Georg Glaeser · Werner Nachtigall

The Evolution and Function of Biological Macrostructures

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Translation from the German language edition:
Die Evolution biologischer Makrostrukturen - ein Fotoshooting
by Georg Glaeser and Werner Nachtigall
© Springer-Verlag GmbH Deutschland, ein Teil von Springer Nature 2018.

ISBN 978-3-662-59290-8 ISBN 978-3-662-59291-5 (eBook)
https://doi.org/10.1007/978-3-662-59291-5

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The registered company address is: Heidelberger Platz 3, 14197 Berlin, Germany

Below the left eye of the hermit crab (*Clibanarius misanthropus*), you can see a paddle-like leg joint (see p. 56). The appendage acts as a pump with which water from which oxygen has been extracted is expelled through the gill cavity.

Preface

Different ways of looking at animals and plants

Many people are dazzled by the beauty of nature. Those with an interest in biology will probably take out their binoculars or magnifying glass and have a closer look at what nature has to offer. Among nature lovers, nature photographers may be regarded as a "species" of their own: They not only want to document what they see, but strive to create pictures that hold artistic value while simultaneously capturing the biological complexity of their motifs. The goal is to arrive at a photograph that is both informative *and* aesthetically pleasing.

Looking at nature with "innocent joy"

was what brought mathematician Georg Glaeser and biologist Werner Nachtigall together. Both are passionate nature photographers, and they have known each other since their previous collaboration on *The Evolution of Flight*, the second volume in a series of "biological photoshoots." The work on this project revealed an abundance of macroscopic, and even microscopic, elements that play a significant evolutionary role – just consider the impact of feather microstructures during a bird's flight – but not all of these elements could be accounted for in the book's discussion of flight processes.

The macroscopic world – little-known but often highly influential

The two authors would like to fill this gap with the present book, which will shed light on the astonishing diversity present on the macro level – a hidden world that only few people know about in great detail but that is just as real as the world of big objects that surrounds us.

Comparing different formations of organs

A first look will reveal the appearance of an animal or a plant. The biological discipline of comparative morphology is concerned with the description of such appearances. The first book of this series (Glaeser/Paulus: *The Evolution of the Eye*) illustrates how fascinating such comparisons can be by considering the different formations of visual organs.

Speed and acceleration

Animals and – to some extent – plants have the ability to move, sometimes at great speed and occasionally with astonishing acceleration. This is where high-speed photography comes in. In the book *The Evolution of Flight*, Glaeser, Paulus, and Nachtigall already explored the thrill of rapid movement, capturing the motion of animals in flight using telephoto lenses and series-production cameras.

Macrostructures through the lens of technical biology

In biological sciences, the term 'macrostructure' refers to any structure that measures several millimetres or only a few centimetres in size and to which a specific function can be assigned. The close examination of macrostructures requires a magnifying glass and occasionally the low magnification of a microscope. Especially on the surfaces of living organisms we can find a confusing and yet fascinating variety of such structures.

We have tried to describe a representative selection of these structures from the point of view of technical biology and broaden the reader's understanding further through photographs. For this purpose, we used macro and micro cameras.

Evolution and macrostructures

Microstructures are also subject to evolutionary processes, but it is not uncommon for these processes to push the boundaries of what is physically possible. This aspect will frequently be raised and discussed throughout this book.

Biological evolution is often regarded as an “upward development.” However, it is not, in fact, a goal-oriented process, let alone a progression towards a specific higher goal. Evolution is merely the *modification* of a given system over generations that generates minor morphological, and sometimes also physiological and behavioural-physiological, differences between species.

All genetic heritage is subject to variation

This is due to the fact that each unit of hereditary information (gene on a chromosome) can mutate randomly (such mutations may be caused by natural radiation). Through the genetic recombination that occurs during sexual reproduction, the mutated gene is then randomly transmitted to the offspring. It is safe to assume that minor gene mutations continually appear in all individuals of a species.

No offspring is identical to its parents

The mutations are usually so minimal that they often go unnoticed when we look at our offspring. Yet, every offspring is ‘something else’. If a mutation confers reproductive advantage, we consider this to be an *evolutionary success*.

Evolution is induced but also limited by physical conditions. The impact of these physical conditions on the processes of evolution is still underestimated.

