, natural selection and adaptation are completely bounded. However, at this point in our discussion these arguments are considered inadequate and actually unsound, because we have already introduced the process of adaptation without a proper introduction and evaluation. Therefore we need direct proof of the state of being adapted and a refinement of our definition.

Adaptation has a number of shades of meaning. It can signify a structure working or acting in a specific surrounding. This so-called 'primitive' meaning is aprioristically derived from the observation (Maynard Smith, 1958). The observation is not queried nor the idea that the action services the organism. Frequently activity has to be taken in a rather passive sense; structures, and particularly shapes, are truly fitting in an environmental situation rather than acting to obtain something from the environment for the organism, e.g. plants and animals grown in restricted spaces, streamlining for swimming, shapes for burrowing. There would be little reason to discuss this shade of meaning any further, were it not for the fact that there are numerous publications only reporting the activity and implying proven adaptation. In fact a great deal of the physiological and functional-morphological literature belongs to this category. The underlying thought is always that nature does nothing in vain, so that any activity or even the presence of a structure must have an effect for the organism (see for discussion Dullemeijer, 1974). Whether this is correct is connected to the second grade in meaning, viz. that the action is beneficial for the organism, thus more than 'simple' observation that it has an effect. With the term beneficial generally two meanings are indicated: the activity is necessary to maintain the integrity and survival of the organism and the species, and the activity is convenient but in a way dispensable. The latter meaning is very questionable and the most difficult to prove or disprove. However, accepting this meaning considerably affects the attitude to further questions.

For the majority of structures it is not difficult to prove their necessity. Crude experiments and simple observations convince us of their indispensability. It is common knowledge that lungs serve for air breathing and cannot be missed, that kidneys serve excretion and cannot be missed. But it becomes already slightly less easy to say that e.g. the tail of a lizard is necessary and that certain appendages in arthropods are indispensable. In plants such a problem cannot be solved at all. It becomes more difficult when organs or structures are numerous such as lymph glands, hairs, scutes and segments in lower invertebrates. Each single element certainly can be missed but it may be rather inconvenient for the organism. Whether the lack of these structures can have harmful effects in the long run or in specific circumstances remains a possibility. It is known e.g. that in man the early ectomy of a lymph gland (appendix, tonsil) is making the best of a bad job.

The problem becomes even more complicated when we realize that any organ or structure has many features and that most of these features are strongly connected. One of the features can be necessary whereas the other can be missed, or even can be disadvantageous to the organism. In this respect there is a wide spectrum of features which are functionless and thus non-adaptive to harmful, be it mainly in the long run. One would even be inclined to say that in the long run every organ has a property (Dullemeijer, 1974), an aspect, a feature, which is harmful for the organism and which besides the wearing effect, is responsible for its death.

The third grade in meaning of the concept 'adapted' relates to efficiency. Several authors restrict the meaning to those cases in which it can be said that the function is performed with a specific and relatively high efficiency. Efficiency is difficult to measure for a number of reasons:

a. efficiency can relate to total energy expenditure,
b. efficiency can relate to effectivity in time and space, e.g. speed of activity,
c. efficiency can relate to the amount of material put into action, and
d. efficiency is a relative concept in respect to various species, various functions and various moments.

A proof of adaptation in the sense of efficiency will thus always be preceded by choice of a reference to which adaptation can be measured. The common method is a comparison of closely related or analogous situations from which the conclusion is derived that one structure or function is more efficient than the other under well-defined conditions. Alteration of conditions tends generally to change the efficiency difference. In accordance with this notion, Bock and Von Wahlert (1965) defend the point of view that the energy balance is the best parameter to define adaptation. They write: 'Hence we define the degree of evolutionary adaptation, the state of being, as the minimal amount of energy required by the organism to maintain successfully the synerg if a single biological role of a faculty is considered, or to maintain successfully its niche if the whole organism is considered. The adaptation is, of course, the faculty.'

To my knowledge there is no clear, well investigated example available which shows efficiency differences in total energy expenditure and subsequently related to differences in adaptation. Some approximations may be read off from physiological measurements which record the total oxygen consumption and the release and loss of energy to the physiological adaptation. Such approximations have also been described in cases where animals were kept to exercise certain functions, such as locomotion under well-described conditions. How academic the solution is that uses the energy balance for defining the concept adaptation, becomes apparent when we try to imagine how the energy balance should be measured and subsequently compared. To make the balance we need to have the proportion of input to output. Input can be measured as total amount of energy which can be maximally taken up by the animal, and output as the total amount of movement. The use of these parameters can be criticized severely. It is not fair to consider all the food or all the potential energy as profitable for the organism. Differentiating between absorbed and wasted energy is a better method, but does not help much, so we can follow the energy flow sheet (fig. 10) and reach net energy. We then arrive at the point where we meet the same difficulty for the output. Do we take the useful mechanical energy (how to determine?) and add growth and development? Suppose we could come to a reasonable balance, is it fair then to compare a cow to rabbits as in the amusing illustration of Kleiber (1961) (fig. 11)? Are cows better adapted because they have gained relatively more weight or are rabbits better adapted because they move better? Such a comparison is useless. The possibility remains that the comparison is made between very closely related species or individuals, an argument which agrees with Bock and Von Wahlert's opinion, because they directly connect 'adaptation' to 'natural selection'. But suppose that the individuals do not differ in energy balance and they do in finding better places for their offspring, then we would have to conclude that the latter group is better adapted. Thus it is easily said that the degree of adaptation is the minimal amount of energy to maintain successfully the synerg, but it can hardly be measured. There are other difficulties to restrict the concept adaptation to 'energy balance'.

The first part of the definition by Bock and Von Wahlert is clear if we know that a synerg stands for the relationship between selection force and

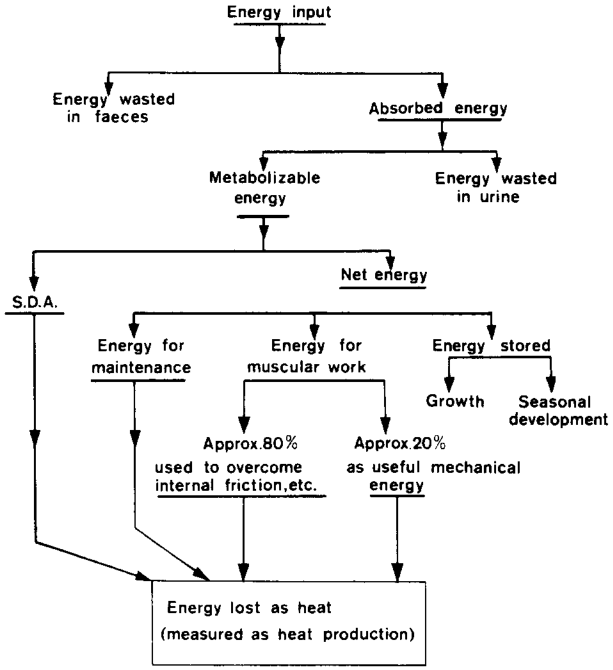

Fig. 10. The energy flow chart of *Carassius auratus*. After Davies (1964) from Florey (1966).

	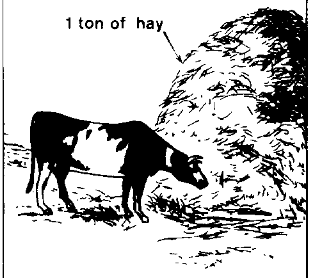	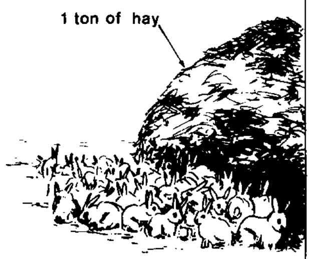
Animals	1 steer	300 rabbits
Total body weight	1300 lb	1300 lb
Food consumption per day	16⅔ lb	66⅔ lb
Duration of 1 ton of food	120 days	30 days
Heat loss per day	20000 kcal	80000 kcal
Gain in weight per day	2 lb	8 lb
Gain from 1 ton food	240 lb	240 lb

Fig. 11. Difference in consumption and use of food between two mammalian species. After Kleiber (1961), from Florey (1966).

biological role (= function). We shall further analyse this relationship and try to imagine the operation of the synerg, in order to see the full consequence of this thoroughly documented definition for our problem.

A selection force is an agent which eliminates,[4] from a group of phenomena, one or some, such that a shift in the average group characteristic takes place. The problem shifts then to the question of how a biological role can be eliminated without eliminating or changing the faculty (= functional component). If this is possible then there is indeed a relevant relationship between biological role and selection force. If not, then the selection force affects the faculty with the result that the biological role cannot be performed, or has to be changed. The effect does not stop at the level of biological role as in Bock and Von Wahlert's scheme (fig. 12). In the text Bock and Von Wahlert are aware of this. Their diagram is a diagram of concepts rather than of operational effects. This means, however, that Bock and Von Wahlert also measure the success of the synerg as the 'fit' of the biological role as an expression of activity, to the selection force as an expression of the environment, and for this term 'fit' we have the excellent term 'adaptation'. The term synerg seems then superfluous. Thus from now on we say that adaptation is the working of the functional component with a minimal amount of energy. We are still left with the definition of 'successfully' and the measuring of the minimal amount of energy. If the former term is defined in terms of energy balance then the circle of logic is closed, and in terms of maintenance or amount of offspring we have a circular definition. Yet, theoretically Bock and Von Wahlert's definition of the *degree* of adaptation gives us a means of escaping the circular argument.

We can observe the maintenance of a functional component (not of a synerg) or of the organism supposing we have a measure for 'reasonable living'. Theoretically we continue establishing the amount of energy needed

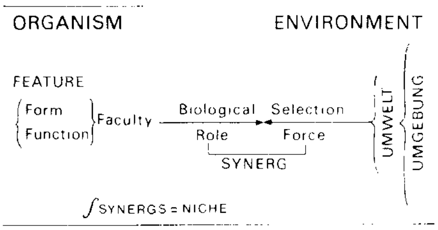

Fig. 12. The relationship between function, form and natural selection according to Bock and Von Wahlert (1965).

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[4] We use here the term 'eliminate', although natural selection, and thus selection force, is generally defined in terms of probability of disadvantageous versus advantageous operation (Mayr, 1963). This extreme connotation does not invalidate the argument presented here.

for such 'reasonable living'. Thus, the degree of adaptation is expressed in amount of energy, but strongly connected to the described conditions (reasonable living). 'Adaptation' then cannot be the faculty, but rather the concept which describes the relation of the faculty (= functional component) to the environment in terms of the amount of energy. It does not need much imagination to see that such a notion goes back to Maynard Smith's aprioristic arguments. Do we need to add 'the amount of energy'? Apparently not for the recognition of adaptation as such, but comparatively to describe the degree of adaptation it seems a reasonable parameter. Comparison is compulsory and this requires comparable conditions. As we have seen, a requirement which is very difficult to obtain, and also of very limited application.

The causal relation between selection force and biological role seems to be somewhat more complicated than Bock and Wahlert suggest in their scheme. The selection force is a specific factor in the environment (Lewontin, 1978). The question now is on which aspect this force has an effect: on the biological role, the action or the structure? These latter concepts have different logical statuses. Structure is a three-dimensional material element. When this structure changes one or more of its properties in an almost reversible way over a short time we talk about action. There is the possibility now that the action is affected without an effect in the structure. Biological role means that the structure and/or activity have an effect on the organism so that it continues to survive; thus it affects structures or processes which are considered necessary for the maintenance. Biological role cannot be affected unless the activity or the structure is affected under the same boundary conditions. It is of course always possible to change the boundary conditions but this will amount to the effect on other structures or functions. It also seems possible that the aim of the activity is not reached but then the environment must change, or in other words the selection factor has changed. So, with constant boundary conditions and with non-changing selection factors, biological role is always affected through influences on activities or structures. We conclude that logically the concept of biological role is a concept describing a relation, whereas activity and structure belong to the domain of material, directly observable, phenomena. The maintenance of the organism by means of the operation (as a causal factor) of the functional components is called the biological role of these components. This is also in agreement with Bock and Von Wahlert when they say 'adaptation is, of course, the faculty'. Transposed into our terminology it says that the faculty (our functional component) holds the relation with the environment. Again, this relation is called the adaptation and the faculty is considered to be adapted to the environment. The relationship between the functional components and the environment is called adaptation. Thus, when we talk about the biological role or function of an active structure (a functional component) we mean its relationship to the other functional components of the organism. The latter relationship can take the shape of a causality or a structurality in the sense of a synthesis in systems (cf. Zweers, 1979).

The fourth grade in the meaning of adaptation is survival chance. Organisms or species which have hardly any chance of survival are said to be badly adapted, those with a good chance are said to be well adapted. The question now arises: is the chance of survival always directly connected to the efficiency of energy consumption? One would be inclined to accept this relationship, but the presence of the enormous variety of organisms with almost incomparable energy expenditures points to a much more complicated relationship. As Lewontin (1978) correctly remarks: 'the concept of adaptation implies a preexisting world that poses a problem to which an adaptation is the solution'. The difference of adequateness of an adaptation between two types can thus only be evaluated when they occupy exactly the same habitat or have exactly the same niche. This will never be the case, as many ecological observations show. Then it does not make much difference for survival chances in terms of competition whether one type would spend somewhat more energy than the other. Their survival will thus mainly depend on their ability to cope long enough with the various environmental factors to get the chance to produce sufficient offspring. We reach the conclusion that energy saving is thus only of importance for organisms which are in a competitive situation, or which spend so much energy that they do not have a chance to survive sufficiently long to produce offspring. Competition plays a part between individuals of the same species. It only happens when two types belong to the same ecological population. Consequently natural selection will have comparatively the greatest impact when such a competition occurs. Then total energy expense may have a paramount influence. But adaptation is generally observed and defined as a species attribute, seldom as a feature of individuals, although the theory of evolution demands the latter. This does not exclude the possibility that individuals of different species or populations are competitive over a short period relative to one specific environmental factor. If this environmental factor becomes crucial for survival or predominantly important, species are then in competition. Energy expenditure seems to be one of several factors. Before such a conclusion is drawn it seems appropriate to investigate the total life cycle of the individuals of the population to establish the importance of the competitive factor. As soon as species are ecologically far enough apart this parameter is less dominant. In the majority of situations, adaptation is rather a question of technical fitting than of energy efficiency. This kind of understanding adaptation can be gained from studies into functional morphology and related disciplines.

In the concept 'adaptation as activity or becoming adapted', there are as many shades of meaning as in the static concept. Each graduation of the concept 'adaptedness' can be transposed into an aspect of the dynamic concept. Particularly in Anglo-American literature, the meaning of adaptation refers always to the dynamic graduation without indicating especially one or other case.

In neo-Darwinian theory the cause for adaptation is always natural selection on spontaneous random variation. In extreme opinions adaptation and natural selection are defined inseparably (Bock, 1976), so only those features are called adaptation which have originated from the effect of natural selection or better, still conversely, there is no adapted feature which has not arisen by the operation of natural selection.

I follow Lewontin (1978). He writes: '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.' And Lewontin adds to this: 'Natural selection does not lead inevitably to adaptation.' The question arises then whether it is appropriate to pose the reverse question, viz. are there any adaptations which have originated without the necessary operation of natural selection?

To answer this question it is necessary to agree about the definition of the concept of natural selection. Natural selection is the selecting of certain phenotypes from a population by the influence of environmental factor(s), through their chance of producing offspring, such that a shift in genetic composition in the population takes place. According to Lewontin, in general it leads to a better adaptation but it does not necessarily have to, it can also lead to a worse situation and ultimately lead to extinction. This latter opinion does not hold if natural selection is defined as extinguishing only the relatively badly adapted organisms and has such a paramount effect that indeed all rather badly adapted organisms are extinguished. This is why Bock (1976) connects natural selection and adaptation. Moreover the opinion includes the assumption that all selected individuals contributed to the genetic pool before they were selected. Selection of individuals who produced their offspring before selection does not have an effect on the change of the population. This kind of selection cannot therefore be called natural selection.

A canalization of developmental processes by interaction of parts (Waddington, 1968) or a limitation by lethality through disharmonic development cannot very well be called natural selection because of the absence of an environmental factor. However, for each element in an organism the others form its environment. Thus if such an interaction selects individuals and contributes to genetic change, this selection is natural but internal. In this way canalization could be called natural selection, having directed that particular development and thus 'chosen' this one out of many other alternative developments. However, the alternatives have never been real, but only theoretical. Such a directed development is not in contradiction to natural selection and if the new organism can fill an open niche then it is an important source of evolution. To classify this process under natural selection is to be discouraged because then the concept of natural selection would almost coincide with the concept of adaptation and encompass the same meanings as the concept living. It loses its particular strength as an explanatory theoretical concept due to the fact that in each investigation beforehand natural selection can be appointed as the explaining factor without an increase of insight.

