[127] *Acta Biotheoretica 34: 233–248 (1985).*

CONSTRUCTIONAL MORPHOLOGY: THE ANALYSIS OF CONSTRAINTS IN EVOLUTION

DEDICATED TO A. SEILACHER IN HONOUR OF HIS 60. BIRTHDAY

WOLF-ERNST REIF*, ROGER D.K. THOMAS** and MARTIN S. FISCHER*

* Institut für Geologie und Paläontologie der Universität Tübingen, Sigwartstr. 10, D-7400 Tübingen, West Germany.

** Department of Geology, Franklin and Marshall College, Lancaster, Pennsylvania 17604, U.S.A.

ABSTRACT

Evolutionary change is opportunistic, but its course is strongly constrained in several fundamental ways. These constraints (historical/phylogenetic, functional/adaptive, constructional/morphogenetic) and their dynamic relationships are discussed here and shown to constitute the conceptual framework of Constructional Morphology. Notwithstanding recent published opinions which claim that the "discovery" of constraints renders Neodarwinian selection theory obsolete, we regard the insights of Constructional Morphology as being entirely consistent with this theory. As is shown here in the case of the *Hyracoidea*, formal analysis of the constraints which have framed the evolution of various characters extends our understanding of the evolution of a taxon.

1. INTRODUCTION

The term "constructional morphology" has been used with several different but related meanings which have collectively given rise to considerable ambiguity. The purpose of the present paper is to clarify these different meanings of the term and to outline an analytical approach to the study of the origins and evolution of organic form that has been designated as "Constructional Morphology". This particular approach was first suggested by Seilacher [56] and has been developed further by Reif [43,45,46] , Thomas [62] and Thomas and Reif [63,and in preparation] . (A similar concept, with a different name, was already developed by Van der Klaauw [25,26,27] and Dullemeijer [11,12] .)

1) Some have employed the term constructional morphology to emphasize the functional and architectural integration of organic structures, as analogues of machines (see Reif, in press, for a review). Bock and

v. Wahlert [3] and Peters *et al.* [38] have indicated complementary ways in which organic form may be explained within the framework of evolutionary biology. One analyses the biological role of an organ by testing possible answers to the question: "What is the utility of the organ?" This search for adaptation is the province of functional morphology, as this field is usually conceived. Alternatively, one seeks answers to the question: "How does the organ work or operate?" This question seeks to understand the design, the physical and chemical processes, and the action of the organ. The attempt to answer this latter question has been called constructional morphology. It represents the morphological aspect of biophysics and physiology. Whereas modern experimental biophysics and physiology are largely reductionistic, constructional morphology focuses on higher levels of integration [38]. This concept of constructional morphology is independent of the postulate of evolutionary change. It has a long history (Reif, [47] extending back at least to the work of Cuvier and Geoffroy, Russell [53]). It is noteworthy that a very broad research program was developed in the 1870s, and that direct comparisons between organs and technological inventions have long been a standard method. The application of this sort of analysis in paleontology was long neglected but Böker [4] and D. v. Kripp [28] seem to have been pioneers of its revival in this century.

2) The entomologist Hermann Weber chose the term "Konstructionsmorphologie" for a new approach to morphology. After WWII he developed a research program that was only incompletely worked out and published due to his early death [67,68,8]. The fullest account is given in unpublished notes distributed at a lecture series [48]. Weber's goal was to provide a new methodological basis for morphology, so that the necessarily descriptive science of morphology could compete with the more fashionable areas of experimental biology. Weber rejected evolution (*i.e.* the theory of descent) as an axiom of morphology, because he wanted to avoid the naive speculative phylogenetics which, according to him, had plagued morphology since the time of Haeckel. Also Van der Klaauw [26,27] took this position and he simultaneously introduced a holistic approach, which had a strong influence on his students (see [13,14] for reviews). The only sound basis for a method which Weber found was typology, which he tried to free of all its metaphysical connotations. The first step in Weber's method is to provide an exact, empirical description of the taxon.

Building on this objective basis, causal determinants of form are incorporated step by step. First one analyses morphogenesis, ontogeny and the alternation of generations. Then one develops a plan of construction which incorporates function, mechanical operation and the change of form and function during ontogeny. Weber did not distinguish between the function and the biological role of a character, so it is not clear how ecological data could be incorporated into this functional analysis.

