


The Evolution of Flight

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Springer

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Foreword

A trio of authors

This book is organized similarly to its predecessor, "The Evolution of the Eye". Once again, the following statement applies: Animal evolution itself cannot be captured in photographs, but its results certainly can. In this book, we have focused on the evolution of flying, various forms of which have independently been "invented" in the animal kingdom. Mathematician and passionate animal photographer Georg Glaeser has joined forces with the experienced evolutionary biologist Hannes Paulus and the exercise physiologist and flight biophysicist Werner Nachtigall in order to approach this topic with words and pictures in a way that is both generally comprehensible and scientifically sound.

Naturally, the book will not only consist of purely biological accounts, but will also touch upon aspects of Technical Biology. The discipline of Technical Biology describes and explains natural forms and processes in light of physical-technical expertise. Especially in gaining a better understanding of animal flight, certain viewpoints and parameters derived from the physics of technical flight can prove particularly helpful, even though they will only be applied in this book to make some simple and fundamental comparisons. Inspirations from biology that could have an impact on technology ("bionics") may also be drawn; however, they won't be discussed in any detail in the present book.

Photographing beyond a biological perspective

In this book as well, all of the photographs have been taken by Georg Glaeser (who also designed the book's layout). His approach to photographing animals combines empathy with artistic (and sometimes also mathematical) enthusiasm, rather than following the criterion of making pictures that are zoologically as easily identifiable as possible. The flight of the scarab on the left page or that of the barn swallow on this page are not just interesting in terms of their flight technicalities (the picture of the scarab shows how the beetle's wings function with the elytra closed). Additional information is provided by shadows and reflections on the surface. The numerous pictures that the photographer has taken of scarabs suggest that, before they rise into the air, these beetles tend to rotate in such a way that the sun shines on their backs, thus casting a symmetrical shadow. This habit probably helps the beetle to navigate using orientation cues from the sky, and the Ancient Egyptians, who associated the scarab with their sun god, surely noticed this as well.

Some animals had to be drawn

Flying animals, like all others, have developed over the course of millions of years. In the Carboniferous period, dragonflies whirred through the air. Birds evolved during the Jurassic period. Pterosaurs first appeared even earlier in the Triassic period and became extinct towards the end of the Cretaceous period. In the present day, many of

Seba's short-tailed bat (*Carollia perspicillata*)

Blister beetle (*Mylabris oculata*)

these animals can only be reconstructed and "drawn" – a task undertaken by the artist Markus Roskar. He also created illustrations of animals such as flying snakes and gliding ants, which could not be captured in high quality by camera.

Sometimes "multiple images"

Flying is a very dynamic process. Individual snapshots, while important and sometimes very spectacular, are often not as useful for the analysis of complex motion processes as "animations", which typically consist of a series of photographs taken and displayed in rapid succession (and sometimes films in super-slow motion). Insofar as technically possible, photographs may also be merged to illustrate motion processes – as was done, for instance, in the picture on the left-hand side.

Approaching a topic from different perspectives

This book may be read as a survey of flying animals across the evolutionary tree. In addition and alternatively to that, the authors would like to shed light on the evolution of flying from different perspectives and to draw comparisons between the different results of this evolutionary process. This shall primarily be done by means of photographs, which are occasionally complemented by schematic drawings. Since the focus will be on the photographs, the texts are concise while still including essential information.

Bibliography and web links

Bibliographical references to relevant literature and websites allow the reader to explore the topics that are covered in the book in more detail. Since online content is subject to change and may be deleted, the book is accompanied by a website, which keeps track of such changes.

Double-page principle

This book need not be read from front to back, as it is designed based on the double-page principle. Occasionally, cross-references are made to other pages. To facilitate the understanding of scientific terms when starting to read the book in the middle, it is recommended to consult the index to see where such terms are previously dealt with in the text.

An unbelievable variety

This book is meant to highlight and illustrate the various forms of flying that can be found in nature. For their contributions and help in creating this book, we would like to thank the following people (in alphabetical order and without academic titles): Daniel Abed-Navandi, Gudrun Maxam, Axel Schmid and Sophie Zahalka. Stefanie Wolf from our publisher Springer Spektrum has provided valuable and dedicated support during the planning and publication of the project. The limited number of pages required a very strict selection of photographs to be included in the book. However, numerous additional photographs can be found on the website that accompanies this book: www.uni-ak.ac.at/evolution

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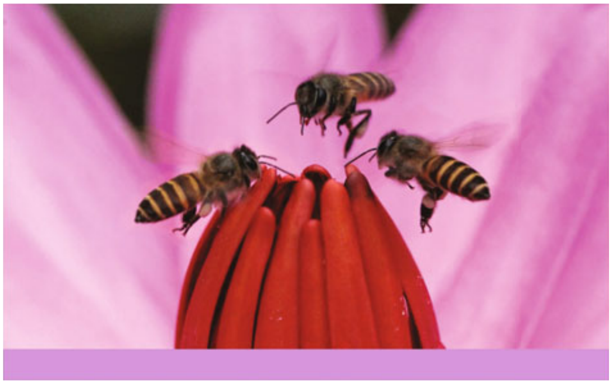

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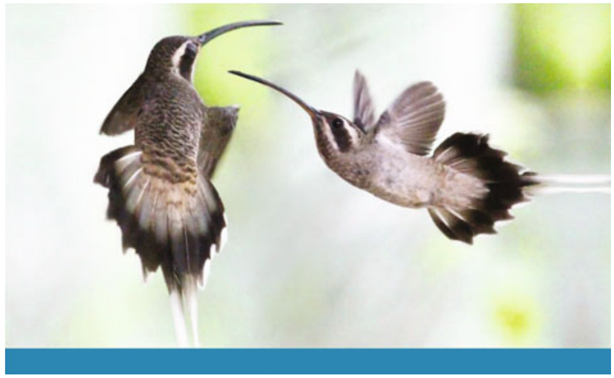

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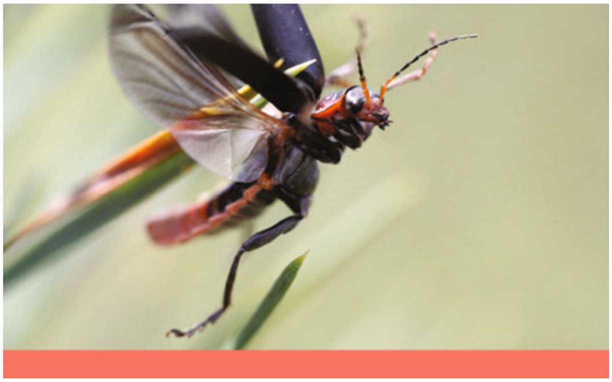

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It was only about 50 million years ago that bats and flying foxes took to the skies. Insects have been flying for a period seven times as long, and birds for a period four times as long. The pterosaurs, which had been flying through the air for some 170 million years, disappeared due to drastic climate changes towards the end of the Mesozoic Era. Navigation by means of ultrasound has enabled bats to conquer darkness.

