Ecomorphology: Integration of form, function, and ecology in the analysis of morphological structures

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Abstract: Ökomorphologie: Integration von Form, Funktion und Ökologie bei der Analyse morphologischer Strukturen

Aufgrund der enormen Komplexität von Organismen ist es in der heutigen Biologie unumgänglich geworden, mehr und mehr reduktionistische Ansätze zu verfolgen. Dies kommt in ihrer zunehmenden Zergliederung in Einzeldisziplinen zum Ausdruck. Extrem reduktionistische Ansätze dürfen jedoch nicht das Ende biologischer Forschung markieren, sondern sollten zugleich der Anfang für einen weiteren integrativen Ansatz sein, der das organismische Niveau berücksichtigt (vgl. SAUER, 1992). Auch in der Morphologie gewinnt eine integrative Sichtweise, welche die Form und Funktion morphologischer Strukturen in ihrer Beziehung zur externen Umwelt betrachtet, immer stärker an Bedeutung. Aufbauend auf klassischen morphologischen Disziplinen wie der deskriptiven und funktionellen Morphologie versteht man unter der ökologische Morphologie allgemein die Lehre von der Wechselbeziehung zwischen der Morphologie eines Organismus und seiner natürlichen Umwelt. Während die Funktionsmorphologie die Analyse exakter Struktur-Funktionsbeziehungen zum Inhalt hat, geht es in der Ökomorphologie um die Untersuchung der Funktion von Organismen im ökologischen (Umwelt) und/oder evolutionären Kontext (Historie), wodurch eine Förderung des Verständnisses der ökologischen und evolutionären Konsequenzen ihres Bauplanes erreicht werden soll. Dieses Forschungskonzept wird im Rahmen dieser Abhandlung anhand von Fallbeispielen vor allem aus der Gruppe der Staphylinoidea erläutert.

Key words: adaptation, Coleoptera, ecomorphology, evolutionary morphology, functional morphology, Insecta, morphology, Staphylinidae

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Organisms are complex entities whose study has necessitated an increasingly reductionistic stance in modern biology (CAPLAN 1987). As a consequence, biology as a science has been split up into numerous sub-disciplines. However, this extremely reductionistic philosophy must not be taken as marking the endpoint of biological research but should be reappraised as the beginning of a new integrative approach encompassing the entire organism (SAUER 1992). This view has been promoted since the second half of the 20th century with the rise of new disciplines such as ecophysiology and ethoecology. Moreover, in morphology, an integrative approach with regard to the form and function of organisms in their relationship to the external environment is becoming increasingly important (e.g. KARR & JAMES 1975, MOTTA & KOTRSCHAL 1992, REILLY & WAINWRIGHT 1994).

General outline of ecomorphology
Morphology is a biological discipline that aims at an understanding of the biology of organisms on the basis of their structural appearance (MAIER 1994). Ideally, any aspect that determines the formation and change of morphological structures should be considered, including genetics, function, phylogeny, ontogeny, ecology and ethology. This list makes it clear that morphology has to "co-operate" with several other research areas in biology. However, no standard morphological methodology exists. Therefore, morpholo-

