

Schmidt-Kittler, N., & K. Vogel, eds. (1991): *Constructional morphology and evolution (Konstruktionsmorphologie und Evolution)*. Springer-Verlag, Berlin — Heidelberg — New York. XI + 409 S., 147 Abb., 3 Tab., DM 248,—.

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The book contains 24 contributions — arranged in 4 parts — which were originally presented at a symposium on “Constructional morphology and biomechanics: concepts and implications”, held in 1990. Subject of part I are the “Concepts of constructional morphology”.

In his contribution on “Explanations in Konstruktionsmorphologie and evolutionary morphology”, Walter J. BOCK gives an outline of modern philosophy of science and emphasizes that every branch of biology dealing even partly with evolution has to realize the principal difference between nomological-deductive and historical-narrative explanations. BOCK argues that the German term “Konstruktionsmorphologie” does not refer to the same range of meanings as the English “constructional morphology”, which can easily be seen by translating “construction site” or “road under construction” into German. Therefore he pleads in favour of the original term “Konstruktionsmorphologie”. Within this research program, valid explanations have to be nomological-deductive. Problems will immediately arise when historical-narrative explanations are introduced, since the complete research strategy of Konstruktionsmorphologie aims to yielding nomological-deductive explanations. A different approach is provided by evolutionary morphology. BOCK advocates a proper distinction between Konstruktionsmorphologie and evolutionary in order to achieve nomological-deductive explanations or historical-narrative ones, respectively. His analysis of terminology, linguistics and history of the morphological approaches dealt with is an outstanding example of an introduction to scientific methodology and a clear basis for further discussion. — Werner NACHTIGALL's essay on “Functional aspects of morphology” lists numerous quotations of the original definitions of morphological terms. So, it is of special value for all students of history of science. It rather reflects a certain way of thinking than it contributes to terminological or epistemological clarity. — In his “Outline of morpho-constructional analysis”, Norbert SCHMIDT-KITTLER emphasizes the specific properties of this concept, the main purpose of which is to describe “Functions of organic features in terms of transformation of energy input into effect output on the strength of physical principles”. Thus, it constitutes a synthesis of mechanics, energetics and morphology. Admittedly, synecological relationships — and even the main part of the autecological parameters — of the organism under consideration are left out. In SCHMIDT-KITTLER's article there is a certain gleam of “higher” philosophical claims. However, they do not add to the merits of this article. — Klaus VOGEL wrote something like a counterpart to Walter BOCK's chapter. VOGEL starts from an explicit definition of “constructional morphology: . . . the study of organisms and their parts as coherent systems and subsystems that obey statically and dynamically (at rest and in movement) physical principles and processes”. This definition claims to be based on Hermann WEBER's concept of “Konstruktionsmorphologie” as a synthesis of pure — descriptive — morphology and comparative functional analysis. The author totally ignores BOCK's distinction of nomological-deductive and historical-narrative explanations in morphology. All of the apodictic claims in VOGEL's contribution apply only as long as nomological-deductive explanations are intended, e.g. the first of his six “concluding theses”: “morphology is mechanics”.

The 9 chapters of part 2 deal with “Bioconstruction: operational interconnections, behavior, environment”. R. McNeill ALEXANDER introduces the concept of “dynamic similarity in the analysis of animal movement”. “Two motions are dynamically similar if one could be made identical to the other by multiplying all lengths by one factor, all times by a second factor and all forces by a third one”. These factors, and certain relations thereof, are combined in a number of expressions which characterize complex physical conditions of dynamic similarity. Such expressions are e.g., the Reynolds number pvl/μ , where p is the density and μ the viscosity of a fluid, v the velocity and l a length of a body moving through the fluid. These expressions facilitate the diagnosis of dynamic similarity. ALEXANDER gives examples for some types of movement (running, flight and swimming), showing that the dynamic similarity hypothesis at present seems to be confined largely to walking and running. It would, however, be worth to apply this concept also to the testing of homology, as long as