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The topic is and will continue to be exciting

The fact that animals – and ultimately humans as well – can rise to the air as if gravity did not exist has always exerted enormous fascination on us. Biophysics has allowed us to understand and analyse this fact. Moreover, it is quite "typical" for the stunning capacity of evolution to use every imaginable niche and push it to its limits by placing, step by step, "one stone upon another."

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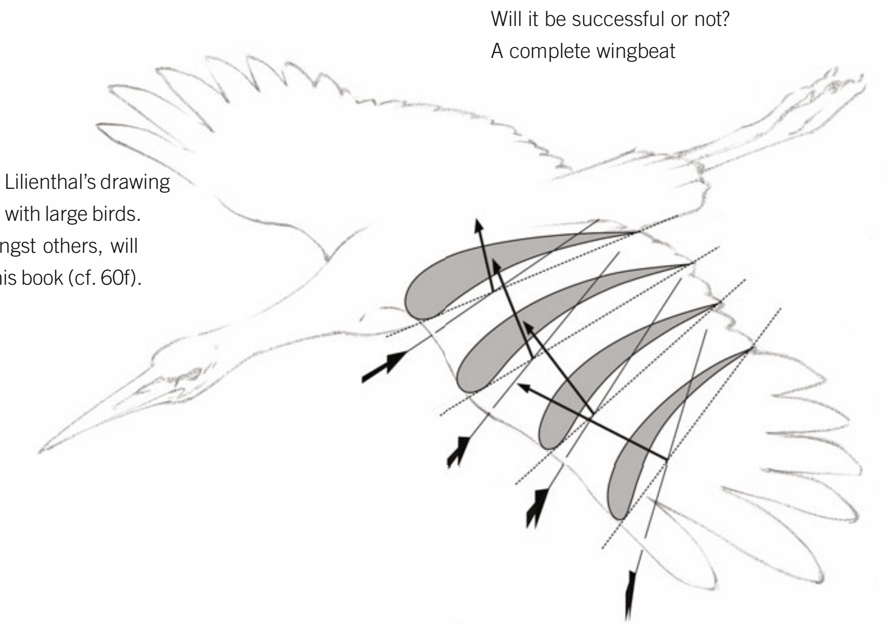

A "classic": Otto Lilienthal's drawing of lift-generation with large birds. This topic, amongst others, will be explored in this book (cf. 60f).

1 400 Million Years of Flight Evolution

Fourfold development to perfection

It must have been about 400 million years ago (mya): Certain insects started to develop wings, and not long after, almost all insects had gained the ability to fly. Birds evolved 200 mya, pterosaurians (from which birds do not have descended) probably even 230 mya. The fourth phase of this evolutionary process finally introduced flying mammals with the evolution of bats over 50 mya.

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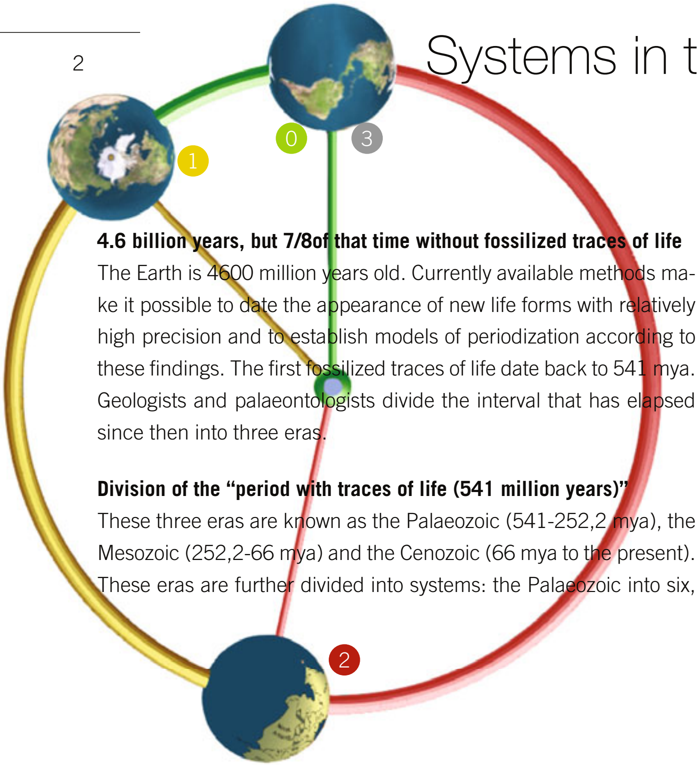
Systems in the geological timescale



4.6 billion years, but 7/8of that time without fossilized traces of life

The Earth is 4600 million years old. Currently available methods make it possible to date the appearance of new life forms with relatively high precision and to establish models of periodization according to these findings. The first fossilized traces of life date back to 541 mya. Geologists and palaeontologists divide the interval that has elapsed since then into three eras.

Division of the "period with traces of life (541 million years)"

These three eras are known as the Palaeozoic (541-252,2 mya), the Mesozoic (252,2-66 mya) and the Cenozoic (66 mya to the present). These eras are further divided into systems: the Palaeozoic into six, the Mesozoic into three, and the Cenozoic into three as well. Since these eras hold some significance for the evolution of life and will be referred to throughout the book, they shall be listed here with their time limits and some keywords as regards the appearance of typical life forms (those with wings printed in colour). The table follows the geological time scale that can be found on Wikipedia, but it is worth noting that there are several, slightly differing approaches and terminologies.

