PENSOFT

SENCKENBERG
world of biodiversity

Leibniz Association

A technomorphic conceptualisation of biological 'constructions' and their evolution

Festschrift in Honour of Professor Dr. Wolfgang Maier
Edited by Ingmar Werneburg & Irina Ruf

Manfred Drack[1], Oliver Betz[1]

1 *University of Tübingen, Institute of Evolution and Ecology, Evolutionary Biology of Invertebrates, Auf der Morgenstelle 28E, 72076 Tübingen, Germany*

http://zoobank.org/EEA42FFD-58C3-4501-9147-07A760896A68

Corresponding author: Manfred Drack (manfred.drack@uni-tuebingen.de)

Academic editor Ingmar Werneburg | **Received** 25 May 2022 | **Accepted** 3 August 2022 | **Published** 9 September 2022

Citation: Drack M, Betz O (2022) A technomorphic conceptualisation of biological 'constructions' and their evolution. Vertebrate Zoology 72 839–855. https://doi.org/10.3897/vz.72.e86968

Abstract

Here, we build on earlier work concerning notions of engineering design and investigate their conceptual connection to evolutionary biology. The basis for this work is an engineering design schema covering the central concepts of function, working principle and construction. Its relevance for evolutionary biology is explored by connecting these concepts to the so-called design space that is used in engineering optimisation. This tool makes it possible to distinguish various optima of performance and to visualise their robustness with respect to disturbances or changes in parameters. The robustness of morphological 'constructions' with regard to changes of shape is shown by means of examples from engineering and biology. The characteristics of various 'landscapes' in the design space is then related to the concept of evolvability, whereby we explore analogies between systems biology and morphology. A general property of phenotypes from the molecular to the organismal level seems to be that their 'construction' facilitates both their robustness and their exploration of the design space while maintaining the performance of the relevant functions at a high level.

Keywords

biomimetics, design space, evolvability, function, morphology, optimisation, working principle, robustness

Introduction

In a broad sense, the so-called technomorphic approach in biology has a long history, as is indicated by the word 'organ', which stems from the ancient Greek ὄργανον for tool or instrument, originally 'that with which one works' (OED 2021). An organ in turn can be defined via a function (Toepfer 2011: 2,746). Such analogies, in both directions, extend beyond the usage of words: Aristotle compared the functioning of catapults with the movements of animals, and traces of such thinking can also be found in Plato's *Timeaus* (Canguilhem 2008: 79). Pronounced statements stem from La Mettrie's approach in *L'homme machine* from 1749 (La Mettrie 1912), which is probably

the most radical account (other than notions of Descartes) of humans as machines.

For an understanding of the way that biological 'constructions' work, we can sometimes usefully consider organisms heuristically *as if* they were machines, so that analogies between biological and technical systems can be drawn in various contexts (e.g. Reuleaux 1900, Vogel 2013). One of these considerations is the technomorphic approach suggested by Wolfgang Maier (Maier and Zoglauer 1994). Another, more recent, example is the 'living machines' approach of Prescott et al. (2018). Such a mechanistic procedure has also been followed in a travelling exhibition launched by the Field Museum in Chicago (The Field Museum of Chicago 2014).

Before we dig deeper, however, a warning that was made by an eminent theoretician and that is still valid today should be considered: "One can say that the machine theory, on the one hand, provides a useful heuristic tool for the study of organic entities, although as a theoretical model, it has had an almost devastating effect on the development of biology: it has caused those researchers who are biased by the mechanistic idea to be left struggling with scholastic pseudo-problems, even to this day, whereas, on the other hand, it has prevented the perception of actual problems in organic nature (Bertalanffy 1932:55, own translation). The criticism expressed here refers to the insight that organismic structures and functions have to follow physical and chemical laws but that these aspects alone are not sufficient for a holistic understanding of organisms involved in various ways in developmental, evolutionary and ecological contexts. Hence, a well-balanced holistic organism concept needs to be conceived that considers organisms as functionally integrated hierarchically organized systems embedded in historical (ontogenetic and evolutionary) processes (Maier 1999).

Nevertheless, by keeping in mind that comparisons between biological and engineered systems can also have negative results, i.e. the technical approach does not help us to answer biological questions, we can still legitimately investigate those engineering concepts that can be used in biology without ontologically having to claim that organisms are (nothing but) machines.

In the present contribution, we build on earlier work concerning notions of engineering design and investigate their conceptual connection to evolutionary biology. Being functional morphologists and biomimeticists, we mainly consider the morphological or phenotypic levels of living entities, although the approach seems general enough also to cover other areas of biology on the molecular level.

We have previously introduced a (technomorphic) point of view that mainly conceptualises the field of biomimetics (Drack et al. 2018, Drack 2019). As this method has been shown to be useful in the field of biomimetics, we have further developed it in the present context in order to explore its suitability in the analysis of morphological structures in evolutionary biology (Drack et al. 2020), including the implementation and evolution of these structures. The goal is to connect the commonly used engineering design concepts of *function*, *working principle* and *construction* with *optimisation* and *robustness*, because such concepts might also be central for our understanding of evolution. These concepts can also be linked together via the so-called design space (Martins and Ning 2022), which can, in turn, be used by biologists in order to understand phenomena in evolution.

We propose that robust optima at a construction level are widespread in living nature. To be able comprehensively to analyse these optima, we develop below a conceptual framework that might be useful for further (comparative) investigations within biology and, additionally, for comparing biological with engineering systems.

First, we briefly describe the engineering design schema together with the central concepts that it deploys (*function*, *working principle*, *construction*). Second, the connection of the core concepts of this schema are related to biological evolution. Third, the concepts of *optimisation* and *performance* are introduced by means of connecting *function*, *working principle* and *construction* to the design space. Fourth, characteristics of the design space are investigated with respect to differences between biological and engineering constructions. Thus, the connection between evolvability and robustness is analysed with respect to the way that biological systems can evolve in general without negative influence on their performance. Fifth, the connections of the concepts developed on the basis of the design space are evaluated with regard to possible refinements of related concepts of evolutionary biology.

The conceptual framework developed here is a synthesis based on ideas from various disciplines including engineering design, engineering optimisation, morphology, evolutionary biology and systems biology. Our overall aim is to establish a useful theoretical and conceptual framework for further investigations not only in biology itself, but also in the subject linking biology and engineering, namely biomimetics.

The engineering design schema

We first need to introduce some core terms from engineering as a basis for further considerations of the optimisation and robustness of (evolving) biological systems. A conceptual schema from engineering design (Pahl et al. 2007a) with five distinct levels has been used to analyse engineering and biological items, mainly for conceptualising the field of biomimetics. This is illustrated in Fig. 1, by using Velcro® as an example (Drack et al. 2018, 2020). The two columns on the left list the five levels of engineering design and their typical formats of representation. In the biological model, the overarching system consists of the interaction of a dog and a burdock plant leading to seed dispersal. The construction level indicates details of the interacting parts and their properties. Observations therefrom reveal that the function in question is "to attach object reversibly". The working principles in

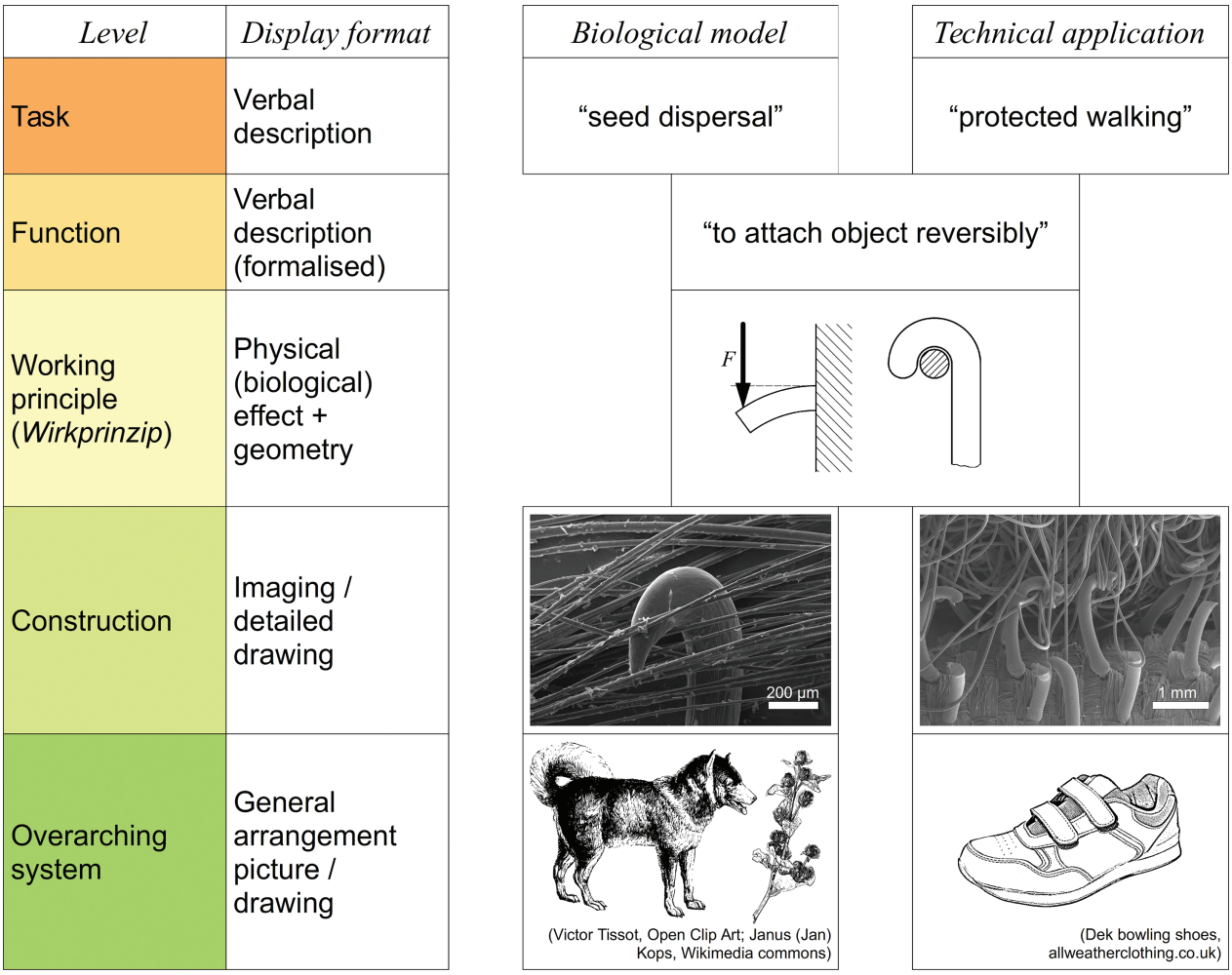

Figure 1. Engineering design schema employed for biology, engineering and biomimetics (Drack et al. 2018, Drack 2019). For further explanation, see text.

this case are elastic bending and positive interconnection as represented by the two drawings. The task is "seed dispersal". In its technical application, Velcro® is used, for example, in a shoe as the overarching system. Whereas the technical *construction* and task differ from the biological (role) model (termed "concept generator" by biomimeticists), the *function* and *working principles* remain the same and, hence, these are at the core of biomimetic knowledge transfer (Drack et al. 2018). For our current purposes, we need to consider (1) the particular *function* needed for the *construction* (or the concrete design) in order to perform a task, (2) the *working principles* (or mechanisms, i.e. abstract causal relations) and (3) the *construction* level (specifying the parameters of the interacting entities). Function is used here in a specific manner similar to that in engineering design in which functions and working principles are kept apart (Pahl et al. 2007a). A vast literature exists on function (e.g. Krohs and Kroes 2009), but no commonly accepted definition. For the current purpose, it suffices to state that a function can be fulfilled via various working principles and is expressed as a verb + noun combination describing an action that needs to be done. A working principle concerns a basic physical, chemical or biological effect that can be used to fulfil a function (Pahl et al. 2007b) and involves a fundamental cause-and-effect relationship that also exists even when not harnessed for a function. In contrast to abstract working principles, constructions embody working principles in particular ways and with particular parameter settings (e.g. size, material characteristics).