There is another argument to restrict the concept of natural selection and at least to leave evolution without or with little influence of natural selection an open possibility. The theory of evolution stands on two bases: random variation and natural selection, which is a strictly determined process. There is no aprioristic argument that the first base could not be changed into a concept containing a determined or at least stochastically directed variation. Much of modern genetics, molecular biology and functional morphology (constraints theory) is supporting such ideas. In a complete mirror picture, natural selection could be thought of as being random which would meet Lewontin's case that natural selection does not inevitably lead to adaptation. We therefore stay with the usual definition of natural selection as selection by the environment and affecting the gene pool.

Disharmonic development, change of genes (mutation) leading at early stages to death and also origin of new forms caused from genetic changes and 'allowed' to live in new or open ecological niches will not be classified under this definition of natural selection. The concept is too important in biology to do else; it is one of the few real biological concepts and we must not dilute it by reading more into it than the original definition, because of the danger of losing its strength. On the other hand, the other possibilities for evolution should not be excluded beforehand. The acceptance of the other possibilities can protect us from a too dogmatic viewpoint, in particular when it comes to application, e.g. in human society (cf. Ruse, 1979, in Sociobiology). We shall return to these aspects when we have further analysed the role of functional morphology.

Here it needs to be said that naturally the operation of natural selection presupposes a variability among the organisms which must have its basis in the gene pool. Selection of individuals with identical genomes but with variations induced by the environment does not change the new generations.

Modern genetics does not exclude the possibility that changes of the genes occur by the influence of factors inside the organisms and especially by factors from the environment, be it not directed by the factors to which the new forms should be improved.

The issue still remains whether the randomness of the variations demanded by neo-Darwinian evolution theory (Mayr, 1963) is a valid hypothesis. In fact, the variations are strongly limited by the constructional constraints.

IV.3. Function and series

From the foregoing discussion we have seen that the relations described in fig. 4 cannot be maintained neatly and cannot be considered completely separately. The reason is that the mentioned concepts in functional morphology and evolutionary biology do not constitute clear straight linear series of similar logical succession. Moreover, not all relations are relevant, which becomes apparent when a shift of concepts in one discipline is not followed in equal measure by a shift of concepts in the other discipline.

The relation between form and series (or sequence) has a direct importance for biology. The relation between form and mutation and transformation is also very relevant, although not discussed in this article. But the relation between form and natural selection can only be made via the concept function, thus implying an unavoidable shift in the list of concepts of functional morphology when such a relation is considered. The same holds for the relationship between form and adaptation. Therefore, this seems to be the proper moment to see how 'function' behaves with respect to the concepts of evolutionary biology.

As generally accepted we shall distinguish in the function concept the two modalities: *activity* and *biological role* (Jeuken, 1958; Bock and Von Wahlert, 1965; Dullemeijer, 1974). The connection of the two and the relation to structure will not be considered at this point of the discussion.

The relationship between activity and series shows great similarity to the relationship between form and series. The construction of a series presupposes various activities, which can be classified as being on the one hand sufficiently similar, and on the other hand definably different. We obtain here again a typology, viz. of activities, which may be ordered idealistically or realistically. In an idealistic series the activities can be ordered according to the choice of the investigator with a parsimony criterion, if chosen. We may expect to find in this ordering a tendency to give priority to qualitative criteria in reference to biological roles. Within the group of a specified criterion, a quantitative one will be used. A clear criterion based on consanguinity or affinity is generally absent because of the descriptions of most activities by investigators not interested in typology, and because of the absence of a *comparative functiology* (as morphology). In comparative physiology the aim of research leads to a causal explanation. Yet it seems possible to borrow a number of examples from comparative physiology, such as sight or locomotion. Sight or seeing can be ordered from simple light perception to the directed perception of patterns (Beklemischew, 1958-1960; Florey, 1966 and many textbooks). Thus the first element in the series of activities is sensitivity for light (restricted to a specific spectrum or not), e.g. animals attracted by light or trying to avoid lit areas. The following element can be seen as the perception of the direction of the light source. Simultaneously or thereafter we can classify the activity to distinguish between light-dark gradations and the perception of colours. The ability to concentrate the light rays by diffraction and the following ability to form images completes the sequence. Such a series occurs parallel in many animal phyla. It varies in these phyla with respect to number of members in the series and the ultimate perfection of sight. In all groups it is non-linear, which makes the interpretation difficult. More important, however, is the spasmodic impression of the sequence due to the separation of the activities from structures. In the textbooks the activity (physiology) is always treated in connection with the structure (morphology) so much so that to the latter generally is given priority. Idealistically a sequence of activities has hardly any meaning, unless such an activity sequence is also founded on Platonic ideas. Remarkably such a philosophy has never had any relevance in function-biology. Idealism has always been directed towards structures, probably due to the static nature of this philosophy.

Realistically the sequence of activities has always had much attention, because the activity together with the biological role is considered as the factor of the chance of survival, in other words the factor on which natural selection operated. The realism was, however, not focussed on relationships but on the realism of the survival value. The demand for a philosophically realistic approach is, however, that there is a connection (consanguinity) among the members of the sequence. Up till now it was impossible to determine this consanguinity other than measuring the structures, even when it was measured on the organization level of the genome. This is due to the fundamental connection of the natural sciences to matter, or in a more limited sense to the unseparable connection of activity with structure. Thus, the sequence of activities separated from their structures becomes a sequence of analogies. The following example is typical. Böker (1935) was the first who tried to construct a typology and sequences of activities and biological roles as such. To distinguish structural typology and homology from his function series, he called his sequences 'biologische Reihen'. The interesting aspect of these 'Reihen' is their potentiality to serve as models for sequences of activity and biological roles in which a specific improvement is reached under influence of natural selection or orthogenetically.

In its idealistic nature the sequence can be accepted and can function as a source for initiating new hypotheses. To be realistic more and different information has to be added. Böker tries to provide this by adding representative specimens to the sequence (thus not the actual structures). From the foreword of his book I conclude that he did indeed consider the sequences as representing real evolution, but he does not give any evidence of their genetical connection, nor is there any evidence of a constructional nexus. Thus, he surpasses the borderline of the system making a change in philosophy necessary, as we similarly observed for the Hennigean system. Nobody should have difficulty in seeing that Böker's Reihen cannot meet the challenge of this change and that we are dealing here with a 'false' evolution, because the specimens were already classified differently on principles of blood relationship (consanguinity). Both Hennig's and Böker's systems are very similar in this respect, but otherwise they are completely different, indeed in many ways they are the opposite of each other. In Böker's system the prohibited jump from idealism to realism is most apparent if the sequence consists of organisms of totally different taxonomic taxa. In series of closely related specimens this change of philosophical system plays hardly any role; there is a fair chance that the series holds for both systems. Then the change of system can only be disqualified on methodological grounds.

However, Böker's system provides the functional morphologist with an excellent tool to compare constructions and to set up series, so long as the latter are not interpreted phylogenetically.

IV.4. Functions – evolution

The following example shows us that new information or a new hypothesis must be added to make the construction of sequences meaningful for evolutionary interpretations.

Edwards (1976) analysed the locomotion of salamanders with the aim of understanding the evolution of terrestrial locomotion, particularly the selective pressures which led to terrestrial locomotion. Two aspects are distinguishable in the introduction, viz. which factors 'forced' the rhipidisteans to move to land, and which were the demands put on the locomotory system. Both aspects are supposed to coincide. Thus there are at least two selection pressures which could have coincided. Then comes the question of how the locomotion was achieved including the potentiality of the structures in the ancestors. The method for obtaining some insight into these problems uses modern organisms as models for a hypothesized phylogeny. It is supposed that the selected organisms can indeed be used as representing the types of locomotion. Edwards feels that salamanders can serve the purpose, basing his argument on analyses and opinions of Jarvik (1942, 1968), Parsons and Williams (1963), Estes (1965) and Bolt (1969) that the salamanders are derived from the eryopoid temnospondyls closely resembling the members of the family Dissorophidae.

Edwards describes three aspects of salamander locomotion: propulsion, gait and lateral bending of the vertebral column. These aspects apparently all refer to propulsion, so that the latter two form aspects of the former. Propulsion is achieved by three methods: girdle rotation, limb retraction and humeral-femoral rotation. The methods can be combined or occur separately. The gait analysis shows that the animal has generally three feet on the ground, but sometimes only two simultaneously. It occurs together with all three propulsion methods. Lateral bending is connected to girdle rotation. Most bendings are more or less standing waves but change into travelling waves at fast speeds. The proportion of propulsion methods changes with speed with considerable overlappings.

The propulsion methods in salamanders can now be compared to the methods in the ancestors from which they are supposed to have originated, or they can be compared to any method in an attempt to make some kind of sequence. Edwards is not clear about this point. We have the impression that he tends to make the former comparison. The procedure he follows is suggesting a similar locomotion in labyrinthodonts based on similarity in structure, among which are the cristae ventrales on the humeri and femora, the screw shape of the glenoid fossa and the S-shaped articular surface of the head of the humerus and their sprawling posture. He also concludes that the first gait was a trot, because of the supposed travelling waves in rhipidisteans and such waves observed in salamanders. Thus Edwards did not only compare activities but connected these to the structures.

Edwards asked the question: What pushed the rhipidisteans on land?, but he has not yet answered it. It is very likely that he supposed that locomotion was a prerequisite to come on land and that other ecological factors forced them to go, or that he considered this type of locomotion a possibility to go on land. In both cases natural selection on locomotion has not been the primary factor for terrestrial life, but a necessary condition for the animals to be able to go on land. In a negative way selection operated, i.e. those who did not have this ability sufficiently were extinguished.

Natural selection remains also here the most probable explanation although other explanations cannot be neglected. If we specify the kind of activity with its biological role as we have seen in the example studied by Edwards, there is a good chance that we cannot explain the evolution of such an activity by natural selection, because it did not react on that activity. It is highly probable that the locomotory system is so flexible or plastic that by other factors it is shaped into its relevant shape. I shall return to this connection of elements and the consequences of natural selection later.

The conclusion from this example is: description and comparison of activities are necessary but insufficient, the connection with structure and the biological role are necessary. It follows then that a description of the mutual relationship of the functional components must be the next step in the procedure.

IV.5. Functional components – series

IV.5.a. The analysis of the functional component. On various occasions (Dullemeijer, 1974), I have described the methods and procedures to analyse the relationship between function and form in a functional component. It does not seem necessary to discuss these procedures at length, but some indication of the methodology is relevant because of the interweaving of the construction of sequences, the evaluation of adaptation and natural selection.

Two approaches are usually used to describe the relationship. The first is the *inductive* or *comparative approach* or method (Dullemeijer, 1974). This method is naturally the primary one, which actually any layman uses. It is founded on the belief in confidence of direct empirical observation. Organisms, parts of them and various elements are described, registered and classified. The same procedure is applied for the activities and the biological roles of these organisms and their parts. Comparison and connecting the two classifications results in a conclusion describing the relationship between form and function. Subsequently an investigation is started into the explanation of the relationship, e.g. in locomotory organs, the relationship is explained by the rules of kinematics. Clearly this approach meets all the difficulties of distinguishing, classification and ordering that I have already discussed in the preceding paragraphs.

In the first place the choice or selection of the structures is crucial for the results. Some insight or knowledge of the comparability of the structures and the connected activities is an absolute prerequisite. The choice can be made on the structures only and on the activities only (Böker, 1935). Although the choice as such will be based on a variety of arguments (cf. Dullemeijer, 1972, 1976) it is not generally thought to be a difficult one, although it is theory-laden. This difficulty is more apparent in the delineation of the two aspects with regard to the organizational levels and taxa, as well as spatially. A number of procedures are involved, all of which have a more or less typological nature. Naturally it is practically impossible to describe all the details of the forms and the activities. Selection, delineation and description of detail are given in view of the specified aim. This implies, unfortunately, the danger of bias, but without a goal specified beforehand the investigation would turn into infinite chaos. The description of the structure and the activity must be given in a balanced way concerning the details. This is difficult to foresee, however, and must be regulated during the investigation. Imbalance of description of both aspects frequently occurs. Morphologists are inclined to present very accurate and detailed descriptions of structures with far less detailed description of activity. Many structural details and parameters do not figure any more in the conclusion and if they do, it seems that many structures can perform the same activity. Examples of the latter are analogous organs such as respiration organs: lungs, gills, skin, allantois, accessory gills, tracheae. It is concluded that there are many different forms for the same activity. This conclusion is correct but incomplete. The forms are described in greater detail than the activities. If the latter were described with the same detail we would find a one-to-one relationship and the idea of analogy would be eliminated.

This is always the case in analogous organs. The reverse situation is less frequent, because investigators of the activity, mainly physiologists, cannot avoid the material and structural basis, although we could do with better description of the structures. Apparent examples can be found in some studies of neurophysiology, where the activity is measured in great detail but the structural substrate is insufficiently known. We therefore see these students turn to structural analyses.

One main example from our experience can elucidate the situation further so that the consequences can be estimated. To be able to depress the lower jaw, birds have to use the kinetics of the skull by protracting the quadrate slightly (Bock, 1964; Zweers, 1974; Zweers *et al.*, 1977). This movement seems to be identical in many birds, but it differs quantitatively somewhat. The structural substrate seems to be similar, but on closer observation reveals also some differences. In Anatidae an antero-dorsal ligament is responsible for the blocking, which necessitates a shift of the rotation axis rostralward; in Ardeidae it is mainly the shape of the knobs forming the lock, and in parrots we find a ligament running almost caudally. In the two latter cases the shift of the axis is also slightly different. The question now arises whether such details must be taken into account in the construction of sequences. Or to what degree must functional components be similar to place them in linear or branched sequences. It is a similar problem as in the construction of all idealistic sequences, because the information on genetic connection (consanguinity) is lacking, unless we use the suggestions presented by taxonomists. The latter information closes the circle of reasoning without any profit or progress in certainty, because in the majority of taxonomic classifications direct information on genetic relationship is lacking too. The solution to this dilemma again is trial and error, i.e. begin to compare and regulate according to the results. This practice is found in several studies, althougn the chances of a valid comparison can be increased considerably by knowledge of the classification of the group of organisms.

If the aim is to construct a sequence then it is general usage to start the analysis on a so-called '*generalized form*' (Dullemeijer, 1956, 1959; Liem, 1973; Lombard and Wake, 1976, 1977; Barel *et al.*, 1976, 1979; Zweers, 1974). This generalized form is the reference specimen. It is analysed in great detail so that subsequently a comparison with closely related forms can be made rather easily. In the reference specimen both form and activity have to be described in great detail and in a balanced way. The reference example is sometimes called a *model* in which all elements expected to occur in the related organisms must be present (Lombard and Wake, 1976, 1977; Zweers, 1979). Consequently the model is always placed as the original form, from which the others are derived. This position is not challenged by definition. The series remains typological, but it is clear how the derivation was arrived at.

The study of Lombard and Wake (1976, 1977) concerns the functional morphology of the prey capturing in the lungless pletodontid salamanders. These animals project their tongue very quickly, for which they use a complicated construction of the hyoid apparatus and specially developed muscles. The aim of the study is twofold, almost similar to the study by Liem (1973), viz. to understand the structure by deriving it from the activity as an efficient means of capturing prey and secondly to understand the variety of tongue structures in related forms as an evolutionary diversity. The skeletal elements of the tongue are from anterior to posterior a medial, unpaired basibranchial, to which at each side two ceratobranchials are connected. The two ceratobranchials converge and meet in a connection to a long, rod-shaped epibranchial. Anterior to the spoon-shaped basibranchial is a very small lingual cartilage and to both sides extends a radial (fig. 13). Paramedially and dorsal to the basibranchial lies the anteriorly broad ceratohyal, extending posteriorly in a narrow curved rod. In the median, far caudally between the epibranchials we find the cross-shaped urohyal.

The main muscles are the rectus cervicus profundus and the subarcualis rectus I. The former muscle is a direct continuation of the muscle which arises as far as the ischium. It attaches anteriorly to the dorsal surface of the basibranchial just behind the lingual cartilage (fig. 13). The subarcualis is wrapped around the epibranchial in a complex spiral. The apparatus is connected to the lower jaw and the rest of the body by a complex muscular system and some ligaments.