Palaeozoic (53.4%):

- Cambrian 541 - 485.4 – marine conchifera, worms, and algae
- Ordovician 485.4 - 443.4 – graptolites, trilobites
- Silurian 443.4 - 419.2 – placodermi, insects, first terrestrial plants
- Devonian 419.2 - 358.9 – ammonites, first apterygote insects, fish, tetrapods, tree ferns
- Carboniferous 358.9 - 298.9 – amphibians, first winged insects, ancient dragonflies, forests of club mosses and horsetails
- Permian 298.9 - 252.2 – amphibians, reptiles, coniferous trees

Mesozoic (34.4%):

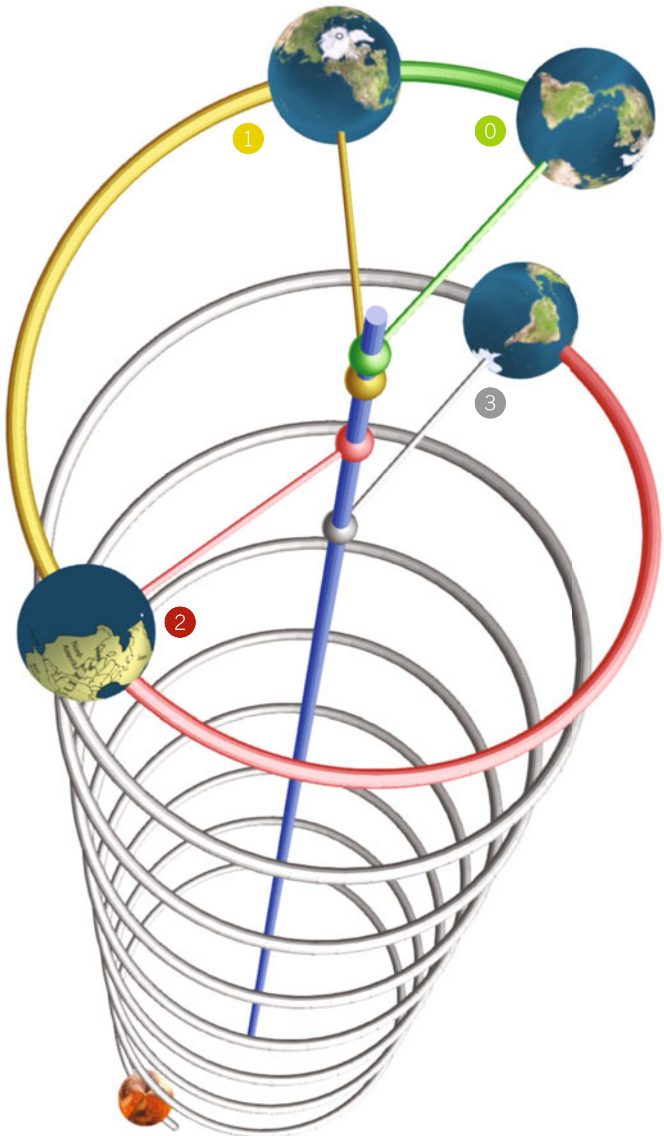
- Triassic 252.2 - 201.3 – reptiles, dinosaurs, ichthyosaurs, pterosaurs
- Jurassic 201.2 - 145 – dinosaurs, early birds, early mammals, ferns
- Cretaceous 145 - 66 – marsupials, angiosperms

Cenozoic (12.2%):

- Paleogene 66 - 23.03 – flowering plants, primates, bats
- Neogene 23.03 - 2.588 – Hominidae
- Quaternary 2.588 - 0 – mammoths, ice ages, human beings

Illustration of these periods

Lets relate the "lifespan" of our planet to one single earth day. If the origin of Earth 4600 mya starts at 00:00, it is not until about 21:45 that the first winged insects appear. The first flying fish a bit later. The first birds and the last pterosaurs around 23:00. Gliding mammals may be found around 23:35. That is to say, the protagonists of this book have been living in the last $2\frac{1}{4}$ hours before midnight. (As a side note: According to this time scale, *Homo sapiens* do not appear until 3.6 seconds before midnight.)

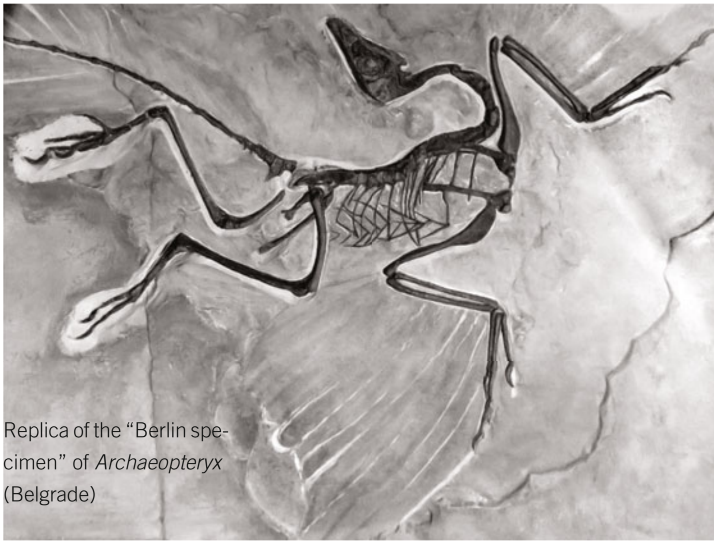


Only a tiny fraction of all animals survives

A billion animal and plant species are believed to have arisen (and largely gone extinct) at one time or another since the beginning of the Palaeozoic 541 mya. A much greater number of animal skeletons must have been "produced" in the process, which begs the question of what circumstances can prevent the complete decomposition of a living being's body after its death so that components, forms or structures of that body are retained: To date, more than a hundred thousand fossil species have been scientifically documented, but this represents only a tiny fraction of all animal remains that are "fossilized" (or using a broader term, "petrified", i.e. mineralized). Fossils are primarily found in sedimentary rocks (formed by the deposition of material at the surface of the Earth or under water).

When does "fossilization" succeed?