Relevance of engineering design schema for evolutionary biology

The concepts of function, working principle and construction are also helpful for understanding biological evolution. For instance, Duncker (1994) has pointed out the importance of distinguishing between a functional and a causal level, which here connect to the function and working principle concepts, respectively. Functions are usually fulfilled by the interaction of several structural parts at the level of the construction, according to working principles. If von Uexküll (1928) had not previously introduced the term *Wirkmal* with a different meaning, it would be well suited to designate the structural embodiments of working principles (in German: *Wirkprinzip*). Alternatively, 'constructional character' and 'constructional trait' might be useful terms for designating those structures that play a role in fulfilling functions. This

makes it possible to distinguish them from the character and trait concepts, which are not necessarily connected to a function, in phylogenetic homology research and from the descriptive term 'morphem' (Richter and Wirkner 2013, 2014).

Apart from overall functions (e.g. "to metabolise food", "to sense the environment"), novel sub-functions can arise during evolution. For example, the predecessors of birds were at first unable to fly. However, once the forelimbs of these vertebrates had attained the characteristics enabling them to fly, the scope of the evolutionary variation of the 'construction' wing became limited (cf. Riedl 2000: 259). Not all constructions were now possible because of the implementation of a working principle, namely that by which wing profiles create a favourable ratio of lift to drag force within an air flow. The wings could thus not deviate far from a certain shape and the muscles, bones, etc. needed to be arranged in certain geometric relationships to each other. Hence, a bundle of constructional traits is strongly interconnected and cannot be changed to any great extent evolutionarily as long as these birds wish to fly. A functional burden (Riedl 1975, 1977) has emerged. Nevertheless, within the overall framework of a construction that is constrained by underlying working principles necessary to generate a certain function, a number of degrees of freedom exist with respect to the quantitative parameters (and their combinations) that are employed to realise the working principles and that, for example, generate certain mechanical lever conditions necessary for locomotion or feeding. Evolutionary morpho-physiological disparity can therefore be generated across the species within a clade without compromising function, a macroevolutionary principle well-known as the "many-to-one mapping of form to function" (Wainwright 2007, Wainwright et al. 2005).

Any (newly emerged) function channels the underlying morphological structures in a certain way by means of employed working principles. When a function is no longer relevant, its underlying structures may become released from their constraints and might either be reduced or evolve in the context of other functions. An example of such changes in function involves the cone-shaped pointed teeth of dolphins (personal communication, Wolfgang Maier, Tübingen). The phylogenetic ancestors of dolphins possessed, in their upper and lower jaws, teeth (tribosphenic molars) with cutting edges that fulfilled a specific function, namely "to cut up food". Once this function was no longer needed, the working principle and the associated construction (cutting edges) could be abandoned. Extant dolphins can no longer cut up their food, with their teeth, and apparently no longer need this cutting function.

Functions can be preserved for a long time in phylogenesis, but they can be fulfilled by different working principles. During the pollination of plants, one function can be described as "to transport pollen grains to the target". In the case of wind-pollinated flowers, this requires the pollen grains to be evenly distributed in the air and to hover until they reach a stigma with a good probability. Accordingly, the pollen grains must be 'constructed' following the (working) principles of aerodynamics. In pollination achieved by animal vectors, the same function is fulfilled differently and employs different working principles. The pollen grains no longer fly through the air by themselves, rendering the laws of aerodynamics meaningless for them. Instead, working principles now play a role that, for example, improve their attachment to the body of the animal pollinator. "To adhere to an animal's body" thus becomes a new sub-function of "to transport pollen grains to the target". Evolutionarily, both the transition from wind pollination to animal pollination and the reverse pathway are known (Wragg and Johnson 2011).

Functions of an organism can, as in the previous examples, relate directly to the external environment, which is the subject of research in the field of ecomorphology (cf. Reilly and Wainwright 1994, Betz 2008). However, functions and their implementations can also be largely independent of the external environment and can then be referred to as 'internal functions'. Consider, for example, the function of a mammalian heart valve.

The consideration of function in the context of evolutionary research, the subject of analogy research (e.g. Koepcke 1974), is an under-represented field of research. This was recognised early on by Bertalanffy during his development of a systems view of biology: "It would be beneficial if, in the future, a greater experimental and theoretical interest were once again devoted to the problems of functional adaptation" (Bertalanffy 1932:320, own translation). This means that, in addition to homologies, analogies should also be investigated, because "similarities in form, particularly if they are not derived from the same evolutionary origins, appear to reveal certain rules with regard to the shaping of these forms [*Bildungsgesetze*]; these rules then dictate the course of certain evolutionary trends" (Bertalanffy 1933:75, own translation).

In order to link the notions of function, working principle and construction more comprehensively to evolutionary biology, we need to introduce the concept of optimisation as the next step.

Optimisation and its connection to the engineering design schema

The previously introduced concepts of function, working principle and construction can be connected via the design space to resolve optimisation problems. For this purpose, the field of engineering optimisation needs to be explored in some breadth.

Optimisation has been broadly defined as: "the efforts and processes of making a decision, a design, or a system as perfect, effective, or functional as possible" and more narrowly, as "the specific methodology, techniques, and procedures used to decide on the one specific solution in a defined set of possible alternatives that will best satisfy a selected criterion" (Licker et al. 2003). The decisions made with regard to the particular shape of Velcro® hooks and loops (Fig. 1) serve as an example. Even with given similar functions and working principles, constructions can vary to some extent. One reason for this might

be optimisation processes with respect to different performance measures, whereby performance is defined as any quantitative measure of how well a function is accomplished (Irschick and Higham 2016). We therefore need to investigate the way in which the concepts of optimisation and optimum fit into the engineering design schema introduced above (Fig. 1).

In engineering, we can easily find out what has been optimised and with what objective(s), because these questions have guided the designer. In biological systems (e.g. the shapes of diatoms or the leaves of a tree), difficulties are encountered in determining whether and to what extent the systems have been optimised and the value of their adaptive peak. This requires solid knowledge of the function or biological role (Bock and Wahlert 1965) of the structures under consideration followed by comparative performance measurements (or theoretical modelling) in the biological context (e.g. Irschick and Higham 2016).

An instructive example for optimisation in engineering is the optimisation of a roof shape illustrated by Bletzinger et al. (1995). A rectangular ground plan is given and mathematically pre-defined. Bézier curves are used for the roof shape (Fig. 2). Two parameters (or design variables; Martins and Ning 2022) can be changed: the height of the roof in the middle of the short side of the ground plan (x_1) and the height of the roof in the centre of the rectangle (x_2). Otherwise, the roof is defined by the Bézier curves, which connect as higher or lower arches the longer sides of the ground plan. An engineer can, for instance, optimise the structure for minimum strain energy, which is equivalent to the minimum deformation of the roof. The roof would then look like a saddle ($x_1 > x_2$ in Fig. 2). Optimisation might also be aimed to achieve equal stress distribution, which would lead to a roof shape that is more similar to a dome ($x_1 < x_2$ as actually shown in Fig. 2). Alternatively, the roof could be optimised for minimum weight, resulting in a roof shape resembling part of a cylinder ($x_1 = x_2$ and both small in Fig. 2). From these considerations, we can clearly see that the designer has to choose the objective (and performance measure) to be achieved by the proposed optimisation. A subjective decision will thus be made between one of these three objectives.

The optimum and optimisation always refer to something particular: a particular objective (function). Moreover, those parameters that can be changed to achieve the objective have to be clear. For a simple case like a roof, this can easily be shown in a 3D diagram. The resulting design space in the roof example can have two axes for the two parameters that can be changed. The third (vertical) axis of the diagram indicates the optimisation objective by means of a quantitative measurement regarding the performance of the objective. In the simple two parameter case, one can consider a landscape (Fig. 3) in which one searches for the parameter combination with the highest peak, which represents the best performance, i.e. the optimum. The optimisation process can be considered as finding a quick way from a given (random) combination of parameters to the optimal one.

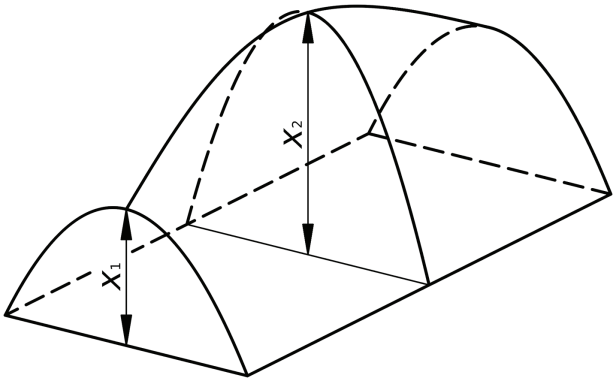

Figure 2. Model for the roof optimisation problem. For further explanations, see text.

In general, optimisation is the determination of the parameter settings that correspond to a well-optimised system. This landscape depiction is useful when only two parameters are involved. In instances of more than two parameters, which is usually the case, the design space becomes a hyperspace. Here, we can usefully consider a space with clouds of greater or lesser density (high density representing high performance), with optimisation algorithms searching for the area of highest density.

From a biologist's perspective, the question arises as to whether the engineering concepts of optimisation can be adapted to biological optimisation problems in real organisms. Cases of optimisation towards a single performance measure are difficult to find in biology. One example used by Nachtigall (1995) is the haematocrit, i.e. the volume percentage of red blood cells in the blood. This parameter has an optimum with respect to oxygen flow, i.e. the maximum amount of oxygen transported through the vessels per unit time. In cases of few erythrocytes, they move rapidly because of the resulting low viscosity of the blood but, together, they carry little oxygen. Many erythrocytes can carry a large amount of oxygen but they move slowly, because the viscosity of the blood is now high. The optimum of the haematocrit can be determined experimentally and theoretically and compared with haematocrit values found in organisms. These values have been shown to be at the optimum, i.e. maximum oxygen flow, in pigs and sheep (Nachtigall 1995).

