Prof. Dr. Klaus H. Hoffmann

Have no Fear of Zoology

A stroll through the animal kingdom for teachers & students

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KLAUS H. HOFFMANN

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A STROLL THROUGH THE ANIMAL KINGDOM FOR TEACHERS AND STUDENTS

Have no Fear of Zoology: A stroll through the animal kingdom for teachers and students
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CONTENTS

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His research in entomology, animal physiology and molecular ecology resulted in 160 original publications, 46 reviews, book contributions and three books. Prof. Hoffmann is an Associate Editor of the journal "Zeitschrift für Naturforschung C (Biosciences)". Since 2015, he has been a Senior Expert of the Senior Expert Service (SES) in Bonn.

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1 OBJECTIVES

Zoology is the science of animals. Zoological questions are addressed not only by researchers of standard zoological disciplines (e.g. taxonomy and systematics, morphology and anatomy, developmental biology, physiology and neurobiology, ecology), but also in related disciplines such as microbiology, genetics, cell and molecular biology as well as in biochemistry and medicine.

For example, when biochemists or physicians work with cell cultures, they often use insect cell lines. Techniques of cell and molecular biology and molecular genetics used in human medicine have frequently been first developed in experiments with invertebrates. An example of this is the method of RNA interference. In the area of improved animal protection, many test methods in the field of pharmacology and environmental protection, are carried out with invertebrates. For example, organisms of the zooplankton are used as bio-indicators for water pollution.

Microbiology includes protozoology, that is, the study of single-celled eukaryotic organisms (organisms with a nucleus). The fruit fly *Drosophila* is one of the most important model organisms in genetics. Recently, attempts have been made to use so called secondary substances from invertebrate animals, especially from marine organisms, for drugs and antibiotic in human and veterinary medicine.

After an introduction into the animal system, this book presents the most important animal groups in 15 chapters and shows their importance for scientists and physicians. The physiology and biochemistry of animals is discussed as well as their economic importance and their importance in their ecosystem. The book concept is based on two lecture series "Biology for Medical Students" and "Zoology for Biochemists", which were offered for studies in human medicine at the University of Ulm (1978 to 1994) and biochemistry at the University of Bayreuth (1994 to 2012). The book is also suggested for teachers of biology at all school levels, as well as students of veterinary, forestry and agricultural sciences or biotechnology.

Each chapter starts with a short presentation of the learning objectives and a keyword index of relevant terms and includes review questions that enable readers to test their own acquired knowledge. Suggested solutions for the review questions are found at the end of the book. Naturally, no claim to completeness can be made for any chapter. References to specific literature are given only in a few cases. For further information refer to a selection of up-to-date textbooks of zoology. Some pictures were modified from these textbooks and served as a source for the illustrations in this book.

- Peter W. Hochachka and George N. Somero: Biochemical Adaptation. Princeton University Press, Princeton, New Jersey 1984.
- Charles F. Lytle and John R. Meyer: General Zoology Laboratory Guide. 16th Ed. McGraw-Hill, New York 2012.
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- Cleveland P. Hickman, Larry S. Roberts, Susan L. Keen, David J. Eisenhour, Allan Larson, and Helen l'Anson: Integrated Principles of Zoology. 16th Ed. McGraw-Hill, New York 2017.
- Frederic H. Martini, Judith L. Nath and Edwin F. Bartholomew: Fundamentals of Anatomy & Physiology. 11th Ed. Pearson Education International, San Francisco 2017.

In many, if not all zoological articles, the free encyclopaedia Wikipedia is a good guide: https://en.wikipedia.org/wiki/Zoology. Moreover, the online Khan Academy Biology is recommended: https://www.khanacademy.org/science/biology. However, online encyclopaedias should be generally viewed critically.

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2 EVOLUTION, SYSTEMATIC ZOOLOGY AND THE ANIMAL CELL

2.1 LEARNING OBJECTIVES AND KEYWORDS

The chapter introduces the evolution of organisms, shows the systematic classification of the animal kingdom and presents the structure and function of an animal cell.

- Species, race, allopatric and sympatric species formation, adaptive radiation
- Phylogeny, homology, homonomy, analogy, convergent development
- Plesiomorphy, apomorphy
- Cladogram, monophyletic, paraphyletic, polyphyletic
- Selection, mutation
- Archaea, Bacteria, Eukaryota, Protozoa, Metazoa, Protostomia, Deuterostomia, Bilateria, Ecdysozoa, Lophotrochozoa
- Unit-membrane, diffusion, carrier transport, cytosis, centrioles and centrosomes, endosymbiotic theory.

2.2 SPECIES, THE BASIC UNIT OF LIVING ORGANISMS

Characteristics of animal life are inter alia growth and reproduction, self-movement, metabolism with heterotrophic nutrition, stimulus perception and stimulus processing as well as behavior (instinct and learning). Animals are **heterotrophic organisms** depending on organic substances of other organisms for nutrition.

More than 1.5 million animal species are currently listed, with a further 10 to 30 million species living on the planet. More than 50 percent of all known animal species are insects.

The term "species" refers to a group of organisms (taxon) which are similar in morphological, biochemical and genetic characteristics. Populations that live in the same area of distribution are mutually fertile and reproductively isolated from individuals of other species. New species arise within a habitat by **geographical isolation** (**allopatric**) or by **endogenous barriers** (**sympatric**) (Figure 1).