Bird skeletons, such as the ones pictured on this page, can survive intact or virtually intact for relatively long periods of time (at the top a bird skeleton when it was first found and on the right the same skeleton half a year later). However, in the long run, these skeletons will completely disappear as they are exposed to the effects of weathering. In this book, we will occasionally make reference to real fossils, such as the famous primeval bird *Archaeopteryx* (as an example of the "missing link", cf. p. 166) or relatively rare forms of organisms preserved in their original form in amber (cf. pp. see page 55f. and see page 41f.). Fossilization can only occur if the animal body is protected from further decomposition. So the dead remains must have been washed away to oxygen-free zones at the bottom of the Jurassic sea or they must have sunk into an oil-rich swamp (as it occurred to the numerous fossils found in the Messel pit near the German city of Darmstadt). The remains could then have been encased by showers of fine sedimentary lime particles or, at a later geological period, become embedded in oil shale, where they were eventually "petrified" with increasing pressure.



Replica of the "Berlin specimen" of *Archaeopteryx* (Belgrade)

Relative and absolute age dating

As an obvious "rule of thumb", the oldest layers of undisturbed sedimentary rocks can be found at the very bottom and the youngest layers at the top. Thus it is possible to categorize fossils in one layer in relation to those found in another layer. The long half-life of certain elements, such as uranium, thorium, and potassium, allows the absolute age of such rock layers to be determined.

Evolution – a constant process

Evolution – or: How do phylogenetic changes occur?

Evolution is defined as the change of organisms over time. It was recognized very early on that plants and animals had undergone a variety of such changes without knowing what had triggered these changes. It was recognized that offspring differed from their parents and that changes in any one generation are small compared to the differences observed across species. However, it was not until Darwin that the question of what triggered these large-scale changes between species could be answered. Darwin's theory of natural selection provides a causal explanation of how evolutionary change can occur.

Natural selection: Consequences for genetic composition

Natural selection is basically the difference in reproductive success when comparing two individuals from the same species. If this difference is not based on mere coincidence but on the fact that those individuals that are better suited to their environments produce more offspring than the other individuals of the same species. If this behaviour is heriditary, it will have consequences for the genetic composition of the next generation. So, this reproductive advantage, also known as 'fitness', must be hereditary.

Phylogenetic changes

Darwin's theses

In 1859, Darwin set out several theses regarding changes in organisms over time:

- Evolution means the changes that occur within populations of organisms over time. These changes are facts and not theories.
- These evolutionary changes occur in small steps. The extent of these steps can be correlated with the difference between parents and their offspring.
- A rise in the number of species results from the splitting of phylogenetic lineages, which occurs in addition to the evolutionary changes within those lineages.
- The mechanism underlying these phylogenetic changes is the process of natural selection, which Darwin defined as opposed to 'artificial selection' in the breeding of pets and agricultural crops.
- All organisms have descended from one common ancestor. The diversity of organisms is due to phylogenetic developments that have taken place over millions of years following the chemical evolution that has led to the origin of life. Hence, all organisms are related to one another.

The image shows a male *Neurothemis terminata*, a relatively large Southeast Asian dragonfly. Dragonflies already existed in the Carboniferous (especially "giant dragonflies" with a wing span of 72 cm) and they have barely changed since then. Not all dragonflies in the Carboniferous period were giants. Some of them were of "normal size". The giant size of the early dragonflies is sometimes believed to have been due to the higher levels of oxygen in the air (this would also apply to other insects during that period). However, some 150 mya ago, dragonflies seem to have become smaller in size without any significant decrease in oxygen levels. An alternative explanation could be that, with the appearance of the first birds, smaller species of dragonflies began to have an advantage as their larger and slower peers fell prey to birds.

All life comes from the sea

The Galápagos Islands have a strong historical connection with Charles Darwin. This photograph shows the famous rock formation known as “Darwin’s Arch”, situated near Wolf Island.

Below you can see the aquatic life that resides in these waters: a group of eagle rays (*Aetobatus Narinari*) in the foreground, a great hammerhead (*Sphyrna mokarran*) in the back.
All life on this planet began in the sea. The oldest known vertebrates date from the early Ordovician of about 450-470 million years ago. Cartilaginous fishes (rays, sharks) first appeared during the transition from Silurian to Devonian some 420 million years ago. It is no coincidence that the sight of swimming rays may trigger associations with flying. Leonardo da Vinci once said: “Observe the swimming of the fish in the water and you can understand the flight of the bird in the air.”

"Missing links"

Palaeontological evidence

During Darwin's lifetime, evidence to support his theses could be already obtained from palaeontology. Layers of rock serve as windows of time from the past, which can be precisely dated by means of modern methods. Clearly, only the most primitive organisms can be found in the older (earlier) layers of rock. Remains of the earliest vertebrates appear in later (younger) layers and birds and mammals even later.

Vertebrates at a later point in evolution

Even during Darwin's lifetime, these rock layers served as evidence to support that vertebrates had evolved after invertebrates, that birds had not appeared until the different groups of dinosaurs had already established themselves, and that such datable fossils could be used as conclusive evidence of evolution.

The first "missing link"

The discovery of the first primeval bird (*Archaeopteryx*) came in quite handy, as Darwin claimed that there had to be so-called "missing links" for his theses about evolution and natural selection, according to which major animal groups did not evolve independently but are united by connecting links, to hold true. Numerous such connecting links have since been discovered and can thus no longer said to be "missing links".

Scientifically verifiable opposition

Darwin's theses were and continue to be a scientifically verifiable opposition to creation myths, such as the Biblical Genesis and numerous other myths from around the globe, which hold that all species are the product of an individual creation event and have remained constant ever since. These claims have sparked a debate that continues to this day and has relatively little to do with science.

Establishment of the theory of natural selection

Breeders of animals and plants during Darwin's lifetime already knew that changes in traits could be attained by means of selective breeding. They would breed until, by chance, they managed to produce individuals that displayed the desire traits. That is, breeders would wait fo so-called "hot spots" to appear among their "samples" and then use these "hot spots" with the desired traits for further breeding. It is now known that these "hot spots" were actually mutations, i.e. heritable changes in an organism's reproductive cells. Through ongoing selection from one breeding cycle to the next, breeders gradually managed to attain their desired traits. Darwin assumed that similar mechanisms could be found in nature.