The analysis proceeds from an ontogenetic time-scale (development) to the evolutionary time-scale (relationships among taxa). This is accomplished not by deduction from the theory of descent but by induction (analysis of morphological similarities). The fact of evolution (Theory of Descent), phylogenetics (Reconstruction of Relationships), and causal factors of evolution (Theory of Selection, Theory of Speciation) are not clearly distinguished in Weber's writings. This explains in part Weber's reservations about what he called "evolutionary methods". It is obvious that Weber did not seek to contribute to the causal explanation of evolution, nor did he want to develop an "evolutionary scenario" (*i.e.* an integrated account of the phylogeny and evolutionary ecology of a taxon). His goal was to provide a non-speculative description of the phylogeny of a group of taxa. Consequently, the next step is to arrange the analyzed types in an hierarchical order. This pattern leads to the recognition of a "Prototypus", from which "all other forms" can be derived. The prototype is then interpreted in phylogenetic terms as the "paleotype". Now the fact of evolution is accepted and the ideal connections between the types are reinterpreted as genealogical relationships. Progress beyond this "evolutionary tree of types" is only possible if paleontology provides appropriate data. If the prototype can be equated with a real fossil taxon, it becomes the "ancestral form". The last step is to describe the phylogenetic history of the diversity of the group.

3) The paleontologist A. Seilacher, who had attended Weber's lectures, introduced the term "Konstruktionsmorphologie" as the title of yet another research program [56]. His basic premise was that a functional interpretation was a necessary but not a sufficient explanation of organic form. Organic form could be understood only if it was seen as the result of the operation of three factors: adaptation, phylogenetic history, and "Bautechnik" (principles of morphogenetic fabrication). Seilacher's Bautechnik-aspect introduces a significant component that is independent of the action

of natural selection. It recognizes the laws of geometry, natural materials, and growth processes give rise to patterns that are in some cases "non-adaptive", like certain colour patterns in molluscan shells. Seilacher's goal was to go beyond traditional functional and constructional morphology, to provide a more complete and flexible framework for the analysis of organic form, recognizing the roles of independent factors and incorporating dynamic processes of individual development and evolutionary change. For a similar concept of the "Leiden school" see Dullemeijer ([14] , with many references) and Zweers (this volume).

2. ORGANIC FORM, EVOLUTION AND CONSTRAINTS

We have further developed Seilacher's concept and the present account in part summarizes a longer paper in progress. Two questions which complement one another lie at the core of our conceptual framework: (1) "What absolute constraints, if any, limit the range of possible organic forms?" and (2) "How is the course of evolutionary change constrained by the nature of its processes and their action in *this* world?" Our inquiries, provoked by these questions, lead to the recognition of a set of constraints on form, which can be classified in different categories. These constraints help to explain a variety of evolutionary phenomena, such as suboptimal structures, convergence, parallel evolution, chanelled evolutionary pathways, and the geometrical patterns that characterize organic structure.

This approach to the explanation of form is in full accord with the Synthetic Theory of Evolution. In no way does it contradict the theory of evolution by natural selection, broadly construed. We view this approach as a natural extension of modern evolutionary theory. It integrates functional and constructional morphology (in their classic senses) with ecology in an explicit evolutionary context.

When Seilacher [56] first published his essay, the role of constraints in evolution was accorded little interest. Authors like Waddington [66] , Weiss [70] and Olson [37] who challenged the then dominant (pan-) selectionist view were regarded as mavericks in the community of evolutionary biologists. The adaptationist view of that time is well exemplified by the work of Cain [7] . Mayr [33,p.2] listed "mutational limitations" and "epigenetic limitations" in a table of evolutionary factors that had been proposed by earlier authors, but these topics received no further comment here and little elsewhere in the book. One of the first to draw attention to "nonadaptive aspects of evolution" in the context of the NewDarwinian synthesis was Van Valen [64]. Recent textbooks (*e.g.* [10,22,29,30,60]) include no discussion of the roles of constraints on the process of evolution by natural selection. Rare exceptions are Salthe [55,p.315-328] in his chapter "The best of all possible worlds", and Futuyma, [16,p.386-387] who addresses "failures in adaptation" and related subjects. Only recently has the concept of constraint received much attention in various areas of evolutionary biology (functional morphology, developmental biology, ecology). Reacting to a provocative caricature by Gould & Lewontin [21] of attempts to explain form, behaviour and evolutionary change in terms of adaptation, Mayr [36] has defended the adaptationist program. He claimed that the notion of constraint is not in conflict with the synthetic theory and he listed five kinds of constraints (*cf.* [1,5,14,41,43,56,62]; see also Mayr, [34]):

1. A capacity for nongenetic modification (ecophenotypic response).
2. Multiple evolutionary pathways. The adoption of a particular solution may greatly restrict the possiblities for subsequent change.
3. Stochastic processes.
4. The target of selection is always the individual as a whole, rather than a single gene or an atomized trait.
5. Cohesion of the genotype.