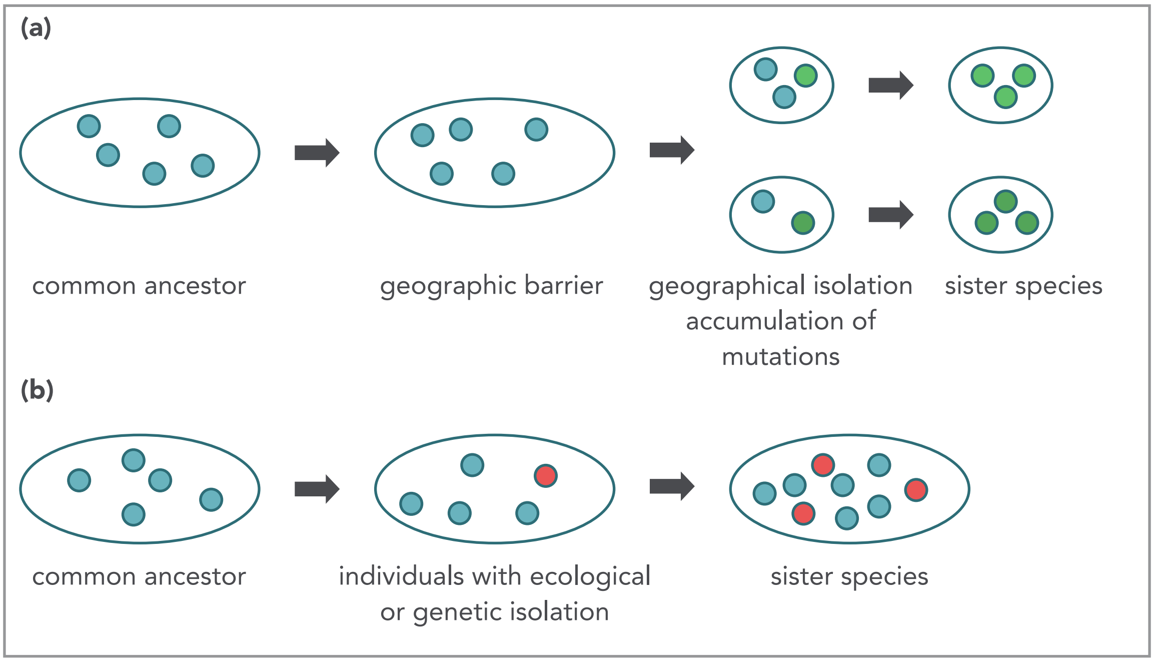

Figure 1: The two types of new species formation, allopatric (a) and sympatric (b). After Munk, Ökologie-Evolution, Thieme, Stuttgart 2011.

The identification of animal species is regulated by internationally agreed rules, which are based on the work of the Swedish scientist Carl von Linné (1707–1778) (**binary nomenclature**). The first word of a scientific name (which is derived from Latin or Greek) denotes a genus, that is, a group of closely related species. The second term defines the species and is often based on a characteristic feature of the species. For example, the species name *Gryllus bimaculatus* describes the so-called two-spotted cricket (see Photo 16). The name of the species is followed by the name of the first describer and the year of the first description (*Gryllus bimaculatus* de Geer, 1773), sometimes abbreviated, e.g. (L.) for Linnaeus (Linné). Species names are written in italics in a scientific text. Subspecies have a third name, so they are called trinominal.

Biological species are grouped into higher groups (genus, family, order, class, phylum, and kingdom) in the biological system (Table 1), but also into subspecies, varieties or cultivation forms. The term "race" is also used as a subdivision designation within species.

The individual development of the organisms is called **ontogenesis**, and their ancestral tree is called phylogenesis.

Kingdom (Regnum)	Animalia	Animals
Phylum	Chordata	Chordates
Subphylum	Vertebrata	Vertebrates
Class (Classis)	Mammalia	Mammals
Subclass (Subclassis)	Eutheria	Placentals
Order	Primates	Primates
Suborder	Anthropoidea	Higher primates
Family	Hominidae	Hominids
Genus	Homo	Humans
Species	*Homo sapiens*	"wise man"

Table 1: Example for the taxonomic categories for the classification of humans, *Homo sapiens*.

2.3 SPECIES FORMATION AND ADAPTIVE RADIATION

In the **allopatric** species formation (Figure 1), geographic barriers such as mountains, deserts or water between islands and mainland can separate species, so that the subpopulations arise in separated areas, i.e. in **allopatry**. An example of allopatric species formation is the occurrence of two species of squirrels (*Ammospermophilus harrisii* and *A. leucurus*) in the Grand Canyon (USA).

There are several possibilities for the **sympatric** species formation (Figure 1), i.e. the emergence of new species in the area of the species of origin:

- Spontaneous genetic isolation of individuals within a population.
- Transition from bisexual to parthenogenetic (single-parent) reproduction by mutation.
- Species bastardization between closely related species.
- Spontaneous polyploidy (more than two sets of chromosomes per cell).

For example, the tetraploid tree frog species *Hyla versicolor* emerged from the hybridization of a diploid eastern and a diploid western species *Hyla chrysoscelis* in the southeast of the USA.

Strong sexual selection and special habitat annidation (ecological species formation) can also lead to a sympatric species formation.

In the case of **adaptive radiation**, several new species are formed from an ancestral form by annidation into different ecological niches in a geologically short history. One example of adaptive radiation is the fourteen species of Darwin finches, which today are found on the Galapagos Islands and are derived from a common ancestor. They differ primarily in their beak shape, indicating their different ways of obtaining food.

2.4 SYSTEMATICS OF THE ANIMAL KINGDOM AND THE FORMATION OF A PHYLOGENETIC SYSTEM

In the beginning, the evaluation of relationships between different species used only morphological or anatomical criteria. Today, ontogenetic criteria such as embryonic development, and, in particular, molecular characteristics (matchings of proteins and gene sequences), and fossils, play an important role in the assessment of relationships.

Homology is defined as any similarity between structures of organisms in different taxa that is derived from similar structures in their shared ancestry. To verify homologies, the characteristics are assessed according to three criteria: **criterion of position**, **criterion of specific quality** and **criterion of continuity**. Only if the similarities between organisms are homologous (and not analogous, see below) can these characteristics be used for kinship analyses. Homologous are for example the swim bladder of fish and the lung of terrestrial animals. In homologous traits with a common phylogenetic origin there can be a change of function.

Non-homologous features with the same function are termed **analogies** and have no meaning for systematic classification. Examples of analogous structures are the lens-type eyes in cephalopods and in vertebrates, or the wings of insects and birds. Homologous and non-homologous structures which have developed into (morphologically) similar structures as an adaption to the environment are termed **convergent** developments and likewise have no significance for systematic classification.