The *Archaeopteryx* constitutes a significant connecting link in the evolutionary lineage from feathered dinosaurs to present-day birds. However, as long as these connecting links are not known, that is, as long as they are still missing links, we can do no more than formulate hypotheses. The discovery of the *Archaeopteryx* thus not only revealed a prominent connecting link, but has also given support to the idea that birds have evolved from dinosaurs.

"Survival of the fittest"…

Differences in reproductive success

Since Darwin, natural selection has explained the difference in reproductive success that can be observed among individuals of a population and that depends on their genetic quality or fitness. This reproductive difference is, hence, no mere coincidence, but the consequence of these individuals' genetic constitution, and it will also have an effect on the genetic structure of a natural population's future generations. Those individuals that produce more offspring contribute to increasing the number of individuals that carry the more suitable genetic material. Since populations tend to remain constant in size, the proliferation of one kind of individuals necessarily implies the gradual disappearance of others that produce fewer offspring. That is to say, successful mutants gradually replace the less successful ones.

"Survival of the fittest"

Darwin referred to this as the "survival of the fittest" or "struggle for life". This survival of the fittest is not about animals fighting tooth and nail for survival, but a competition for reproductive success. So, rather than actual fighting, there is a competitive trial of strength. The winners are, for instance, those individuals that could run away from a cheetah as opposed to those that could not. The same principle applies to the cheetah, of course. Those cheetah that are faster than their prey are more successful in raising their offspring. Put very simply, this means that only the winners or the group of winners can successfully reproduce. It is usually enough for this group to produce more offspring than the others, and among their offspring it is once again only the fastest that survive as winners.

Selection based on environmental factors

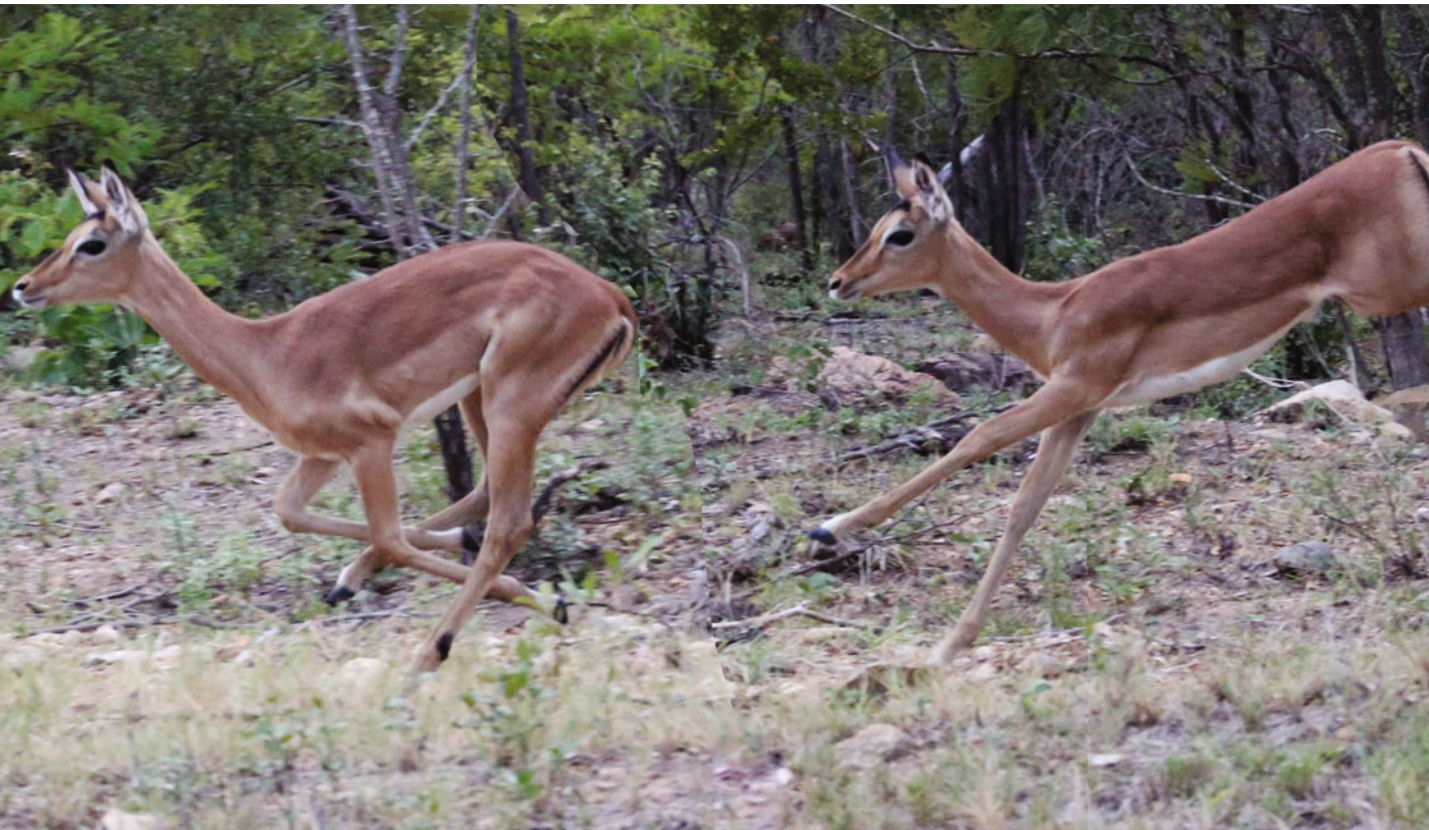
The process of selection that is artificially guided during breeding by human beings is carried out in nature through the environment. This natural environment consists of so-called biotic and abiotic factors. Abiotic factors include, for instance, temperature and humidity. Biotic factors are based on the relationship between organisms living in this environment (particularly, their competition for resources).

Selection only occurs with genetic variation

Natural selection can only occur or be effective if the individuals of a population are not the same and differ in their genetic qualities. One 'trick' of nature that introduced such variation in the early history of living organisms was the invention of sexuality based on the division into two different genders that are joined in the reproductive process of meiosis (reduction division).