gists require versatile research programs that are based on structural phenomena but that reach out to other biological levels to provide the necessary integration (cf. Fig.1). This integrative understanding of morphology is also the key concept of the relatively young field of ecological morphology (shortened to ecomorphology). The term ecomorphology was coined in the 1940s (van der KLAAUW 1948). According to a more modern definition, it comprises the analysis of the interrelationship between morphological form and its natural environment to enable the understanding of the mutual contribution of both these aspects (MOTTA & KOTRSCHAL 1992). In this context, ecomorphologists are primarily interested in analysing patterns of resource use of organisms, i.e. their capacity to use resources from their external environment. Thus, ecomorphology refers to one of the fundamental questions in ecology, viz. which factors determine the actual resource use of organisms (SCHOENER 1986, WAINWRIGHT 1994). Whereas functional morphology investigates the exact relationship between form and function (e.g. HOMBERGER 1988), ecological morphologists focus on the function of morphological structures in an ecological (environment) and evolutionary (history) framework in order to promote our general understanding of the ecological and evolutionary consequences of animal construction (WAINWRIGHT 1991; BOCK 1994). In this context, the term "function" does not imply the physical and chemical properties of a morphological structure (as in functional morphology) but, instead, refers to its "biological role", i.e. its use in the natural environment (GOLDSCHMID & KOTRSCHAL 1989). A major goal in ecomorphology is to find adaptive explanations for specific forms, i.e. to consider the external environment as the main evolutionary causation of the observed morphology. However, in order to evaluate the role of phylogenetic history as an additional or alternative explanation, phylogenetic relationships have to be reconstructed among the investigated taxa, if such information is not available in the literature. These relationships can then be used as a template for explanations concerning the evolutionary origin and diversification of the investigated ecologically relevant structures.

How do we make the connection between the morphology of an organism and the ecological and evolutionary consequences of its morphology? REILLY & WAINWRIGHT (1994) suggest a generalised integrative scheme for analysing ecomorphological interrelationships as a series of interconnected levels of inquiry (Fig.1). Proceeding from (i) the description of the morphological traits of interest of the organism, these levels of analysis are arranged according to (ii) their functional roles and (iii) performance consequences, to (iv) their effects on actual resource use and (v) fitness.
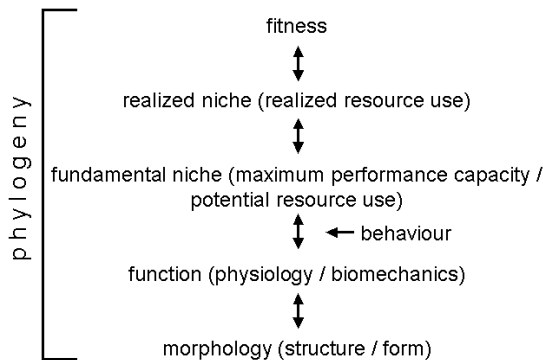

Fig. 1: Interconnected levels in ecomorphological research (modified after REILLY & WAINWRIGHT 1994). Note the possible integration of phylogeny at all levels of investigation and the consideration of behaviour as a filter allowing the selection of the way in which a morphological structure is actually used from the diversity of possible functions. For further explanation see text.

In contrast to the opinion of many ecologists, our knowledge of the functional morphology, anatomy and biomechanics of many animal structures is rather poor (cf. BOCK 1990). In view of the relatively new development of ecological morphology, ecologically interested morphologists therefore often need to perform thorough studies of the functional morphology of ecologically relevant structures. A sound analysis of the ecological and evolutionary consequences of these structures is only possible on this foundation (BOCK 1990; REILLY & WAINWRIGHT 1994).

In the following, I illustrate these different steps of ecomorphological research by using case studies from my own research on Staphylinoidea (Coleoptera).

Case study 1: **Descriptive comparative morphology of the mouthparts in spore-feeding Staphylinoidea**