Another important issue in engineering is multi-criteria (= multi-objective) optimisation (Alfaris 2010), which occurs once more than one criterion or objective needs to be achieved. Taking the roof example from above, we find that, if both equal stress distribution and minimum strain energy, are objectives, a good overall solution is hardly possible. Different methods are available to cope with such problems. For instance, the importance of the different objectives could be weighted with, say, 30% and 70% and expressed in only a single performance measure. Optimisation might then produce a mediocre performance for both criteria. Importantly, no single optimal solution can generally be achieved in multi-criteria optimisation. The choice as to which objective has to be weighted more highly involves the subjective decision of the designer and, furthermore, the engineer has to choose

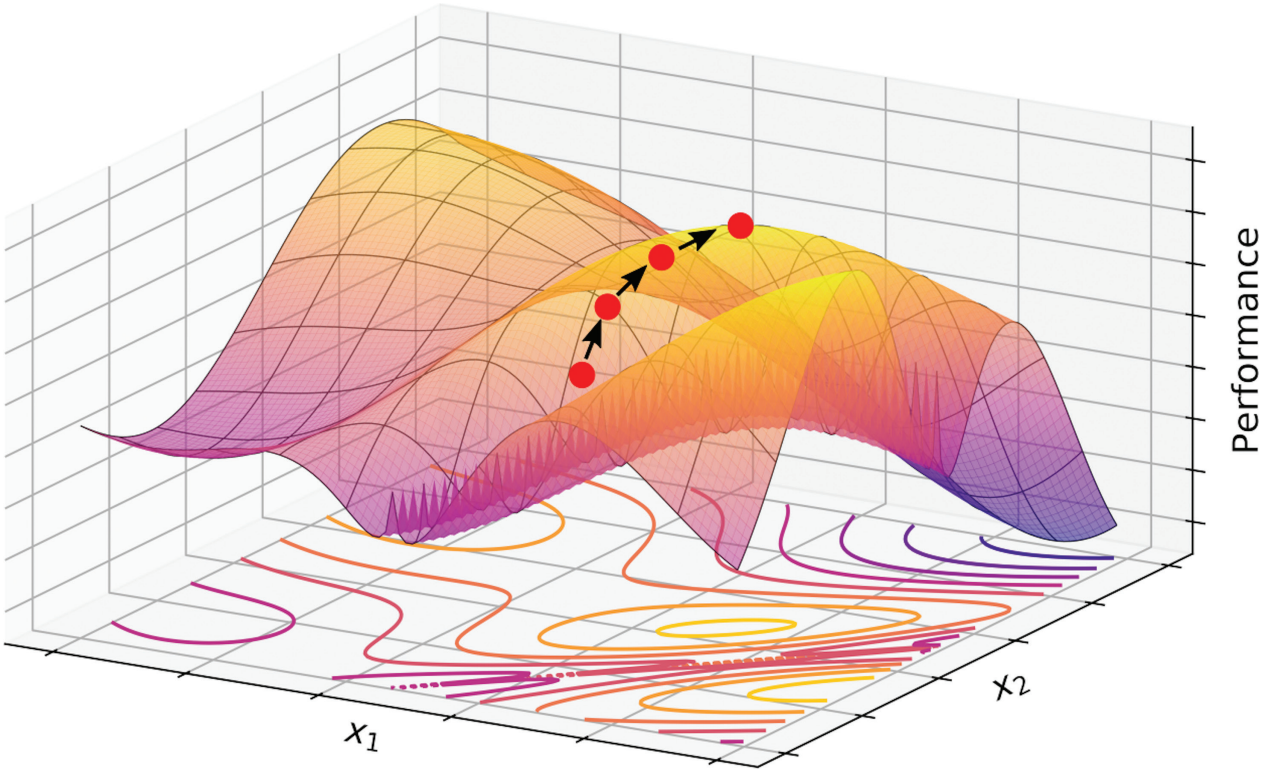

Figure 3. Hypothetical design space example valid for both engineering and biology illustrating the optimisation of two parameters x_1 and x_2 of a construction. The parameters can be of a different kind, including length measurements, material properties, optical properties, etc. The third, vertical axis shows a measurable performance. The two parameters x_1 and x_2 can be changed, with each combination resulting in a different performance value (red dots). With two parameter dimensions, a surface results from different parameter settings that can be depicted as a 'landscape'. Optimisation is the process indicated by the arrows. By changing the parameters, an ever better performance can be achieved, leading to an optimum at the top of a 'hill'.

from a set of solutions that are only more or less optimal. In biology, multi-criteria optimisation problems are the rule. They do not lead to only one best 'solution' and usually involve suboptimal compromise solutions. For example, the shells of sea urchins might have been optimised with respect to multiple objectives involving not only mechanical stability, but also ontogenetic factors (Grun et al. 2016).

Since the engineering design schema (Fig. 1) turns out to be a useful conceptual framework, the question arises as to whether it can also be linked to optimisation problems in general (both engineering and biology). The conceptual levels that need to be considered here are *function*, *working principle* and *construction*, which can be easily linked to the design space (Fig. 4). A function such as "to attach an object reversibly" provides indication for an objective and a performance measure. A particular performance measure can be interpreted as a quantified specification of a function. For an engineering construction, one could, for instance, use a performance measurement such as "attachment force after 1000 cycles of attaching and detaching" for the function "to attach an object reversibly". The performance of, for example, Velcro® tape will be considered satisfactory if it retains its high attachment force, even after 1000 cycles of use. For the construction of the biological concept generator, a somewhat different performance measure is conceivable, because the burr has to attach to the fur of the animal only once or twice in a reversible manner.

On the level of the working principle (Fig. 1), the connection to the design space is straightforward. Working principles directly indicate the parameters that can and need to be changed in the process of optimisation. For instance, parameters that can be changed in the Velcro® example include the diameter of a single hook, the diameter of the loop, the aspect ratio of the hook and material parameters such as Young's modulus or the overall hook density.

The levels of both the function and working principle provide the performance criterion and the parameter dimensions of the design space. The working principle determines those parameters that have to be considered and altered during the optimisation process, whereas the function indirectly determines a measure for the performance that needs to be optimised.

Finally, at the construction level, the parameters determined by the working principles are set to specific values represented by a particular point in the design space. In the final construction, the parameters are set in such a way that performance is high, i.e. the construction fulfils the function well. Hence, the concept of optimisation via the design space can be seen as connecting the three levels of the scheme, namely function, working principle and construction (Fig. 4).

In this context, we should distinguish between the concepts of effectiveness and efficiency. Effectiveness refers to a quality, whereas efficiency can be quantified and can therefore, in specific cases, serve as a performance

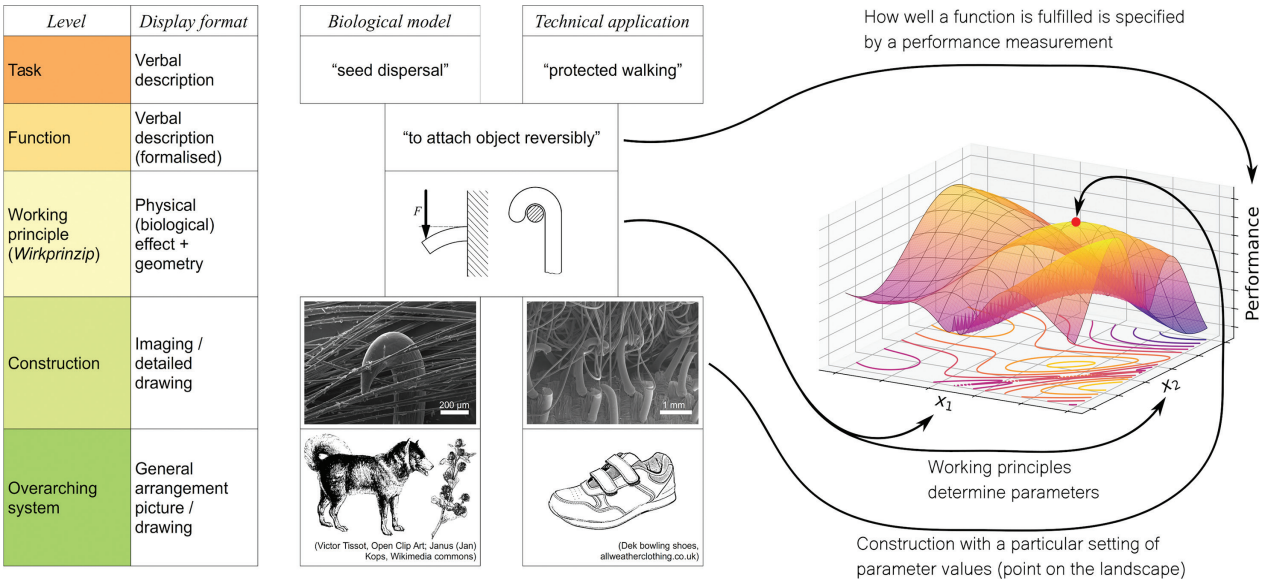

Figure 4. Summary of the relationship between the engineering design schema on the left (cf. Fig. 1) and the design space on the right (cf. Fig. 3). For further explanations, see text.

measure (cf. Fig. 3). A certain function can be fulfilled by means of alternative working principles and, usually, by a combination of them. In engineering, functions are commonly considered as being neutral with respect to the various working principles that can be used. "To attach an object reversibly" might be achieved via the working principles of mechanical interaction mentioned above in the Velcro® case but might also be based on alternative working principles such as those involving wet adhesion or the attraction of magnetic forces. They all indicate cause and effect relationships that can be implemented to achieve the particular function. Other working principles such as optical ones are not effective for the mentioned function, because they cannot contribute to fulfilling it. Hence, the mechanical, adhesive or magnetic working principles are all effective (i.e. they produce a useful effect with regard to fulfilling the function), whereas the optical working principles are not. The effect resulting from the employment of a specific working principle determines the highest level that the overall performance can achieve. Hence, the performance of a certain construction with respect to its function depends first on the selected working principles and can then, second, be further modified by fine-tuning the combination of the parameters that are indicated by the working principles (e.g. the material parameters in the Velcro® example). Effectiveness defines the overall quality of the working principle to be selected in order to fulfil a certain function (can a selected working principle produce a necessary effect at all?), whereby a working principle defines a quantifiable performance range that can potentially be achieved under the actual boundary conditions. For instance, for the conversion of solar (radiant) energy to electrical energy, working principles can be used that involve the heating of water in order to run steam turbines. Alternatively, a working principle that involves the photoelectric effect could be employed. Both these working principles come with different limitations to their efficiency, which in these cases can serve as a performance measure obtained here by dividing energy output by energy input. The theoretical maximum efficiency (η_{max}) using a steam turbine is given by the Carnot cycle and is limited by the lower (T_0) and upper temperature (T_1) in the cycle: $\eta_{max} = 1 - T_0/T_1$ (Grote and Antonsson 2008: 268). Using the photoelectric effect, the Shockley-Queisser limit allows for a maximum efficiency η_{max} of about 35% (Dau et al. 2019: 35). Functions can be achieved in differently efficient ways depending on the type of working principles used and the setting of their parameters.

Constructions using other working principles require the consideration of other parameters. For instance, the dimensions in the design space for the parameters that need to be optimised are different in the case of the steam turbine compared with photovoltaic construction. However, if the function stays the same, then the performance measure (in this case energy efficiency) also stays the same. Note that efficiency is one type of performance measure, others can be visual acuity, jumping hight, etc.