Nature-inspired technology

This book contains many examples from technical biology. This field explains the characteristics and functions of biological forms by drawing on insights from engineering physics and engineering, or at least tries to offer a better understanding of them than would have been possible without this kind of knowledge and know-how. This became obvious in some of the examples in this book. A biological study of how the domestic pigeon’s alula enables the bird to perform special flight manoeuvres could fill an entire monograph, but a physical-technical explanation demonstrating the dependence of the lift coefficient on the angle of attack boils down to a few lines.

Bionics

The reverse approach, bionics, has flourished in recent decades. Nature offers an infinite wealth of inspiration for technological advances. However, this transfer of principles from nature to technology must be conducted in an appropriate manner.

Several examples discussed in this book have already generated bionic innovations, such as the van der Waals adhesion of gecko setae (p. 38), which has inspired adhesive tape that sticks even under water and on oily surfaces; the alula feathers of birds (p. 101) which served as a model for the high-lift slats of aircrafts; and the torsion buckling of bird of paradise flowers (p. 152), which has been adapted for the folding mechanism of self-regulating façade-shading systems.

The design of this book

is once again based on the tried-and-tested 'double-page principle': Each double-page is usually dedicated to one topic. Photographs and/or sketches are used to illustrate key ideas and are often complemented by explanations of the underlying evolutionary process. A benefit of the double-page principle is that the reader is not required to read the book linearly from cover to cover. One can start reading from a random point and then look up the cross-references provided on a second reading.

Bibliographical references are given at the end of the book. We tried to keep the texts short to focus the reader's attention on the pictures, but also strove for readability. For this reason, we avoided using formulas and an abundance of numerical data, and relied instead on concise and informative texts. At several points in the book, we added drawings that were made in a uniform style. The creator of these drawings is Werner Nachtigall; he used a thick eyebrow pencil and coarse paper. The templates that he created with these utensils were then significantly reduced in size. As you will see further on in this book, the result of this process are sketches with a unique graphic quality.

Georg Glaeser, who specializes in wildlife photography, was not the only photographer this time. Some of the photographs in this book were taken from Werner Nachtigall's vast archive of pictures, which include detailed close-ups of preserved animal and plants. Some images of preserved organisms were captured using electronic microscopes. However, we preferred using pictures of living organisms whenever possible.

Acknowledgements

We wish to thank Hannes F. Paulus, who co-authored the first two books of the "Photoshoots of Evolution" series. For this book, we could count on his expert knowledge and experience in the classification of species. A number of other people deserve special thanks. We are most grateful to (in alphabetical order and without academic degrees) Daniel Abed-Navandi, Peter Calvache, Gudrun Maxam, Tamara Radak and Eugenie Maria Theuer. Stefanie Wolf from Springer Spektrum has also been tremendously helpful and dedicated, offering support throughout this project.

The two authors wish you a delightful reading experience with plenty of aha moments!

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Whatever nature "constructs", it must be "brought into shape" first. Morphological structures may serve a protective function, but they are hardly ever completely rigid. They are set in motion through muscular traction or changes in internal pressure. These processes can be explained by the principle of the lever. Following this principle, we typically find levers of different lengths when it comes to generating wide-ranging motions or transferring high forces.

Chapter 2: Sticking, Filtering, Drilling

Individual "building blocks" must be mechanically resilient. If they are made up of individual elements, they need strong internal adhesion. It is frequently the case that very diverse structures need to be coupled – for example, the leg of a fly and the surface of a leaf. If the connection between two units holds, complex structures such as fish traps or drills can be built. These are not supposed to adhere to other materials. The adhesion of pollen to the hair covering of insects (e.g., bees) belongs into this category.

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Gripping, stowing, and storing food 63

The principle of gripping prey plays a decisive role for movement and food gathering. Just think of the way that orangutans brachiate or the lightning-fast movements of a mantis when snatching prey. Food gathered must be stored, and for this purpose, repositories and containers must be stretched. Space must also be provided for structures that are not in use at certain times; on this account, they are often folded, as in the membranous wings of beetles.

Chapter 4: Signalling, Swimming, Flying, Exploding

Fluids are similar in principle 83

Creatures move on land, in water, or in the air. The organs involved in these movements vary accordingly, and as a result, so do their macrostructures. From the point of view of physics, water and air are fluids and as such, they are similar in principle. This similarity has evolutionary ramifications, for example in the context of the resilient, optimised shape of moving bodies. These can, for example, be observed in hydrophilids and in recumbent and swimming birds.