Following this description, Lombard and Wake proceed by a theoretical consideration of the possible movements (fig. 14). Therefore they schematize the skeletal elements to straight bars and suggest the degrees of freedom of movement in the connections between the bars. They base these possible movements on observations of sections and preparations of animals with

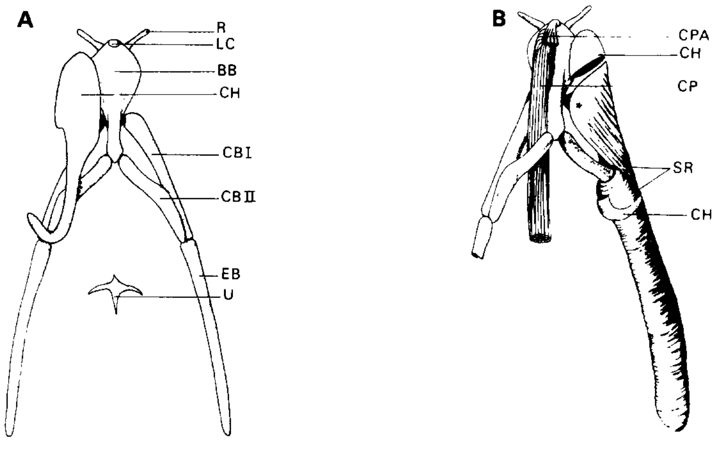

Fig. 13. (a) Dorsal view of the hyobranchial skeleton of *Eurycea bislineata*. The ossified urohyal lies approximately in the same plane as the basibranchial. The other elements are cartilaginous. (b) Dorsal view of the principal muscles. BB, basibranchial; CBI, CBII, ceratobranchial I, II; CH, ceratohyal; CP, rectus cervicus profundus; CPA, rectus cervicus profundus anterior; EB, epibranchial; LC, lingual cartilage; R, radial. SR, subarcualis rectus I; U, urohyal. From Lombard and Wake (1976).

protruded and retracted tongue. From the course of the muscles and their relative sizes they hypothesize about the working of these muscles. All this information is brought together in hypotheses on the working, for which the species *Eurycea bislineata* is the standard. It seems best to cite partly their summary of this hypothesis of the dynamics.

1. The hyobranchial skeleton is folded during the feeding sequence. Folding is achieved by opposition of joint 3 to the midline (fig. 14).

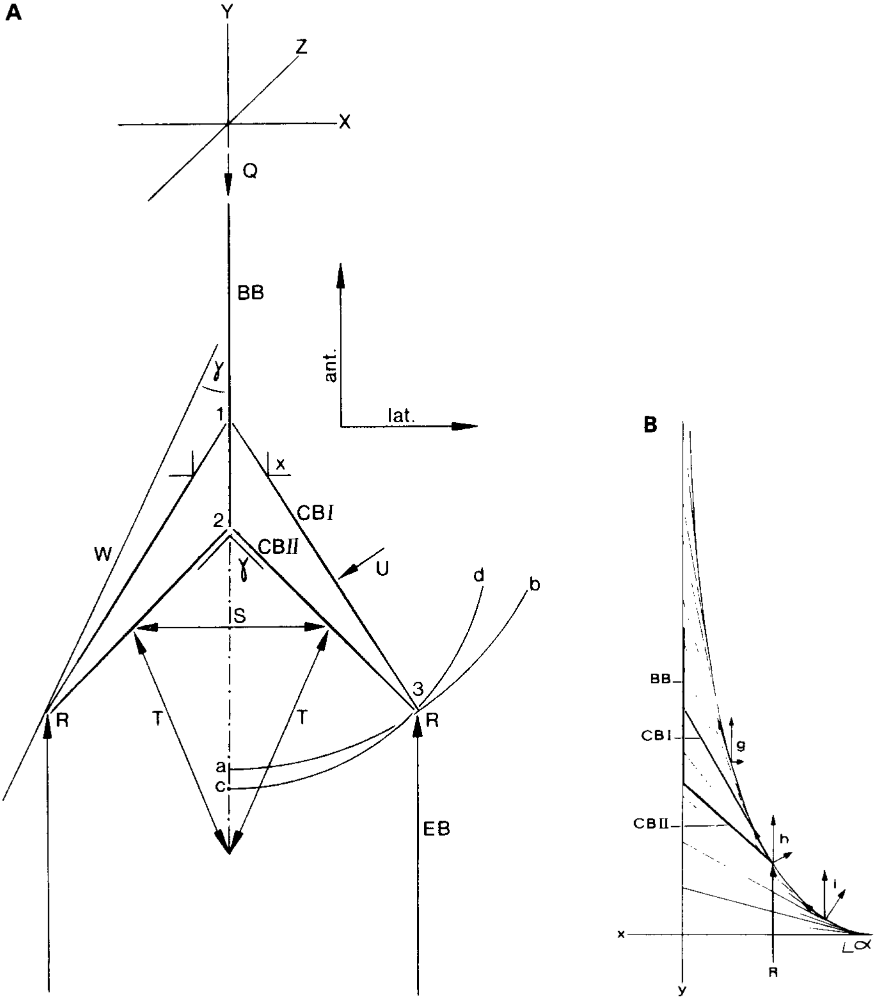

Fig. 14. (a) The principal elements of the plethodontid hyobranchial skeleton. From Lombard and Wake (1976). (b) A tractrix and method of construction. The light construction lines are of equal length and are always tangential to the curve. 1, 2, 3, joints; a, b, course of the ceratobranchials I and II in medialward folding; g, h, i, vectors normal and tangent to the tractrix; Q, R, S, T, U, main vectors; other abbreviations in fig. 13.

2. In the folded state ceratobranchial II lies superior to ceratobranchial I. Accordingly, during folding the basibranchial is rotated about joint I such that the distal tip is directed ventrally.
3. The precise degrees of folding are determined by the proportion of the skeletal elements and the relationships of their joints.
4. Projection of the tongue is accomplished by the subarcualis rectus I muscle.
5. The ceratobranchials move along bilateral tracks, which have the form of a tractrix (fig. 14).
6. Retraction of the tongue is accomplished by the rectus cervicus profundus.
7. Unfolding is accomplished along a complete or partial bilateral track that is coincident with the second ceratobranchials when the hyobranchial skeleton is at rest.

By means of microscopical sections of specimens with protruded, partly protruded and retracted tongues the authors have tested these hypotheses. Indeed they found a large agreement; only some problems on minor aspects remained. From their observations they could also give a reasonable suggestion about the direction of the forces and, consequently, the small forces acting in unfavourable directions. These latter forces can easily be absorbed by the stiffness of the connective tissues around the joints. This confirmed hypothesis of the manner of working of the apparatus is called a model, which they describe as follows:

1. The mouth opens.
2. The subarcualis rectus I muscle contracts, both squeezing and thrusting the epibranchial cartilages forward to propel the tongue from the mouth.
3. The ceratobranchial-epibranchial joints on each side ride along a morphological track formed by the lateral wall of the cavity of the subarcualis rectus I muscle. This track has the shape of a segment of a tractrix. Movement along the track forces the joints toward the midline. The distal elements of the apparatus are folded in three dimensions during this process.
4. While folding, CB II comes to lie superior to CB I and BB rotates about joint I so that its distal tip is directed ventrally. This occurs before the tip of the tongue has passed the margin of the jaw.
5. Contact is made with the prey on the axis of projection. Capture is accomplished by a mucous coating on the tongue pad.
6. The rectus cervicus profundus muscle contracts, returning the apparatus with the captured prey to the mouth. Integrity of the folded skeleton is maintained by the investing epithelial sheath which reduces disruptive forces.
7. During retraction, the epibranchials are separated and directed into the cavity of the subarcualis rectus I muscle either by a mass of connective tissue associated with the heart, or elastic recoil of the epibranchials themselves, or both.

8. The distal, folded elements of the skeleton are forced apart to the resting position by the same process.
9. The forces generated while bringing the apparatus to a complete stop are absorbed by the connective tissue mass and the heart.

This model is now used by the authors as a basis for a comparison of the diversity in feeding mechanisms among the lungless salamanders. The model is used in a *deductive methodology*. The authors try to imagine changes in the model if improvements are supposed to occur. They hold the opinion that these improvements indeed took place by the operation of natural selection. Improvement of protrusion of the tongue and more successful capturing of prey involves a longer reach or increase of distance over which the tongue can be protruded, a faster protrusion and what they call an increase in directional versatility, which could mean wider range of movement or more precise aiming at the target. These improvements find their expression in changes of the structures within the boundaries of the general salamander 'bauplan', the so-called spatial constraints and the variety of possibilities within the construction of the model. The expressions (or their various options) can be predicted to a certain degree or the predictions can now be compared to the actual situation. It can be shown now that some structures cannot or can barely change in size, shape or structure and this isometry indeed is found, e.g. in the length of the basibranchial. Other structures must change considerably, e.g. in the length of the epibranchial, the length of the retractor muscles, the place of attachment of the genioglossus and the connection of the tongue with the margin of the lower jaw. On the other hand there seems to be some degree of freedom which by and large can be predicted, but not in many details. Thus a predictable lineage is found. The lineage is not linear, in fact almost every group shows its own detailed characteristic deviation from the main line. It must also be remarked that the predictions from the model did not only concern improvements of protrusion, but also allowed for the 'less advanced' types to be understood.

There are also exceptions to the general predicted trend, e.g. *Hydromantes* seems to be such a species with many deviating features, whereas in others some minor structures seem to have a degree of freedom which could not be fitted in completely. The majority of features, though fitting in nicely, apparently belonged together in one structural totality.

The lineage is read from what they call the generalized tongue in a conservative group to the specialized tongue, the most protrusile one.

The eight discrete modes in terms of biomechanics 'conform to a large degree with current views of phylogeny' which gives the authors 'confidence that their approach is "robust" '. At a certain point (mode IV) a splitting of the main lines has been observed (EB I vs. EB II) which is believed to be an ancient adaptive choice, and also 'mode IV retained the generalized option and specialization has been constrained as a result'. Lombard and Wake assume that this was due to the retention of aquatic larvae, because the 'ceratobranchials play important functional roles and CB I is larger and has more generalized functions than does CB II'.

This study is important because it shows nicely the value of the deductive methodology for evolutionary studies (Dullemeijer, 1974; Dullemeijer and Barel, 1976). It also points to a new way of looking at structure and it lifts general description to a level of functional as well as evolutionary explanation (Gutmann, 1966; Franzen *et al.*, 1976). Fortunately the authors have not hidden the shortcomings and the gaps in their explanation.

Apparently we need much more detailed information about the food and feeding; we need more insight into the connections and constraints in the construction to understand the specific evolution. We also need another method to prove indeed that natural selection was the effecting agent. Being a deductive methodology it shows also all the risks of it (Dullemeijer, 1974), but I feel that the authors are too modest in their evaluation of their own approach by referring to 'current views of phylogeny' or by using such terms as 'advanced', 'conservative' and 'generalized'. The results and the applied methodology as such can be justified by the important insight and explanations obtained. In fact the mentioned evolutionary terms should not be used during the functional morphological analysis, but only be introduced when the results are interpreted from an evolutionary angle (which they promise to do in a third article to which I am anxiously looking forward).

From this comparison a lineage of feeding mechanisms can be established. It turns out that the model represents just a relatively advanced stage. In other words, many groups have a less specialized protrusion mechanism. The series consisting of eight groups begins with a group with slightly protrusile tongue. Folding hardly occurs. The tractrix is followed by ceratobranchial I. The tongue has a short connection with the lower jaw and flexibility of the tongue tip hardly occurs. The successive groups are arranged in order of magnitude of these aspects. Thus folding becomes complete in group IV, and simultaneously the tongue is largely freed from the jaw margin. The muscles of retraction are longer and the tongue pad becomes a complicated structure with lateral flanges and flaps movably supported by the lingual cartilage and the radial cartilages. The situation in group IV actually represents the model.

The authors distinguish a group V which at first glance is similar to group IV – there is no increase in protrusion or folding. However, this group has a number of minor characteristics which are comparable to those in the groups II, III and IV. Such small deviations from the linear arrangement occur in several groups. Therefore the arrangement should not be read linearly, although the general tendency is an increase of protrusibility of the tongue.

In group IV the protrusion is extensive, folding occurs before protrusion, the ceratobranchial II follows the tractrix and the RCP muscle is the only retractor and has become very long. In group VII the tongue pad has become larger and the basibranchial is long and narrow. The last group VIII again is a group which combines various features of the two former.

Thus we see also in Lombard and Wake's study that the choice of the functional component depends on the aim, in fact, the kind of sequence to be described. The size and the composition of the taxa or grouping, the detail and the accuracy of the inference are all related to the ultimate aim. Having in mind the construction of a lineage of functional components they come up with a different grouping from the usual taxonomic one, they consider other structures in different relations than usually is done in formal morphology. Such choices are of course open to variations, addition etc. and thus various authors can reach different conclusions, so much so that basically they cannot reach immediately agreement. The required detail of the information about structure and function is loosely connected to the size of the taxa. With higher taxa, where distantly related organisms or organs are compared, one cannot expect that detailed information is of much relevancy or that much insight in details of the forms and functions in the sequence can be obtained.

Many factors differing in the various plans of organisms interfere with the interpretation of a particular relationship between form and function, so that in the various groups we see great differences in these relationships. The particular relationship is affected by the conditions of the general plan situation, in which this relationship has to be fitted in. This aspect amounts to the acceptance of many boundary conditions. It is awkward for the construction of sequences; it is generally experienced as a deforming factor, although essential for understanding the functional components. It can also be interpreted as the occurrence of multiple functions to which the specific function-form relationship has to be determined (Zweers, 1979). The limit between specific functions and boundary conditions can shift during the procedures, e.g. if one tries to explain the shape of a part of the human lower jaw, one can take the resistance against muscular force as the specific function and the presence of the glenoid joint and the dentition as boundary conditions, together with the applied formulae of mechanics and the characteristics of the bony material. There is, however, no principal reason to consider the joint and the dentition also as functions and the remaining factors as boundary conditions. Thus we can extend the boundary conditions to the entire environment of the jaw. Many students therefore show the tendency to select groups of closely related representatives (Bowman, 1961; Darwin finches; Zweers *et al.*, 1977; Barel *et al.*, 1976; Lombard and Wake, 1977), so that these conditions can be considered the same. Only some have chosen to extend the comparison over many phyla (Gutmann, 1972, 1976), which requires a different approach (see p. 234). Thus the question of relationship of the groups precedes the choice and if the problem of genetic similarity or consanguinity is posed, this choice serves as a test to justify the original supposed consanguinity (the functional morphological complex criterion of Hecht and Edwards, 1976; Szalay, 1976; Romero-Herrara *et al.*, 1978). Again, we see thus that the inductive procedure and the results from it about the relationship between function and form do not contribute to the construction of sequences and phylogenies. The sequence was already present and the aim of functional morphology is to describe the relation between function and form. This relation as such is of no use to evolutionary biology but it describes a particular type of adaptation. *Functional morphology and evolutionary biology so far have their own domain and their own principles of explanation* (Dullemeijer and Barel, 1976).

In all studies we find a necessary tendency to switch to the *deductive methodology* (Dullemeijer and Barel, 1976). This method has in short the following steps (Dullemeijer, 1974): the activity is described and from this a theoretical form, *model* or *paradigm* is constructed with an assumed relation factor (fig. 15), then the model is compared to the real form. Again, for the construction of the model many other factors are used, known as the boundary conditions. These boundary conditions are generally sufficient to restrict the model to one, in the case of more possibilities they have to be selected on other arguments, or all have to be considered in the comparison. The boundary conditions are the kind of material, spatial restrictions, connections to other functional components (systemizing concept of Zweers, 1979) and the mathematical formulae (Dullemeijer, 1974). Notwithstanding the exact description of the function and the boundary conditions, it is necessary to introduce a principle of optimal design to restrict the number of models.

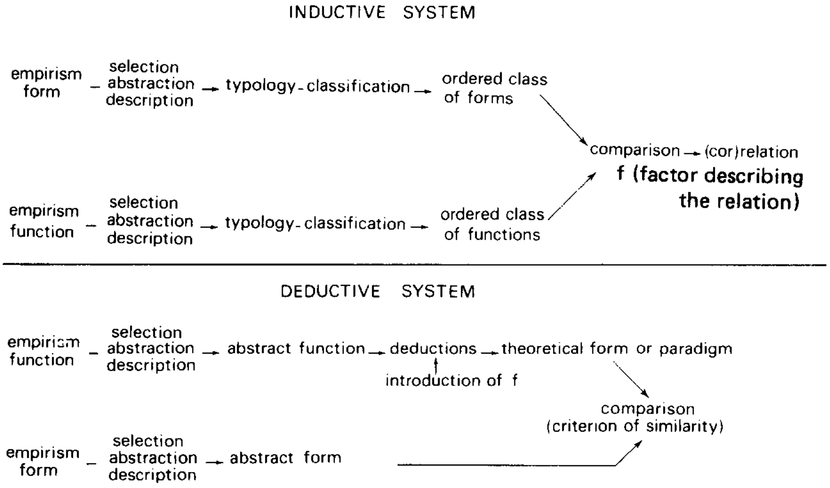

Fig. 15. Successive steps in the procedures of the inductive and deductive systems.