The described concept of effectiveness can also be applied to biological evolution in which, in theory, one working principle should be selected that allows the fulfilment of a function with high performance. Once this working principle is in action, its underlying parameter values are under selective pressure to further improve (optimise) the overall performance of the system employing the given working principle. The selection of a certain working principle in evolution might be attributable to chance (whereby exaptation (Gould and Vrba 1982) can be understood as working principles that are in place within an organism but with a function yet to come), to selective pressure (according to slight differences in the resulting performances of the working principles) or to certain environmental or organismal conditions.

For our understanding of macroevolution, we will find it instructive to analyse to what extent performance differences between clades have resulted from the selection

of differently effective working principles or from the adjustment of more efficient parameters within the underlying working principles. For example, in predatory *Stenus* rove beetles (Coleoptera, Staphylinidae), a shift has occurred from the ancestral way of prey-capture by means of direct seizure with the mandibles to a novel (derived) prey-capture apparatus that involves the combination of new working principles such as the catapult-like protrusion of the elongated labium and the firm adhesive attachment of the prey to sticky cushions at the tip of the labium (reviewed in Betz et al. 2018). The selection of these novel working principles has probably made it possible for rove beetles to catch elusive prey such as springtails in a highly efficient and rapid manner, despite many life forms of these beetles being physiologically limited with respect to their overall agility and reaction ability (Betz 1998). The newly evolved labial prey-capture apparatus has been further adjusted within the selected working principles improving its efficiency (i.e. its performance) with regard to prey-capture success. These adjustments have involved an increase in the parameter values of the labium length (increasing its range), in the size of the sticky cushions and in the number of adhesive trichomes on their surface (increasing their adhesive strength) (Betz 1996, Koerner et al. 2017). Explanations concerning the origin of evolutionary novelties in biological organisms (e.g. Wagner 2010) should thus involve a closer inspection of the working principles that generate novel functions.

Biological evolution can lead to burdens or constraints (Riedl 1975, 1977, Held 2009). Once the working principles have been selected, they cannot easily be changed for others and they thereby determine the dimensions of the design space. Thus, effectiveness and performance (or in specific cases efficiency) can be limited, leading to 'solutions' in biology that are not, from an engineering point of view, optimal. However, within these constraints or burdens, the performance can increase during evolution, although it will not increase as much as it would have if an alternative working principle or new combinations of working principles had been initially used.

In engineering, as previously mentioned, a set of parameters of a construction is optimised towards multiple criteria during multi-criteria optimisation. All dimensions for the parameters stay the same but have to be optimised with respect to other (conflicting or concurrent) criteria. In biological evolution, another case of optimisation might also be relevant, here referred to as entangled optimisation (Fig. 5). This case of optimisation cannot be depicted in two dimensions easily. In Fig. 5, we hypothetically consider x_1 and x_2 parameters that are employed for optimisation with respect to performance measure A, with some optimal peak at a particular setting of x_1 and x_2. Now, let us consider that parameter x_1 is also involved in some other construction that is used with some other working principle that involves parameters x_1 and x_3 relevant for optimisation with regard to performance measure B. The optimal peak for B requires a certain setting of x_1 and x_3. However, the peaks of performance measures A and B each require different values of x_1. In such a case, it is in principle impossible to attain a maximum for both performance measures. This is different from multi-criterion optimisation, which concerns the same (and not only partly shared) parameters that are optimised with regard to different criteria. For sound localisation in vertebrates, for instance, it is advantageous to have the ear drums set far apart from each other, as this makes the detection of the direction of a sound more precise. However, the parameter of the distance between the ear drums is also connected to the parameter of head width. Since head width is subject to many other restrictions, it cannot be optimised (from an engineering perspective) to achieve an optimal solution for both requirements. To avoid such entanglements, the term module in the sense of largely independent units serving particular functions can be useful with respect to optimisation in both engineering and biology, as can, the term functional unit (as a mechanical unit or evolutionarily stable configuration) identified via shared functional interactions (Schwenk 2001). Such modules need to be distinguished from modules or modularity used in a gene-related sense (Futuyma 2007:517). "By modularity we mean a genotype-phenotype map in which there are few pleiotropic effects among characters serving different functions, with pleiotropic effects falling mainly among characters that are part of a single functional complex" (Wagner and Altenberg 1996).

In biology and engineering, certain parameters can be subject to neutral variation, i.e. certain values do not affect the final performance of the system, as has been introduced above in the context of many-to-one mapping. One example involves the branching patterns of blood vessels at the aortic arch (Popieluszko et al. 2017). Some humans have different patterns with regard to the branching of these vessels, i.e. the vessels have different geometrical parameters but with no major influence on performance (or health). An example from engineering refers to the elasticity of water pipelines. Plastic and steel have different Young's modulus values and yet both materials can be used and perform well in pipes for transporting water under pressure.

To conclude, optimisation is a problem that is relevant for both engineering and biology. The engineer has to choose one or more objective(s) in accordance with a desired function and even has to consider multi-criteria optimisation problems that involve trade-off solutions. Hence, the envisaged optimum and the optimisation process are subject to the technical aims of the designer. For a biologist, the determination of the particular 'objectives' in the evolution of a particular structure can be challenging. Continuous adaptation to the environment is often important and might be indicated by the performance measures that can be investigated by biologists. For instance, the hook shapes on burs (geometric parameters) are well adapted enabling the wide dispersal of seeds. This links performance to fitness. Arnold (1983, 2003) has developed a concept that theoretically and practically connects particular morphological structures via their performance capacity to the fitness of a whole individual, i.e. an organism. Although the fitness consequences of subtle morphological differences between organisms are difficult to measure, we can assume that the measur-

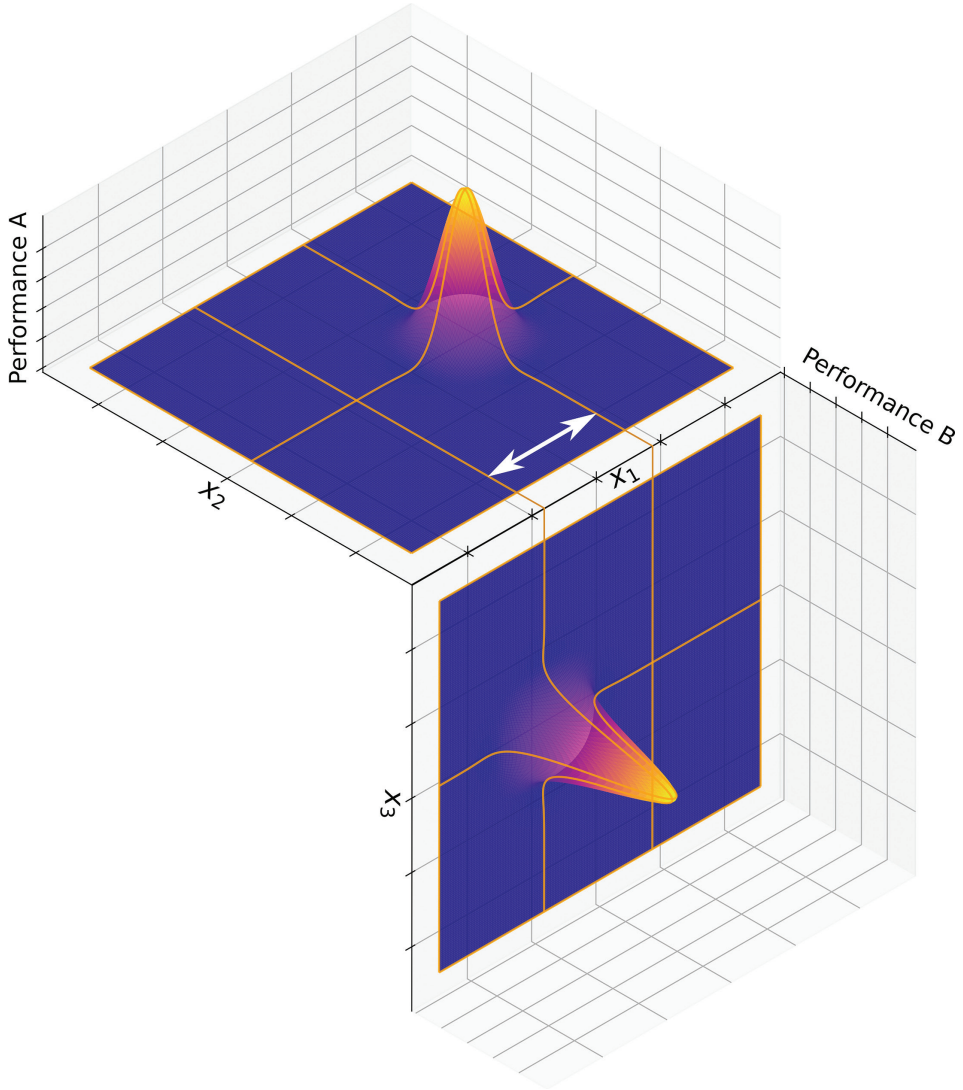

Figure 5. General illustration of the optimisation problem, here called entangled optimisation, aimed at achieving different performance measures with partly shared parameters. Two performance measures A and B are considered, in addition to the three parameter dimensions. Parameter x_1 is relevant for both performances, whereas x_1 and x_3 can be changed each only affecting one performance. The white arrow indicates that not both optima can be reached simultaneously. For further explanations, see text.

able individual performance differences that result from morphological differences do indeed contribute to fitness.

So far, we have dealt with optimisation and the design space in a general way. Design spaces and their 'landscapes' can, however, be diverse, extending from very narrow parameter areas with high performance to broader areas with neutral variation. These areas of neutral variation are related to the concept of robustness, which will be explored next.

Design space characteristics, robustness and evolvability

Based on the approach of connecting the engineering design schema with the design space, we will now explore the relationship between the design space and the concept of robustness. Design spaces can have different characteristics depending on the deployed working principles (Fig. 6). These characteristics need to be considered if we are to understand the connection between design spaces and robustness. The design space in our examples focuses on only two parameters (x_1 and x_2) for easier visualisation. Key ideas that are also valid for high-dimensional design spaces can, however, also be developed with only two parameters.