Any morphological research program usually starts phenomenologically, including the observation, description and documentation of the morphological structures under study. Even at this descriptive level of investigation, valuable ecological and evolutionary knowledge can be achieved, especially if we follow a comparative approach. Although not a causal analytical approach, the methodology of comparison has the potential to recognise similarities attributable to common descent (homologies) and to common function (adaptive similarities or analogies). Moreover, adaptations might be recognised by their correlation with certain parameters of the external environment. Finally, the evolution of morphological characters might be understandable by mapping them on independently established phylogenies (cf. Fig.2).
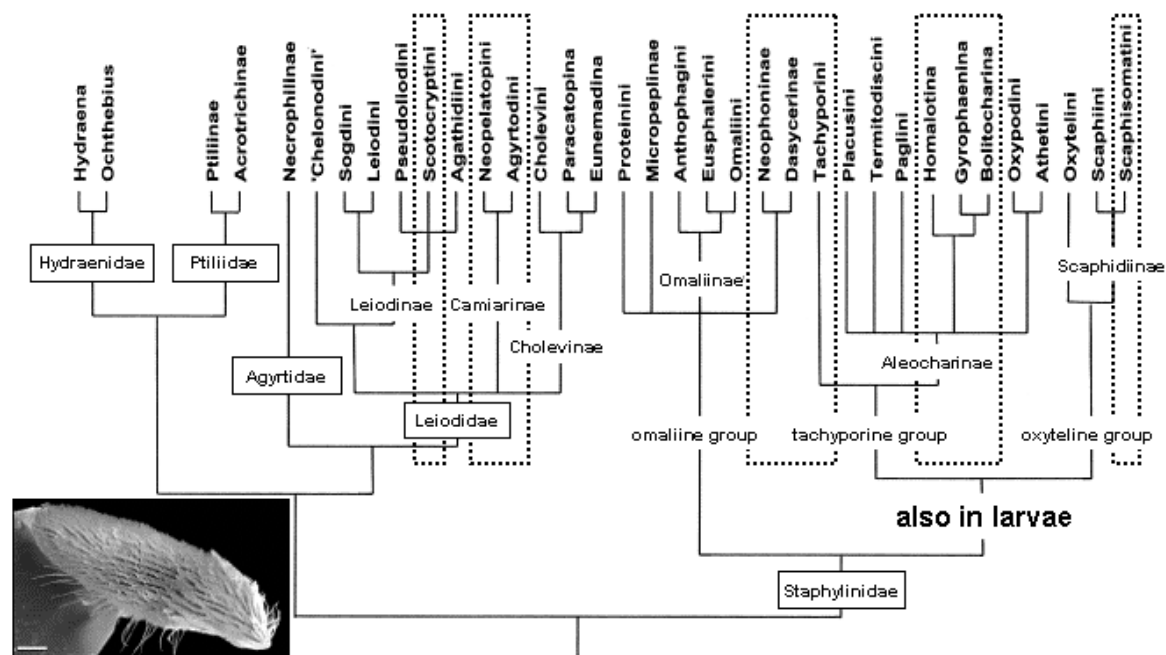

Fig. 2:   Example of the mapping a specific morphology on a phylogenetic tree. Distribution (black-rimmed tribe names) of laciniae modified into oblong "spore brushes" (bottom left) across the phylogeny of spore-feeding staphylinoids under investigation. The lack of these structures in non-spore-feeding outgroups and their convergent occurrence in obligate spore-feeders support the view that they might represent true adaptations towards brushing fungal spores from the substratum. For further details see BETZ et al. (2003).

In order to evaluate the influence of different phylogenetic and ecological starting points on the formation of the mouthparts in the guild of fungal spore-feeders among the coleopterous superfamily Staphylinoidea, we performed a scanning electron microscopic analysis (SEM) of the involved trophic structures in spore-feeding larvae and adults of the Ptiliidae, Leiodidae and Staphylinidae in order to describe the fine structure of their main functional elements (Betz et al. 2003). On the basis of a phylogenetic scheme, our analysis shows that shifts from general microphagy towards sporophagy are not necessarily constrained by nor strongly reflected in mouthpart morphology. Nevertheless, in several of these lineages, the organs of food intake and grinding have experienced particular derived fine-structural modifications that have convergently evolved, probably in response to specialised mycophagy, such as spore-feeding. These modifications involve (i) advanced galeal rakes, (ii) galeal or lacinial "spore brushes" with arrays of stout bristles (Fig.2), (iii) reinforced obliquely ventrad oriented prosthecal lobes and (iv) the differentiation of the molar grinding surfaces into stout teeth or tubercles. Even specialised predatory mouthparts with reduced mandibular molae have not formed an insuperable constraint for the evolution of sporophagy. This is illustrated by the evolution

of secondary trituration surfaces on other parts of the mandibles or the maxillae in larvae and adults of representatives of the tachyporine and oxyteline group.