The usual presentation of the phylogeny of organisms and their relationship to each other in dichotomous branches (cladograms) reflects the identification of monophyletic groups via **synapomorphy** (shared possession of a derived feature in sister taxa). The characteristics of a **monophyletic** group (Figure 2a) are that the taxa go back to a common ancestor (parent type) and all descendants of this parent type are contained within this group. Improper classifications are for example systematic groups which are not all progeny of a parent species (**paraphyletic** groups; Figure 2b), or which are from different ancestral species (**polyphyletic** groups; Figure 2c).

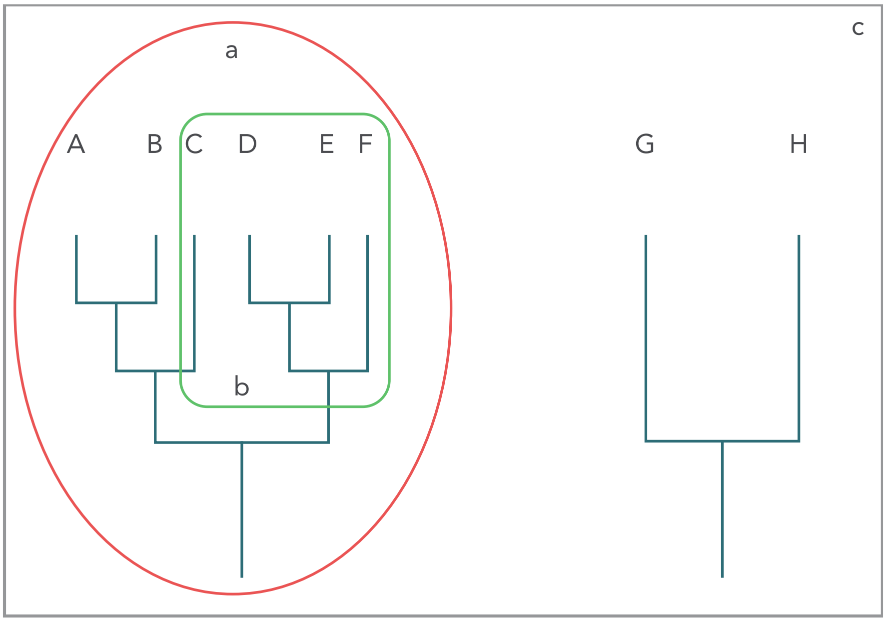

Figure 2: Phylogenetic relationships between different taxa (A to H): monophyletic (a, red circle), paraphyletic (b, green border) und polyphyletic (c, grey border).

Synapomorphies represent a key element of phylogenetic systematics. Synapomorphies are derived characteristics that two taxa have in common because they occurred for the first time in their common ancestral species. If, for example, you want to clarify the relationships between the pigeon, the dog and the cat (vertebrates), the characteristic "fur" serves as a synapomorphy between dog and cat (mammals). Characteristics, which also occur within two taxa, but do not allow a statement for closer relationships, are called **plesiomorphies**. An example is the possession of feathers, which is not suitable for the establishment of relationships within the birds.

A **cladogram** in the strict sense is not equivalent to a tree of life (dendrogram), since only the branches of a tree of life reflect the lineages that occurred in evolution.

2.5 MECHANISMS OF EVOLUTION AND THE TREE OF LIFE (DENDROGRAM)

Biological evolution reflects the developmental history of living organisms, thus revealing the changes in gene sequences over generations. It is an approach to a scientific explanation for the origin and change of living beings in the course of the earth's history. Changes in the genetic material of living organisms can be caused by spontaneous point mutation, segment mutation, genomic mutation, horizontal gene transfer, sexuality, heterozygosity and gene coupling, as well as chromosomal crossing over in the meiosis, but also by environmental influences such as UV radiation or mutagenic substances.

The two fundamental theories for the explanation array of species in the animal and plant kingdoms were first suggested by Charles Darwin (1809–1882), and are based on the derivation of all organisms by modification of common ancestors (descent theory) and on natural **selection** among descendants (selection theory). In the case of an overproduction of offspring and hereditary variations among the offspring, selection of the best adapted to the environment leads to natural selection ("**survival of the fittest**"). Animals that are better adapted to environmental conditions have a higher fitness and are more successful in reproducing.

According to the current concepts, a cell without nucleus was the last common ancestor at the base of all living organisms. Its early progeny split into two prokaryotic (cells without nucleus) groups or domains, the **Bacteria** and the **Archae**a. From the latter, once called **Archaebacteria**, originated the **eukaryotes**, that is, all organisms with a nucleus. Early eukaryotes absorbed certain bacteria, which were retained as mitochondria and chloroplasts (endosymbiotic theory). These cell organelles are now used for energy production and photosynthesis. A fusion between Archaea and bacterial cells is also discussed. The oldest fossils of prokaryotes are about 3.5 billion years old, single-cell eukaryotes (Protozoa) originated about 2 billion years ago. Multicellular organisms (Metazoa) originated about 1.5 billion years ago, the oldest animal fossils are about 600 million years old (Ediacarium).

The first monophyletic dendrogram of organisms (Plantae, Protista, and Animalia) was designed by Ernst Haeckel in Jena in 1866 (Knoop & Müller 2009, p. 59). Based on changes in the body structure, four main branches were postulated in the dendrogram of the animals: the first division into **Parazoa** (animals without tissues) and **Eumetazoa** (animals with tissues), the separation into **Radiata** (radial symmetrical animals) and **Bilateria** (bi-symmetrical animals), the distinction of **Acoelomata** (without a body cavity) and **Coelomata** (with a body cavity), and the branching of the Bilateria into **Protostomia** and **Deuterostomia**. The rapidly increasing abundance of data from genome sequencing makes it necessary to constantly revise the phylogenetic classifications of animals.