To illustrate the various design spaces in the following, we use simple examples from engineering and compare them with biological structures. Dovetail slides (Fig. 7) are commonly used in various devices and machines. In these constructions, flat surfaces are employed, because they are easy to manufacture. The shapes are basically described by two parameters: length (x_1) and angle measure (x_2) for each part A and B (Fig. 7), i.e. x_{1A}, x_{2A} and x_{1B}, x_{2B}, forming four dimensions in an overall design space. To adjust the proper form-fitting dimensions, parameter x_{1A} can usually be fine-tuned by a screw, even after manufacturing. A dovetail connection can, however, also be

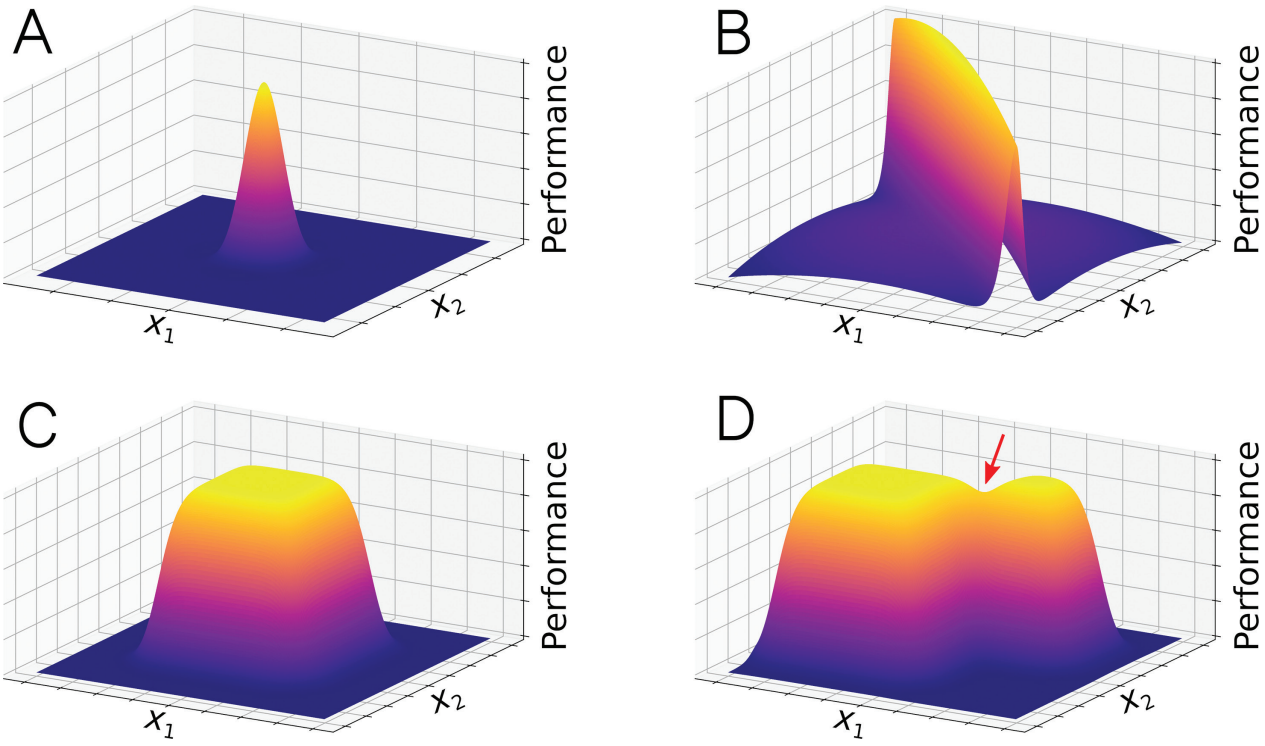

Figure 6. Various hypothetical design spaces for two parameters x_1 and x_2. **A** Single optimum peak in the design space. For two parameters, only one particular narrow setting leads to a high performance. **B** Ridge-like optimum. When the two parameters are concurrently changed, an extended optimum can be achieved, but not when only one is changed. **C** Flat optimum with a high plateau. Both the parameters can be changed within wide boundaries, still leading to an optimum. This indicates the robustness of performance with respect to parameter changes. **D** A 'corridor' (arrow) that links two flat optima. Performance might decrease a little, but still be comparatively high. Interlinked areas of high performance facilitate evolution in various ways, increasing evolvability.

constructed without this fine-tuning feature (Fig. 7 right) but, in this case, manufacturing needs to be extremely precise and further adjustments for wear are not possible.

Single optimum peak

For this simplified engineering dovetail slide example (Fig. 7 right), imagine that part A is given without an additional adjustment device and part B has to be designed and manufactured anew. High performance would mean minimum backlash, although sliding is still possible. In this case, the two parameters for part B (x_{1B}, x_{2B}) must not vary to any large extent. This can be visualised as a single small peak in the design space (Fig. 6A, when x_{1B} and x_{2B} are depicted as x_1 and x_2). When the two parameters are well chosen, the resulting sliding performance can reach a high optimum. However, any minor perturbation, expressed as a change in either of the two parameters, will impair the performance and, thus, this kind of construction is not robust with respect to changes in x_{1B} and x_{2B}.

Ridge-like optimum

Now imagine a case in which x_{1A} and x_{1B} can be optimised together in the dovetail slides. When these parameters are changed simultaneously, several optimal solutions are possible. In the design space, this would resemble a ridge (Fig. 6B, when x_{1A} and x_{1B} are depicted as x_1 and x_2). The range of parameter value combinations for a good result is small but is larger than for the single peak case. A slight change in only one parameter would, however, lead to a lowered performance. Moreover, note that the ridge in the example of Fig. 6B is not of a constant height, which means that tiny (but still fitting) x_{1A} and x_{1B} lengths would easily lead to damage in part B, because a narrow dovetail would be prone to deformation and fracture. The ridge-like surface in the design space is typical for any engineering fit in which one part has to fit into another with small tolerance ranges (Grote and Antonsson 2008). Although ridge-like design spaces are common in technical devices (e.g. shafts in bearings), their robustness with respect to changes in the relevant parameters is only low.

Flat optimum with a high plateau

Similar 'constructions' to the dovetail slide can be found in the mouthparts of various insects, for example, in the sucking mouthparts of true bugs (e.g. Wenk et al. 2010). The connections between the maxillae (Fig. 8) can be compared with the engineered dovetail slides, as they allow linear gliding past each other. However, the groove-and-tongue structures of the maxillae differ in detail from the engineered dovetail slides with respect to shape. One can compare the two constructions, i.e. the hemipteran and the engineered system and consider their robustness

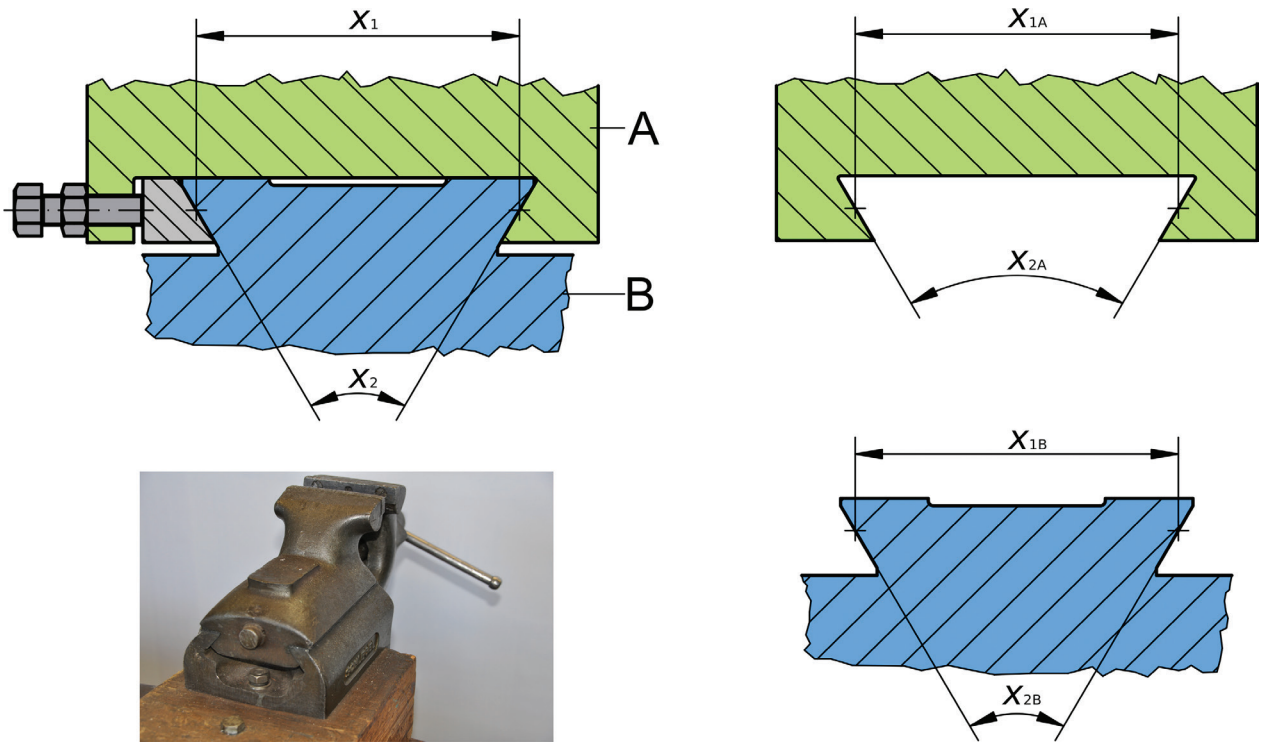

Figure 7. Dovetail slide as used in engineering. Top left: A commonly used construction with a screw for fine-tuning. Right: Two components **A** and **B** of a simplified dovetail slide. Bottom left: A vice with dovetail slide as used in workshops

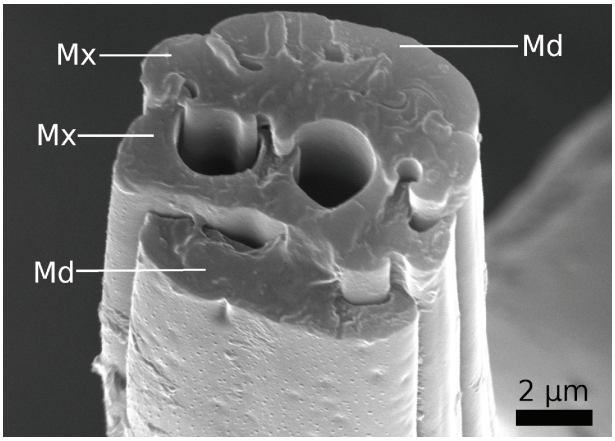

Figure 8. Scanning electron micrograph of cross section through the mouthpart stylets, with the maxillae (Mx) and mandibles (Md), of the heteropteran *Aradus cinnamomeus* Panzer, 1806 (Aradidae). Groove-and-tongue structures connecting the two maxillae allow for linear sliding movements

with respect to changes in their geometric parameters. In the hemipteran stylets, the curvatures of the groove-and-tongue structures probably allow for a wider range of variation in geometric parameters while still giving good performance with regard to sliding in a precise manner. Compared with the engineering construction, no flat surfaces glide past each other. Hence, more than two parameters can vary. Potentially, material compliance can also allow for adjustments of length measures. Unlike technical constructions, biological materials are often soft and elastic, so that the relevant material parameters such as Young's modulus might allow for robust constructions that still work well, even when, for example, a radius in the groove-and-tongue structures changes.