The optimal design is always somewhat arbitrarily determined, it depends on how well the activity has to be performed and how efficient the functional component has to work. Somewhere the principle is an expression of adaptation. The deductive method is also called the non-comparative method (Dullemeijer, 1974) because it can be and is essentially considered as one case.

For the construction of the sequence the method is not sufficient, just as the inductive method by itself does not contribute to sequence formation. The members of the sequence have to be chosen already before the method is applied. Yet, having selected a number of related organisms for the construction, there is a difference in the construction of the sequence with either method. With the inductive method new aberrant cases can change the entire sequence without obtaining any insight into the aberration, whilst on the contrary, in the deductive method it becomes immediately clear why we have an aberration and which factor is responsible for it (Lombard and Wake, 1976, 1977). In the latter method it is also possible to construct a sequence which is founded on inferences from the functional morphological analysis. The activity, the boundary conditions and the conditions of optimality particularly are parameters suitable for arranging the construction in a certain order. We cannot avoid the subjective idealistic ordering but the quantification gives us a better argument for the sequence, especially in the combination of the mentioned parameters (Dullemeijer, 1959; Lombard and Wake, 1976, 1977; Gutmann, 1976). The direction of the sequence is not quite certain yet, but the chances are better if the sequence is read in the direction of improvement of the conditons of optimality, more efficient realization of the actual form and if the direction is given by the constraints of the construction. There is a *constructive constraint* in the boundary condition, but it is not yet clear whether we can call this an *evolutionary constraint.* Efficiency is difficult to measure and the effect of the constraints in the construction are generally recognized (Franzen *et al.*, 1976; Gutmann, 1976), but rarely demonstrated. Only in those cases where the effect of constraint in the construction is known, or in cases where there is suboptimality, can we hope to have a measure for polarity for the sequence. The only cases we have available to date are compromise situations. In these the activities are performed suboptimally. A shift in the compromise can improve one or other activity, or by differentiation the functional components can be separated. Examples are rare, and little attention has been paid to these phenomena. Indeed, there are a number of sequences of recent forms where optimum shifts are presumed to occur, but due to the application of the inductive method instead of the deductive one the proof of such a shift is not given. Yet we shall discuss some examples, notwithstanding the deficiency in the inference.

The best of such examples seems to be Bock's study (1960) on the second joint between the lower jaw and the base of the skull in *Rhynchops*. In many birds we find a ligament connecting the processus basipterygoideus of the lower jaw with a process on the basisphenoid. In *Rhynchops* the processus are enlarged and meet each other, forming a true articulation.

Bock suggests a function of this articulation as being a bracing mechanism to counteract the force during feeding. *Rhynchops* catches fish by flying with its lower jaw in the water. A prey is caught when it bumps against the jaw. For this activity an energy absorbing and bracing mechanism seems to be very useful. We find comparable structures in other birds, like gulls and terns, although less developed. Clearly we can read the sequence in the direction of improvement of the structure for catching fish. Yet this example is not the one we need to prove the case. Although in Bock's reasoning a brief moment of deductive reasoning must be present, the main argument is based on the derivation of the activity from the structure, knowing the method of catching prey. Indeed there is the possibility of a straight deductive reasoning. If we try this we see that in the series of models the optimal design principle is the same. It is the demand, the activity, which changes. The sequence therefore is based on the quantification of the activity or the improvement of the function and not on improvement of the structure. The boundary conditions which should be necessary to explain the specific position of the articulation are not known yet, so that also from these parameters no polarity of the sequence can be derived.

We meet the same difficulties in my study on the viperid head (Dullemeijer, 1959), notwithstanding the application of the deductive method. The ectopterygoid in various Viperidae has roughly the same shape, details varying among the species. The ultimate model, and thus also the real shape, is an integration and partly an addition; each activity is optimally performed within the boundary conditions. Again the sequence can only be constructed by quantifying the activities rather than changing the optimalization.

From these two cases we find that we need an example in which the deductive method is applied including *suboptimalization*. This does not exist by definition, but there are numerous examples of biological suboptimal *realizations*. Examples of these suboptimal realizations can only be found in *compromise* solutions. The peculiar situation now is that everybody agrees that there is a host of compromise structures, indeed that almost any structure is a compromise, and that organisms as a whole are always compromises in their ecological situation, but nowhere is it used to construct sequences.

A very simple example of a compromise situation is found in the position of the ilium in mammals. In small mammals, the ilium is oriented almost parallel to the vertebral column, but in the big animals the ilium stands perpendicularly to the column. The position is important for standing and locomotion. For standing the perpendicular position is the most efficient (less bending strain). For locomotion a parallel condition is best (efficient force application). The latter condition would be very inefficient in large animals because of the strong bending strain and consequently the enormous increase of the thickness of the bone. But this implies an unfavourable position for locomotion. The reverse holds for small animals, unless these move very slowly. In the latter case they can have a perpendicular position (e.g. chameleon). The most frequent position assumed is about halfway. Both functions are suboptimally realized. All these intermediate positions can be placed in a sequence, which can be read in the direction of locomotion or of standing. In these directions there need not be a better overall efficiency, one of the functions is better performed, the other in fact worse, and thus is less optimally realized. The optimalization for the model is the same. However, in these cases it would also have been possible to obtain the same result by assuming a suboptimality in the model. The latter method has serious drawbacks. The measure in which suboptimalization must be introduced is unknown and, by definition then, the compromise cannot be found anymore.

It is most likely that the degree of adaptation, defined in terms of efficiency or energy balance, is the same in any of the compromise situations. Thus this degree does not give us a hold for the determination of the polarity.

There remains, however, the possibility that the sequence has to be read in the direction of a constructive adaptation to one of the functions, e.g. in the example to standing with an increase of size. This is a most unlikely situation, however. It would imply that we can place the various functions or the environmental factors in a polarized series. For such a proposition we need, of course, direct evidence that the organisms have indeed moved to the other environment.

A last possibility seems to be to chose improvement as the measure for the polarity. This has been proposed by Lombard and Wake (1977) and Zweers (1979) and for a broader comparison by Gutmann (1976) and Bonik *et al.* (1976). It is supposed that the environment stays the same with respect to the observed function. The function is improved by change of the construction, e.g. tongue protrusibility for capturing prey (Lombard and Wake, 1976, 1977), straining and picking capacity (Zweers *et al.*, 1974, 1977), locomotion (Gutmann, 1966, 1972, 1976). The improvement does not have to automatically imply a more efficient or a more economic performance of the original function, but in fact will in general imply more specialization. In the three examples mentioned, there is most probably a mixture which makes the maintenance of the organisms with the original function understandable.

Lombard and Wake (1976, 1977) presuppose similar kinds of prey to be captured in more or less comparable situations. Thus, the function as such is improved. However, in view of the non-linearity and the variation in structures, one may suspect that detailed research into the prey and the way of catching prey would force us to conclude that we are dealing with a change rather than an improvement. There is no improvement of function, but a specialization. By and large the same holds for the locomotory function (Gutmann, 1972). From Zweers' example it is particularly clear that we are dealing here with a change or shift of activity, such that specialization takes place. The mallard is able to strain food, to pick up particles or to graze. It can do this by means of its moderately wide beak, the sieve apparatus, a moderate pumping system, etc. The shoveller is not able to graze or to pick up large particles, but his sieving ability is much better than that of the mallard (Zweers, in press). Along with a change in beak shape go changes in muscle proportions, tongue structures, etc. The diving duck can hardly strain at all. Its beak is narrow and pointed, the sieve apparatus small and the muscles constructed for powerful picking and holding. We cannot say, however, that in their own domain one is better than the other. Only when they are compared for all three activities is one better, in the sense of specialization, than the other.

In the example of waterfowl the mallard is a generalist. It probably has a better chance of survival, so if this criterion is chosen for improvement the sequence would read in the direction of the 'generalist'. The results of all these efforts to establish the polarity is that we can indeed make reasonable and biologically interesting sequences, even though we never can be sure that we have a real lineage. The best chance of obtaining a real lineage remains of course in these cases where a real, solely improvement in efficiency occurs, during which the activity has to remain qualitatively the same.

The acceptance of the latter condition is dependent on the amount of detail required, the already-defined extension of the problem and the choice of the groups and level of organization (we return to this aspect on p. 233). Knowing this, it is no longer important which species or form is taken as the generalized one, so long as it is not supposed that 'generalized' is equal to 'primitive' or 'original'. We cite the examples presented by Dullemeijer (1959), Zweers (1977, 1978), Lombard and Wake (1976, 1977), Barel *et al.* (1976, 1977).

IV.5.b. Direct evidence. The additional information to establish the polarity, and in particular the reality, of the sequence can only be provided by the so-called direct evidence so long as we do not have other evidence for a constraint direction in evolution. This direct evidence must be evaluated of course with all the precautions mentioned by various authors (Patterson and others).

We shall consider two examples, a study by Robinson (1975, 1977) on plesiosaurs and by Crompton *et al.* (1963, 1978) on synaptid reptiles. They show the deductive method and the formation of sequences respectively.

Robinson's study (1975) on the locomotion of plesiosaurs is a deductive approach and thus has a predictive trend for the explanation of structures.

Any design of an evolutionary series as an improvement could not yet be made, due to the lack of clear transitions from one type of locomotion to the other. There is a functional dichotomy, as she calls it, between the locomotion types of rowing and subaqueous flight. Although there are theoretically intermediate types there are many features in practice which make these types separate in structure and function.

In table 1 we have copied Robinson's table 4 in which she summarized the differences between the rowing and the flying types. In this list we recognize the description of how principally both types differ in their operations and how the structures have to be (optimalization principle) in order to perform these functions. The theoretical model is demonstrated in technical constructions, which are used as a reference for the comparison of the structure of the fossils. Some prediction could be developed beforehand, because the technical construction already shows a size dependency in the efficiency of the type. Given this type difference in terms of efficiency it is possible to indicate how the systems could be improved (third part of the table). Accepting the technical analogy, expectations about the morphology can be made (morphological implications) and these can be compared to the actual situation.

Robinson has selected four plesiosaurs of which the entire skeleton is well preserved and shows many features important for reconstruction of muscles. Moreover, she used two plesiosaurs of which the paddle outlines could be observed. The plesiosaurs show great similarity in their limb and girdle structures, which are summarized in table 2 borrowed from Robinson. All these structures agree with the expectations for a subaqueous flying type but not very well for a rowing type. Considerable details in the morphology could also be explained by supposing this type of behaviour.

Muscle reconstruction on the basis of observable scars and rugosities (places of attachment) on limbs and girdles and comparison to primitive reptiles endorse the conclusion. It is noteworthy that Watson (1924) and Tarlo (1958) arrived at another reconstruction by starting from the opinion that rowing was the type of locomotion. They did not observe a number of muscle attachments. This points to the danger in the procedure, viz. that the accepted type of function influences the suggested reconstruction, which should be done, of course, completely free of any presupposed interpretation.

Robinson did not use her findings for interpreting the direction and course of the evolution, although she made a few remarks about the primitive stage which were supposed to be less efficient. It seems therefore that the methodology she applied can indeed show us the direct derivation of specific structures and that much of the detail in the structure can be weighed. A large number of details within the boundaries of the general form remains puzzling, but it can be concluded already that these structural features can be explained only by relating them to subordinate or more detailed functions

Table 1. Summary of the principles of rowing vs. flying. From Robinson (1975).

Rowing	Flying
Oar:	Hydrofoil:
1. Purpose: To exert backward force on the water; to create maximum turbulence and drag; to remain 'fixed' in the water.	1. Purpose: To create lift; to create as little drag and turbulence as possible; to move rapidly thru the water, accelerating it backward.
2. Shape: Flat plate, uniform in breadth from proximal to distal ends, or broadening distally.	2. Shape: Cambered plate, tapering toward its distal end.
3. Orientation: At right angles to its direction of motion.	3. Orientation: At an angle of 10° – 20° from the direction of fluid flowing past it.
Stroke Orientation and Characteristics	Stroke Orientation and Characteristics
1. Components: a. Propulsive stroke: antero-posterior; force imparted to water. b. Recovery stroke: postero-anterior; no force imparted to water.	1. Components: a. Downstroke: Posteroventral; force imparted to water. b. Upstroke: Posterodorsal; force imparted to water.
2. Rotation: 90° necessary.	2. Rotation: 120° or more required.
3. Sweep: restricted to ± 45° from the perpendicular.	3. Sweep: The larger the better; increase of wind disc is favorable.
4. Form: Straight line in horizontal plane, or figure – eight elongated in horizontal plane.	4. Form: Figure-8 elongated in the vertical plane; if 8 is inclined, angle of wing may compensate.
Force and Power	Force and Power
1. Objective: To impart maximal force backward on water.	1. Objective: To accelerate a large amount of water backward.
2. Options: a. Increase mechanical advantage. b. Make muscles pinnate c. Add a second joint or move the first joint. d. Decrease velocity ratio. e. Increase muscle cross-section.	2. Options: a. Increase wing disc. I. Length wing. II. Increase vertical sweep. b. Increase velocity of wing c. Increase angle of attack
3. Mechanical analogy: Levers.	3. Mechanical analogy: Propellor.
Morphological Implications	Morphological Implications
1. Limb oar-shaped	1. Limb hydrofoil-shaped
2. Major muscle masses post to glenoid	2. Major muscles masses dorsal and ventral ventral to glenoid
3. Muscle insertions strongest ventrally	3. Muscle insertions equally strong dorsally and ventrally
4. Rotation of joint: 90° vertical to horizontal	4. Rotation of joint: 70° in one plane to ± 50° in the other
5. Sweep of limb restricted, either physically or with muscle arrangement	5. Sweep is limb unrestricted; physical and muscular restraints lacking
6. Force of muscles exaggerated; compromise; force and velocity	6. Compromise: speed and sweep; force to overcome drag

in their course of change during evolution. Here again we get the impression that there are analogous developments particularly when she compared

Table 2. Similarities of functional-morphological features in fore- and hindlimbs and girdles in plesiosaurs. From Robinson (1975).

1. Fore- and hindlimbs almost identical in shape and construction but not necessarily in size.
   a. All elements in the horizontal plane; flattened elements are flattened horizontally.
   b. Hyperphalangy, especially in digits 2, 3 and 4.
   c. Phalangeal elements short, rounded pillars.
   d. Phalanges in overlapping pattern anteroposteriorly.
   e. Phalanges united within foil-shaped 'wing' tapering distally and thinning toward posterior border.
   f. Podial elements flat and interlocking.
   g. Epipodials short and flattened.
   h. Propodial-epipodial joints often marked by retained pisiform, 'accessory ossicles' (Andrews, 1910) or sesamoid elements.
   i. Distal ends of propodials anteroposteriorly flared.
   j. Propodials with large ventral muscle scar near head.
   k. Propodials with dorsal process (humeral tuberosity, femoral trochanter) capped with cartilage and confluent with the articular head, and upon which muscle scars are visible dorsally.
   l. Propodial heads at large angles to their shafts.
2. Pectoral and pelvic girdles similar in shape and construction, and in several features, mirror one another.
   a. Dorsal elements (ilium and dorsal blade of scapula) small relative to other endochondral girdle elements.
   b. Dorsal elements removed from joints; dorsal blade of scapula well anterior to glenoid, ilium at posterior border of acetabulum.
   c. Broad ventral plastron.
   d. Posterior plastral elements (coracoids) larger in pectrum, anterior elements (pubes) large in pelvis.
   e. Scapula with large ventral porcess mirroring the posterior ischial plate.
   f. Articular surfaces asymmetrical.
   g. Interarticular thickened ridges divide pectrum and pelvis into anterior and posterior basins.
   h. Right and left halves of girdles meet at an angle in the midline.

Chelonia, *Zalophus* and *Spheniscus*. She has, however, sufficient evidence that the differences are due to other constructional demands (boundary conditions for the specific locomotory functions) related to other functions, e.g. shell structure in *Chelonia*, terrestrial locomotion in *Spheniscus*.