Chapter 5: Storage, Constructions, Building materials

Like humans, plants and animals "build rooms" in which they can store substances, for instance. There are lightweight constructions and above-ground constructions, as well as heavy earthworks. All these constructions must be stable; some require great tensile strength to hold the structure together. Cellulose is the main building material of plants. Animals use chitin or calcareous material, such as the bone substance of vertebrates or the calcareous skeletons of corals.

Chapter 6: Packaging, Primordia, Unfolding Mechanisms

In nature, especially in connection with macrostructures, we can find a variety of elements acting as a kind of packaging for fragile structures. The way fruits and seeds fill surfaces and enclose spaces shows how stacking is done in nature, utilising space in an optimal way. When these organisms mature, their packaging must unfold. This unfolding can be achieved through growth processes or pressure increases, as well as tension equalization – these can typically be found in certain flowering mechanisms.

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In recent years, the exploration of the macrocosm in all its different forms has had manifold implications for the increasingly blurry dividing line between nature and technology. Investigating structure-functional aspects of nature is one of the chief aims of technical biology. Bionics is then used to technically implement the insights reached. In this final chapter, we give a few examples of such structures.

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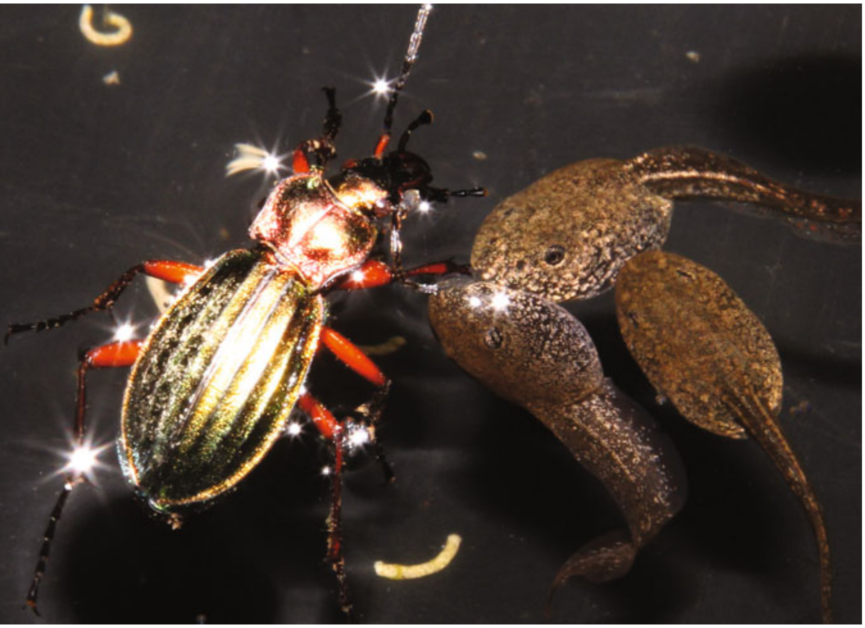
G. Glaeser, W. Nachtigall, *The Evolution and Function of Biological Macrostructures*, https://doi.org/10.1007/978-3-662-59291-5_1

1 Shape, Movement, Lever

Moving morphological structures through levers

Whatever nature "constructs", it must be "brought into shape" first. Morphological structures may serve a protective function, but they are hardly ever completely rigid. They are set in motion through muscular traction or changes in internal pressure. These processes can be explained by the principle of the lever. Following this principle, we typically find levers of different lengths when it comes to generating wide-ranging motions or transferring high forces.

Morphological structures



The thoracic sclerite of ground beetles

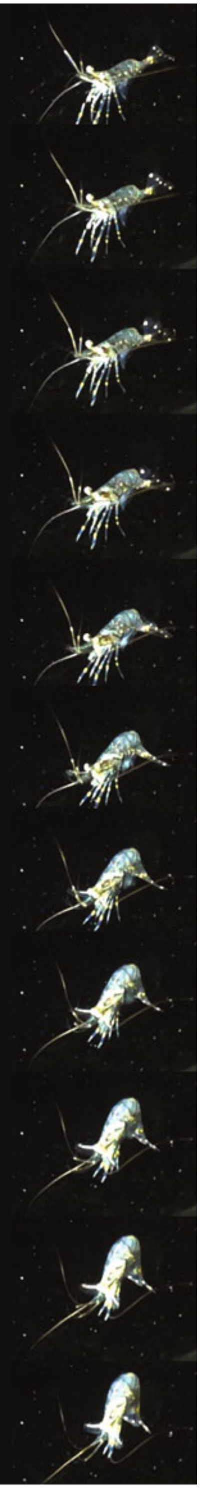
This is the part of the shell that covers the beetle's thorax, from which three pairs of legs protrude. Like all morphological structures of insects, the thoracic sclerite is made of chitin. It has merged from several embryonal layers into a self-contained and stable part that is shaped like a shallow bowl with a reinforced rim. A series of muscles is attached to its inner surface.