similarity of all kind is regarded to be the only valid test of homology (BOCK). — Some aspects of constructional morphology (sensu VOGEL) are useful even on the level of single cells, as Jürgen BEREITER-HAHN shows in his chapter on "Cytomechanics and biochemistry". He outlines that all properties of cells, even of single ones, are shaped by a complex network of interaction of factors controlling biomechanics and form. This network includes mechanical properties as well as chemical activities and genetic information. The author states that "classical logics may be insufficient to describe the cause/effect relations established in self-organizing systems". Unfortunately, I could not find any substantiation of this statement in this article. — The position of the 'Frankfurt School of Phylogenetics' is expounded in the contribution of one of its founders, Wolfgang Friedrich GUTMANN ("Constructional principles and the quasi-experimental approach to organisms"). He places emphasis on the so-called hydraulic theory which explains nearly every organismic unit in terms of hydrodynamics. Notwithstanding the stimulating role of this approach within the science of form and function and its many undoubtedly correct — albeit often trivial — consequences, the author arrives at some strange points. He states, for example, that "constructional morphology is not allowed to start from form . . .", or "a nonmorphological morphology has to be set up which will remain devoid of form". These claims will hardly facilitate communication and cooperation between the 'Frankfurt School of Phylogenetics' and other constructional morphologists whatsoever. — Wighart VON KOENIGSWALD and Hans Ulrich PFRETSCHNER exemplify the interaction of genetic determination and functional adaptation by studying structure and mechanical requirements of the enamel of mammalian teeth. The Schmelzmuster reflects certain detectable stress forces, and it also conserves certain — phylogenetically — prior adaptations. The latter can be used to reconstruct phylogeny (like any other morphological character). — C. R. C. PAUL treats the apertures of gastropod shells from a functional-morphological perspective. The results are amazing, they allow to meet the never vanishing opinion that gastropod shell morphology were evidence for non-functional — and therefore luxurious — characters. Especially data on aquatic — mostly marine — snail species demonstrate that "snail shell apertures have an instantaneous function associated with emergence and retractions of the body and a growth function during construction of the shell". Here, by the way, the meaning of the term "construction" is clearly different from the usage in e.g. VOGEL's essay. — Dieter Stefan PETERS asks if "behavior plus 'pathology'" were "the origin of adaptations". His main examples — deviations in bill shape in birds — illustrate that the advantage of a character can only be assessed in relation to a certain environment. Therefore, whether a character is "pathological" or a "key innovation" depends on the requirements it has to cope with. Since part of these requirements naturally arise from the environment (or better "umwelt") the whole debate on "primacy of organisms" vs. "concept of adaptation" is hard to understand. If, as PETERS says on p. 147, "adaptation is not the morphological representation of certain environmental properties", it is entirely inexplicable how it ever could be noticed that in spite of specific differences in the morphology of certain bees "the habit of oil foraging could be predicted on the basis of inspecting specimens in museum collections", as he states on p. 149. — "The function of labyrinthodont teeth" turns out to be "an adaptive answer to a constructional or morphogenetic constraint in evolution" in the study of H. PREUSCHOFF, W.-E. REIF, C. LOITSCH and E. TEPE. The authors show that labyrinthodonty was evolved several times in groups where fangs with low jaw bones were developed. In low jaw bones the mechanical properties large fangs require could not be reached by immature teeth which are simply smaller than foldless adult teeth. So, in at least four different evolutionary lineages the immature teeth became labyrinthodont, which allowed large fangs with low jaw bones. The mechanical values of adult teeth without dentine folds do not differ from teeth with plicidentine. Adult labyrinthodonty may, therefore, be explained most plausibly as a morphogenetic remnant of earlier functional requirements. — J. M. V. RAINER discusses flight and echolocation in bats in respect to different evolutionary scenarios. The production of sufficiently loud calls like those necessary for echolocation is apparently only possible when a bat is flapping its wings. Consequently, flight patterns, acoustics of echolocation calls and foraging strategies form a complex of coupled adaptive domains. This exciting study suffers only from numerous inconsistencies in argumentation, especially in the phylogenetic part. The author cites in extenso sources supporting the view that Megachiroptera plus Microchiroptera are not monophyletic, but he widely ignores those speaking in favour of monophyly. He emphasizes the importance of the retinotectal pathway in the brain of Megachiroptera and Primates, but he obviously missed that these resemblances have been doubted by other investigators (THIELE et al., Verh. Deutsch. Zool. Ges. 84, 381 f., 1991). On p. 180 RAINER writes it were "difficult to conceive that a highly specialized microbat could successfully give up sound in favour of vision". On p. 183 the "absence of echolocation" is treated "as a synapomorphy of megabats", which undoubtedly means that they gave up this way of gaining information. P. 185 starts with the statement that "megabats show no obvious primitive . . . characters in comparison to microbats". I wonder how the author copes with the claw on the second finger in Megachiroptera. Moreover, the possession of large eyes, as opposed to the small ones in Microchiroptera, is easily explained as a plesiomorphy of all eutherian mammals. So, RAINER's phylogenetic discussion is better read with great reservation. — A. WISSER and W. NACHTIGALL provide with their analysis of the

biomechanics of the wing joint in flies an outstanding example of a synthesis of morphology and functional analysis. Detailed structural data are given as well as mechanical values. The chapter is furnished with a great number of illustrations, photographs and drawings. However, some of the graphs are a bit complicated and therefore their understanding requires a certain amount of time.