Rearranging the parental chromosomes

Meiosis is a special type of cell nucleus division, and it differs from the more common type of cell nucleus division, known as mitosis, in that the number of chromosomes is reduced by half. This implies a rearrangement, i.e. a new combination of the paternal chromosomes. The results of this type of cell division and the rearrangement



of the genetic material are the germ cells or gametes.

Each individual is genetically unique

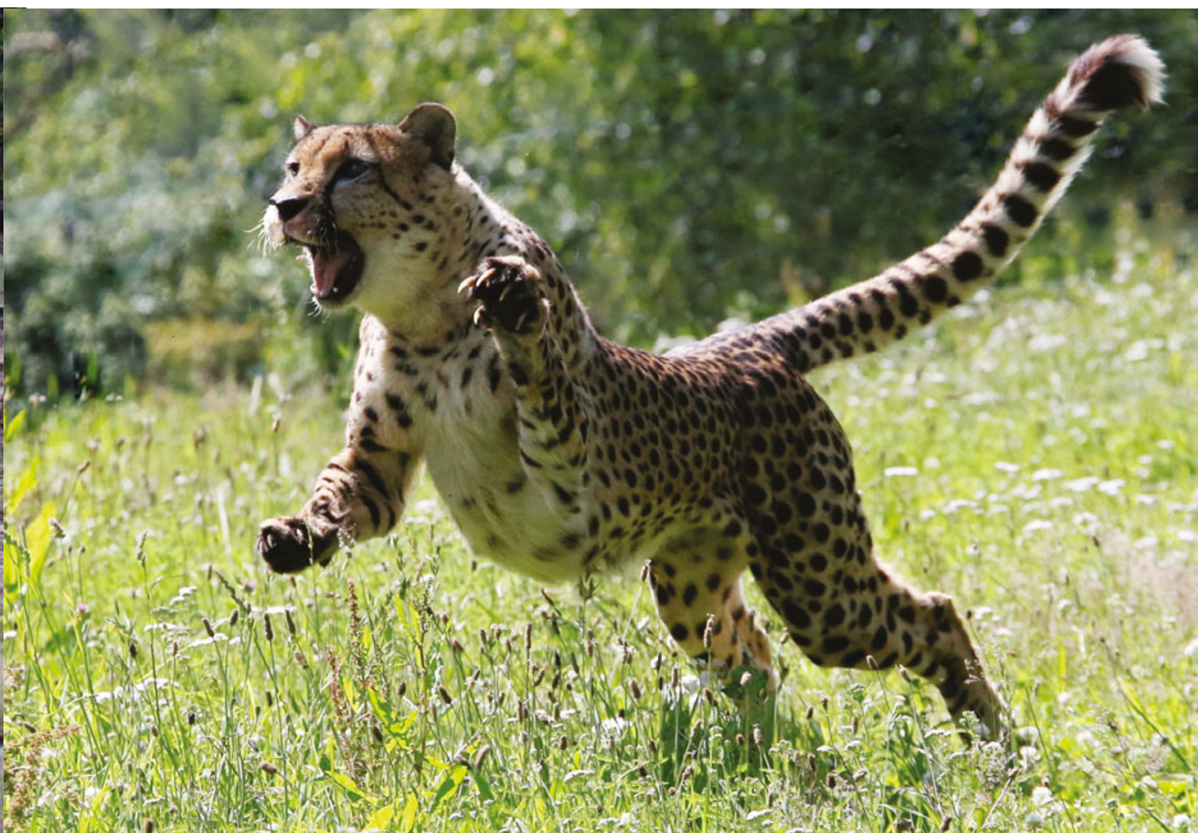
Such cell nucleus division allows infinite possibilities of genetic variability. This shall be illustrated by means of a very simple example. Each individual is genetically unique. In order to see this, one only needs to look at us human beings. No individual is like another. Each individual has his or her own finger print. Thus in simple genetic terms, each individual is a separate and unique genotype. An example of a gene (1 locus) with one allele will yield 3 different genotypes among the offspring, which can be labelled as AA, Aa, and aa. Out of these three genotypes, two are homozygous (AA and aa) and one is heterozygous (Aa). A stands for dominant, a for recessive traits. So, for n genetic loci, there are 3^n genetically different individuals.

Exponential growth

That is, for $n = 20$ there are several billion genetically different individuals and for $n = 30$ more than 200 trillion. However, each individual consists of at least 1000 heterozygous genetic loci, which could yield 3^{1000} genetically different offspring. Since this number is so inconceivably great, it is reasonable to define the probability of two individuals being genetically identical as zero. Similar observations can be made with regard to the sorting of alleles. Two alleles per genetic locus yield 2^{1000} possible combinations of how these alleles can be arranged during reductive division, that is, before the production of sperm and ova. This number, too, is practically infinite. Each sperm, each ovum is genetically unique. All this taken together points to a source of practically infinite possible variations. If we take genetic mutations into account, the number of possible variations will increase even further. So, natural selection draws from a practically inexhaustible source of genetic diversity.

The opposite of chance, albeit a statistical process

The products of natural selection, that is, those individuals with more offspring than others within the same population, are not a matter of coincidence. It could be said that natural selection is actually the very opposite of coincidence. Still, natural selection is a statistical process, in which, as in a game of dice, individual cases cannot be said to be meaningful. In this process, merely the range of genetic variants is based on chance. It is impossible to predict which alleles will combine during meiosis and if and what kinds of mutations may occur. Such phenomena are simply a result of coincidence. However, which of these variants will eventually assert themselves in the process of reproduction is no longer a matter of chance. So, claims that human beings are the product of mere chance in evolutionary history are based on a misconception of what natural selection is and how it works.



Flying squirrels …

When "the ability to fly" gives an advantage for survival …

When the possession of wings or organs for gliding gives an individual an advantage for survival, this will statistically lead to such individuals producing more offspring on average so that this trait is then further passed onto their descendants. If the evolutionary pressure to escape a predator is high, the possession of such organs is likely to assert itself quickly within a population, and it will also contribute towards the gradual improvement of these wings or gliding organs.

Flight organs determined by "parameters"

What kind of flight organs will evolve in this process is determined by various conditions and, of course, by the type of environment in which the organism in question lives. Physical laws provide a conditional framework channelling the evolution of wings and gliding organs, which are always subject to the laws of physics. Already existing limbs may also act as organismal preconditions in the evolution of wings, which are then adapted from these pre-existing structures.