Based on the sequence data of the 18S rDNA, hox genes, mtDNA, the myosin II gene and the arrangement of the mitochondrial genes, a tree of life of the animals was developed in 2004, which distinguishes three large groups within the Bilateria: Deuterostomia, **Lophotrochozoa** (Lophophorata and Trochozoa) and **Ecdysozoa** (animals with molting) (Wink 2006, p. 31) (Table 2). Deuterostomia include the echinoderms, hemichordates, and chordates. The Lophotrochozoa unite organisms with a lophophore (e.g., Bryozoa), with a trochophore larvae (e.g., annelids and mollusks), and other groups, e.g. the Plathelminthes. The Ecdysozoa unite all organisms with molting, e.g. the arthropods and nematodes. Within the Lophotrochozoa and the Ecdysozoa, however, there are still uncertainties in the arrangement of individual taxa. Equally unclear are the monophyly of the Porifera and the position of less well-studied groups, for example the Gastrotricha.

Regnum: Single cell "Animals" (Protista, **Protozoa**) (ca. 40,000 species)

Regnum: Multicellular Animals (Parazoa und Metazoa)

Phylum **Porifera** (sponges, Parazoa) (5,000 species)

Eumetazoa

Phylum **Cnidaria** (coelenterates) (1,000 species)

Bilateria

Protostomia (protostomes)

Lophotrochozoa

Phylum **Plathelminthes** (flatworms) – Acoelomata (20,000 species)

Phylum **Nemertini** (ribbon worms) – Acoelomata (900 species)

Phylum **Rotifera** (wheel animals) – Pseudocoelomata (2,000 species)

Phylum **Annelida** (segmented worms) (18,000 species)

Phylum **Mollusca** (mollusks) (13,000 species)

Ecdysozoa

Phylum **Nematoda** (round worms) – Pseudocoelomata (20,000 species)

Phylum **Tardigrada** (water bears) – (600 species)

Phylum **Onychophora** (velvet worms) (200 species)

Phylum **Arthropoda** (arthropods) (1,000,000 species)

Deuterostomia (deuterostomes)

Phylum **Echinodermata** (echinoderms) (6,300 species)

Phylum **Hemichordata** (hemichordates) (100 species)

Phylum **Chordata** (chordates) (55,000 species)

Table 2: The most important phyla in the animal kingdom
(only the phyla are listed, which are discussed in this book).

2.6 STRUCTURE AND FUNCTION OF THE EUKARYOTIC CELL

2.6.1 ORGANELLES OF THE EUKARYOTIC CELL

Eukaryotic cells have organelles and the region between organelles is compartmentalized. The structure and shape of eukaryotic animal cell is maintained by the cytoskeleton, which consists of microtubules, microfilaments, and intermediate filaments.

Cell organelles	Functional units (biomolecules)
Nucleus with nucleolus	Ribosomes (proteins, ribonucleic acids)
Mitochondria	Centrioles (microtubules; proteins)
Endoplasmic reticulum (ER)	Cell skeleton (proteins)
Golgi apparatus	Cilia and flagella (microtubules; proteins)
Lysosomes	
Peroxisomes	

Table 3: Cell organelles and units of function in an animal eukaryotic cell.

Cell organelles (Table 3, Figure 3) are usually surrounded by a membrane (bilayer lipid membrane, unit-membrane). The cell nucleus, mitochondria and chloroplasts (plant cell) likewise have a double membrane.

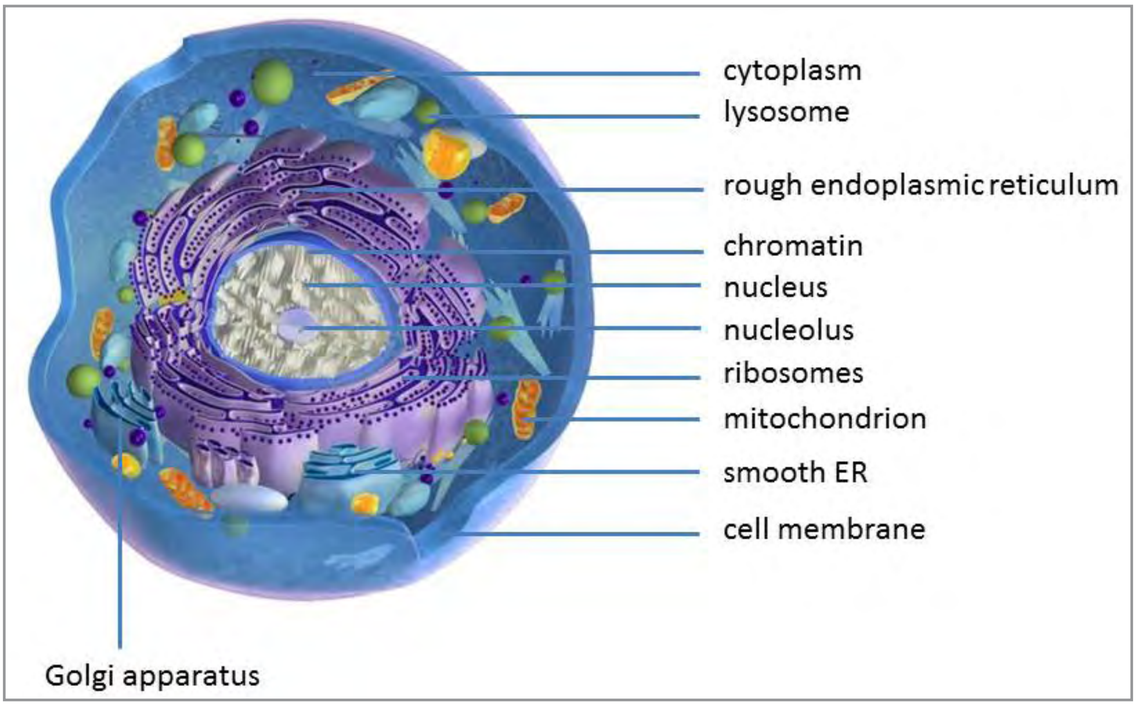

Figure 3: Structure of an animal cell (Clipdealer GmbH, Munich, Germany).