The flurry of recent interest in constraints is also reflected in Mayo [32] "Natural Selection and Its Constraints".

3. A NEW THEORY OF EVOLUTION?

Philosophers of science have long tended to see all scientific enterprise in the light of physics. However, it is now becoming clear that physics cannot be regarded as *the* model science. Historical sciences like biology and geology differ significantly from physics ([57]; see discussion in [35]). Nevertheless, controversy continues among biologists and philosophers of science over the nature and utility of theories in natural history, especially over evolutionary theory, which incorporates numerous subsidiary theories and hypotheses.

Over the past few years, the synthetic theory has repeatedly been declared "effectively dead" [19], "on the verge of crumbling" [20], "insufficient" [24], as no longer acceptable (see [6,51]), or as an "altdarwinistisches Dogma" [23]. Recently Webster & Goodwin [69] have vigorously attacked the synthetic theory. "The organism as a real entity, existing in its own right, has virtually no place in contemporary biological theory" (p.16). "Genetic and environmental concepts exhaust the explanatory repertoire of the (neo-Darwinian) paradigm vis-a-vis form" (p.31). "We regard the theory of evolution, and in particular neo-Darwinism, as having extremely limited explanatory power with respect to the problem of form to which it was originally addressed. This limitation arises as a consequence of the absence of any adequate theory of the means of production of 'typical forms' and is such, we would maintain, as to render debatable the claim that neo-Darwinism is the unifying theory in biology" (p.44). Webster & Goodwin argued for a structuralist approach: "The general aim of structuralist theory is to make the order of a unified system intelligible. It aims to express a formal system in which 'the actual is explained or interpreted as an instance of the possible' [39]" (p.41). "A structuralist conception of living organisms with its emphasis on the logical, the universal and the necessary, implies that the organismic domain as a whole has a 'form', and is therefore intelligible (which does not mean predictable) and that the 'content' - the diversity of living forms, or at least their essential features - can be accounted for in terms of a relatively small number of generative rules of laws" (p.46).

We have quoted here extensively from Webster & Goodwin [69] for two reasons. First, the concept of these authors, who are developmental geneticists, parallels that which we developed in Reif [43], Reif and Robinson [50], and Thomas [62]. Second, however, we see this structuralist approach to the problem of form as being complementary to the synthetic theory and *not* as a contradiction of it. Ever since the time of Darwin [9] debate has continued over the content *and* status of the theory of evolution. The Darwinian theory in its various forms (neo-Darwinian; Modern Synthesis; recent Modern Synthesis, *sensu* Mayr, [33]) has been rejected by some authors for a number of reasons. Among these are: (1) the notion that the theory cannot be refuted or that it cannot be proven; (2) that it is incomplete; (3) that it produces wrong results; (4) that adherents of the theory neglect important aspects of organismic structure. Debate on the status of theories is a common phenomenon in natural history. Expansion of a theory may or may not involve refutation of the old theory and its replacement by a new one. We regard it as a virtue of the Darwinian Theory that it satisfactorily integrates the results of disparate modes of analysis. This does not mean that the theory is in any way vague or arbitrary.

Webster and Goodwin [69] see the structuralist approach as an alternative to both atomism and holism, which have dominated the history of biology. "Structuralism is concerned with order, its generation and transformation. It rejects both atomism and holism. Following Piaget [39], we may characterize it in terms of three key concepts: wholeness, transformation and self-regulation" [69:40]. Mayr [34:333] in his defense of the adaptionist program claimed: "A partially holistic approach (in other words, an adaptationist program which takes constraints into consideration) that asks appropriate questions about integrated components of the system needs to be neither stultifying nor agnostic. Such an approach may be able to avoid the Scylla and Charybdis of an extreme atomistic or an extreme holistic approach". These theoretical formulations differ in emphasis and terminology, but it is by no means clear that they prescribe different research programs. They differ fundamentally, however, in the positions taken in relation to the Synthetic Theory. This can mean either that acceptance or rejection of the theory is irrelevant (which most likely it is not) or that we still do not have satisfactory criteria by which the merits of such a theory can be objectively judged.