A broad optimum would, of course, be much better than a small peak or a narrow ridge in the design space. To illustrate this, first consider a piston pump in engineering (Fig. 9A) in which a piston moves back and forth within a cylinder, thereby changing the volume within the cylinder periodically. An inlet and an outlet valve open in such a way that the liquid moves in one direction only. In engineering, both pistons and cylinders are often made of metal, and the diameters of both have to be chosen in such a way that movement is possible, despite the gap between them being small in order to prevent liquid escaping between the piston and cylinder. Such an arrangement is not very robust with respect to changes of the parameters "outer diameter of the piston" (considered as x_1) and "inner diameter of the cylinder" (considered as x_2) (resembling the design space in Fig. 6B) or to deformations that result from impacts from the exterior. Salivary pumps in hemipterans have an arrangement different from that of technical piston pumps (Fig. 9B). The materials are not rigid and their functional elements are integrated and not separate. The gap between the 'piston' (*P* in Fig. 9B) and the 'cylinder' (*Cu* in Fig. 9B) is wide and the cylinder does not need to be sealed. Hence, even if the diameter of the piston is slightly changed, it can still move, without the performance of pumping with high efficiency being affected, since the piston does not touch the cylinder as in the engineering case. Furthermore, the engineering parts have to have constant diameters throughout. This is not necessary in the salivary pump, because the 'cylinder' is not used as guide for the 'piston'. Hence, no direct equivalent to x_1 and x_2 of the engineering case can be found

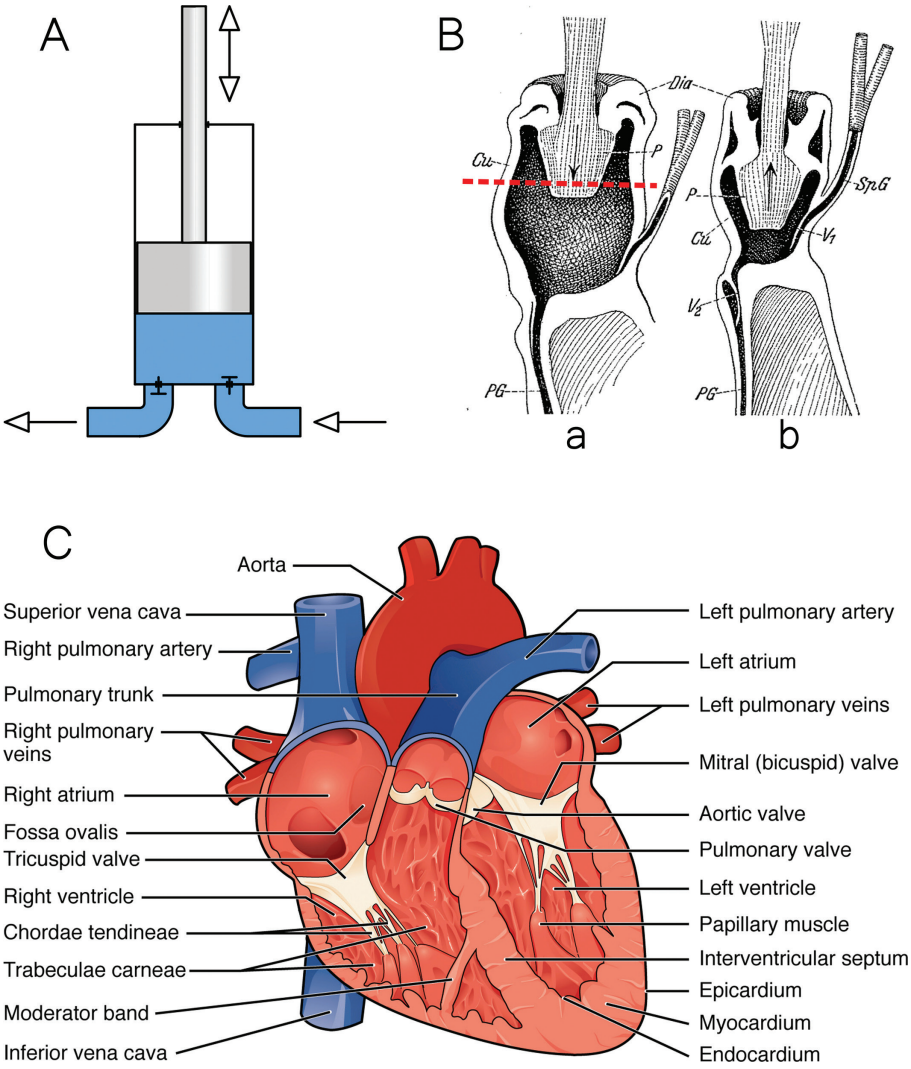

Figure 9. Schematic drawings of oscillating pumps in both engineering and biology. **A** Piston pump in engineering can, for instance, be used to pump water. **B** Salivary pump in Hemiptera. a: piston retracted; b: piston position with relaxed muscle. *Cu* cupula, *Dia* diaphragma, *P* pistill, *PG* efferent salivary duct, *SpG* afferent salivary duct, V_1 V_2 valves (from Weber 1930). **C** Frontal section of the human heart (from OpenStax College 2013, CC-BY-3.0). For further explanations, see text.

for the salivary pump. Moreover, changes in the inner diameter of the cylinder of the bug would not result in a significant drop in performance. Hence, a flat optimum would result if both these parameters were plotted (from a particular cross section as indicated by the red dotted line in Fig. 9B) in the design space (Fig. 6C). Such an optimum is much more robust with respect to changes, in this case of diameters, than is the case for the single optimum peak. However, with a rigid metal construction, one can produce higher pressures that are not achievable by the biological salivary pump 'construction', because material deformations attributable to changes in pressure are low. In engineering, diaphragm pumps (Eifler et al. 2009) use soft parts similar to those of the hemipteran salivary pump. Conversely, to our knowledge, nothing similar to the conventional engineering piston pump exists in biological 'constructions'.

The vertebrate heart (Fig. 9C) also uses periodical volume contractions for pumping, but in a different way. No piston is involved, but rather the whole muscular surrounding of the blood volume contracts and the movements of the valves lead to a flow of blood in one direction only. From an engineering perspective, the many (morphometric) length measures (e.g. diameters of the left ventricle in various cross sections) also do not seem to be highly constrained, i.e. limited to small ranges. Whereas the piston would no longer move in case of a small diameter reduction of, say, 0.1 mm of the cylinder in an engineered piston pump, a similar reduction in the size of a ventricle might not greatly alter the overall performance of the heart. Therefore, in the design space for many size parameters of the heart, a flat optimum (Fig. 6C) can be expected, similar to that of the hemipteran salivary pump. A supporting fact for this claim is that, although hearts shrink during ageing, this does not affect their performance, as investigated for the size of the left ventricle (Peverill 2021).

A comparison of technical scissors and cutting edges in biological teeth serves as another example. The two cutting edges of scissors are rigidly connected via a screw that does not allow other than one degree of freedom to work properly. If any of the geometric parameters changes (e.g. caused by a loose connection or the deformation of the blades), the cutting performance deteriorates. Analogous to technical scissors, many vertebrates have teeth with edges, whereby the edges of two opposing teeth are used to cut up food (Maier 2017, 2020). In contrast to the scissors, the cutting edges are not necessarily arranged with high precision. For example, precise occlusion is lacking in many herbivorous lizards that cut vegetation

with laterally multicuspate teeth. The position and the form of the upper and lower teeth in this example can vary widely before the cropping performance declines (Schwenk 2001). Furthermore, although teeth are hard and rigid, they are connected to the jaw bones via an elastic periodontium (Lippert 2003:602), which makes slight movements of the teeth relative to the jaw possible. Moreover, the lower jaw can be moved in various directions as a whole, directing the cutting edges to those places in which they are needed. Hence, this example shows that some morphological parameters can vary widely without affecting the performance relevant for food ingestion. However, having more than one degree of freedom of the scissors, the movements of jaws in different directions have to be controlled in a more sophisticated manner via various muscles. Additionally, much more precise and straight cuts can be made with scissors, but such precision is hardly needed by organisms.

Robustness

In general, a high flat elevation in a design space with two parameters (x_1, x_2) indicates an optimal area that is robust (Fig. 6C), i.e. with a high plateau, so that parameters can be changed within wider limits without compromising performance. The size of the plateau area can be used as a measure of robustness, because it is quantifiable. In the presented design space diagrams (Fig. 6), a search for robust solutions entails one looking for flat maximum areas in the design space. In multidimensional design spaces, the landscape analogy no longer holds although the basic concept remains the same. In the mentioned engineering examples (dovetail slide, technical piston pump), such a flat optimum area is non-existent, because of the way that they are constructed. On the other hand, the biological example of the salivary pump allows a flat optimum for considerations of, for example, the diameters of piston and cylinder.

Examples for robustness are not limited to morphological features but are probably widespread in biology. For example, robustness plays an important role in the field of systems biology in which dynamic behaviours are investigated, mainly on the molecular scale (e.g. Alon 2007). For example, particular arrangements of signal transduction pathways on the molecular level can contribute to robustness against noise (Paul et al. 2016). Biochemical reactions arranged in a sequence need especially fine-tuned values of parameters (reaction rate constants) to work well in transmitting a signal, for example, from the outside of a cell to its nucleus. Theoretical considerations show that such arrangements are not robust with respect to slight changes in parameter values. However, in real biological systems, we find that network-like arrangements of chemical reactions filter out noise without the need for fine-tuned parameters in order to perform well (Paul et al. 2016). The possibility for a certain degree of "sloppiness" in the parameter values without negative consequences for the overall performance seems to be an important feature in real biochemical systems and their models (Gutenkunst et al. 2007). Chain-like *versus* net-like arrangements of chemical reactions, which can be seen as realising different working principles, have different "connectivities" or topological configurations. When the performance is 'optimised' (by evolution or in computer simulations), the reaction rate constants can be considered as parameters of the design space. Other arrangements of the chemical reactions lead to different design spaces in which, in the robust case, the optimum is large, since (sloppy) parameters can vary widely but still maintain a good performance.

In an even more general perspective, going beyond morphological structures and systems biology, the approach developed here may turn out to be useful for the broader debate on robustness. Up to now, no commonly accepted definition exists for robustness. The illustration via the design space (Fig. 6) might, however, be useful for its more precise conceptualisation in general. Robustness has been characterised as the "ability to withstand attacks, perturbations and offences without being disrupted or heavily modified" (Bertolaso et al. 2018:2). According to a more specific definition from systems biology (and engineering), robustness is a "property that allows a system to maintain its functions despite external and internal perturbations" (Kitano 2004). Since robustness represents a fundamental system level phenomenon, it is also relevant for the central organism concept in biology (Bertolaso et al. 2018:2). Organisms need to be robust with respect to changes or disturbances from both the exterior (e.g. temperature changes) and the interior (e.g. physiological changes), i.e. they still need to be able to perform their functions well. The above definitions comprise both external and internal perturbations, which can be visualised by changes of the parameter values in the design space, together with possible alterations of the resulting performance. In a macroevolutionary context, perturbations can be interpreted with respect to long-term changes of organismal 'constructions'. A design space with robust areas (flat optimum) would thereby indicate the scope of variation possible without compromising performance (e.g. swimming performance of cephalopods with respect to shell parameters, as analysed by McGhee 2007).