Morphological structures can furthermore be described in a quantitative way, leading thus to the field of morphometry. Morphologists can collect quantitative data on one or more characters that can afterwards be evaluated by using uni- or multivariate statistics (cf. LEISLER & WINKLER 1991). In traditional morphometry, one usually determines simple distances, counts or angles that have functional meaning (e.g. biomechanical levers) or might otherwise be appropriate for describing the morphological diversification of a taxon. For instance, the distributional pattern of species across the morphological space constructed *via* principal component analysis (PCA) might allow resource or habitat specialists to be recognised according to their isolated position within it. On the other hand, wide gaps within the morphospace might indicate that certain phenotypes are not realised within this group of organisms (RICKLEFS & MILES 1994), possibly because of constraints for ecological, historical or design reasons.

In Fig.3, I have combined principal component 1 (PC 1) with PC 4, which together account for 44.3% of the total morphological variation within a larger set of morphological variables collected in approximately 100 species of spore-feeding staphylinoid beetles. The resulting morphospace sorts these species according to PC 1 representing body size, lateral eye protrusion, leg length and antenna length and to PC 4 standing for body width and the leverage of the mandibles. The latter character is of special functional significance, since it is indicative of the force that the beetles can exert to break hard spore walls open with their basal molae. In particular, several representatives of the ptiliids and leiodids appear to have evolved forceful mandibles, whereas several staphylinids have mandibles that might be adapted to act at higher velocities (cf. GRONENBERG 1996 for the trade-off between force and velocity in insect mandibles).
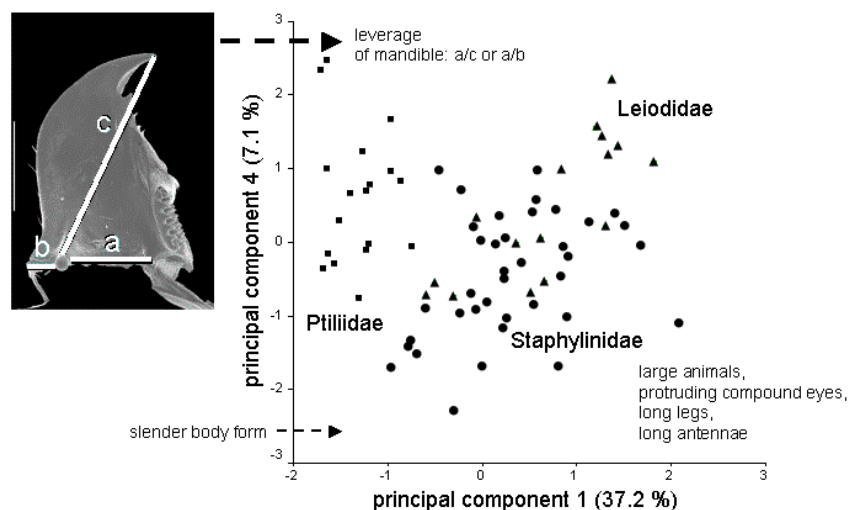

Fig. 3:   Scatter plot of the first and fourth principal components of the external morphology of spore feeding Staphylinoidea adults. Each dot represents a different species of Ptiliidae (square), Leiodidae (triangle) or Staphylinidae (circle). Image on the left shows the ventral aspect of a mandible with three inscribed levers (a-c), originating at the ventral condylus. For further explanation see text.