We see our own structuralist approach to the problem of form to be fully consistent with an evolutionary process in which selection is the sole *efficient* cause of change. Thomas and Reif [63] elaborate three categories of constraints: (1) historical/phylogenetic; (2) functional/adaptive; (3) constructional/morphogenetic. These will be discussed here. We do not regard this as a mere exercise in classification. On the contrary, a framework of constraints is necessary, because although the constraining factors may be treated as discrete variables, they are closely interrelated and complement one another. Many recent authors have emphasized the role of one or other of these factors, paying insufficient attention to their complex interactions.

4. HISTORICAL/PHYLOGENETIC CONSTRAINTS

The genome and epigenetic, developmental processes are highly buffered and stabilized systems. Minor disruptions are corrected by homeorhetic processes (*sensu* Waddington [65]); larger disruptions (on all levels) lead to a breakdown of the developmental process. Lethal mutations are only one example of such a breakdown. This stabilization of developmental processes (see Alberch [1] for a discussion) necessarily plays a strongly conservative role in evolution. Hence all organic forms have a strong historical component.

If we are to determine whether morphology evolves by small increments or in larger jumps, we must know how far the inhereted epigenetic "machinery" can be changed without a collapse. What consequences for adult structure follow from a given change in the epigenetic machinery? What kinds of changes are likely to occur; what are unlikely? Answers to these questions will come from the synthesis of genetics, epigenetics and evolutionary studies. There has long been an interest in the influence of developmental processes and timing on evolutionary change. In recent years this has led to several important publications, *e.g.* [5,18,40]. For the area of inquiry circumscribed by Raff & Kaufman's title: "Embryos, Genes and Evolution", Reif [49] has suggested the name: "Evolutionary Epigenetics".

Numerous phenomena of evolution can be largely explained by the conservatism of the inherited genome and epigenetic machinery, among them vestigial organs and atavisms, the constancy of Baupläne, and the stability of adult form within species. Striking instances of parallel evolution highlight the fact that potential adaptations are strongly predetermined by the genetic and epigenetic make-up of a taxonomic group [1].

5. FUNCTIONAL/ADAPTIVE CONSTRAINTS

The analysis of functional/adaptive constraints focuses on the interactions among parts of an organism and those between the organism and its environment. Every part of an organism has a biological role that requires some particular mechanical function. The variety of mechanically viable forms is limited *a priori*. However, the number of possible forms is further reduced by the condition that the parts must function in a given context, by which adaptive changes are constrained. The effect of these constraints varies, depending on a given situation. They may keep the number of multiple adaptive pathways [2] small; they may leave only one possibility open (*i.e.* they channel evolution); or they may prevent further change altogether. Convergence is usually understood as a result of adaptation in response to similar constraints. In this perspective, selection drives form towards a common optimal design, as in the eyes of vertebrates and squid, and the torpedo body-shapes of tuna, mako sharks and cetaceans. It is usually forgotten that other constraints play an important part in convergence. There may simply be only one possible solution to a given structural problem due to the laws of geometry, physics and chemistry (see below).

Concepts of optimal design, behaviour, or life history strategy have long served as models in ecology and evolution (see Stearns [58] for a review). Evolution by natural selection does not predict the achievement of optimal design. Organisms simply have to be "good enough" to survive. This means that they must be as good as or slightly better than their competitors. Nonetheless, we do find numerous examples where an observed trait is in close accord with an optimal model [59]. In other cases optimal models fail. In such cases a "satisfying model" applies, in which "the search for an optimum is replaced by the search for a stopping rule, for a way to tell when a good-enough alternative has been found" [58:13]. This means that students of adaptation should not only devise optimal models but have to learn to develop models which are "good enough" in a given situation, *i.e.* in a construction, in an ecological situation *etc.*

Optimal designs set standards for comparison in an important research strategy applied in palaeontology, the paradigm method of Rudwick [52]. In order to determine the function of a fossil organ, one constructs models that would perform alternative possible functions optimally. The function with the paradigm that is approached most closely by the actual structure is inferred to be most probable. Such a method should only be applied if one also takes other constraints into account. Concisely, optimal models constrained by historical and morphogenetic factors lead to satisfying models. Satisfying models are not alternatives to optimal models but are rather more sophisticated modifications of them. The problem remains that it may be rather simple to design an optimal model but it is often very difficult to discover the appropriate constraints.

6. CONSTRUCTIONAL/MORPHOGENETIC CONSTRAINTS

Historical/phylogenetic and functional/adaptive constraints act in a given context and they hardly ever set absolute, inescapable limits to evolutionary change. This is not the case for constructional/morphogenetic constraints, which are ahistorical and express limits placed by the laws of physics, chemistry, cybernetics and geometry on evolutionary change.