Part 3 contains 6 essays on "Bioconstruction: morphogenesis", starting with Klaus BANDEL's demonstration that the morphology of the molluscan shell does not only reflect adaptations to certain environmental impacts and phylogenetic history, but also ontogenetic changes. Data about the latter can be extracted from shape and structure of the shell. Even the type of embryonic development leaves its traces in the first mineralized shell. In detail, there are some loose terms in this article, e.g. on p. 218 f. it is stated that "each level of ontogeny follows its own evolution and has its own phylogeny" (this is nonsense as long as 'phylogeny' means 'history of taxa', as normally defined). However, even a number of similarly vague wordings do not lessen the importance of BANDEL's analysis. — Karel F. LIEM shows in his "Functional approach to the development of the head of teleosts" how internal and external determinants of development interact. In the jaw apparatus there are certain strategic anatomical points ("hot spots") which are of special importance for the force transmission during biting and suction. Interestingly, LIEM comes to the conclusion that "it is impossible to assign a dominance hierarchy of form over function or vice versa". — Adolf SEILACHER introduces a new conceptual framework, which he calls "(bio) morphodynamics". It describes the way of interaction between "phylogenetic tradition", "fabrication", "function" and "effective environment", where "fabrication" means the formation of "biomaterial" to patterns by means of mechanical and chemical regulation. This concept appears to be partly vague (how to separate "external function" from "effective environment"?), partly trivial (the "inclusive program" has to meet the requirements of the "effective environment" on the basis of its "bauplan" which is part of the "phylogenetic tradition") and only partly stimulating. In fact, examples are given that are neither new nor surprising ("pneu" versus "dome" models in echinoids, "zebra patterns" in human fingerprints, zebra heads and stegocephalian skulls). It remains open if or how the outlined morphogenetic mechanisms can be decoupled from the process of adaptation. SEILACHER just admits that they "may become tamed towards a specific function by Darwinian selection". — Diethard TAUTZ treats in his "Genetic and molecular analysis of pattern formation process in *Drosophila*" the increasingly exciting field of developmental genetics. The growing insight into the interplay of regulation genes, structure genes and epigenetic processes open a new look at evolution on this level. E.g., it was found that "a number of processes are specified in redundant pathways which can partly substitute each other". These "can provide a versatile frame for the evolution of developmental traits, since they allow the divergence of one component, while the other remains functional". — R. D. K. THOMAS and W.-E. REIF's essay on "Design elements employed in the construction of animal skeletons" is perhaps the best example of "theoretical morphology". The authors attempt to uncover the range of variation and constraint in forming skeletons by first considering theoretically the number of possible variants (i.e. situation, material, number, shape, growth, assembly and interplay of elements) and then finding examples in nature. The result is a matrix of possible combinations from which the likelihood of homology vs. convergence can be estimated. Like all other such attempts, the present one suffers from the principal 'naturalistic fallacy': how to decide whether a certain combination does necessarily not occur or is just accidentally not the case. Consequently, the authors claim their attempt to be a "useful heuristic device" rather than to serve as a new 'morphogenetic law'. — "A theoretical morphological approach to tooth replacement in lower vertebrates" by David B. WEISHAMPEL offers another case of the application of general models and mechanisms to a special morphogenetic problem. Instead of the traditionally discussed competing explanations – the Zahnreihe-theory and the clade-theory – the author presents a model starting from the postulation of inhibition zones controlling the vertical and horizontal spacing of tooth germs. This model can simulate all replacement geometries of extant and fossil "lower" vertebrates. It represents one more step from purely descriptive "rules" towards an understanding of the underlying causal mechanisms.

Part 4 is entitled "Bioconstruction: evolution" and contains 5 chapters. P. DULLEMEIJER discusses extensively the relation between universal, general, and local constraints in forming a biological construction. Although providing several examples, e.g. nearly the same data set of fish jaw morphology as K. F. LIEM refers to, this contribution is mainly an essay on methodology and epistemology. The author picks up concepts of other contributors in a fruitful and effective way. Sadly enough, only few others did so. — Hans-Rainer DUNCKER's analysis of "Constructional and ecological prerequisites for the evolution of homoiothermy" is not only the longest but also the most isolated chapter of the book. The author does not even cite one of the other contributors. Nevertheless, he shows in a simply convincing manner that the different compartments of 'homoiothermy' in birds as well as in mammals could not be developed independently of each other. Rather functional couplings and, consequently, temporal hierarchies determined the evolutionary origin of the 'homoiothermy-syndromes'. One of the most puzzling consequences of this approach is the conclusion that the avian feather is not primarily an adaptation to reduction of heat loss, since the