The convergent evolution of wings in three vertebrates

This is what happened in the evolution of wings from pre-existing front limbs among vertebrates. Three groups of vertebrates convergently evolved such flight organs: pterosaurs, birds, and bats. Their wings, though very different in their respective structures, gave these three animals the ability to fly. The flight organs of winged insects, also known as Pterygota (a term derived from the Greek word for wing), have a whole different origin, and how these wings may have evolved is still up for discussion.

Gliding mammals existed long before bats

Gliding organs have also evolved in multiple ways independently from one another. Well-known examples are the approximately 37 species of flying squirrels (also known as Pteromyini; members of the family Sciuridae, to which regular squirrels also belong), with most species occurring in Southeast Asia and the Himalaya region. Two species can be found in South America and there is even one (*Pteromys volans*) that is common from Northern Europe to Japan. Their size ranges from 7 cm (*Petinomys* and *Petaurillus emiliae* from North Borneo) to almost 60 cm (*Petaurista petaurista* from Southeast Asia), not counting the length of the tail. What they all have in common is a membrane of skin that attaches from the front legs to the hind legs and can be expanded like a sail. This extension of skin, which acts like a paraglider, allows them to jump from one tree branch to the next and to glide up to 100 metres, with their long tails providing stability during flight. Also worth mentioning is the insectivorous mammal (*Volaticotherium antiquus*), an ancient gliding mammal that actually bears no relation to the flying squirrel. This gliding mammal lived some 125 million years ago and reached a size of 12-14 cm. So this ancient animal could already be found flying across the air some 70 million years before the appearance of the first bats, but, like present-day flying squirrels, it glided rather than flew.

Nachtigall W. **Gleitverhalten, Flugsteuerung und Auftriebseffekte bei Flugbeutlern**
In: Nachtigall, W. (Hrsg.): Biona-report 5. Bat flight - Fledermausflug. 171 - 186. Akad. Wiss. Lit. Mainz, Fischer, Stuttgart (1986)

… and other gliders.

Rodents or marsupials – a convergent evolution towards gliding

Flying squirrels from the genus *Pteromys* and wrist-winged gliders from the genus *Petaurus* both glide by stretching the skin membrane between their front and hind legs. They look much alike, and with up to 20 cm body height and tails of similar length they are roughly the same size. Yet they are not directly related to each other, one being a rodent and the other a marsupial. According to studies, these animals can reach a gliding distance of at least 1.5 m with 1 m of height loss. So, their glide ratio would be no more than 1.5. However, from television films, we have also gathered evidence for significantly higher (better) gliding ratios. These animals can regulate their gliding flight by changing the curvature of the gliding membrane or moving their tails, which allows them to jump from one tree trunk, land on another and then climb up again.

Gliding reptiles

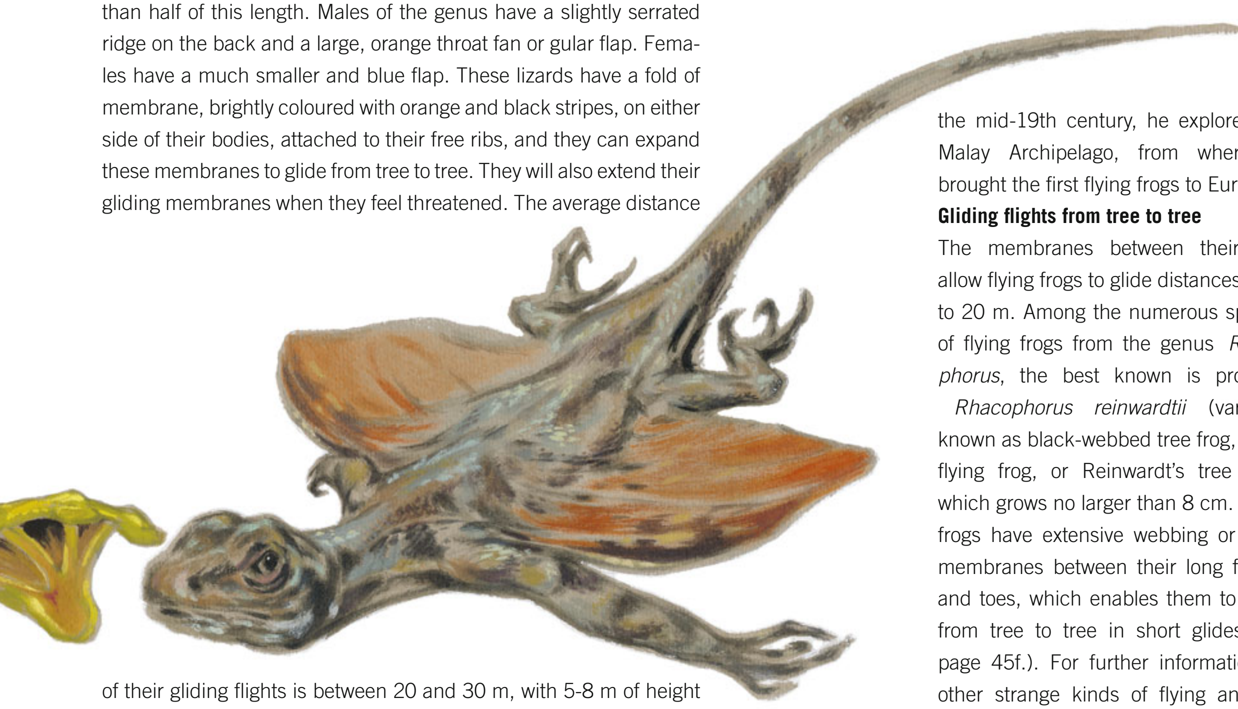
The flying dragons or gliding lizards from the genus *Draco*, with around 42 species distributed across Southeast Asia, are also gliders. They are members of the family Agamidae (lizards). They can reach a length of over 20 cm, with their thin tail accounting for more than half of this length. Males of the genus have a slightly serrated ridge on the back and a large, orange throat fan or gular flap. Females have a much smaller and blue flap. These lizards have a fold of membrane, brightly coloured with orange and black stripes, on either side of their bodies, attached to their free ribs, and they can expand these membranes to glide from tree to tree. They will also extend their gliding membranes when they feel threatened. The average distance of their gliding flights is between 20 and 30 m, with 5-8 m of height loss. The maximum distance, however, can be up to 60 m. By twisting its tail, the flying draco lizard can control the stability of its flight. The movement of its tail and gliding membrane also allows the lizard to target specific destinations and avoid obstacles midglide. The fossil of the Cretaceous iguanians lizard, *Xianglong zhaoi*, in China, which is also believed to have used membranes stretched across elongated ribs for gliding, points to another example of convergent evolution.