2.6.2 FUNCTIONS OF THE CELL ORGANELLES

The cell **nucleus** contains DNA (deoxyribonucleic acid). During cell division (mitosis and meiosis) the DNA condenses and can be visualized in the form of chromosomes, and after replication and cell division the DNA is separated into the daughter cells. Replication (amplification of DNA) and transcription (synthesis of RNA) take place in the cell nucleus. The **nucleolus** can be distinguished by its rDNA as a precursor of the ribosomes. The **mitochondria** also contain DNA (mtDNA). The main task of the mitochondria is the production of chemical energy in the form of ATP (adenosine triphosphate).

The **endoplasmic reticulum** (ER) serves important function with regard to signal transmission. The **ribosomes** are located on the rough ER and represent the site of protein biosynthesis (**translation**). The smooth ER is involved in the degradation and removal of harmful end products of the cell metabolism. Enzymes of the smooth ER are involved in the synthesis of various lipids (including steroid hormones). The task of the Golgi apparatus, which is closely connected with the ER, is to form vesicles in which proteins are transported. The endoplasmic reticulum also divides the cell cytoplasm into compartments.

In the **peroxisomes** there are more than 50 different oxigenases, enzymes responsible for the oxidative degradation of organic compounds (cell detoxification). **Lysosomes** contain digestive enzymes in a mostly acidic pH range, which digest both foreign and cellular molecules (biopolymers) into monomers.

An electron-dense (EM) cytoplasmic region near the nucleus is called the **centrosome**, which contains the paired **centrioles**. Centrosomes are microtubule-organizing centers (MTOC) and organize the mitotic spindle in cell division in most animal cells. Plant cells usually do not contain centrosomes. **Cilia** and **flagella** are cytoplasmic protuberances of the plasma membrane and contain cytoskeletal elements (9 + 2 arrangement of microtubules, see Figure 4). They are used primarily for movement of the cell or surrounding fluids.

2.6.3 CELLULAR TRANSPORT SYSTEMS

The compartmentalization of the eukaryotic cell by membranes creates separate and independent reaction spaces in the cell, but makes transport of nutrients, chemical messengers, etc. more difficult. Cellular transport mechanisms across membranes include passive and facilitated **diffusion, active (carrier) transport** for smaller molecules, and **pinocytosis** or **phagocytosis** (exo- and endocytosis, transcytosis, vesicle transport) for fluids and for larger molecules. Active transport mechanisms require chemical energy (ATP). Transport can then take place against a concentration gradient, whereas diffusion can only take place in the direction of a concentration gradient.

2.7 REVIEW QUESTIONS

1) What are the causes of changes in the genome of an organism during its biological evolution?
2) Describe the system of the Linné-based naming of species.
3) How do monophyletic, paraphyletic, and polyphyletic taxa differ from each other?
4) Which biomolecules are involved in the construction of the ribosomes and what is the function of the ribosomes?
5) What mechanisms of cellular transport are possible against a concentration gradient?

3 PROTOZOA / PROTISTA

3.1 LEARNING OBJECTIVES AND KEYWORDS

In this chapter unicellular organisms with a nucleus are presented, some of which have animal and plant features. They already have important characteristics of animal life, such as heterotrophic nutrition, self-movement, or sexual reproduction. Many Protozoa can cause serious diseases in humans as parasites.

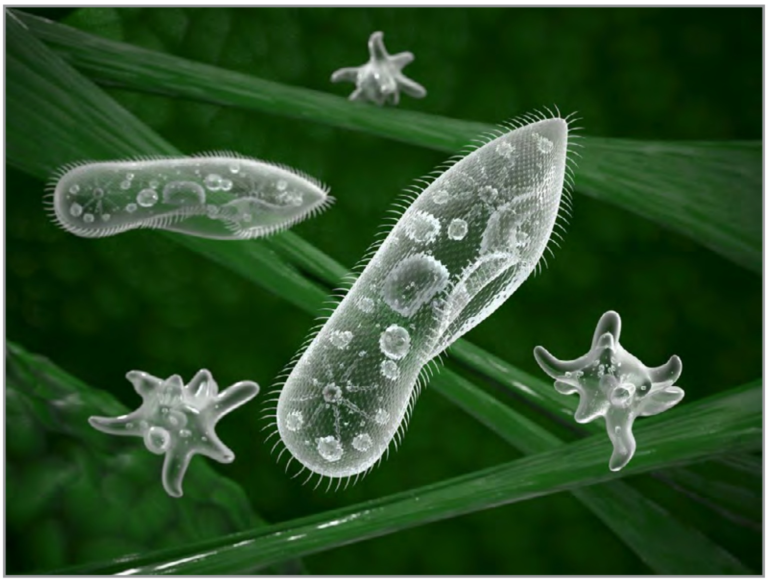

Photo 1: Representatives of Protozoa, *Paramaecium* und *Amoeba* (Wire_man / Shutterstock.com).

- Choanozoa, Amoebozoa, Archaeplastida, Chromalveolata, Rhizaria, Excavata
- Pseudopods: lobopods, filopods, axopods, rhizopods
- Mechanism of amoeboid movement and locomotion with cilia and flagella
- Hologamy, merogamy, isogamous, anisogamous, homophasic and heterophasisic alternation of generations
- Trypanosomes and *Plasmodium* (Apicomplexa).

3.2 CHARACTERISTICS AND SYSTEMATICS OF THE PROTOZOA

Protozoa are unicellular eukaryotic organisms, which are usually not autotrophic (for example, no photosynthesis) and are motile. They are on the border between plants and animals, for example, among the flagellates autotrophs (with chloroplasts) and heterotrophs occur in the same family.

Protozoa live solitary or in colonies. Their size ranges from a few micrometers up to 13 cm (*Cycloclypeus carpenteri*). They have one or more nuclei each separated by a nuclear envelope from the cytoplasm. In the cytoplasm, in addition to the typical cell organelles of a eukaryotic cell, contractile vacuoles are found, especially in the fresh water species, which serve for excretion or osmoregulation, as well as extrusomes (trichocysts), used to catch prey or for defense. The cell is bounded by a cell membrane (plasmalemma with a glycocalix on the outer side). Cellular exciters, such as pseudopods, or cilia and flagella, are used for movement.