These bowl-shaped parts withstand traction and compression forces without breaking or deforming. As their name implies, ground beetles commonly live on the ground, but they also like to burrow into loose earth. When they do so, their thoracic sclerite both acts as a shovel and protects their internal organs from the pressure of the surrounding soil particles. For this reason, ground beetles have evolved a thicker thoracic sclerite than other species that do not burrow but are light enough to float on water.

The cephalothorax of spiders

Arthropods, which comprise insects, spiders, centipedes, millipedes, and crustacea, moult at more or less regular intervals; it is only by shedding their exoskeleton that they can grow. Before the old layer of chitin is cast off, the new exoskeleton, which is still soft and pliable, is "inflated" by an increase in the animal's internal pressure. Once it has grown to size, the new layer hardens. The discarded cuticles, also called exuviae (see below), preserve the animal's morphology with all its fine details. On the exuviae of the spider's cephalothorax (a fused head and thorax) that is depicted from the side here, the crest of the apodeme, to which the muscles are attached, and the tiny domes of the spider's "eyes" are clearly visible. Yet, all that is left is just a thin membrane of translucent chitin: Where the eyes used to be, we see the corneae that were also cast off. The spiracle tubes of insects are similarly shed during moulting. You can clearly see them protruding from the exuviae of dragonfly nymphs, where they look like tiny white cords. Once chitin has hardened, it is no longer pliable. That is why arthropods must moult their hardened exoskeleton in order to grow: Moulting is simply the consequence of evolution's "choice" of chitin as the building material of arthropods.

Flexible shells and levers



The flexibly joined segments of shrimp shells

Each segment of a shrimp is covered by a plate, but the individual segments are joined together flexibly. You will notice that if you order a prawn cocktail, which consists of the tail end of mid-sized shrimps. During flight from predators, this tail is flexed to form an almost perfect spiral, which enables the shrimp to jump backwards rapidly; then, it is quickly straightened out again to produce powerful swimming strokes. The picture below shows a mechanical shrimp (*Cinetorhynchus rigens*) performing several such "tail flips" in front of the photographer's camera. However, such movements last no more than a few hundredths of a second: It took the rockpool prawn on the left just 1/100 of a second to do the tail flip captured by the image series (the series was shot with 1000 images per second)! The photographs on the next page show a large sea mammal moving in a way that bears a remarkable similarity to the shrimp's tail flip. Dugongs swim by undulating their entire spine down to the tail fin. Shrimps, on the other hand, propel themselves through the water by flipping their tails or paddling with their hind legs in a metachronal rhythm.

Like a knight's armour

Evolution has equipped many arthropods with flexibly joined shell segments. These segments are either interlocked with each other or joined by articular membranes that vary in thinness. They protect individual body parts like a knight's armour while still providing sufficient flexibility. They thus manage to fulfil contrasting demands, offering an evolutionary playground for further optimization.

A shrimp's toolkit

Let's have a look at the rockpool shrimp *Palaemon elegans* depicted on the right (see also p. xiii): We can see two pairs of pincers situated near the shrimp's mouth. The front pincers with the blue and yellow stripes are the largest. The secondary pincers are fine and transparent. These tools allow the animal to grab microscopically small prey that lives in seagrass meadows. Female shrimps carry fertilized eggs attached to the short limbs of their lower bodies. These limbs beat back and forth periodically to fan fresh water over the fragile embryos.