avian thorax (indicating flight ability) must be evolutionarily older than homiothermy. This consequence is not discussed by the author, but anyway could inseminate the current discussion about the evolutionary origin of flight in birds. — Karl EDLINGER stresses “The mechanical constraints in mollusc constructions – the function of the shell, the musculature, and the connective tissue”. Like some other representations of ‘constructional morphology’, he argues lively against traditional morphologists whose suggestions are dequalified as “totally unexplained” hypotheses. This were acceptable if the author’s phylogenetic ideas were better substantiated, but they are not. K. EDLINGER’s “alternative phylogenetic relationships” are pure statements, relying on certain assumptions. Thus, they are as apodictic and axiomatic as those he criticizes. For example: although he – correctly – emphasizes that “none of the reconstructions can be directly deduced from the fossil record”, he states without any empirical data that “the constructional stages of the sequence never possessed a waist”. This is the type of mere statement on which the whole argument is based. — P. W. SKELTON evaluates “Morphogenetic versus environmental cues for adaptive radiations”. Unlike most of the other authors, he starts from a cladogram (of Aptian-Cenomanian recumbent rudist Bivalvia), thus discussing a series of concrete cladogenetic events. Despite some – from a Hennigian point of view – odd usages of terms (e.g. “polyphyletic origin” of a taxon, “convergent taxa”), the author stays close to classical methodology and terminology. In a similarly reconciling way he concludes that “adaptive radiation – when it can be identified as such – requires both morphogenetic (or other intrinsic) innovation and a receptive environment. Yet the appearance of either may serve as an effective cue for the radiation, contingent upon prior existence of the other, acting, so to speak, as an enabling circumstance”. In my opinion, this relation of mutual enhancement applies to all sorts of internal vs. external factors of evolutionary transformation. — If a traditional Hennigian systematist would discuss the phylogenetic relationships of “some metazoan phyla” without even mentioning the results of the molecule-based studies she or he would clearly be blamed to violate the rules of good science. James W. VALENTINE describes “The sequence of body plans and locomotory systems during the Precambrian-Cambrian transition” without even mentioning the possibility that the Spiralia are monophyletic. VALENTINE’S contribution does not contain any inspiring phylogenetic proposition or hypothesis on constructional novelties which could compensate for its serious flaws.

Naturally, a book containing 24 contributions of different authors from different parts of the world, different schools of thinking and different fields of science, can hardly be homogeneous. In fact, “Constructional morphology and evolution” presents a variety of approaches and topics. Of course there are differences in style and quality. But on the whole, this book can stimulate discussion and exchange of information in “constructional morphology” (if not “Konstruktionsmorphologie”). It might as well offer a valuable source of knowledge to scientists from adjacent and other fields. However, a considerable number of contributors – among them even the editors – do not give the impression that it was their intention to overcome traditional battlefields in evolutionary biology.

Vogel, K. (1991): Konstruktionsmorphologie – Ein Schlüssel zum Verständnis der biologischen Evolution (Constructional morphology – a key to understanding biological evolution). Sitzungsberichte der Wissenschaftlichen Gesellschaft der Johann Wolfgang Goethe-Universität Frankfurt am Main, Band 28, Nr. 2. Franz Steiner Verlag, Stuttgart. 22 S., DM 24,—.

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Der Autor unternimmt mit diesem Bändchen den „Versuch, Morphologie in der Biologie wieder ‚gesellschaftsfähig‘ zu machen“. Dies soll geschehen, indem organismische Strukturen in erster Linie als Konstruktionen gesehen werden, die mechanischen (bzw. statischen oder anderen physikalischen) Erfordernissen genügen müssen. Jede Abweichung einer organismischen Form von der unter sparsamsten Annahmen energetisch günstigsten muß unter Energieaufwand erzwungen werden. Der Nutzen eines solchen Energieaufwands wird vom Autor fast ausschließlich in einer Verbesserung des „Internbetriebs“ gesehen, im Unterschied zur klassischen Evolutionsbiologie, in der ein möglicher Nutzen fast stets in einer Verbesserung der Auseinandersetzung mit der Umwelt, des „Externbetriebs“ also, gesucht wurde und wird.

Der vorliegende Aufsatz enthält – gemessen an vielen anderen Publikationen der Frankfurter konstruktionsmorphologischen Richtung – nur wenige, m. E. unnötige, Polemiken gegen die „klassischen“ Denk- und Arbeitsweisen in der Evolutionsbiologie. Dagegen zeigt er überzeugend die Chancen einer physikalisch-ingenieurwissenschaftlich orientierten Morphologie als „Gerüst“ für eine Wissenschaft vom Organismus.