The pseudopods, which serve locomotion, but also for prey capture, are very different in shape:

- Lobiform **lobopods** contain endoplasm surrounded by ectoplasm. They represent the typical pseudopods of the Amoeba (Amoebozoa) (Photo 1).
- **Filopods** are of filiform shape and contain hyaline ectoplasm. They are movable at their base and are typical for the group Testacea.
- **Axopods** are rod-shaped. Flowing cytoplasm forms an outer mantle and transports substances from the axopodia into the cell body and vice versa. The fixed inner axis of microtubules (axonema) ends in the cytoplasm or the nucleus. Axopodia are used primarily for prey capture and only secondary for movement. They occur frequently in the Radiolaria and the Heliozoa.
- **Rhizopods** are similar to the axopods, but tend to ramify. They are found in the Foraminifera, more rarely in Radiolaria and Flagellata, and are also mainly used for prey capture.

The former classification of the Protozoa as a monophyletic strain with five classes (Sarcomastigophora / Flagellata, Sarcodina / Rhizopoda, Sporozoa, Cnidosporidia and Ciliata) was replaced by a scheme in which the Protozoa are seen as a polyphyletic taxon. Roberts & Janovy (2005, p. 43) use the phylum names Chlorophyta, Retortamonada, Axostylata, Euglenozoa, Apicomplexa, Ciliophora, and Dinoflagellata. One of Simpson & Roger's (2004, p. R693) classification systems is based solely on molecular data and presents groups termed Opisthokonta, Amoebozoa, Archaeplastida, Chromalveolata, Rhizaria, and Excavata as the six main groups of the eukaryotes, all of which also contain unicellular organisms.

A further revision of this classification was recently reported by Adl et al. (2012, p. 429) and is presented in Table 4.

	Super groups	Examples
	Amoebozoa	Tubulinea Mycetozoa
Amorphea	Opisthokonta	Fungi Choanomonada Metazoa
		Apusomonada
		Breviata
	Excavata	Metamonada Malawimonas Discoba
Diaphoretickes		Cryptophyceae
		Centrohelida
		Telonemia
		Haptophyta
	Sar	Cercozoa Foraminifera "Radiolaria"
		Alveolata Stramenopiles
	Archaeplastida	Glaucophyta Rhodophyceae Chloroplastida
Eukaryota with uncertain systematic classification		

Table 4: Classification of the Eukaryota. After Adl et al., 2012, p. 429.

3.3 AMOEBOID MOVEMENT

Amoeboid movement describes a creeping movement of cells, as found in many amoebas, but also in numerous cell types of the Metozoa (macrophages, lymphocytes, embryonic cells, cancer cells). It is due to the displacement of cytoplasm and the contraction of **actin** and **myosin** filaments (filiform proteins, which are also found, for example, in the skeletal muscles of the vertebrate animals).

In response to an external stimulus (light, chemicals), amoebas form a cytoplasmic **pseudopod** in the direction of the stimulus (**hyaline cap**, “anterior end”). In this process, actin filaments are degraded in the cell. The protuberance of cytoplasm leads to hydrostatic forces, whereby endoplasm with the free actin molecules is pressed into the pseudopodium (pressure flow hypothesis, shear-sliding hypothesis). The free actin molecules aggregate again in the pseudopodium and the actin-binding protein leads to gelation of the cytoplasm (becoming ectoplasm) (sol-gel conversion).

At the other end of the cell opposite the pseudopodium (**uroid**, “trailing end”) actin and myosin molecules provide for contraction and thus for a flowing movement of the cell. The necessary membrane rearrangements are carried out by vesicle transport. Amoeboid movement requires a solid substrate for the cell.

3.4 MOVEMENT BY CILIA AND FLAGELLA

Movement by **cilia** (short and many per cell) or **flagella** (up to 2 mm in length and few per cell) are found in the Ciliata and Flagellata, respectively (Photo 1). Many cells of the Metazoa are also provided with cilia (e.g., bronchial epithelial cells of the mammals) or move by means of flagella (e.g., sperm cells). Cilia and flagella are extracellular structures that are anchored in the cell membrane at the basal body.

Basal bodies correspond to the centrioles in their structure and serve as microtubules organizing centers (MOC) for the construction of cilia and flagella (9 × 2 plus 2 arrangement of **microtubules**; axoneme) (Figure 4). The nine outer doublet microtubules are connected by radial spokes with the two inner microtubules (central microtubules). Interactions between the outer double structures by means of dynein arms (motor protein) lead to a lateral movement of the cilia In the case of flagella, the motion is often planar and wave-like, whereas the motile cilia often perform a more complicated three-dimensional motion with a power and recovery stroke. Cilia of a cell often stroke synchronously (wave movement in a cilia field). The consequence of cilia and flagella is either locomotion of the individual or, in the case of a resting individual, a current in the surrounding medium.