In a subsequent study Robinson (1977) could show partly by inductive, partly by deductive, reasoning that many features, if not all, of the major skeletal construction, and the difference between the long-necked and short-necked plesiosaurs could be attributed to their way of locomotion. In the two groups, plesioauroids and the pliosauroids respectively, the force transmission is different. However, the difference has, as boundary conditions, the difference in feeding and food; probably the plesiosauroids were agile, catchers of large prey and could develop high speeds in short periods (sprinters) whereas the long necked pliosauroids were endurance swimmers and 'grazers' of small prey.

The investigation into the evolution of the new jaw joint and the ear ossicles in mammals by Crompton (1963, 1978) concerns the inductive formation of a series with a slight element of deduction. But first the fascinating story of the transitional forms from reptiles to mammals as told by Crompton and Parker (1978) is worth repeating briefly. As has already been known for over a century, several reptilian jaw bones were transformed in mammalian earbones (Reichert's theory, fig. 16). Parallel to it a differentiation in the dentition into incisives, canines, premolars and molars and a change of the musculature took place. Reptiles have many bony elements in their lower jaws of which the dentary carries the dentition, composed of more or less similar teeth which can be replaced such that everywhere new ones can be added. Replacement occurs, however, in a regular pattern. The posterior lower jaw parts are partly membrane bones surrounding Meckel's cartilage of which the caudal thickening ossifies to the articular. The latter bone articulates with the quadrate which in its turn is dorsally jointly connected to the posttemporal or squamosal bone. Behind the quadrate we find the tympanic membrane in the centre, supporting the extracolummella or extrastapes. This extrastapes is a cartilaginous or bony extension of the stapes running from the oval membrane of the inner ear. The stapes is generally considered homologous to the hyomandibular, which lies in fishes between the skull and the quadrate. Ancient reptiles did not possess a tympanic membrane, it occurs only in modern and extant forms. In mammals, all the posterior lower jaw bones, the quadrate and the stapes have become exclusively ear bones. Only the dentary remains a jaw bone and forms a new articulation with the squamosal. This transformation was already established by Reichert and confirmed by many other authors on ontogenetical grounds.

It was also held as the evolutionary course, but up to the beginning of the sixties, direct proof was lacking. There were some suggestions of a functional explanation by Broom (1930) and Parrington (1946), but these were not quite satisfactory. In 1963 Crompton published his analysis of *Diarthrognathus*, a fossil which is a real link and from then on new evidence was rapidly added by Crompton and Parker (1978), Allin (1975), Barghusen

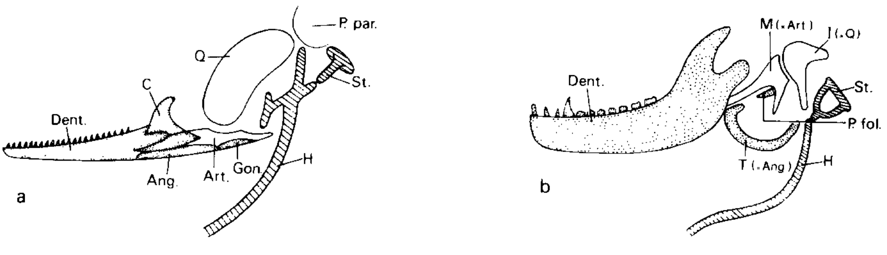

Fig. 16. Schematic representation of the homology between the jaw bones of reptiles and the ear ossicles in mammals according to the theory of Reichert. From Van der Klaauw (1945) after Gaupp (1913).

(1968) and Parrington (1971) which showed without doubt the correctness of this transition. Still the question remained: What was the functional reason for this sudden change, this key innovation? Present knowledge of the changes of dentitions and musculatures allow a fair suggestion about the functionality.

Two lines of reptilian development are distinguished (fig. 17), one in which the tympanic membrane arises behind the quadrate, leading to modern reptiles, the other leading to the mammals in which the tympanic membrane develops just ventral to the jaw joint between two processes of the angular bone. The latter becomes the mammalian tympanic ring. Articular and quadrate become the malleus and the incus respectively. The depressor muscle disappears and the jaw despressor is formed from the hyoid muscle system: the musculus digastricus. The adductor muscles originate in the reptiles inside and on top of the jaw. In the mammals the external adductor complex is extended to the temporal region whereas the medius part develops into the masseter complex.

The functional change is thought to consist basically of a differentiation into the two functions, hearing and food uptake, which are performed simultaneously by the same bones in the reptilian condition. It is supposed that the stem reptiles could only pick up ground vibrations by their jaw bones, and later developed two types of tympanic membranes. The quadrate-articular joint therefore had to be unloaded. Therefore the muscles had to be rearranged. This was possible by a differentiation of the dentition into a biting part and a chewing part, so that the chewing pressure and the muscle force were in equilibrium without a resultant force through the jaw joint between quadrate and articular. A new position of a resultant force, although much smaller than the original reptilian one was conducted through the dentary-squamosal connection.

Crompton was now able to construct a sequence of fossils in which all these transformations could be shown as an almost continuous series (fig.

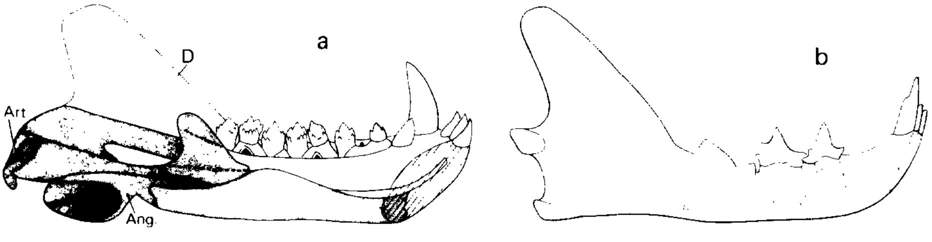

Fig. 17. The transition from the reptilean lower jaw (a) to the mammalian mandible (b). After Crompton (1978). Stippled, lacteal dentition; unstippled, permanent or replacement teeth. Darkly stippled, various reptilean bony elements, among them the articular (Art) and the angular (Ang) forming the notch for the future mammalian tympanic membrane. D, outgrowth of the dentary.

18). Differenences of opinions still exist about the development of the tympanic membrane (Parrington), the precise representations in the series (Barghusen), the dominance of the functions (Allin), but the general trend seems to be well documented.

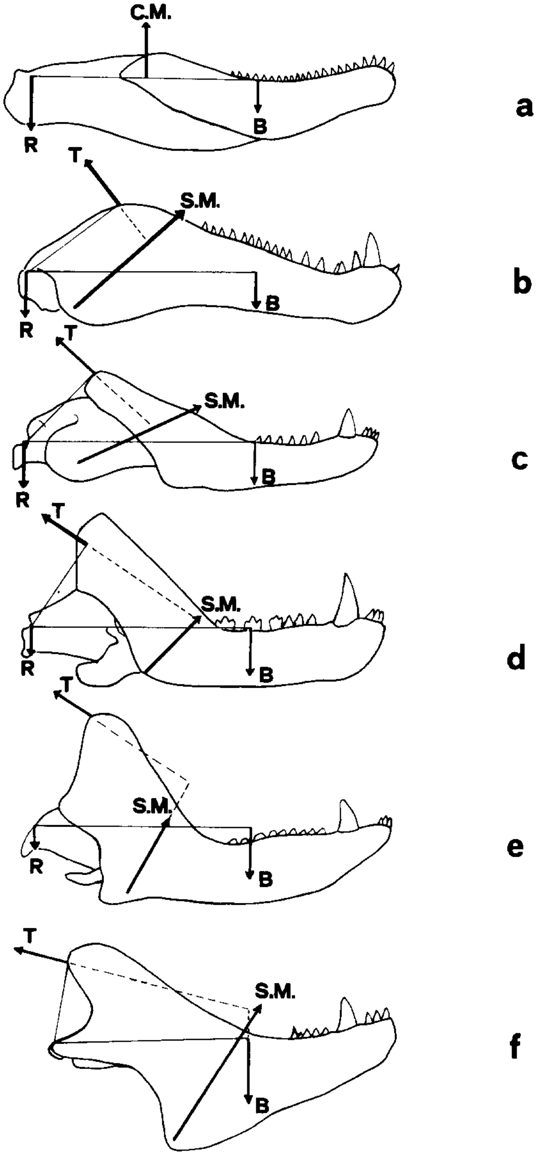

Fig. 18. Evolutionary series of lower jaws of mammal-like reptiles, after Crompton (1962). a, *Labidosaurus*; b, *Dimetrodon*; c, a therocephalian?; d, *Thrinaxodon*; e, *Trirachodon*; f, *Diarthrognathus.*

This impressive study shows clearly the importance of an understanding of evolution by means of functional morphology. Given this important meaning it is now our task to delineate the boundary conditions for the procedure and thereafter try to indicate the possible progression in this kind of biology.

The procedural steps in Crompton's and Allin's studies can be listed as follows: a selection of the representatives in the phylogenetic series, the delineation of the area to be analysed, the reconstruction of structures not immediately available in the fossil record, the derivation of possible functions of the system, the implication of these functions for the structures, the evaluation of the sequence and, as a last though not essential step, the formulation of hypotheses on the biological meanings and the causes of this particular evolution. Some of the procedures we have discussed already in 1974 (Dullemeijer, 1974), but since then (Crompton, 1963) great progress has been made in the investigation (Crompton and Parker, 1978) and the relationship of functional morphology and evolutionary biology has been analysed further (Dullemeijer and Barel, 1976).

The selection of representatives is not a very important issue anymore. The same procedure has been followed as described by Hecht and Edwards (1976) and Szalay (1976) and although alternatives could probably be described (Barghusen, 1968), the general trend would still not change. Only those investigators interested in the succession of the particular species and details in these groups could hold a different opinion. Those interested in the explanation of the described transformation can at least use these representations as a series of models or a homologous series (with all the inductive and subjective interpretation already discussed).

The delineation of the area is more difficult. Here we meet the same problems as in the functional morphology of extant adult forms when studied from a holistic philosophy. In this area we are dealing with a part of a network which covers a great deal of the head and in terms of survival almost the entire animal. This is a handicap for all workers in functional morphology. Pragmatically and intuitively we select a part; this is not a serious disadvantage so long as we are willing to accept that many factors outside the selected area can influence the system. The larger the area and the more parameters we can take into account, the better the explanation. This progression we also observe in Crompton's analysis from 1963 to 1978.

In the system under discussion we have two important, probably dominant functional components, which is a great advantage for the analysis over other studies as we shall see further on. It implies little influence from other functions, only a few boundary conditions, but an important effect on the surroundings which must be able to undergo this effect. Probably many other important features had to change, or be present to 'allow' this transformation.

The reconstruction of, in general, soft parts is a technical problem rather than a methodological one. As has often been explained, paleontologists use the results obtained from the analysis of recent forms to interpret their material. The only handicap is that some of the relations can only be read in one direction (see also Kemp, 1969). In the example mentioned this is no great handicap, because the main functional components consist, for the greater part, of hard well-fossilized structures. More difficult is the functional interpretation. Here Crompton and others use partly a deductive method and although not mentioned particularly their method has great similarities with the paradigmatic one proposed by Rudwick (1964). The general function is derived from an analogy to recent forms, but more detailed derivations necessary to understand the sequence rely on a suggestion about the function. From this suggestion a theoretical model of the structure is derived. In the same way as in the study of recent material there is a great danger of circular reasoning, the more so because of the derivation of the general function by analogy. Unfortunately there is hardly any alternative, and with a dominant function there is less risk. However, when it comes to interpretation of details opinions can differ considerably. Comparing analyses of the feeding mechanism, the use of muscles and the dentition (Frazetta, 1959, 1966; Jordansky, 1964; Dullemeijer, 1959; Van Drongelen, in prep.), it is not difficult to imagine other force diagrams than Crompton did which can also explain the other loading of the jaw and the development of the masseter muscle. It may even be necessary to look for an alternative explanation of the loading of the jaw joint, as in recent species the joint is never completely unloaded during all jaw movements (Weys and Dantuma, 1975; Hiiemae, 1978). The same holds, but probably to a lesser degree, for the interpretation of the ear ossicles. This is not saying that Crompton's interpretation is unlikely or that it should be rejected, but it points to alternatives on which future research should be focussed. This case shows clearly that only by functional morphological interpretation can we hope to get some insight in these transformations.

The causal explanation of the sequence depends of course on the mentioned procedural steps. From the material as such and from the foregoing methodology no causal factor can be derived. It may indeed be natural selection operating on a plastic or mutational material; it is also possible that the construction had already such a built-in adaptability that the organisms could readily extend to other ecological niches. To decide between the selectionist and neutralist point of view needs further argument (Romero-Herrera *et al.*, 1978), although the large change in genotype seems to make some effect of natural selection necessary.

Crompton's study can be summarized as an example of a continuous series in which we can understand the transition by a functional separation of the functional components. It seems that evolution follows the constructional constraints in the direct ancestor of each member, and thus the construction of each ancestor is an absolute prerequisite for the following member. There is no constructional improvement, but a differentiation. Whether there is ecological improvement by a better energy balance remains an open question.

IV.6. Functional component and evolution

These aforementioned studies show that two dominant functions explain the greater part of the structural differences and many, if not all, details of the structure of the bony, fossilized elements. Supposing we could set up a sequence, the question may be asked, are these two main functions an indication of selective pressures in the area of feeding and locomotion?

Again we must conclude that natural selection gives a reasonable explanation, but that other solutions are not excluded. Taking a rather extreme opinion implies that every functional component has arisen by the operation of natural selection. The opposite extreme position is that due to the complicated constructional interrelationship of the members in the pattern the variation, although random, must produce a specific functional component or set of functional components. There are a number of reasons why we cannot chose between these alternatives. We shall discuss this in the final section. Here it suffices to note the impossibility of deriving such a choice from a study without considering the functional components, for we have chosen and selected the functional components as adapted features. Only in these cases where we could prove suboptimal situations might we suppose a less rigid connnection to natural selection; in all other cases any feasible conclusion cannot yet be drawn.

As was argued previously, there are moments in science where the concepts are so wide and universal (adaptation and natural selection) that nothing is gained over the simple observation that animals live or have lived. Such a situation does not stimulate further research. Therefore we must try to fill in the actual factors operating in variation, mutation and natural selection and how they operated. Unfortunately we can only speculate, because in most cases we do not know them and frequently we have to be satisfied with the description and analyses of the function and its relation to structure. This is what functional morphology here can do, and at best give some wild suggestions about the real agent during evolution.

IV.7. Pattern – series

The studies of Crompton and Robinson have already revealed the apparent connection of various functional components at various levels of organization. It was found that sometimes there was a tendency to separate these functional components, and sometimes there was a combination in which various degrees of integration and compromise constructions are found (Dullemeijer, 1974). The recognition of these combinations of functional components in one system can now purposely be made the object of research.

We call this a holistic or system-theoretical approach (Meyer-Abich, 1940; Van der Klaauw, 1945; Von Bertalanffy, 1952, 1960, 1968, 1973; Dullemeijer, 1956, 1968, 1974; Koestler, 1967; Koestler and Smythies, 1971; Weiss, 1969). There are such differences between these approaches (Dullemeijer, 1974) that they vary from approaches which can hardly be distinguished from the analytic-atomistic approach to systems in which a completely new terminology has been developed.

It is important first to describe briefly the methodology of the holistic approach to appreciate the methodology and the results obtained for evolutionary biology. Here also there are basically two methods: the inductive and the deductive method. The inductive method consists in selecting a number of organisms, distinguishing functional components, listing many structural details of them, correlating the features of these functional components by comparing the organisms, connecting the functional components by putting the correlation in a sequence and setting up a hypothesis to explain the correlation and describing them as networks. The deductive method follows a number of similar steps, but when it comes to describing the correlation, the effect of a change in one functional component for the entire network is theoretically designed and then compared to the actual forms. If deduction is properly carried out it can be used to infer future or expected forms supposing that evolution follows these lines. In still another presentation it can be imagined how certain functional components should be improved and to evaluate this effect for the entire organism. Such a procedure, sometimes called construction morphology, can teach us the potentialities and constraints in the evolutionary process and the role of selection pressures (Gutmann, 1966; Dullemeijer, 1974; Lombard and Wake, 1976, 1977). Again the relationship between functional morphology and evolutionary biology will be demonstrated with a few examples.

There are only a few examples described in the literature where a holistic approach has been applied and even less where morphological networks have been described. There is no analysis where indeed the entire organism is studied.

The network diagrams and flow charts have been common pictures in all kinds of sciences and technologies in recent decades. They are discussed in system theory and graph theory. Most of these diagrams can really be called flow charts, only a few are construction networks. An analogy with the design and operation in a factory may elucidate which kinds of networks we can expect to occur in biology and which particular in morphology.