It may be argued that geometry and cybernetics are abstract mathematical fields, that what is here subsumed under "geometry" and "cybernetics" belongs to physics. Nevertheless we will speak of geometric and cybernetic laws here. The ahistorical constraints can be grouped into three categories:

a) The physical and chemical properties of available materials (elements, chemical compounds). Size limitations placed by physical laws on structures of all levels (cell sizes, sizes of locomotory structures, *etc.*). Size dependent phenomena such as adhesion, viscosity, and inertia (see Table 2 of Koehl, in [5:223]).

b) The number of possible growth programs for organic structures is limited. Each program yields a limited range of different solutions. This aspect has been designated as Theoretical Morphology (*sensu* [42]; see [44] for references).

c) Cybernetic laws control development, homeorhetic processes, maintenance, and repair of the organism. We are far from having a clear understanding of these laws.

Acquisition of particular materials, growth programs and regulatory systems in the course of evolution constitute historical events, which subsequently result in historical/phylogenetic constraint. This historical aspect should not be confused with the clearly ahistorical aspect, inherent in the properties of the original materials, growth programs, and regulatory systems.

Convergence is often not the result of a common functional, adaptive constraint ("the optimal solution"), but may rather result from common constructional/morphogenetic constraints ("the only possible solution"). Analogous growth programs give rise to similar structures in very different taxa [50].

In a recent paper on the relation between ontogenesis and patterns of evolutionary change, Alberch [1] has argued "that developmental constraints and interactions impose severe limits on the action of directional selection and can set up phyletic trends" (p.664), Alberch's examples involve the interaction of several different factors. Functional/adaptive, historical/phylogenetic, and constructional/morphogenetic constraints all operate on developmental pathways. A non-random change (*sense* Alberch) on an inherited developmental pathway is directed by (1) the inherited genetic and epigenetic machinery, which by historical accident happens to have properties such that it can be changed only in certain ways, or (2) by the functional integration of the inherited epigenetic pathway with other processes, or (3) by the cybernetic properties of the epigenetic processes themselves, whose law-like structure limits the range of future changes.

7. A SYNTHETIC VIEW OF CONSTRAINTS

The relative roles of the various determinants of form are most easily established for what we call "*Comparative examples*", where structures of different taxa are compared. Parallel evolution of structures that have evolved independently in closely related taxa clearly expresses historical/phylogenetic constraint. As shown above, convergence may express either evolution towards an optimal design, if it is determined by functional/adaptive constraint, or it may express the only possible solution to a structural problem and thus reflect constructional/morphogenetic constraint.

"*Non-comparative examples*" have to be studied individually because no appropriate comparisons are possible. Here, it is much more difficult to evaluate the relative importance of the three types of constraint. In the morphological (and ethological) perspective developed here, all evolutionary changes, however they are initiated, ultimately involve changes of function in response to a new adaptive situation, involving environmental change, exploitation of a key innovation, or selection towards optimality, for instance.

The first question asked is: "What structure, including its developmental pathway, is inherited?" As a second step, one seeks to establish the "past adaptation", the adaptive significance of the structure before its change of function. In the third step, one analyses the demands that are placed on the structure by its new function (*sensu* [13]). If these functional requirements are relatively unspecific and if the developmental pathway is strongly canalized, a change of function requires only minor changes in structure, in which case historical/phylogenetic constraints dominate (Solution no. 1). If the functional requirements are strong and specific, a change of function can be brought about only if the historical/phylogenetic constraints are relatively weak. The modification of structure which results is either controlled by functional/adaptive constraints, in which case it evolves towards an optimal design (Solution no. 2), or by constructional/morphogenetic constraints, in which case a "good enough" structure will evolve (Solution no. 3). In this model, historical/phylogenetic legacies are regarded as past adaptations, modified at each step in evolution within limits set by the three types of constraint. The three solutions are never absolute determinants of form. In each individual case, a compromise develops among the influences of the three factors.

8. CONSTRAINTS IN THE EVOLUTION OF HYRAXES

Hyrax evolution illustrates the effects of several kinds of constraint. Living hyraxes are rabbit-sized, plantigrade herbivores with very good climbing capabilities. They live in protected environments such as tree-crowns in the tropical rain-forest and caves within rocky mounds of the African savanna. Hyraxes are thought to have evolved from three-toed, digitigrade steppe-runners [15,61].