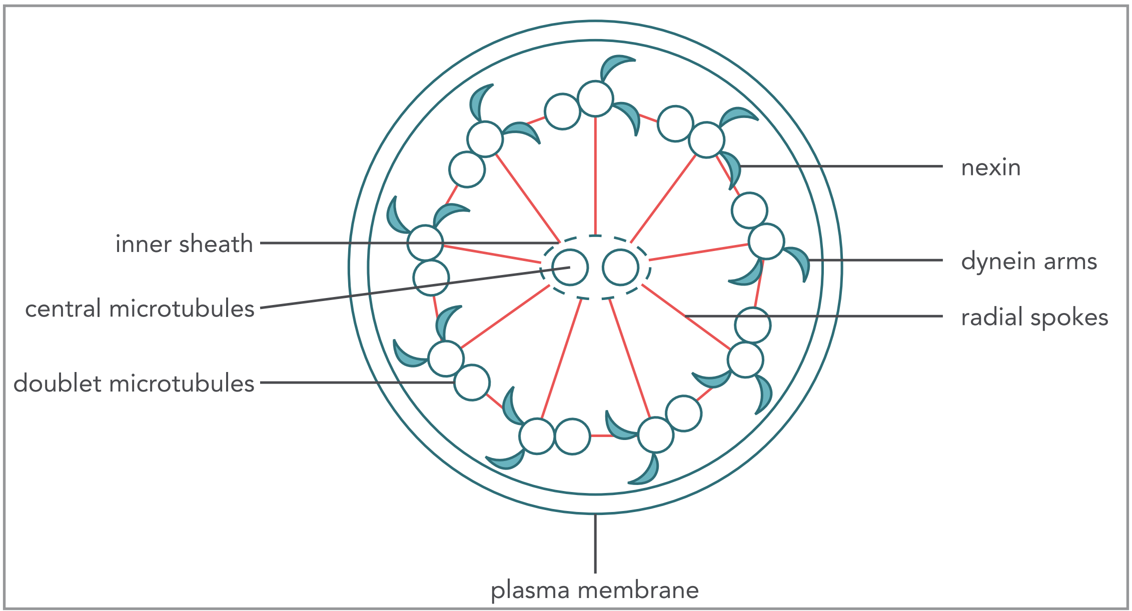

Figure 4: Cross section of an axoneme.

3.5 SOME METABOLIC FEATURES IN THE PROTOZOA

The food intake occurs in the heterotrophic Protozoa by diffusion or pino- or phagocytosis. In the case of Protozoa with a solid cell envelope, a cell mouth (**cytostome**) is formed for the absorption of food; a cell-anus (**cytopyge**) is used to excrete indigestible food. The food moves through the cell in food vacuoles and is digested there. The release of undigested residues is carried out by means of an egestion vacuole.

The **contractile vacuole** of the Amoeba, a pulsatile vesicle with collection channels and ampulla, absorbs excess water that has entered the cell and returns it to the environment at regular intervals. In particular, it is used to regulate the water balance (**osmoregulation**) in freshwater forms.

3.6 MULTIPLICATION AND REPRODUCTION

The multiplication of Protozoa can take place asexually and sexually. Asexual reproduction assures the survival of the species by the division of cells from agamonts. Protozoa that multiply asexually are potentially immortal. Cell division may be by equal or unequal longitudinal or transverse division, but also by budding or multiple fission.

In sexual reproduction three different forms, **hologamy** and **isogamous** and **anisogamous merogamy** are distinguished (Figure 5). In hologamy, fertilization occurs without the formation of special sex cells; two complete parent individuals merge into a zygote (copulation, fertilization process). As a rule, in Protozoa, however, movable, specialized sex cells (gametes) are formed by division of gamonts, which are equal in size (isogamous merogamy) or of different size (anisogamous merogamy or heterogamy with formation of micro- and macrogametes). Usually the male sex cells are smaller than the female.

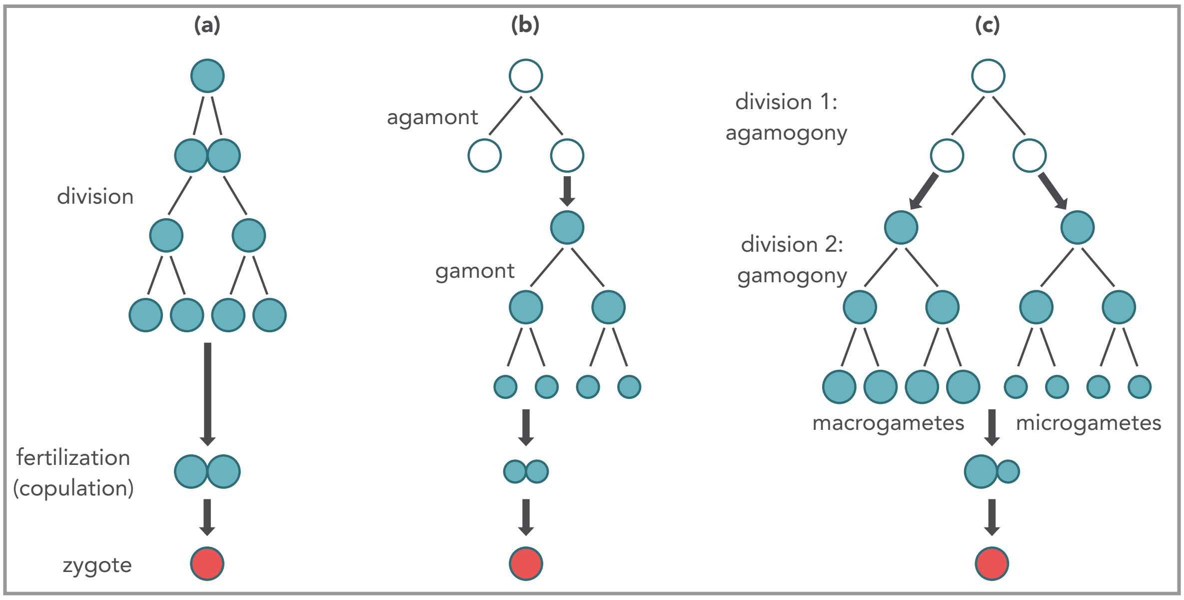

Figure 5: Forms of sexual reproduction: Hologamy (a), isogamous merogamy (b) and anisogamous merogamy (c). After Storch, Welsch, Kurzes Lehrbuch der Zoologie, Elsevier-Spektrum, München, 2005.

A particular form of sexual reproduction, **conjugation**, is found in the Ciliata. The process does not result in an increase in numbers but is a simple exchange of genetic material between two individual cells. Ciliata have a macronucleus (metabolic nucleus) and a micronucleus. The macronucleus is reabsorbed, and from the micronucleus a haploid female stationary nucleus and a male migrating nucleus are formed by nuclear division (meiosis and mitosis). A bridge of cytoplasm forms between the two ciliates, and one gametic nucleus from each cell passes into the other cell. The two gametic nuclei in each cell unite, thus restoring the diploid number of chromosomes. The micronucleus undergoes two mitotic divisions to produce four micronuclei: two of these will form the new micronuclei of the cell, and the other two will become the new macronuclei. Following the process of conjugation, normal binary fission proceeds.