The design generally starts with a list of demands translated into specifications. The specifications must in some way be such that they belong together, are connected, but do not hinder or overlap each other. The general picture for that is a diagram built up of blocks and connected by arrows (fig. 19). The blocks represent the members, the demands or the specifications and the

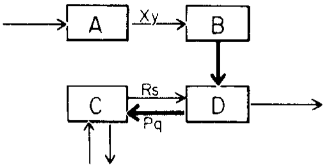

Fig. 19. Simple diagram of a system. The blocks represent the members in the system, which are connected (arrows) by features or properties of the members. The closeness of the relationship can be indicated by the thickness of the arrows.

arrows show their relationship. When we have a factory in mind, the blocks stand in general for required activities and the arrows for the mutual influence between the activities. A number of other networks are derived from this diagram of activities: first, a flow chart which shows the handling of the products through the factory; second, a flow chart picturing the energy stream or other supplies; third, the diagram of the connection of the apparatus; fourth, a diagram picturing the employee organization, fifth, the construction diagram of the building. The latter diagram must include the demands for the others. These factors all figure in the design phase. If now the factory has to be built, the constructor sets up another diagram for the planning of the building and the supply of building materials. We could extend these diagrams to the operation and sales management and the operation of the whole organization and the building. All these diagrams have their analogy in biology.

We shall now distinguish two groups of networks, the one in which the activities and processes connected to the handling of the products are pictured, which we call *flow charts*, meaning that the products 'flow through' the organization, and the other in which the construction of the building, the machines and the employees is figured, which we shall call *networks* and particularly for morphology we shall call the network of the building a *pattern*. From the analogy it is clear that an understanding of the pattern can be obtained if we have insight into functional demands, constructional demands and the material of which it is built. These three aspects are treated in the various subareas of functional morphology.

As any pattern in biology originates from another pattern in ontogeny and phylogeny it is not difficult to extend the procedure to these dimensions. In this area of research alone, a holistic or system biological approach can contribute much to evolutionary biology (pace Reed, 1978). It is likely that this approach will make Ghiselin's so-called selective retention law (Ghiselin, 1969) understandable. The analogous phase of the constructor planning is the area of genetics and ecology in biology.

How can we design a pattern? The first step has already been taken by establishing the relationship between function and form into functional components. The combining of functional components with the aid of the analysis of their interrelations by the methods mentioned results in such a pattern. It is the result of the synthesis after the analysis of the functional components. Three examples of the work in our laboratory will be presented.

In 1956 I published an investigation into the functional morphology of the head region in the common viper. The result is presented in fig. 20. In this animal a number of main functions were distinguished, indicated by the three-dimensional blocks. The relationship between the structures was analysed, for some in great detail, but for others only suggested. Much work has still to be done. It turned out during this analysis that the functional components were connected by different structural features, called properties, such that the presence of a specific feature of the structure in one component could be considered a demand for a feature in the structure of another component. As almost each member of a component is connected by a member of another component, this demand of one component in the other does not stop there. The second component will be a demand for a third in which the demand of the first is included, although in a different and less intensive way. Thus a functional component cannot exactly be delineated but shows the characteristic of a field decreasing its constructional consequences (its presence) from a centre, extending almost through the entire pattern (Dullemeijer, 1959). Characteristic for the pattern is the degree of freedom and the degree of dependence each member of a component and each component has. If the figure of the pattern is drawn with only comparable consequences (= demands) (in the figure the arrows) then the outgoing arrows represent the degree of freedom and the ingoing ones the degree of dependence. The direction of the arrows is found by constructional calculations and logical derivation. It means that one component (or number or element) has constructional consequences for the others if the components must maintain an organized totality. A direct causality does not automatically follow, although in various cases logical and constructional derivation could be equalized to causal influence (see for discussion Dullemeijer, 1974).

Thus we have a simple method to classify the elements (or members) into *dominant* and *subordinate* ones. It should be noted that dominance holds for specific features of an element, so that an element may be dominant for one property and subordinate for another. Subordination does not mean that elements can be missed or are in any way non-functional.

Such a pattern can be constructed for a number of species. The patterns can be compared in differences and similarities and put in a sequence. As could be expected, differences in subordinate elements affect only a small rather local change in the pattern. Differences of dominant elements can be perceived in almost the entire pattern, it looks like a jump in change. To the dominant elements belong those connected to the main functions, particularly the sense organs and epithelially lined cavities.

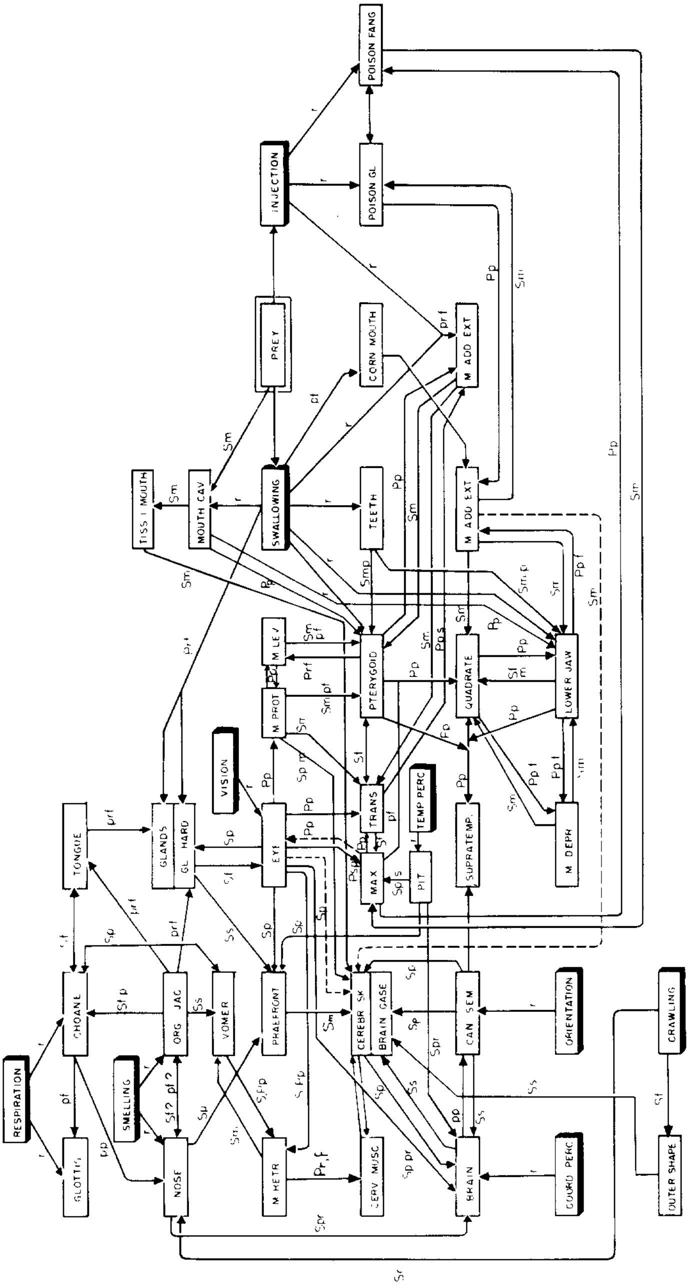

Fig. 20. Pattern of interrelationships of elements and functional components in a crotalid snake. The three-dimensional rectangles represent activities, the other rectangles are the structural members. The arrows are the relations – they run in the direction of the subordinate member. The capital letter is the subordinate feature of the member, the small letter the dominant feature.

From the pattern a rough guess may also be made as to the viability of the organism when some change takes place, even the effect of increase or decrease can be evaluated on this aspect. In the actual case investigated I compared four genera of solenoglyphous snakes. It could be shown that the addition of a pit organ and a change in size related to feeding explained the differences in the patterns. Recently Molenaar (1978) showed that the central nervous system has an entire new nucleus and tract for this organ which has its extension into the forebrain. Thus we can use these two parameters for setting up a sequence. The direction of the series cannot be determined, in fact, there remain several possibilities to order the four genera (fig. 21). For a description of the polarity and the branching in the series there is no direct evidence available. At best we can say that it is very unlikely that the pit organ disappeared, rather than appeared. The effect of the pit organ is indeed very impressive. I feel that by these procedures we can obtain sequences based on real biological phenomena and, although being idealistic, approach the realistic course much closer. The procedure enables us to make hypotheses on the factors involved in the transformations, factors which have a much greater biological reality than the Hennigean dichotomy.

A second example demonstrates the operation of constructional demands particularly those in connection to space, topography and size. The cichlid fishes in the African lakes provide an excellent group for comparative functional morphological studies (Greenwood, 1974; Liem, 1973, 1978; Barel *et al.*, 1976; Dullemeijer and Barel, 1976; Witte and Barel, 1976). Only the genus *Haplochromis* with more than 200 species in the Lakes Victoria and George exploits almost all food-sources and habitats (Greenwood, 1974).

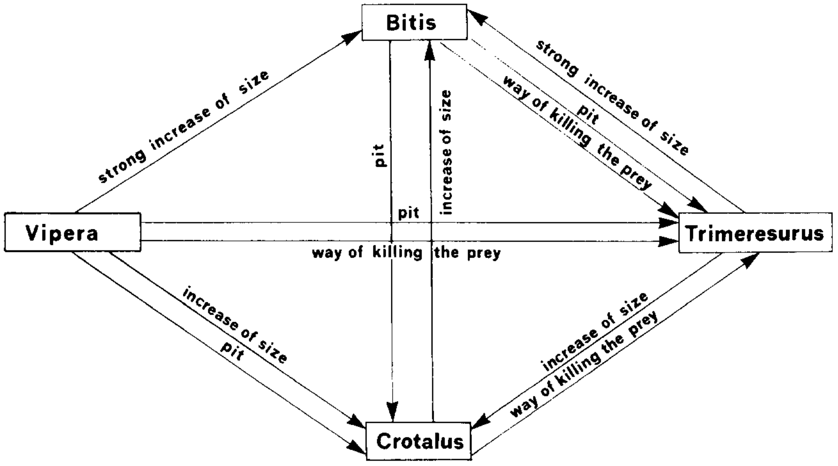

Fig. 21. An idealistic functional morphological transformation of viperid snake heads. From Dullemeijer (1959).

Each species has its own food preferences and shows specific structural adaptations to the way of feeding. Most conspicuous centres are the buccal jaws and the pharyngeal jaws. However, in all parts of the head and cervical regions a reflexion of these habits can be found. Apparently the major, and at first glance most important, constructions, are highly integrated in the entire body. Barel and co-workers (1976) have analysed the interrelationship of the two jaw apparatuses with the surrounding elements (Barel *et al.*, 1976; Witte and Barel, 1976; Hoogerhoud and Barel, 1978). I follow their main examples, the comparison of piscivorous and molluscivorous representatives for the pharyngeal jaws and insectivorous and paedophagous ones for the buccal jaws.

The piscivores differ qualitatively very strongly in their pharyngeal apparatus from the molluscivores, particularly the pharyngeal crushers (fig. 22). The pharyngeal jaws in the molluscivores mentioned work like a mortar to crush the mollusc shells. They possess heavy, voluminous jaws with an extensive saddle-shaped articulation between the neurocranium and the upper jaw. Coherently the musculature is a massive complex composed of many parts, many of them of a pinnate type. These fishes have molarized teeth. The piscivores have relatively slender bones carrying posteriorly curved, cone-shaped teeth. The muscles are smaller, less differentiated and instead of strongly developed adductors it is mainly the retractor and protractor system which is developed. In particular, the size of the entire complex and the insertion areas of the muscles have a considerable effect on the surroundings. Concerning the size, a broader and deeper dimension of the otic region in the mollusc-crushers and partly an internal reorganization is found. For details we refer to Hoogerhoud and Barel (1978). Concerning the muscle insertions, they write: 'To accommodate the insertions of the enlarged branchial muscles of mollusc-crushers, at least five solutions have been realized: a) insertion through aponeuroses (levator posterior); size-increase of the insertion area, b) by enlargement of homologous areas (e.g. the hyomandibulad shell with the levator externus and levator internus), c) 'at the expense' of the insertion area of other branchial muscles (the inverse relation between levator internus and levator externus), d) by adding new structures (the caudal flange carrying part of the levator posterior insertion) and e) by invading new areas (the levator externus of extreme crushers inserts besides the hyomandibulad shell also on the otic bulla).'

The enormous expansion of the pharyngeal muscles has consequences for other functional components, e.g. the intra- and extracephalic muscles of the expansion apparatus are relatively smaller in molluscivores than in piscivores. According to the authors there is an inverse and highly adaptive relationship between the size of the expansion apparatus on the one hand and the size of the pharyngeal jaw apparatus and the abdominal cavity on the other hand.

Apparently an adaptation to being a piscivore as well as a molluscivore

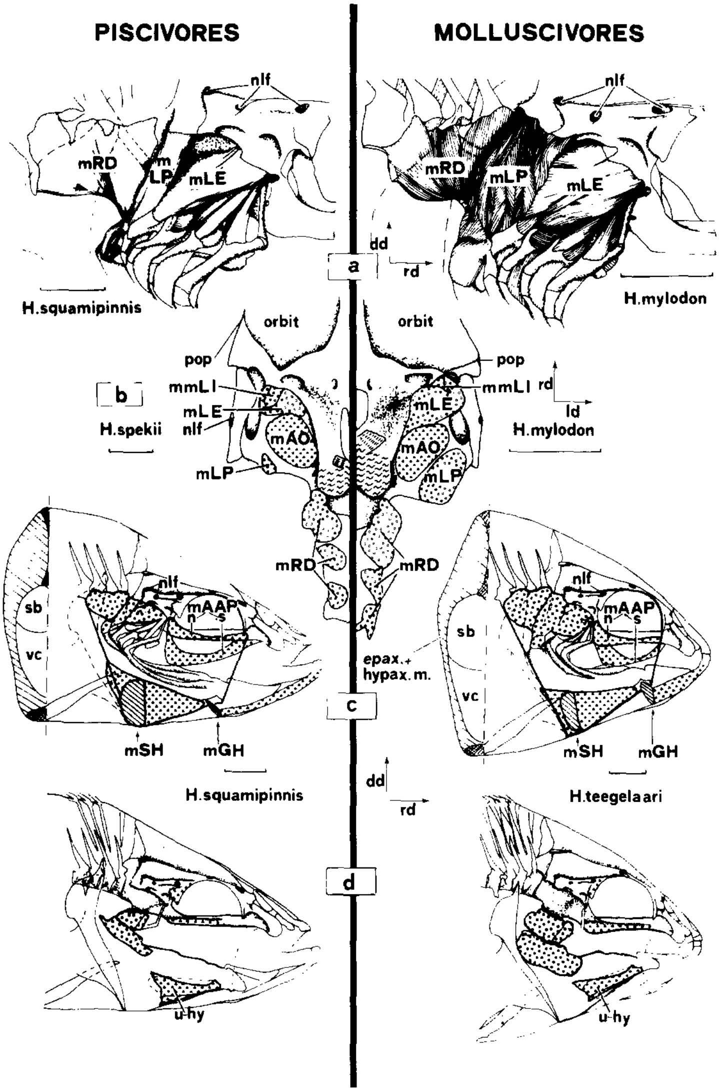

Fig. 22. Comparison of the pharyngeal jaw apparatus and some surrounding structures of piscivore and molluscivore haplochromine cichlids. From Hoogerhoud and Barel (1978). (a) Lateral aspect of the pharyngeal jaw musculature; mLE, musculus levator externus; mLP, musc. levator posterior; mRD, musc. retractor dorsalis; nlf, foramina of the lateral line system. (b) Areas of attachment and main articulation facet at the ventral side of the skull; mAO, musculus adductor operculi; mmLI, musc. levator internus pars lateralis; pop, postorbital process. (c) Position and size of the dorsal extrinsic muscles of the pharyngeal jaw apparatus and of the surrounding muscles. mAAP, musculus adductor arcus palatini with origin (n) and insertion (s). mGH, musc. geniohyoideus; mSH, musc. sternohyoideus; sb, swimbladder cavity; vc, visceral cavity. (d) Pharyngeal jaw apparatus (open circles) and urohyal (u.hy.) (solid triangles) are insertion areas of muscles.

cannot be realized simply due to the restricted available space within the contour of a fish body and the constructional combination of both adaptations. Comparison of insectivores and paedophages show comparable features for the buccal jaws (Barel *et al.*, 1976, 1977; Dullemeijer and Barel, 1976).