One drawback of traditional morphometry is that linear distances might not be homologisable, because they might not be defined by homologous endpoints. Moreover, linear measurements make it difficult to assess the geometry of a structure. For this reason, a new type of morphometry referred to as geometric morphometry (cf. ROHLF & MARCUS 1993) was developed in the 1980s. Here, we place several biologically defined homologous landmarks on the structures of interest by using modern digitizing equipment. The resulting landmark configurations (each landmark being defined by its geometrical two- or three-dimensional coordinates) are corrected for size, position and orientation and can then be analysed *via* multivariate statistics (see ZELDITCH et al. 2004 for an introductory textbook on this approach).

***Case study 2*: Functional morphology of the predatory legs in *Philonthus marginatus* (Coleoptera, Staphylinidae)**

The first step of integration in ecomorphology involves being able to understand the way in which the morphology under study works (cf. Fig.1). Sound functional morphological analyses consider biomechanical and physiological principles in order to develop functional models of the form-function complex of interest (cf. HOMBERGER 1988). These models are simplified abstractions of the real situation but emphasise those functional aspects that are essential for its understanding. They can be illustrated in the form of a biomechanical lever system (cf. Fig.4). Additional methodological approaches in functional morphology involve (i) direct or indirect observations of the working mechanism and (ii) controlled laboratory experiments, possibly with the manipulation of specific functional elements.

The forelegs of representatives of the staphylinid subgenus *Onychophilonthus* are modified into raptorial legs. With these legs, the beetles are capable of striking prey, even those with an especially fast escape mechanism, such as springtails, in a particularly fast manner (BETZ & MUMM 2001). The actual strike takes the form of a rapid (about 9 ms) depression of the unfolding forelegs towards the prey. Contact with the prey is mediated by a large number of adhesive hairs at the underside of the tarsus. During the subsequent withdrawal of the forelegs, the last tarsomere is deflected almost perpendicularly, thereby securing the prey at the front. The high velocity and acceleration of the strike, the presence of a catch-like locking device between coxa and trochanter, the specific mechanics of the coxo-trochanteral joint (Fig. 4) and other peculiarities suggest a spring-loaded system that involves the co-contraction of the antagonistic trochantero-femoral flexor and extensor muscles. Ultrastructurally, the pro-tarsomeres I-III are underlain by an active glandular epithelium, producing a possibly adhesive secretion that is released via numerous tarsal setae at the underside of the tarsi. The beetles are thus capable of fixing the prey at the very moment of contact.
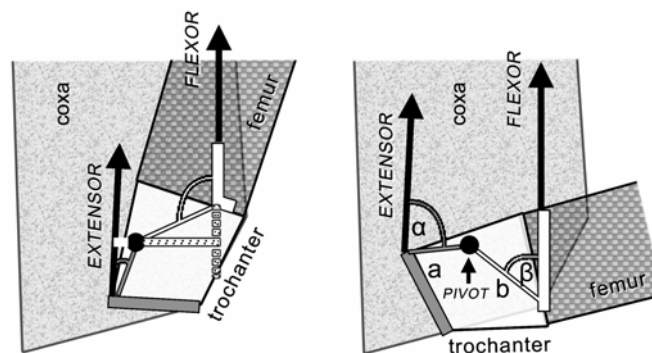

Fig.4: Mechanical analogue of the coxo-trochanteral joint of the raptorial leg in *P. marginatus* suggesting a spring-loaded system that makes possible the observed high velocity of the strike. Depicted are two different states of rotation of the trochantero-femur about the coxa, showing the flexed initial (left) and extended final condition at the end of the rapid depression of the leg (right). Distances a and b represent the mechanical levers of both extensor and flexor system. On the left, the physical levers (horizontal bars) show that, initially, the flexor has a fourfold mechanical advantage with respect to the extensor, which makes the co-contraction of both muscle groups possible without releasing the extension of the leg. For further details see BETZ & MUMM (2001).