Other gliding reptiles …

A different form of gliding has been developed by 8 species of flying geckos from the genus *Ptychozoon*, which are endemic to Southeast Asia. Flying geckos are lizards with flattened bodies that may reach a length of 20 cm. Their tail is almost as long as their trunk. These reptiles are characterized by flaps of skin that grow from their flanks, head, tail, and limbs, as well as webbing between their toes. These skin membranes serve as sails and allow these lizards to travel short distances by gliding. Flying geckos even have the capacity to change direction during flight. They also have broad flattened toe pads equipped with adhesive lamellae.

Flying frogs

Some frog species from the genus *Rhacophorus* found across Southeast Asia have also developed something akin to flying membranes between their toes. Wallace's flying frog (*Rhacophorus nigropalmatus*) in Southeast Asia is named for the British biologist Alfred Russel Wallace. He was a contemporary and rival of Charles Darwin, and in the mid-19th century, he explored the Malay Archipelago, from where he brought the first flying frogs to Europe.



Gliding flights from tree to tree

The membranes between their toes allow flying frogs to glide distances of up to 20 m. Among the numerous species of flying frogs from the genus *Rhacophorus*, the best known is probably *Rhacophorus reinwardtii* (variously known as black-webbed tree frog, green flying frog, or Reinwardt's tree frog), which grows no larger than 8 cm. Flying frogs have extensive webbing or flying membranes between their long fingers and toes, which enables them to travel from tree to tree in short glides (see page 45f.). For further information on other strange kinds of flying animals, turn to pages f.

Dudley R.,Byrnes G., Yanoviak S.P., Borrell B., Brown R.F., McGuire J.A. **Gliding and the Functional Origins of Flight: Biomechanical Novelty or Necessity?** *Annual Review of Ecology, Evolution, and Systematics Vol. 38: 179-201 (2007)*

Emerson S.B., Koehl, M.A.R. **The Interaction of Behavioral and Morphological Change in the Evolution of a Novel Locomotor Type: ``Flying'' Frogs** *Evolution 44 (8), 1931-1946 (1990)*

The largest flying animal of all time

Quetzalcoatlus – "the feathered serpent"

Nowadays, birds, insects, and bats (i.e. mammals) may be regarded as the rulers of the air. In the Jurassic period, however, ancient birds such as the famous *Archaeopteryx* and similar species were only starting to fly. Back then, and well into the Cretaceous period, the air was dominated by reptiles, more specifically by giant pterosaurs, among those the *Quetzalcoatlus northropi*, which, with a wing span as large as 12 m, is considered the largest flying animal to have ever lived.

Jumping upwards from cliffs, standing helpless on plains?

It was assumed that the biggest pterosaurs could only launch themselves by jumping from cliffs. So, if one of them had landed on a plain, it would not have been able to fly up again. However, more recent studies show that these pterosaurs could use their front wings as a pair of front legs. Compared to the wings of birds, the limbs of these pterosaurs were relatively strong.

Or did they launch themselves off "by jumping"?

It is more likely that pterosaurs launched themselves into flight by pushing themselves off the ground *with their four legs*, similar to what flies do with their middle and hind pairs of legs. They must have jumped to great heights to prevent their wings with the delicate membranes from hitting the ground when they started to flap.

Zakaria M.Y., Taha H.E., Hajj, M.R. **Design Optimization of Flapping Ornithopters: The Pterosaur Replica in Forward Flight** *doi: 10.2514/1.C033154 Engineering Science and Mechanics, Virginia Tech, Blacksburg, Virginia (2015)*

On all fours as tall as a giraffe

Launching against the wind, and ideally on steep ground

To jump that high, these pterosaurs needed a strong headwind. If they launched from steep ground, against the wind, they might have been carried as high as large albatrosses, which sometimes struggle to take flight, are observed to do now. For pterosaurs, this struggle may have been eased by their body weight of around 100 kg, which was relatively low in relation to their wing span (believed to have reached up to 13 m).

Like “flying wings”

So, the trunk of these giant pterosaurs was relatively small compared to their giant wing surface, which invites a comparison to flying wing aircrafts, which have no fuselage in the conventional sense. Which is also what their species name, *northropi*, alludes to: J.K. Northrop became famous as a pioneer of the flying wing design. The giant pterosaur was discovered relatively late. In 1971, a student dug up the first fossilized remains of this ancient animal’s wings. Since then, the *Quetzalcoatlus* has been extensively studied and recreated as a model by both palaeontologists and fluid mechanics. Their studies suggest that this pterosaur could fly by flapping its wing, but that it primarily travelled through the air by gliding. Similar to some of the largest flying birds today, such as condors and vultures, the Quetzalcoatlus was probably prone to taking advantage of upslope winds and thermals.

Witton M.P:, Naish D. **A Reappraisal of Azhdarchid Pterosaur Functional Morphology and Paleoecology** *LoS ONE 3(5): e2271.doi:10.1371/journal.pone.0002271 (2008)*
http://www.dinosaurier-info.de/dinothek/pdf_a/2008/001_journal.pone.0002271_di.pdf

Flying Fish

Flying fish

Also worth mentioning as a conclusion to this chapter are "flying fish". The most famous species of flying fish is the *Exocoetus volitans*, reaching a length of about 25 cm. Powerful tail strokes allow flying fish to jump out of the water. They then extend their elongated pectoral fins, with which they are capable of gliding up to several dozen metres above the water surface. They reach "heights" ranging from 1 to 10 m. Flying fish can thus escape many of their predators.

Hertel, H. **Biologie und Technik. Struktur-Form-Bewegung** *Krausskopf, Mainz (1963)*