Figure 23 demonstrates the main differences found in the palatine region, the upper and lower jaw. Again we must conclude that these components are strongly connected and affect a large area in the front part of the cranial region. These patterns and the insight into the dependency of the components enables us to make sequences based on possible transformations of the pattern.

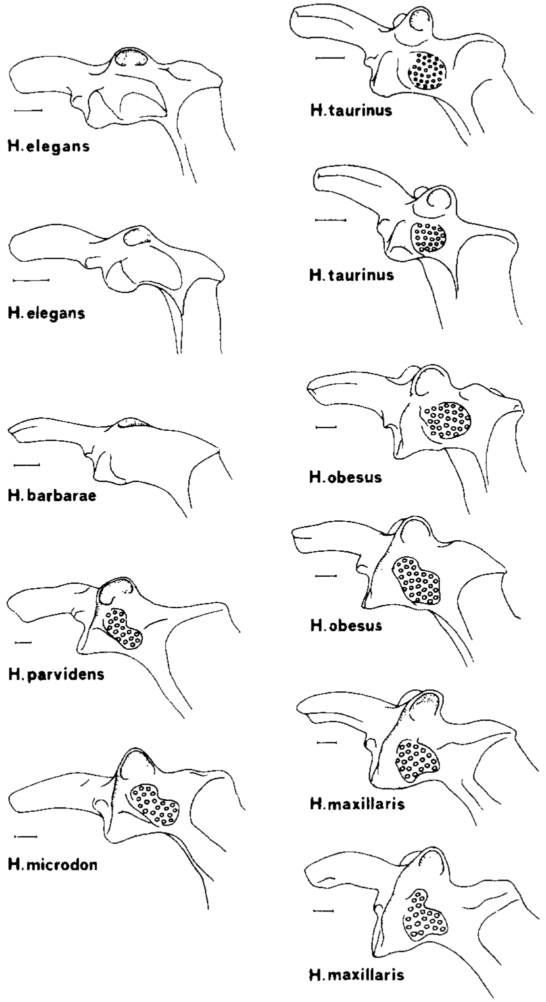

Fig. 23. Main differences in the palatine region in a number of haplochromine species (medial view). From Barel *et al.* (1976). Widely stippled area: vomerad articulation facet; upper densely stippled area: mesethmoid articulation facet; open circles indicate the pit.

The shape of the series is, in the case of the cichlid fishes, not a linear simple one. Actually there are various possibilities, almost all transformations seem reasonable. In such a situation parsimony does not help either.

The cichlid case is most probably one of a vast radiation and many branchings (Greenwood, 1974; fig. 24). The best chance of reaching a realistic conclusion is to find the dominant components. In the cichlid story, in contrast to the viperid story, it will be a quantitative difference. So far there are a number of possibilities to make a reasonable guess at direction or polarity of the sequence of patterns.

The direct evidence is of course most important. The examples presented in studies by Crompton and Parker (1978) and Robinson (1975) show this

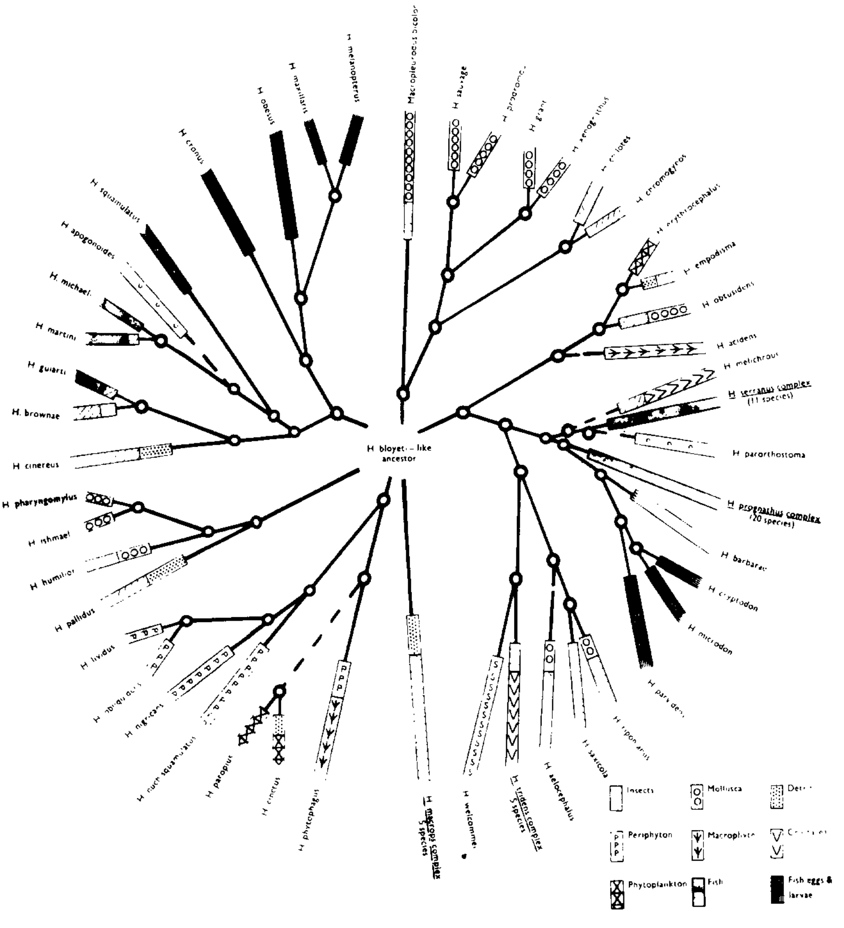

Fig. 24. Species radiation scheme of haplochromine cichlids from Lake Victoria. From Greenwood (1974). The arrangement is mainly on differences in skull and jaw structures. The disconcordance between the morphological classification and that of trophic types is striking.

most clearly, but also show the pitfalls. Although the general trend of an evolution line is apparent, it cannot be concluded that the more advanced forms are always found in the more recent times or that the ancestral form does not occur later than the advanced form. The phylogenetic trees of many mammals show the complexity of the succession. In the phylogenetic tree of the horses (Simpson, 1961; Sondaar, 1969) there are many places where three-toe genera arose after other branches had already undergone a considerable reduction of the number of toes. It is known that these changes are not only time dependent but mainly depend on the geographic ecological circumstances. Such asynchronic developments are known for many groups (Kurtén, 1963), although the general trend remains.

A second argument for polarity is derived from the probability that certain structures can arise. Three aspects can be distinguished.

Rareness, particularly of complicated structures is generally held as an advanced state, e.g. pit organs in snakes, antlers in deer. It is considered very unlikely that the ancestors possessed these structures and that the many descendants should have lost them (compare the criteria by Hecht and Edwards, 1976). Naturally, it is more likely that some groups have obtained these structures as an innovation, such as the pharyngeal apparatus in Cichlids, compared to other teleosts. Apparently rareness must be measured against a related large group which does not possess this structure. Therefore in small taxa it is less possible to use this aspect. If the group has to be split up, then more details have to be introduced and generally quantitative estimations have to be given. The weighing of the structure in this respect remains an enormous problem; there is no general recipe for it (see p. 178).

The second aspect concerns the size of the organisms and their parts. Increase of size is generally considered to be derived, except in island dwellers, where we find the opposite (Sondaar, 1976).

The third aspect is the most important, viz. that the constructive connections of the parts allow only a specific direction of evolution. There has to be constructive continuity, or as Anderson (1967) calls it, a functional gradualism. This aspect has been used in a negative sense, it makes clear why certain directions of development or evolution have not taken place (Bonik *et al.*, 1976). The use of the concept in a positive sense, viz. how the construction has been constrained to the following step in evolution has never been applied to our knowledge, although some authors (Gutmann, 1976) have advocated this opinion. It is understandable, because it presupposes an almost complete knowledge of all the interrelations in networks of one stage, in order to derive the succeeding one. In this respect functional morphology is only just beginning to contribute to evolutionary biology.

Crompton's study shows something of this gradualism and the necessary direction. It is, indeed, almost impossible to think of another direction than from reptiles to mammals irrespective of the fossil record. The ear ossicles can easily be derived from the jaw bones, but the opposite is hard to imagine, mainly of the biological probability. The same holds for the increase of the musculature, the cerebral skull and the dentition. This amounts to the statement that the direction can be read off from the constructive morphological necessity or constraints (cf. Peters and Gutmann, 1971). Methodologically it means an ordering of constructions such that one can be derived from the other gradually for constructive reasons.

If these three aspects do not give a conclusive answer then still another criterion with biological relevancy has to be used. It is the one of better adaptation, resulting in greater efficiency, i.e. a more economic use of energy. A good example is the hydroskeleton theory of Gutmann (1972). In Gutmann's theory we re-find all the aspects of changes in adaptation, functional and constructive gradualism and optimalization (or economization as he sometimes called it) for the derivation of representatives of the main phyla. Gutmann's problem is the broad phylogeny of the entire animal kingdom. From his numerous studies we shall here choose the central one, viz. the derivation of the chordates from the invertebrates.

In short, the theory can be described as the presentation of a series of models, each representing a major phylogenetic step, from a segmented worm-like organism to the bone-ligament-muscle possessing vertebrate (fig. 25). Following Gutmann's description from his 1977 publication, the initial

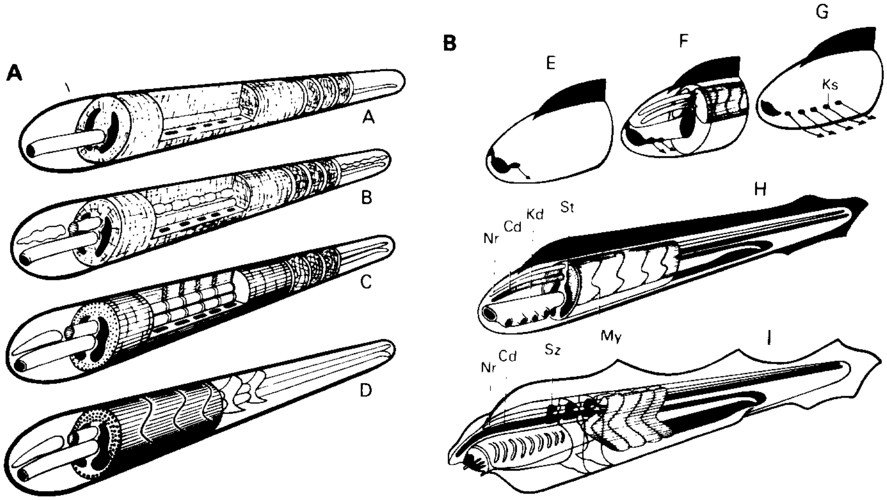

Fig. 25. (a) Models representing stages in the evolution of the chordate construction. A: A worm-like construction with metameric coelomic cavities and muscles running in all directions. B: The notochord develops as a hydrostatic organ in the dorsal mesentery. C: The notochord keeps the body constant in length. D: Segmentally musculature develops. (b) Models representing stages in the evolution of the head region in vertebrates. E, F, G: Gill slit formation (Ks). H: Primitive chordate state with branchial basket (Ka), notochord (Cd), metameric myotomes (Mg), nerve cord (Nr). I: Further developed stage. Sz, sklerocoel.

form is a segmented worm with a hydroskeleton. The coelom contains the pressure resistant fluid, which can be deformed during movement. The muscles form the contractile brace around the fluid-filled body, the dissipiments, the connections to control the transverse extension. This schematic hydroskeleton construction becomes specialized in serpentine movement, such that alterations in the length of the organism cannot be used anymore. This active limitation of the lengthwise alteration allowed a construction which also limited a passive alteration. From a bar of chordoidal cells in the upper part of the enteron the notochord is formed, which splits off from the enteron. The formation of tensile resistant construction enables the coelom to divide into somites and dermatomes. Further division gives rise to sklerocoeles from the remaining space in the myomeres, which are divided in the 'seitenplatte' by tensile resistant bracings. The metanephridia change into the holonephros by fusion of the vasa efferentia from caudal. The nephrotubules remain segmentally placed. Further evolution involves the formation of the neural tube dorsally in the notochord myomer system. It comes to lie in the rather advantageous, supported and protected area dorsal to the notochord, close to the main muscles, so that short nervous connections are possible. After the notochord-myomer skeleton has taken over the hydroskeletal function the gill openings could arise, because then the necessary mechanical conditions were fulfilled. According to Gutmann the gill openings arose from widenings of the mouth which were gradually separated by tissue ridges, those widenings being used during straining of food. Given now the notochord-myomer, sklerocoel development the axial skeleton of the vertebrates can be easily derived. Gutmann supposes as an intermediate a model with a cutaneous skeleton, restricting and effectuating forward locomotion better. Gutmann connects the various models by a gradual transition based on constructive integrity. He argues that specific constructions needed to be there before others for mechanical reasons and that others can only be thought of coming from a well specified preconstruction. The direction or polarity of this evolution is argued for on the principle of a better adaptation. It is a functional aspect, the demand in relation to the environment and the integrity of the successive models which gives the direction to evolution. Since his series of functional entities consists basically of models, the theory makes it possible to prove the reality or correctness of the theory by comparing the models with the actual organisms. This deductive method lies expressively in Gutmann's approach (Gutmann, 1976) and is indeed the only way to obtain an acceptable conclusion (Gutmann and Peters, 1973, 1976; Dullemeijer, 1974). Indeed, it seems that Gutmann's theory gives a reasonable and biologically sound description of the general trends in animal evolution. The models can be found in reality and the functioning, the adaptation and the energy balance can all be measured. Yet it is necessary to analyse the successive steps in the theory in somewhat more detail to see the pitfalls and to assess the necessary future research required to improve or criticize the theory.

From the preceding discussion it is clearly a senseless undertaking to negotiate the difference in approach of Gutmann's theory and the theories in comparative idealistic morphology. The theories cannot be falsified (Hinst, 1978), they generally explain different phenomena in a different way. Rejecting a theory is mainly an issue of satisfaction of the investigator, or a case where a theory surpasses the boundaries of its own area, as we have seen with idealistic morphology. Thus, it is much better that we evaluate the hydroskeleton theory in itself. The first step is the choice of the hydroskeleton as the origin. It is self-evident that this choice is purely inductive or at the most a good guess from the knowledge of the organisms.[5] Although it would be possible to start with another beginning, the argument for this particular beginning is that the derivation would be much more difficult if another start had been taken. Indeed, the first choice is later vindicated by the entire theory. As we have seen, this procedure is always found in deductive methods. It contains the danger of circular reasoning, but it cannot always be avoided. This drawback holds for any alternative theory and in some even more strongly. However, it still asks for a continuous alternative start to challenge the original choice. The next choice is the one of the locomotion function as the dominant one. Again we see an inductive aspect, viz. the decision that locomotion may be dominant, because the majority of animals find their new ecological niches by movement. An alternative theory could be built up by starting from sessile organisms or passively moved organisms particularly in embryonic or larval stages. This alternative should be seriously investigated, if not in the formal morphological way, then in the functional adaptive consideration. Gutmann argues in many places that functionally it is difficult if not impossible to derive the majority of organisms, being active movers from sessile forms. The argument seems to be the rather scattered and rare occurrence of sessile forms rather than the technical or functional impossibility. In terms of model change any direction could be thought of, but the distribution of sessile organisms in the various groups makes an evolution from sessile forms very unlikely.

The further specification of the hydroskeleton as the starting point is an inductive procedure, which must be later justified. Of the many alternatives, e.g. jellyfish structures, acoelomates, this seems to be the only one from which the chordate structure can be derived by a functional gradualism. In later studies Gutmann and co-workers (Gutmann and Peters, 1973; Bonik

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[5] There might be found an acceptable argument for this beginning if it is accepted that life can only be thought to have begun in water as a protein skeleton. From this the structure and the shape of the skeleton can be derived by means of hydraulic properties (Gutmann, pers. comm.). In unicellular but particularly multicellular organisms, specific connections between the cells as a functional construction are necessary.

and Gutmann, in press) have presented evidence for a derivation of the hydroskeleton from acoelomate and protozoan-like organisms.

If I have analysed the procedural steps so far correctly, then it actually means that Gutmann's theory is not completely deductive, but in fact has many inductive steps. The construction of the models is indeed deductive and the procedure of testing the theory is a deduction of falsifiability according to Popper (1969). This inference seems to be the main reason why his theory is difficult to accept by many oppenents. At this point it seems simply an alternative to the oligomere theory or Beklemischew's theory of symmetry. The preferential difference lies, however, in the functional aspect. The hydroskeleton theory demands a gradual transformation of viable functional constructions, thus with a functional integrity. This argument continually plays a dominant role. The origin of the notochord, the stiffening into vertebrae, the origin of the muscular system and the dermal skeleton are all placed in this category. Then there are a number of changes which are possible when a number of conditions are fulfilled, the holonephros, the gills etc. Gutmann considers all these changes as improvements as a result of natural selection.