Accelerating dugongs

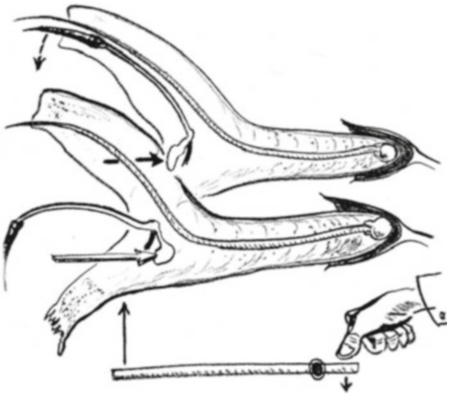
Dugongs, which measure an average length of 3 m, can move their abdomen in ways that invite comparison with shrimps and lobsters. These movements similarly enable a dugong to change its location rapidly: Like a shrimp, the large mammal will flex its abdomen to form an almost perfect spiral and then straighten it out rapidly. Due to their size, dugongs take significantly longer than shrimps to generate the same movement.

Lever arms of different lengths in sage flowers

When a pollinating insect, such as a bee or a bumblebee, lands on a meadow sage (*Salvia pratensis*) flower, the stamens will bend down as if by magic and smear their pollen on the upper side of the insect. Upon entering an older flower, where the carpels are fully developed and the pistil, which supports the stigma, hangs downward, the insect transfers the pollen onto the stigma and thus effects pollination.

The stamens' bending mechanism works as follows: They are connected by a thin ligament that can be twisted. At the bottom, they broaden to form a stiff spoon-like structure, and at the top they elongate along the filament, which carries the anthers at the tip.

If the insect inserts its proboscis into the narrow calyx tube, it has to clear the way by pushing the broad lower spoon of the lever mechanism upward and backward. This will cause the anthers to be lowered to the front. Since the lever arms in this mechanism are of very different lengths, the output force will be significantly higher than the input force. In this case, it means that it takes only small movements of the spoon-shaped lower stamens to make the anthers travel a long path.



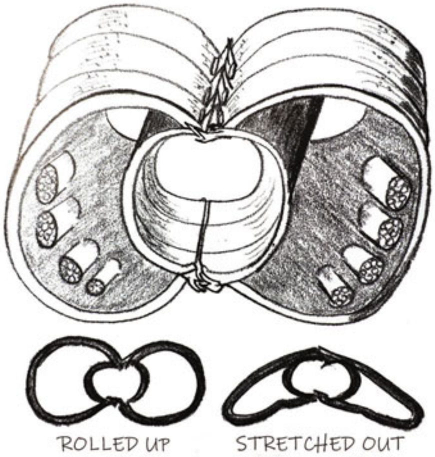
Spiral twisting

Curled-up millipedes

Millipedes (Diplopoda) are a very old group of arthropods. They have existed since the Carboniferous period, and they comprise more than 7200 species today. Since they consist of several segments, they are commonly confused with centipedes. However, the segments of millipedes are rounded, whereas centipedes have flattened bodies. The specimens of the genus *Julus* depicted on this page belong to the family Julidae. Each segment has two pairs of legs attached close together, which is quite unusual. Other groups of arthropods bear only one pair of legs per segment. The solution to this riddle: The visible segments of millipedes are actually double segments (or “diplosegments”, from which their scientific name derives), which are formed by the fusion of two embryonic segments. Upon closer inspection, you can still see a fine fusion line – for instance, at the illuminated segments on the bottom left side of the photograph below. When threatened, millipedes curl up so that their legs are tucked into the interior of the spiral for protection. As the above picture shows, the result is not always perfect.

Butterflies with rolled-up proboscis

The proboscis of butterflies generally consists of two hollow, semi-circular chitin tubes. These tubes are held together by tongue and groove joints, which are particularly interesting from a technical-biological perspective. Most butterflies feed on nectar from flowers, which is sucked up through the cavity of the proboscis. Inside the two tubes, there are two partitions, spiracles, nerves, and small muscles (which are not depicted in the sketch on the right), as well as a series of larger, diagonally oriented muscles. Butterflies usually roll up their proboscis in order to tuck it away conveniently.



Some tropic butterfly species have proboscis of up to 20 cm. As you can imagine, such a long proboscis is at a high risk of breaking in its extended state. The proboscis is straightened through contractions of the diagonally oriented main muscles. These contractions will cause the semi-circular tubes to flatten slightly. As a result, the butterfly's proboscis will unfurl. This process can be easily recreated by rolling up an elongated sheet of paper, grabbing one end of the paper roll with both hands, and bending the outer edges against each other. This will cause the rolled-up piece of paper to unroll. If this bending of the outer edges is reversed, the paper will roll itself up again. In the same manner, the butterfly's proboscis curls back into a spiral by its own elasticity once the main muscles relax. This main mechanism has several other, secondary effects.