***Case study 3*: Performance of tarsal morphology in *Stenus* beetles (Coleoptera, Staphylinidae)**

At the next level of integration of the ecomorphological research program, the performance capacity of the morphology under study has to be measured (cf. Fig.1), an undertaking usually carried out in the laboratory. This approach is the key concept to understanding the linkage between the design of the organism and the ecological and evolutionary consequences of this design. The maximum performance capacity of a morphological structure might determine to what extent the organism is able to perform an ecologically relevant function and to use resources. Examples are the locomotory speed of the legs or the biting force of the jaws. The maximum performance capacity is indicative of the maximal possible (fundamental) niche. On

the other hand, limitations of the performance capacity also limit the range of usable environmental resources.

At this step of analysis, an investigation of the role of behavoiur is also recommended with respect to the decision process that selects, from the diversity of possible functions, the one that has ecological relevance (cf. Fig.1 and WINKLER 1988). Moreover, organisms might be capable of compensating for morphological performance limitations by modifications of their more flexible behaviour.

The final objective of this approach is to assign differences in ecological resource use to those in performance capacity. Here, a comparative approach is recommended i.e. a comparison of individuals within a population, species within a superior taxon or species within an ecological community. As a result, we might achieve a performance gradient that can be related to a corresponding morphological gradient (cf. Fig. 5).

The representatives of the staphylinid genus *Stenus* differ, among others, in their tarsal morphology (slender non-bilobed *versus* widened bi-lobed). In order to evaluate the adaptive value of widened bi-lobed tarsi, the performance of both tarsus morphologies has been evaluated in two different contexts: (i) locomotion on the surface of water and (ii) climbing on vertical (plant) surfaces (BETZ 2002). Measurements of the contact angle at the underside of the tarsi together with observational studies have revealed that, irrespective of tarsus width, all the species are well supported by the surface tension of water while walking upon its surface. Comparative measurements of pulling forces attainable on vertical substrates have demonstrated that widened tarsi have a significantly higher adhesive performance on smooth (plant) surfaces than do slender tarsi. This is attributable to the number of tarsal tenent setae and their specific morphology. These experiments confirm that the major selective demands driving the widening of the tarsi within this genus have come from their firm attachment to smooth plant surfaces (Fig.5).
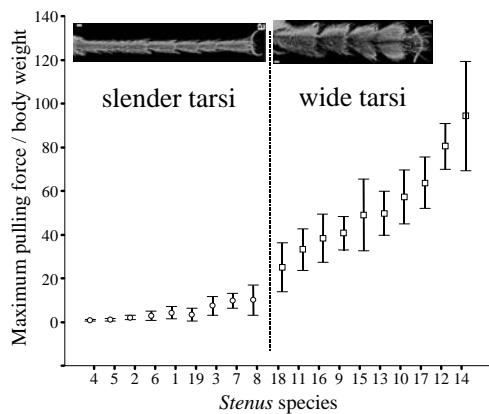

Fig. 5: Maximum vertical pulling forces per body weight as achieved by different representatives of 18 *Stenus* and one *Dianous* species with slender versus wide tarsi on a glass surface representative of smooth plant surfaces. Species with widened tarsi attain significantly higher pulling forces than species with slender tarsi. For further details see BETZ (2002).

***Case study 4*: The relationship between morphology and habitat preference in *Stenus* beetles (Coleoptera, Staphylinidae)**

The following step of integration requires (semi-)field studies in order to evaluate the manner in which the morphology under study is actually used in the natural environment (cf. Fig.1). This is indicative of the actual niche attainable with the possession of this structure. A comparison of the fundamental niche (as established in the previous step) with the realised niche demonstrates the amount of the performance capacity that is actually used under natural conditions and the extent of the congruence of the performance capacity and the attained resource use. If the performance of a structure is not exploited in the field, this might be an indication of the presence of ecological competition.