The question now to be asked is: Is there in place of the notochord, for example, no other structure possible in the model or was Gutmann guided by his knowledge of ontogeny?

How can we test such a hypothesis? The answer is difficult to give, however likely the theory may be. First the imagination to design other models is very much limited, but even more important, it is not yet possible to prove the constructive necessity of this development. If this could be shown in the model, then the real organisms can indeed be used as test objects, otherwise there always remains an uncertain feeling of a shortcut to induction. Our incapacity to show the necessity or the constraint in the constructive series at this level of organization leads to what we called the use of the negative aspect of the functional gradualism. It indicates what seems to be impossible or insurmountable, but not yet what is compelling. A call on natural selection does not protect the theory from this kind of criticism, because this change or tendency must be there before natural selection can operate. Since these changes can be minor, it can be imagined that natural selection is still responsible for the progression, because the new forms can use their energy more efficiently. This is indeed the crux of Gutmann's (1979) arguments.

Two aspects, mentioned almost simultaneously by Gutmann, weaken this argument considerably. First any change, however small, must in some way fit in with the already existing construction, or the construction must also be able to change slightly. Second, 'the adaptational transformations acquired in one environment may allow the organism to change its environmental relations, and to continue a different adaptational process in the new habitat' (Gutmann, 1976). So, again we are obliged to prove the constraint in the changing series of constructions. This will be a task for the future, for which Gutmann's suggested phylogeny provides an excellent basis.

The next important step in the procedure is the testing of the models. Were the models purely deductive, it would give little problem to see the actual organisms as test objects, in the same way as we could test the shape of bony elements. This requirement, however, is not completely fulfilled. A look at the pictures shows that many qualitative and quantitative details can be changed at random, or are not included in the main specifications. A pure deduction would result in much simpler and physically more readily understood models. Some of the details are not very relevant, but many of them need further explanation. Recently Gutmann has added more detailed model extensions, but there still lies a task for future investigations.

Let us then forget the details and use only those aspects of the construction which are really derived deductively by applying physical construction rules to the models. Only then are the real organisms test cases, but not in the falsifying way Gutmann intends to give. Therefore he needs to show that the supposed development could not exist. This is asking too much. I feel that we must be satisfied for the time being with the results already obtained.

Finally, we come to the question of the operation of natural selection and the economy principle. Both concepts can of course only be used in a comparative way. Therefore we need to compare two constructions in exactly the same environment. The latter condition is never fulfilled. What can be said is that with the new structure the organism could occupy new niches for which it is not absolutely necessary that it spends comparatively less energy.

Gutmann uses two definitions of adaptation: adaptation is a decrease in the costs of living with the result of relatively more offspring (Peters and Gutmann, 1973, referring to Bock and Von Wahlert, 1965 and Cizek and Hodanova, 1971) and adaptation is the outcome of the competition between organisms requiring different amounts of energy to live and reproduce (Gutmann and Peters, 1973). These definitions demonstrate quite clearly the need for a reference system. In other words the environment must be specified, and in the case of competition must be the same for both groups. Otherwise the simple solution is a divergence of the groups into two environments. Probably energy use will be less important then, but a condition described by the term habitable is decisive.

For the testing of the models it implies a thorough investigation into the precise adaptation and in case of a model for a large group the necessary generalization of the adaptation of the group. The latter forces strong reductions and abstractions, omitting the specific adaptations of each of the members.

The procedure ultimately results in a conclusion derived from a comparison of models and generalized functional types. Described in this manner the sequence carries all the characteristics of an idealistic series, but there is a paramount difference with the idealism in formal morphology. The models forming the idealistic series in Gutmann's theory are basically deductive models and not generalizations or averages of inductively obtained shapes and forms. Moreover, they consist of functional constructions based on physically sound propositions, thus potentially realizable instead of at best functional, but frequently unfunctional diagrams. Thus, Gutmann's theory falls into the realm of realistic philosophy, albeit with strong abstraction, almost to a third world idealism of Popper (1972). Even when Gutmann's theory could be challenged on the choice of the functions, the details in the design and the test of the models, it forms, by its nature, a bridge between idealism and realism which should be fostered.

IV.7.a. The shape of the sequence. The discussion about the relationship between form and species, function and series and functional component and series did not motivate an analysis of the shape of the sequence. Mostly we could restrict the analyses to linearly ordering the members on equidistancy. In the Hennigean system it was by definition dichotomous and by definition there was an equal distance between the members (see Patterson's diagram of fig. 8). Such a simple representation is the consequence of using one feature or character at a time or bundling the characters in one category so that they could be treated as one. In the sequence of patterns a simple dichotomy or linearity can hardly be expected. This is shown by all the examples discussed so far. It is due to the fact that in the pattern more than one dominant functional component occurs and that the less dominant components quantitatively do not form a sequence with equidistant members.

Thus, two aspects should concern us now: a) the shape of the sequence and b) the spacing of the members in the sequence. Theoretically all sequences can be described dichotomously if one neglects the spacing, the rate of change and restricts the sequence to the pattern as a whole. In fact the dichotomous presentation is the simplest one which can be thought of. However, as soon as more factors are included in the pattern, the sequence soon takes the shape of a complicated network (see example of the viperid snakes) and once this picture has to be accepted, a radiation in many branches at one point must be accepted too (Greenwood, 1974). Now one can always argue that one character or criterion of splitting is more important than the other. Generally, however, there will be no argument to weigh the characters in this way, nor is there any need to do so.

A second argument could be that the multiple splitting can always be broken up in dichotomies when the time taken is short enough, and allowed to be different at the various splitting parts. This amounts to neglecting the rate of change in reference to the group concerned. It is somewhat ridiculous to measure the time sometimes in hours or days and sometimes in ages, or to treat the splitting of phyla in the same order as species (apart from the incomparable unit of evolution). Indeed, drawing the sequence with real time intervals and with different characters will, in many cases, lead to network relationship, particularly if hybridization is accepted as a reasonable factor for the origin of new forms, or to pictures showing radiations in many directions going out from one point. There remains the possibility that a specific shape is reached immediately or along a detour in the lineage. Such real convergences have never been observed up till now and they are most probably undetectable within the available time. But we should not exclude the possibility that, e.g. in the cichlid fishes, a paedophage developed immediately from an insectivore, and also from an insectivore via a piscivore. This would thus constitute a real multiple pathway according to Bock. The foregoing discussion also has some implications for the spacing. These are very different, so that the impression of sudden changes is reached. Do we therefore have to abandon the concept constructional gradualism and introduce the concept saltatorial and punctational? I do not think so. In the patterns we have observed the phenomenon that most parts are affected when one rather dominant functional component is altered. This gives the impression of a sudden saltatorial change, but in fact we are dealing here also with gradualism. However, every part observed separately may give the result that there is an unbalanced rather opportunistic change. A real holistic approach gives different results, the more so if we take into consideration the detail with which we describe the structures. We will see then that in all cases the majority of structures is affected even though it may be less the fürther we go away from the dominant functional component (*centre of realization*, Dullemeijer, 1959).

An example is the hyoid in cichlids, in which Liem (1978) mentions no difference among piscivores and insectivores, and among ambush and pursuit hunters. Liem apparently looked at it to a certain detail, but closer observation revealed that the hyoid is in fact quite different and fulfils a crucial role (Barel, in press). The same holds for the gradualism. The further away from the dominant functional component we go the less we find an effect and then the functional component does have to 'jump' from one function to another. Again the cichlids provide an example. There are indeed transitional forms between piscivores and insectivores (Greenwood, 1974; cf. Liem's statement), e.g. *H. guiarti*. The conclusion must be that all kinds of spacings and shapes can be expected to occur, that 'jumps' seem to occur, but do not exclude the necessity of a functional gradualism.

IV.8 Pattern – evolution

At various places some indication was obtained of a more complicated relationship between patterns and natural selection than between the other concepts in morphology and natural selection. Formerly we could consider natural selection as a straight more or less orthoselection on one character, now in the relationship with pattern natural selection cannot be treated as a simple factor operating on one component anymore.

By definition a pattern is a composition of functional components. The activity of these components varies considerably with respect to quantity and time. Whereas the effect of natural selection can be regarded as the result of the interaction of environmental factors and the functional components or parts of them, a variety of situations will occur. All these differing situations give different stochastic results (Osse, 1978; Zweers, 1979; Liem, 1978). When we now try to determine the fitness, thus estimating the chance of survival of the organisms and the magnitude of selective factors, we must look at various options. The simplest one is that one functional component and one environmental factor control the entire mechanism. The slight differences between species, particularly concerning protective and sexual behaviour, are most likely examples of such situations. We can expect to find among the functional components primarily the dominant ones, but also those more superficially placed, such as skin colour and some minor sense organs which in general hardly have any constructional consequences. It is not necessary, nor is it very likely, that the environment acts on the functional component itself. On the contrary, it is quite reasonable to assume an effect by way of subordinate elements. Ultimately the dominant functional component will be affected, although not directly.

Altogether it seems a wise strategy to focus attention on dominant functional components. Generally there are various dominant components in relation to a variety of environmental factors of which the interaction changes considerably during the life time of the organisms. Even supposing that the subordinate components or elements can follow the changes of the dominant ones due to the plasticity of the former, it still remains an almost hopeless undertaking to disentangle the complicated knot of interactions. Which component will be affected is almost impossible to foresee, unless the pattern shows a strong constraint. The practice of research has followed the reverse course, viz. taking the distinguishing character between the groups and by definition considering only the selective factor for this character. This approach derives from the main interest of most evolutionary biologists, viz. to explain the diversity rather than to understand the maintenance of the organisms. Procedurally this has the advantage of the possibility of applying the comparative method. As only one component and one environmental factor differ among the compared organism the conclusions about the interaction are easy to draw. Such a procedure neglects, thus, the continuous interaction of the other characters with the environment. And more important it denies the possibility that the selective factor attaches to the subordinate components. Another reasonable escape from this difficulty taken by most authors is to take the averaged value of the dominant functional component and the acceptance of a non-variable selective factor for this component (Lombard and Wake, 1976, 1977; Bock, 1976; Liem, 1973; and many others). Such a procedure is introduced axiomatically, immediately derived from the neo-Darwinian evolution theory, viz. random variation with a stable deterministic natural selection.

In fact what has happened in our procedure now is that we have shifted back from our deductive methodology to the original induction of primary observations, which is fatal for our conclusions. The selective force is derived from the distinguishing character including its supposed operation, but the distinguishing character is supposed to have originated due to the selective factor. This circular reasoning is opposite to what Bock (1976) demands for a good science. The only escape is that we try to introduce again the deductive methodology. Therefore we have to screen our methodology again and start again with the problem. This is how to explain the change of one pattern into another, supposing that one or more selection factors operate. For the solution we can either start with the form feature, thus the pattern, or start with the selection factor. In both cases we have a multitude of possibilities.

Starting with the pattern to be explained we can try to derive a new pattern by the operation of natural selection, this being the explanatory theory. The model obtained is compared to the actual pattern. We need not repeat all the pitfalls, they are the same as discussed for the deductive method for establishing the form-function relationship. However, the additional problem here is that, although the theory of evolution is principally not different from any other scientific theory, the kind of natural selection is not in the same way a safe, well-defined factor such as, e.g., mechanical rules in bone mechanics. It needs much experimental work, if at all possible, to prove the degree of operation of the selective factor or factors. But even then the methodology is not purely deductive, because there is no alternative possibility for the hypothesis which can be tested against the original one. Alternative theories can explain the same change in pattern and there has been up till now no method to test the various theories (Hinst, 1978).[6] The argument for natural selection is still the most likely and, as originally with Darwin, there is an analogous argument from breeding practice. In this way we never obtain the strict Popperian test of falsification. The conclusion must be that we cannot deny natural selection, and in the meantime it must be left open that various other theories can explain many phenomena.

The tendency in functional morphology now is to improve the theory of evolution by pointing to the varying nature of a number of potential selective

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6. A theory is sometimes given priority over another one if the former has greater 'strength'. 'Strength' can mean explaining more phenomena, or explaining phenomena lying far apart or explaining more details. This argument unfortunately cannot (yet) be applied in the case of the choice between the selectionist's and the neutralist's explanation. Both are equally strong and it has not yet been decided in which area one can and the other cannot be applied.

factors, to other factors and theories involved, such as constraint evolution, internal mechanism, system effects, etc. I shall not discuss here whether the alternative theories can be founded in genetics as the theory of natural selection; it seems to me that the prospects are good.

Taking one dominant functional component as the distinguishing character on which the natural selection factor operates is justified by two arguments: one is that in deriving one pattern from the other, the other connections apart from the dominant component remain the same and if not, that differences are due to the dominant component, and the second is that the dominant component in the pattern is also dominant over an essential long lifetime of the total living period of the organism, with other adaptations remaining relatively the same. For the first argument the discussed functional morphological analysis should be carried out, and for the second, experimental observations over relatively long periods must give the wanted data.

Many authors begin the latter with what must be described as a fairly good guess by looking at the morphology. Examples are the protrusile tongue in salamanders (Lombard and Wake, 1976, 1978), the pharyngeal apparatus in cichlids (Liem, 1973; Barel *et al.*, 1978), the pit-organ in pit-vipers (Dullemeijer, 1959). We have demonstrated the various shortcomings and pitfalls of this procedure and do not have to repeat it. When from such morphological information a specific adaptation, and thus also an environmental factor is suggested, the entire complex is called a trophic type (Witte and Barel, 1976; Dullemeijer and Barel, 1976; Greenwood and Barel, 1978; Hoogerhoud and Barel, 1978). Such averaging to dominant functional components abstracted from the total pattern can easily give the impression that in the series sudden saltatorial development occurred.

In the series of patterns we have observed a functional gradualism, notwithstanding the apparent jumps in the development. Thus, observation and methodological necessity point to the importance of constraints in the evolution (Romero-Herrera *et al.*, 1978; Joysey, 1976). There is a directed evolution or an evolution between specific marginal values (phylogenetic canalization, cf. Waddington, 1966). The question now arises: Can such a canalized evolution be explained by the neo-Darwinian theory? It probably cannot, because the phylogenetic variation necessary to give the pool, from which the selection can develop a new form, cannot be random anymore. Although the genotypic variation would be random (which is also very unlikely), the ontogenetic development will already single out the majority of variations. If there was an open niche for any variation, then the survival chances are great. In this respect the standard theory of evolution can be revised by suggesting a constraint variation which hardly 'needs' natural selection to explain the survival of a new form.

V. CONCLUSIONS

In the foregoing discussion I have tried to analyse the relationship between functional morphology and evolutionary biology by presenting the main concepts of both fields and connecting these concepts in pairs. Some of these pairs gave us motive for a methodological analysis, some were irrelevant or could only be discussed as intermediates between other pairs.

If only structures were considered it could be shown that the entire procedure remains in the domain of idealistic formal morphology. As has been known for years this does not contribute to evolutionary biology. Structures can be arranged in sequences showing all the characteristics of idealism. Idealistic morphology is a respectable discipline with a well-developed methodology. It cannot, however, be used to demonstrate the course and the cause of evolution without adding different and independent information. However, most important is that the Hennigean system belongs to this philosophical system and thus should be rejected as no more than a preliminary method of classification. A change of philosophical system is needed to bridge the gap with evolutionary biology.

The change implies an introduction of function, an introduction of the concept construction and a description of the sequences in terms of consanguinity, i.e. genetic relationship. Thus there is a need for many functional morphological contributions. Yet, evolutionary biology and functional morphology have their own discrete space with no contact. In functional morphology it is the study of the activity-structure relationship, which does not need evolutionary biology, as well as the explaining description of patterns. Evolutionary biology hardly touches functional morphology in areas where it uses purely physiological, ethological and mainly population-genetical data.

There is, however, a large field where both disciplines are strongly interwoven, ecological functional morphology and adaptations, constructional morphology and natural selection, to mention but a few aspects.

Our analysis has arrived at a point where we are expected to consider random variation as less random in view of the complicated pattern or network of functional morphological analysis, and natural selection as less deterministic because of the strong canalization of evolution as a result of constraints in the relationships between the members in a pattern. If we want to reserve the concept natural selection as distinctive to other explanatory theories, it might well be wise to leave open the possibility that organisms can invade still open niches without much or any selective pressure.

The study of functional and ecological morphology can help us to solve these problems in evolutionary biology, particularly if the morphology and the evolutionary biology are approached with a holistic, system-theoretical or structuralistic approach.

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