Robustness and evolvability

The connection between robustness and evolvability plays an important role in evolutionary biology (Wagner 2005). Evolvability can roughly be considered as the ability or capacity to evolve or, more specifically, the capacity to adapt to changing conditions (Futuyma 2007:517). A paradox appears that, in evolution, organisms need to be robust but evolvable at the same time. This raises several problems that have been addressed in recent years (Wagner 2005, 2016). On the level of the phenotype, a design space with connected (large) areas of high performance facilitates the ability to evolve, because paths through valleys of low performance can be avoided during evolution. The combination of working principles ensuring that such paths with high performance throughout the de-

sign space are possible is therefore beneficial or even a pre-condition for adaptive evolutionary change. The previously mentioned principle of many-to-one mapping of form to function also implies that, in the design space, several parameter combinations of the underlying working principles result in equally high-performance values (Wainwright 2007, Wainwright et al. 2005). This can facilitate the evolvability of forms on the condition that these high-performance areas are not separated by deep valleys in the design space. The combination of parameters (determined by the working principles) of the design space determines the character of the 'landscape' and, hence, constrains the possible evolutionary pathways. The design space can be explored more widely when connecting corridors (Fig. 6D) between (flat) optima are available, i.e. when pathways of high performance are present. Such corridors with relatively high-performance values are more important in biological evolution than in engineering, because engineers do not have to change their constructions from one product generation to the next in a step-by-step manner, but can design them anew. Unlike in engineering, every biological organism during the process of phylogenesis has to be viable and able to reproduce. In this case, the realised constructions and the used working principles have to allow for gradual changes from one robust optimum to another.

Wagner (2016) has shown that, in high dimensional hyperspaces, many feasible, i.e. viable, connections are possible for the phenotypes that he has investigated on a molecular level, although his approach can probably also be extended to the morphological level, as considered here. On the molecular phenotypic level, one of Wagner's questions is: how many proteins (i.e. amino acid sequences) can perform one particular function (Wagner 2016:117)? Astonishing high numbers of such proteins have been detected that, surprisingly, are connected by a network of uninterrupted pathways in which one amino acid is changed at a time (Wagner 2016:123). Such networks in high dimensional spaces cannot be visualised in 2D or 3D diagrams but they can be described with mathematical tools (Reidys et al. 1997). In the mathematically defined space that represents huge numbers of different proteins, the steps consisting of one amino acid change have been found to form pathways and networks in which the functions and performances of the altered proteins are preserved. In plant and animal morphology, analogous features may be found in the design space with quantitative parameters for morphological structures. More than one corridor of high performance, as labelled in Fig. 6D, might be available when considering the many parameters that are often necessary to describe morphological structures that need to be represented by a multidimensional design space. The many corridors could then be connected and might form a network analogous to that found for proteins. This would significantly contribute to the evolvability of morphological structures, because many regions in the design space could be reached without drops in performance. Similar to the more mechanical examples discussed above, the shape of a protein (e.g. an enzyme; in this case, the molecular shape results from 2D and 3D folding) is a decisive factor for its being suited to fulfil a specific function. We can thus assume that analogous hyperspace characteristics, including many corridors, also exist on higher morphological levels, if working principles are utilized in a suitable manner.

Importantly, one central difference exists between engineering optimisation and adaptiogenesis in biological evolution. Whereas the dimensions of the design space are given and do not change in conventional engineering optimisation problems, new dimensions can emerge during phylogenesis. If, for example, morphological novelties evolve, the dimensions of the design space increase. Alternatively, if organisms reduce certain structures (for example, during vestigialization), these dimensions decrease, which means that no fixed, unalterable and pre-defined design space exists in which organisms evolve (Longo 2018).

Connection to standard concepts in evolutionary biology

Natural selection as "any consistent difference in fitness among phenotypically different classes [each with several individuals] of biological entities" (Futuyma 2007:251) with respect to the environment is central for the understanding of adpatiogenesis in biological clades. The conceptual framework proposed here is complementary to these concepts because functional details in the phenotype are investigated. The framework can thus be applied to specific 'constructions' of organisms that contribute to fitness, i.e. the survival and reproductive success of individual organisms.

Applying the introduced design schema to Darwinian evolution, we might ask whether selection during adaptiogenesis primarily acts on the task, the function, the working principle, the construction or the overarching system (Fig. 1). As noted, the working principle describes a basic cause-and-effect relationship (often physical or chemical) and is 'used' (or 'selected from various (differently effective) options') in evolution to generate a certain function via a certain construction, which in turn is achieved in a relevant biological context (i.e. the task). In this context, adaptations are generated when constructions are changed in such a way that the working principle can be better used (i.e. the construction gives a better performance). Hence, the functioning of the construction is quantitatively improved, i.e. its performance increases. Higher performances can lead to improved fitness and, when summed, can become visible as an adaptation (here defined as the "expression of a character that has resulted from natural selection in response to environmental conditions or physiological requirements and that has increased the fitness of the bearer of this trait"; own translation from Zrzavý et al. 2009). Selection primarily acts on both the overarching system and the constructions of an individual organism. Positive contributions to fitness might be attained by introducing changes in the construction / the overarching

system (which also includes behavioural features that employ the constructional features in interaction with the environment) possibly resulting in (1) more (novel) functions (if more working principles come into play) and / or (2) gains in the performance (efficiency) with which the functions are fulfilled (if more efficient parameter values of a certain working principle are selected).

Our design schema can also be related to evolutionary concepts such as adaptation, the adaptive landscape or the adaptive peak. For example, the concept of the adaptive landscape has been widely used to map phenotypes on fitness (e.g. Futuyma 2007, Svensson and Clasbeck 2012), the latter application resembling the design spaces introduced in Fig. 6.

The design space, however, is not about fitness but about the performance of a particular construction from an engineering perspective. A biological analogue of the design space could be a "performance space" in which performance capabilities in an adaptive landscape are mapped onto (morphological) phenotypes (Losos 2009: Fig. 16.3). Since not only one but many 'constructions' and related performances are found in a certain individual organism, their individual contributions to fitness can become complex and difficult to detect. From the engineering multi-criteria optimisation problem, we know that not all single performances can be maximised at once. Moreover, the mutual (antagonistic and synergistic) interactions of performances impede the evaluation of the effect of a single performance on fitness.

Conclusion and outlook

Although all technomorphic approaches have their limitations, because they can never grasp all of the complexity existing in living nature, our approach indicates that they can be useful in some respects. The overall aim of this contribution has been to establish a theoretical and conceptual framework for the analysis of morphological structures in more detail from an engineering point of view. Such analyses might also be useful for further investigations in biology and facilitate the exchange between biology and engineering, i.e. biomimetics. Core concepts from engineering design, namely function, working principle and construction, can be described and used to analyse morphological structures in biology. These central concepts are, furthermore, linked to each other via the so-called design space, whereby the function indicates a quantifiable performance measure and the working principles determine the parameters that can and need to be altered in order finally to achieve an optimised construction. In evolutionary biology, the design space can be used to analyse phenomena such as adaptation and robustness. Constructions that are especially robust can be identified in the design space as flat optima.

Our conceptual framework can be useful for further (comparative) investigations within (evolutionary) biology by means of precise conceptual tools and specified levels of investigation in order to understand the way in which morphological structures work and to compare biological and engineering constructions. Such comparisons might provide new insights in biology possibly leading to technical products based on biological research. Via the recognition and definition of the basic working principles and parameters underlying technical and biological functions, 'constructional characters' and 'constructional traits' can be understood in greater detail and on a heuristic level. Once the employed working principles enabling a certain function are known, the dimensions in the design space can be determined and the effect of the combination of the parameter values for the working principles analysed with respect to engineering questions of optimisation and biological questions of adaptation. In biology, changes in the parameter values in the design space (theoretically, experimentally or empirically by comparisons between individuals, populations or species) can improve our understanding of the adaptiogenesis of living organisms and of the kind of basic working principles that have been taken up during evolution.

The flat optima that allow for sloppy parameter settings seem not only to be present in molecular signal transduction pathways (investigated by systems biology), but can also be found on a morphological level. Our examples show that biological constructions can be more robust than comparable engineering constructions; such findings might be of great interest within the applied sciences (engineering, biomimetics), possibly leading to the design of more robust devices and machines. Flat optima might also facilitate the evolvability of phenotypes when connected by corridors of relatively high performance. In this latter case, pathways or even networks through the design space at high performance levels might open up possibilities for evolution in various directions. The research question as to whether multidimensional design spaces show such characteristics from the molecular to the morphological level remains open.

Acknowledgements

We thank Wolfgang Maier for numerous informal discussions on topics including those dealt with in this article and for sharing his ideas and extensive knowledge on so many aspects of evolutionary biology with us. We also thank the editors of this commemorative volume, Ingmar Werneburg and Irina Ruf, for inviting us to write a contribution and for their editorial work. We thank Ludger Jansen for philosophical clarifications. Fig. 8 was made by Andreas Kunz and Monika Meinert. The research of MD is funded by DFG project 492191929 "Learning from Nature: Epistemological and Ontological Foundations of Biomimetics". Theresa Jones corrected the English.

References

Alfaris A (2010) Multidisciplinary system design optimization (MSDO). Multiobjective Optimization (I). Lecture 14. MIT OpenCourseWare. ESD.77 / 16.888 Multidisciplinary System Design Optimization. CC BY-NC-SA 4.0. ocw.mit.edu/terms. https://ocw.mit.

edu/courses/institute-for-data-systems-and-society/ids-338j-multidisciplinary-system-design-optimization-spring-2010/lecture-notes/MITESD_77S10_lec14.pdf (accessed 26 November 2020)

Alon U (2007) An introduction to systems biology. Design principles of biological circuits. Chapman & Hall, Boca Raton (FL).

Arnold SJ (1983) Morphology, performance and fitness. American Zoologist 23: 347–361. https://doi.org/10.1093/icb/23.2.347

Arnold SJ (2003) Performance surfaces and adaptive landscapes. Integrative and Comparative Biology 43: 367–375. https://doi.org/10.1093/icb/43.3.367

Bertalanffy Lv (1932) Theoretische Biologie. Band 1. Borntraeger, Berlin.

Bertalanffy Lv (1933) Betrachtungen über einige Probleme der Morphologie. Biologia Generalis 9: 70–84.

Bertolaso M, Caianiello S, Serrelli E (Eds) (2018) Biological Robustness. Springer, Cham.

Betz O (1996) Function and evolution of the adhesion-capture apparatus of *Stenus* species (Coleoptera, Staphylinidae). Zoomorphology 116: 15–34. https://doi.org/10.1007/BF02526926

Betz O (1998) Comparative studies on the predatory behaviour of *Stenus* spp. (Coleoptera: Staphylinidae): the significance of its specialized labial apparatus. Journal of Zoology 244: 527–544. https://doi.org/10.1111/j.1469-7998.1998.tb00058.x

Betz O (2008) Ökomorphologie als Analyse der Form und Funktion von Strukturen in ihrer Beziehung zur Umwelt. Entomologia Generalis 31: 129–139. https://doi.org/10.1127/entom.gen/31/2008/129

Betz O, Koerner L, Dettner K (2018) The biology of Steninae, In: Betz O, Irmler U, Klimaszewski J (Eds) Biology of Rove Beetles (Staphylinidae) – Life History, Evolution, Ecology and Ddistribution. Springer, Cham, 229–283.

Bletzinger K-U, Kimmich S, Reitinger R, Ramm E (1995) Form und Funktion. In: Kull U, Ramm E, Reiner R (Eds) Evolution und Optimierung – Strategien in Natur und Technik. Hirzel, Stuttgart, 73–93.

Bock WJ, Wahlert Gv (1965) Adaptation and the form-function complex. Evolution 19: 269–299.