Historical/phylogenetic limitations are shown in cases where morphological (or behavioural) characters are not immediately related to the current ecology of a group. Such discordance may be indicated by comparison between the character of the group under study and equivalent characters of ecologically similar taxa. Hyraxes have a gestation time of 7-8 months. Neonates are fully developed: they can see and are active on the first day and start feeding on the third day after birth; three premolars are already erupted at birth and the fourth starts to erupt; and litter size is small, *Dendrohyrax* having 1-2 offspring, *Procavia* and *Heterohyrax* having 2-3 offspring. These characters are usually found in mammals which live in open areas, like steppes. Groups living in caves (*e.g.* rodents) tend to be r-strategists, with large litter sizes and altricial young. This seeming contradiction suggests a significant ecological shift in the evolution of the hyraxes [4,17,54].

Functional/adaptive requirements imposed by this change in habitat are demonstrated by changes in the mechanics of the locomotory apparatus that makes climbing possible. Cursorial mammals have no clavicle and thus acquire great fore-and-aft mobility in the shoulder joint. The muscles for lateral movement of the arms and legs are reduced or modified to aid in running (*M. deltoideus, pars clavicularis* contributes to *M. brachiocephalicus*). Apart from the goat, hyraxes are the only mammals with no clavicle that climb trees. From their steppe-running ancestors, hyraxes have inherited three-toed feet which lack claws but which have rudimentary hooves. The radius and ulna are ancylosed and thus prevent pronation and supination. To make climbing possible in the absence of claws, the foot has acquired an adhesive sole with a large number of sweat-glands. To compensate for the impossibility of pronation and supination, the wrist joint is fixed in a position intermediate between the horizontal and vertical. When hyraxes walk on the ground or when they "walk" (on their sticky soles) up over rocks, the palms of their hands and feet are in a horizontal plantigrade position. When they climb up trees, they grab the sides of the tree trunk and move their palms into a vertical position. These movements occur by rotation about the wrist and especially about the inter-carpal joints. This inter-carpal movement is made possible by a novel serial arrangement of the carpals, a feature that was not present in their steppe-running ancestors.

Hyraxes inherited at least one character by which they were pre-adapted for climbing. All runners have facets in the wrist joint which prevent dorsal flexion of the hand. Such facets, which are retained by hyraxes, stabilize the hand during climbing and prevent it from tilting dorsally.

Fischer's project is not yet finished, but, from what has been outlined above, the importance of the various limitations is already obvious.

ACKNOWLEDGEMENTS

This is Konstruktionsmorphologie Nr. 174 of the Sonderforschungsbereich 53 "Palökologie", Dept. Geology Tübingen. (Nr. 173 see Thies & Reif, Neues Jahrb. Geol. Paläont. Abh. in press). We thank G. Mickoleit (Tübingen) for critical discussions.

REFERENCES

1. Alberch, P. (1980). Ontogenesis and morphological diversification.- Amer Zool 20: 653-667.
2. Bock, W.J. (1959). Preadaptation and multiple evolutionary pathways.- Evolution 13: 194-211.
3. Bock, W.J., and v. Wahlert, G. (1965). Adaptation and the form-function complex.- Evolution 19: 269-299.
4. Böker, H. (1931). Beobachtungen und Untersuchungen zur Umwandlung der Arten an brasilianischen Meerschweinchen (*Caviidae*) und afrikanischen Klippschliefern (*Hyracoidea*).- Forsch Fortschr 7(14): 203-204.
5. Bonner, J.T. (1982). Evolution and development.- Berlin: Springer-Verlag, 357 p.
6. Brady, R.H. (1979). Natural selection and the criteria by which a theory is judged.- Syst Zool 28: 600-621.
7. Cain, A.J. (1964). The perfection of animals.- In J.D. Carthy and C. Duddington, eds., Viewpoints in biology 3, 36-63. London.
8. Czihak, G. (1957/58). Hermann Weber.- Zool Jahrb Abt Anat Ontog Tiere 76: III-IV.
9. Darwin, Ch. (1859). The origin of species.- London: John Murray.