The preferred hunting sites of the 18 *Stenus* species in Fig. 5 were tested in habitat-choice experiments conducted under semi-field conditions (BETZ 1994, 2000). Accordingly, these species could be assigned to three major habitats, i.e. (i) the debris near the ground, (ii) the open surfaces at the ground and (iii) the herbaceous vegetation, such as reeds. This distinction corresponds well with data based on field collections. A subsequent discriminant function analysis was performed to examine which of several measured morphological variables determined these three major hunting sites of the species. This analysis revealed that plant

climbers were distinct from soil dwellers mainly by their widened tarsi (Fig. 6). Hence, in correspondence with the experimental results shown in the previous section, this morphological feature must be considered a key character for the colonisation of vegetation as a novel ecological zone by many representatives of this genus. Indeed, approximately 70% of the more than 2100 *Stenus* species described belong to subgenera whose representatives have wide bilobed tarsi (V. PUTHZ, personal communication).
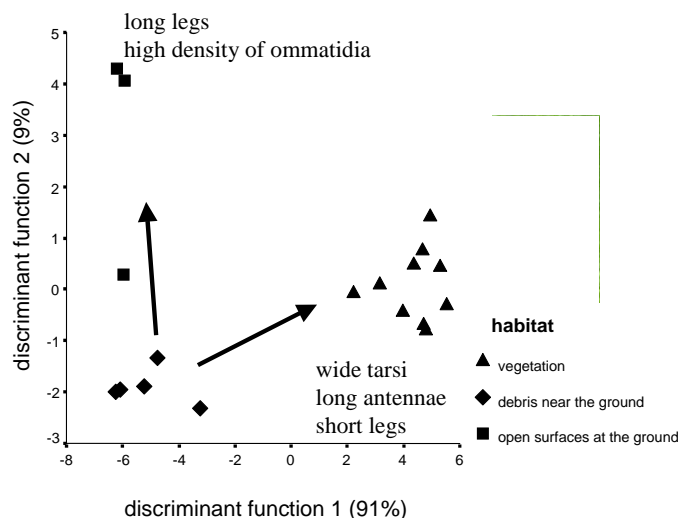

Fig. 6: Separation of the three major hunting sites established in Central European *Stenus* species with a discriminant function analysis. Each dot represents a different species. Tarsus width turned out to be the most important predictor for the separation of the ground-dwelling *versus* the vegetation-dwelling species.

Prospects: Relation of performance to fitness

In order to attain a fundamental understanding of the adaptive value of form-function complexes, it would be of great scientific worth to be able to evaluate the fitness consequences of adaptational changes in morphology. This would be the ultimate test of the adaptive significance of the mechanisms and phenomena revealed at levels 1-4 in the research program suggested by REILLY & WAINWRIGHT (1994) (cf. Fig. 1). However, in practice, it might be difficult to ascribe differences in fitness to morphological graduations as suggested by ARNOLD (1983) (Fig. 7), since reproductive effort and survival depend on many additional factors, such as competition, predatory pressure or energetic considerations, factors that might even interact with each other. However, artificial selection experiments performed under standard laboratory conditions on insects with short generation periods (e.g. *Drosophila*) might aid in moving closer to this objective.
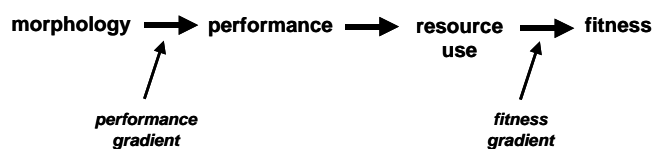

Fig. 7: Theoretical concept of the way in which a deeper understanding of the adaptive value of a specific morphology can be attained by evaluating the influence of morphological variations on performance and fitness. From ARNOLD (1983).

In a macroevolutionary context, fitness might be interpreted in terms of species fitness, which is equivalent to the ecological and evolutionary success of a clade. Unbalanced clade diversities might indicate that one of two sister groups has experienced an largely increased diversification rate attributable to the evolution of a novel morphology, which might have lead to new ecological opportunities. With reliable phylogenies at hand, such hypotheses might be testable by using statistical approaches (e.g. BOND & OPELL 1998).

Acknowledgements

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