Canguilhem G (2008) Knowledge of Life. Fordham University Press, New York.

Dau H, Kurz P, Weitze M-D (2019) Künstliche Photosynthese. Springer, Berlin.

Drack M (2019) Towards a formalisation of biomimetics via engineering design concepts. In: Kesel AB, Zehren D (Eds) Bionik: Patente aus der Natur, Tagungsbeiträge, 9. Bionik-Kongress. Bionik-Innovations-Centrum (B-I-C), Bremen. 92–102.

Drack M, Betz O, Nebelsick JH (2020) Konstruktionslehre, Bionik und phylogenetische Aspekte. In: Werneburg I, Betz O (Eds) Phylogenie, Funktionsmorphologie und Bionik – Texte zum 60. Phylogenetischen Symposium in Tübingen. Scidinge Hall Verlag, Tübingen, 27–38.

Drack M, Limpinsel M, de Bruyn G, Nebelsick JH, Betz O (2018) Towards a theoretical clarification of biomimetics using conceptual tools from engineering design. Bioinspiration & Biomimetics 13: 016007. https://doi.org/10.1088/1748-3190/aa967c

Duncker H-R (1994) Probleme der wissenschaftlichen Darstellung der komplexen Organisation von lebenden Systemen. In: Maier W, Zoglauer T (Eds) Technomorphe Organismuskonzepte. Frommann-Holzboog, Stuttgart-Bad Cannstatt. 299–317.

Eifler W, Schlücker E, Spicher U, Will G (2009) Küttner Kolbenmaschinen. Vieweg und Teubner, Wiesbaden. (7th edition)

Futuyma DJ (2007) Evolution. Das Original mit Übersetzungen. Elsevier, München.

Gould S, Vrba ES (1982) Exaptation – a missing term in the science of form. Paleobiology 8: 4–15. https://doi.org/10.1017/S0094837300004310

Grote K-H, Antonsson EK (Eds) (2008) Springer Handbook of Mechanical Engineering. Springer, Berlin.

Grun TB, Dehkordi LKF, Schwinn T, Sonntag D, Scheven Mv, Bischoff M, Knippers J, Menges A, Nebelsick JH (2016) The skeleton of the sand dollar as a biological role model for segmented shells in building construction: a research review. In: Knippers J, Nickel K, Speck T (Eds) Biomimetic Research for Architecture and Building Construction. Springer, Cham, 217–241.

Gutenkunst RN, Waterfall JJ, Casey FP, Brown KS, Myers CR, Sethna JP (2007) Universally sloppy parameter sensitivities in systems biology models. PLoS Computational Biology 3(10): e189. https://doi.org/10.1371/journal.pcbi.0030189

Held LI (2009) Quirks of Human Anatomy. Cambridge University Press, Cambridge (UK).

Irschick D, Higham T (2016) Animal Athletes. Oxford University Press, Oxford.

Kitano H (2004) Biological robustness. Nature Reviews Genetics 5: 826–837. https://doi.org/10.1038/nrg1471

Koepcke H-W (1974) Die Lebensformen. Goecke & Evers, Krefeld. (4 volumes)

Koerner L, Garamszegi LZ, Heethoff M, Betz O (2017) Divergent morphologies of adhesive predatory mouthparts of *Stenus* species (Coleoptera: Staphylinidae) explain differences in adhesive performance and resulting prey-capture success. Zoological Journal of the Linnean Society 181: 500–518. https://doi.org/10.1093/zoolinnean/zlx006

Krohs U, Kroes P (Eds) (2009) Functions in Biological and Artificial Worlds. MIT Press, Cambridge (MA).

La Mettrie JO de (1912) Man a Machine. Open Court Publishing, Chicago. Online: https://www.gutenberg.org/ebooks/52090 (accessed 12 April 2022)

Licker MD, et al. (2003) McGraw-Hill Dictionary of Engineering. McGraw-Hill, New York. (2nd edition)

Lippert H (2003) Lehrbuch Anatomie. Urban & Fischer, München. (6th edition)

Longo G (2018) How future depends on past and rare events in systems of life. Foundations of Science 23: 443–474. https://doi.org/10.1007/s10699-017-9535-x

Losos JB (2009) Lizards in an Evolutionary Tree. Ecology and Adaptive Radiation of Anoles. University of California Press, Berkeley.

Maier W (1999) On the evolutionary biology of early mammals – with methodological remarks on the interaction between ontogenetic adaption and phylogenetic transformation. Zoologischer Anzeiger 238: 55–74.

Maier W (2017) Der Weg zum Menschen. Ausgewählte Schriften zur Evolutionsbiologie der Wirbeltiere. Scidinge Hall Verlag, Tübingen.

Maier W (2020) Das Säugergebiß als morphologisches Paradigma. In: Werneburg I, Betz O (Eds) Phylogenie, Funktionsmorphologie und Bionik – Texte zum 60. Phylogenetischen Symposium in Tübingen. Scidinge Hall Verlag, Tübingen, 165–186.

Maier W, Zoglauer T (Eds) (1994) Technomorphe Organismuskonzepte. Frommann-Holzboog, Stuttgart-Bad Cannstatt.

Martins JRRA, Ning A (2022) Engineering Design Optimization. Cambridge University Press, Cambridge (UK).

McGhee GR (2007) The Geometry of Evolution: Adaptive Landscapes and Theoretical Morphospaces. Cambridge University Press, Cambridge.

Nachtigall W (1995) Zum Optimierungsbegriff in der Biologie. In: Kull U, Ramm E, Reiner R (Eds) Evolution und Optimierung – Strategien in Natur und Technik. Hirzel, Stuttgart, 137–153.

OED (2021) "organ, n.1" in: Oxford English dictionary online. December 2021. www.oed.com/view/Entry/132421 (accessed 11 January 2022).

Pahl G, Beitz W, Feldhusen J, Grote KH (2007a) Engineering Design: A Systematic Approach. Springer, London.

Pahl G, Beitz W, Feldhusen J, Grote KH (2007b) Konstruktionslehre – Grundlagen erfolgreicher Produktentwicklung – Methoden und Anwendung. Springer, Berlin. (7th edition).

Paul D, Dehkordi LKF, Scheven M von, Bischoff M, Radde N (2016) Structural design with biological methods: optimality, multi-functionality and robustness. In: Knippers J, Nickel K, Speck T (Eds) Biomimetic Research for Architecture and Building Construction. Springer, Cham, 341–360.

Peverill RE (2021) Changes in left ventricular size, geometry, pump function and left heart pressures during healthy aging. Reviews in Cardiovascular Medicine 22: 717–729. https://doi.org/10.31083/j.rcm2203079

Popieluszko P, Henry B, Sanna B, Hsieh WC, Saganiak K, Pękala P, Walocha J, Tomaszewski K (2017) A systematic review and meta-analysis of variations in branching patterns of the adult aortic arch. Journal of Vascular Surgery 68: 298–306.e10. https://doi.org/10.1016/j.jvs.2017.06.097

Prescott TJ, Lepora NF, Verschure PFMJ (Eds) (2018) Living Machines – A Handbook of Research in Biomimetics and Biohybrid Systems. Oxford University Press, Oxford.

Reidys C, Stadler PF, Schuster P (1997) Generic properties of combinatory maps: neutral networks of RNA secondary structures. Bulletin of Mathematical Biology 59: 339–397. https://doi.org/10.1007/BF02462007

Reilly SM, Wainwright PC (1994) Conclusion: Ecological morphology and the power of integration. In: Wainwright, PC, Reilly SM (Eds) Ecological Morphology. University of Chicago Press, Chicago, 339–354.

Reuleaux F (1900) Die praktischen Beziehungen der Kinematik zu Geometrie und Mechanik. Vieweg, Braunschweig.

Richter S, Wirkner CS (2013) Objekte der Morphologie. In: Bruhn M, Scholtz G (Eds) Morphologien. Bildwelten des Wissens 9.2. Akademie Verlag, Berlin, 83–96.

Richter S, Wirkner CS (2014) A research program for Evolutionary Morphology. Journal of Zoological Systematics and Evolutionary Research 52: 338–350. https://doi.org/10.1111/jzs.12061

Riedl R (1975) Die Ordnung des Lebendigen. Parey, Hamburg. (English: Riedl R. 1978. Order in Living Organisms: A Systems Analysis of Evolution. Wiley, New York.)

Riedl R (1977) A systems-analytical approach to macro-evolutionary phenomena. The Quarterly Review of Biology 52: 351–370. https://doi.org/10.1086/410123

Riedl R. 2000. Strukturen der Komplexität. Springer, Berlin. (English: Riedl R. 2019. Structures of Complexity. Springer, Cham.)

Schwenk K (2001) Functional units and their evolution. In: Wagner GP (Ed.) The Character Concept in Evolutionary Biology. Academic Press, San Diego, 165–198.

Svensson EI, Clasbeek R (2012) The Adpative Landscape in Evolutionary Biology. Oxford University Press, Oxford.

The Field Museum of Chicago (2014) The Machine Inside: Biomechanics. https://www.fieldmuseum.org/traveling-exhibitions/machine-inside-biomechanics (accessed 23 April 2022)

Toepfer G (2011) Historisches Wörterbuch der Biologie. Metzler, Stuttgart. (3 vols.)

Uexküll Jv (1928) Theoretische Biologie. Springer, Berlin. (2nd edition)

Vogel S (2013) Comparative Biomechanics. Princeton University Press, Princeton. (2nd edition)

Wagner A (2005) Robustness and Evolvability in Living Systems. Princeton University Press, Princeton (NJ).

Wagner A (2016) Arrival of the Fittest. Oneworld Publications, London.

Wagner GP, Altenberg L (1996) Complex adaptations and the evolution of evolvability. Evolution 50: 967–976. https://doi.org/10.1111/j.1558-5646.1996.tb02339.x

Wagner GP, Lynch VJ (2010) Evolutionary novelties. Current Biology 20: R48–R52. https://doi.org/10.1016/j.cub.2009.11.010

Wainwright PC (2007) Functional versus morphological diversity in macroevolution. Annual Reviews in Ecology and Systematics 38: 381–401. https://doi.org/10.1146/annurev.ecolsys.38.091206.095706

Wainwright PC, Alfaro ME, Bolnick DI, Hulsey CD (2005) Many-to-one mapping of form in function: A general principle in organismal design? Integrative and Comparative Biology 45: 256–262. https://doi.org/10.1093/icb/45.2.256

Weber H (1930) Biologie der Hemipteren. Springer, Berlin.

Wenk P, Lucic S, Betz O (2010) Functional anatomy of the hypopharynx and the salivary pump in the feeding apparatus of the assassin bug *Rhodnius prolixus* (Stål 1858) (Heteroptera: Reduviidae). Zoomorphology 129: 225–234. https://doi.org/10.1007/s00435-010-0115-7

Wragg PD, Johnson SD (2011) Transition from wind pollination to insect pollination in sedges: experimental evidence and functional traits. New Phytologist 191: 1128–1140. https://doi.org/10.1111/j.1469-8137.2011.03762.x

Zrzavý J, Storch D, Mihuloka S (2009) Evolution. Ein Lese-Lehrbuch. Spektrum, Heidelberg.