10. Dobzhansky, Th., Ayala, F.J., Stebbins, G.L., and Valentine, J.W. (1977). Evolution.- San Francisco: W.H. Freeman and Company, 572 p.
11. Dullemeijer, P. (1958). The mutual structural influence of the elements in a pattern.- Arch Neerl Zool 13 suppl.: 174-188.
12. Dullemeijer, P. (1959). A comparative functional-anatomical study of the heads of some *Viperidae*.- Morph Jb 99: 881-985.
13. Dullemeijer, P. (1974). Concepts and approaches in animal morphology.- Assen: Van Gorcum, 264 p.
14. Dullemeijer, P. (1980). Functional morphology and evolutionary biology Acta biotheor 29: 151-250.
15. Fischer, M.S. (1983). Die Extremitätenmuskulatur der *Hyracoidea*. Beiträge zur Fortbewegung und Anpassungsgeschichte.- Unpublished Diploma Thesis,Dept. Biol. Universität Tübingen, 89 p.
16. Futuyma, D.J. (1979). Evolutionary biology.- Sunderland, MA: Sinauer Associates, 565 p.
17. Gambaryan, P.P. (1974). How animals run. Anatomical adaptions.- Translated from the Russian. Jerusalem and London: 367 p.
18. Gould, S.J. (1977). Ontogeny and phylogeny.- Cambridge, MA: Harvard Univ Press, 501 p.
19. Gould, S.J. (1980). Is a new general theory of evolution emerging?- Paleobiology 6: 119-130.
20. Gould, S.J. (1980). The evolutionary biology of constraint.- Daedalus, Spring 1980: 39-52.
21. Gould, S.J., and Lewontin, R. (1979). The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme.- Proc R Soc London B 205: 581-598.
22. Grant, V. (1977). Organismic evolution.- San Francisco: W.H. Freeman and Company, 418 p.
23. Gutmann, W.F., and Bonik, K. (1981). Kritische Evolutionstheorie.- Hildesheim: Gerstenberg Verlag, 228 p.
24. Ho, M.W., and Saunders, P.T. (1979). Beyond neo-Darwinism - an epigenetic approach to evolution.- J theor Biol 78: 573-591.
25. Klaauw, C.J. van der (1948-1952). Size and position of the functional components of the skull. A contribution to the knowledge of the architecture of the skull, based on data in the literature.- Arch Neerl Zool 9: 1-558.
26. Klaauw, C.J. van der (1950). Architectuur van de schedel.- Verslagen Kon Akad Wet Amst 59: 1-5.
27. Klaauw, C.J. van der (1966). Introduction to the philosophical backgrounds and prospects of the supraspecific comparative anatomy of conservative characters in the adult stages of conservative elements of Vertebrata with an enumeration of many examples.- Verh Kon Ned Akad Wet Amst 2e Reeks 57: 1-196.
28. Kripp, D.v. (1933). Die Kaubewegung und Lebensweise von *Edmontosaurus* spec. auf Grund der mechanistisch-konstruktiven Analyse.- Palaeobiologica 5: 409-422.
29. Kull, U. (1977). Evolution.- Stuttgart: J.B. Metzler, 304 p.
30. Leigh, E.G. Jr. (1971). Adaptation and diversity.- San Francisco: Freeman, Cooper and Company, 288 p.
31. Maynard Smith, J. (1975). The theory of evolution. 3rd edition.- Harmongsworth: Penguin, 344 p.
32. Mayo, O. (1983). Natural selection and its constraints.- New York: Academic Press, 145 p.
33. Mayr, E. (1963). Animal species and evolution.- Cambridge, MA: The Belknap Press, 797 p.

34. Mayr, E. (1982). Adaptation and selection.- Biol Zentralblatt 101: 66-77.
35. Mayr, E. (1982). The growth of biological thought. Diversity, evolution, and inheritance.- Cambridge MA: The Belknap Press, 974 p.
36. Mayr, E. (1983). How to carry out the adaptationist program?- Am Nat 121: 324-334.
37. Olson, E.C. (1960). Morphology, paleontology, and evolution. In: Evolution after Darwin, vol 1: 523-545. Chicago: University of Chicago Press.
38. Peters, D.St., Mollenhauer, D., and Gutmann, W.F. (1971). Bau, Konstruktion und Funktion des Organismus.- Natur und Museum 101: 208-218.
39. Piaget, J. (1972). Structuralism.- London: Routledge & Kegan Paul.
40. Raff, R.A., and Kaufman, T.C. (1983). Embryos, genes, and evolution.- New York, London: Macmillan, 395 p.
41. Raup, D.M. (1972). Approaches to morphologic analysis.- In T.J.M. Schopf, ed., Models in paleobiology, 28-44. San Francisco: Freeman, Cooper & Company.
42. Raup, D.M., and Michelson, A. (1965). Theoretical morphology of the coiled shell.- Science 187: 1294-1295.
43. Reif, W.-E. (1975). Lenkende und limitierende Faktoren in der Evolution. Acta biotheor 24: 136-162.
44. Reif, W.-E. (1981). Konzepte und Methoden der Funktionsmorphologie.- In W.-E. Reif, ed., Funktionsmorphologie, Paläontologische Kursbücher, Vol 1, 11-24. München: Paläontologische Gesellschaft.
45. Reif, W.-E. (1982). Functional morphology on the procrustean bed of the neutralism-selectionism debate. Notes on the Constructional Morphology approach.- N Jb Geol Paläont Abh 164: 46-59.
46. Reif, W.-E. (in press). Constructional morphology as a working tool in evolutionary biology.- Int Geol Congress Moscow 1984, Abstracts.
47. Reif, W.-E. (in press). Konzepte und Geschichte der Funktionsmorphologie.- Aufsätze und Reden der senckenberg. naturf Ges Frankfurt.
48. Reif, W.-E. (in press). Konstruktionsmorphologie als biologisches Arbeitskonzept bei Hermann Weber.- Aufsätze und Reden senckenberg. naturf Ges Frankfurt.
49. Reif, W.-E. (in press). Review of: Raff and Kaufman: "Embryos, genes and evolution".- Zentralblatt Geol Paläont. II.
50. Reif, W.-E., and Robinson, J.A. (1975). Geometrical relationships and the form-function complex: Animal skeletons.- N Jb Geol Paläont Mh 1975: 304-309.
51. Rosen, D.E., and Buth, D.G. (1980). Empirical evolutionary research versus neo-Darwinian speculation.- System Zool 29: 300-308.
52. Rudwick, M.J.S. (1964). The inference of function from structure in fossils.- Brit J Philos Sci 15: 27-40.
53. Russell, E.S. (1916). Form and function.- London: John Murray, 383 p.
54. Sale, J.B. (1966). Daily food consumption and mode of ingestion in the hyrax.- J E Afr Nat Hist Soc 25: 215-224.
55. Salthe, S.N. (1972). Evolutionary biology.- New York: Holt, Rinehart and Winston Inc, 437 p.
56. Seilacher, A. (1970). Arbeitskonzept zur Konstruktionsmorphologie.- Lethaia 3: 393-395.
57. Simpson, G.G. (1963). Historical science.- In C.C. Albritton, ed., The fabric of geology, 24-48. San Francisco: Freeman, Cooper & Comp.
58. Stearns, S.C. (1982). On fitness.- In D. Mossakowski, and G. Roth, eds., Environmental Adaptation and Evolution, 3-18. Stuttgart: Gustav Fischer.
59. Stearns, S.C. (in press). The tension between adaptation and constraint

in the evolution of reproductive patterns.

60. Stebbins, G.L. (1971). Processes of organic evolution. 2nd ed.- Englewood Cliffs, NJ: Prentice-Hall, 193 p.
61. Thenius, E. (1975). Die Schliefer: Stammesgeschichte.- In B. Grzimek, ed., Enzyklopädie des Tierreichs, B. 12, 515-524. Zürich, Kindler-Verlag.
62. Thomas, R.D.K. (1979). Constructional morphology.- In R.W. Fairbridge and D. Jablonski, eds., The Encyclopedia of Paleontology, 482-487. Stroudsburg, Penns.: Dowden, Hutchinson & Ross, Inc.
63. Thomas, R.D.K., and Reif, W.-E. (1983). Opportunity and constraint in the evolution of organic form.- Geol Soc Amer Abstr Progr 15: 705.
64. Van Valen, L. (1960). Nonadaptive aspects of evolution.- Amer Natur 94: 305-308.
65. Waddington, C.H. (1968). The basic ideas of biology.- In C.H. Waddington, ed., Towards a theoretical biology, 1-41. Edinburgh: University Press.
66. Waddington, C.H. (1969). The theory of evolution today.- In H. Koestler and J.R. Smythies, eds., Beyond Reductionism, 357-395. London: Hutchinson.
67. Weber, H. (1955). Stellung und Aufgaben der Morphologie in der Zoologie der Gegenwart.- Zool Anzeiger Suppl Band 18: 137-159.
68. Weber, H. (1958). Konstruktionsmorphologie.- Zool Jahrb Abt Allg Zool und Physik der Tiere 68: 1-112.
69. Webster, G., and Goodwin, B.C. (1982). The origin of species: a structuralist approach.- J Social Biol Struct 5: 15-47.
70. Weiss, P.A. (1969). The living system: determinism stratified.- In A. Koestler and J.R. Smythies, eds., Beyond reductionism, 3-55. London: Hutchinson.