In many unicellular organisms there is a regular alternation between asexual (agamogony) and sexual reproduction (gamogony), which is called a **primary alternation of generations**. If the alternation of generations is associated with a nuclear phase change, one speaks of a heterophasic alternation of generations. If both generations have the same nuclear phase, a homophasic alternation of generations occurs.

3.7 DISTRIBUTION AND ECOLOGY OF THE PROTOZOA

Protozoa are overall on the earth where there is enough water. They occur free-floating or on the ground of marine and limnic waters, but particularly the soil water (first settlers in ecological succession). In periodically dry habitats, they survive by forming cysts. The skeletons of certain Protozoa have contributed to the formation of sea sediments and rock complexes (chalkstone, radiolarite). In addition to the free-living forms, many species are found as extracellular or intracellular **parasites** (e.g. Trypanosoma and Apicomplexa) or as symbionts in host organisms. Numerous herbivore (plant-eating) insects (e.g., termites) and mammals (e.g., ruminants) cannot digest their cellulosic food without symbiotic Protozoa in the intestinal tract (Ciliata and Flagellata). The symbionts supply the **cellulases** (enzymes) for cellulose degradation.

3.8 PROTOZOA – PARASITES AND HUMAN PATHOGENS

Many parasitic Protozoa are important pathogens in domestic animals and humans. About 40 human pathogenic forms are known, e.g. the agents of amoebiasis, leishmaniasis, sleeping sickness and malaria (Table 5).

As an example of an **extracellular** unicellular human pathogenic **endoparasite**, the causative agents of the African sleeping sickness, *Trypanosoma brucei gambiense* or *T. brucei rhodesiense* (Flagellata) will be discussed, and as an example of an **intracellular** human pathogenic **endoparasite** the agents of malaria, *Plasmodium* sp. (Apicomplexa).

Trypanosoma is a genus of flagella-bearing unicellular organisms, which occur as endoparasites in various vertebrate animals and are usually transmitted by insects. For *T. brucei* the tsetse fly *Glossina* serves as a vector. A subspecies of *T. brucei* (*T. brucei brucei*) produces the Nagana cattle disease in domestic animals. The unicellular organism occurs in several pleomorphic forms during its developmental cycle.

With a bite of an infected tsetse fly, the metacyclic trypanosomes pass over the skin of a person into the blood, in which they spread as a “slender form” (long slender, **trypomastigote** form) throughout the body. In the further course of the infection, the long slender trypomastigote partly transforms into short, compact trypomastigotes. A tsetse fly is infected when it receives blood with the “short stumpy” form. In the mid gut of the tsetse fly, the pathogens transform into procyclic trypanosomes, which multiply and migrate to the insect’s salivary gland. In the salivary gland the transformation into the **epimastigote** trypanosomes takes place. After a further proliferative phase in the salivary glands, the transformation to the metacyclic form occurs, this form is pathogenic for humans.

Pathogen	Sickness	Transmission path
Trypanosoma	Trypanosomiasis (sleeping sickness)	Insect bite
Leishmania	Leishmaniasis, Kala Azar	Insect bite
Trichomonas	Trichomoniasis	Sexual act
Gardia	Lambliasis (Giardiasis)	Contaminated food
Entamoeba	Amoebiasis	Contaminated food
Isospora	Coccidosis (also in domestic animals)	Contaminated food
Toxoplasma	Toxoplasmosis (also in domestic animals)	Contaminated food
Sarcocystis	Gut sarcosporidosis	Contaminated food
Plasmodium	Malaria	Insect bite
Balantidium	Balantidiosis	Contaminated food

Table 5: Some unicellular organisms, which are pathogenic for humans.

Sleeping sickness in humans occurs in three stages. A few weeks after infection, fever, chills and swelling of lymph nodes occur. In the second stage, the parasite invades the nervous system causing sleep disturbances and cerebral seizures. In the final stage, the patient falls into a coma.

The forms living in the human blood carry a thick layer of glycoproteins (**variant surface glycoproteins**, VSG) on the cell surface, which are constantly changing. The immune system of the host cannot response because it is always "one step behind": it takes several days for an immune response against a given VSG to develop. A special metabolic product, the formation of the alcohol tryptophol, enhances immunosuppression. Tryptophol also appears to support the pathophysiological mechanisms of sleeping sickness (Vincendeau et al., 1999, p. 525).

Plasmodia (Apicomplexa) are intracellular unicellular endoparasites with a complex life cycle that includes an obligate host change between mosquito and vertebrates. The mosquito genus *Anopheles* is the end host (sexual multiplication of the parasite), and humans the intermediate host (with asexual multiplication). Four species of plasmodia cause **malaria** in humans and all belong to the genus *Plasmodium*, namely *P.ovale*, *P. vivax*, *P. malariae* and *P. falciparum* (Table 6).

Characteristic features of Apicomplexa are a conoid, a conical body which obviously facilitates the penetration into the host cell. The conoid, polar ring, micronemes, and other organelles form the **apical complex**. The Apicomplexa also have a specialized plastid, the apicoplast, which has probably developed from a red alga (secondary endosymbiosis). As an obligate endoparasite, however, the Apicomplexa no longer carry out photosynthesis.

Plasmodium species	Form of malaria	Attacks of fever	Mortality
P. vivax	Malaria tertiana	every 48 hrs	low
P. ovale	Malaria tertiana	every 48 hrs	medium
P. malariae	Malaria quartana	every 72 hrs	medium
P. falciparum	Malaria tropica	irregular	high

Table 6: Characteristics of *Plasmodium* species, which are pathogenic for humans.

The developmental stage of the sporozoites enters the human blood stream with the bite (piercing sucking action) of an infected *Anopheles* mosquito and they are carried to the liver. They penetrate into the parenchyma cells of the liver and mature into liver **schizonts**, which are up to 1 mm in size. Each schizont forms hundreds of **merozoites** (exoerythrocytic schizogony). In the next phase of disease, the merozoites enter the bloodstream and enter red blood cells (erythrocytes), where they reproduce again by schizogony. The divisions run synchronously after a few days, which lead to the characteristic periodic fever attacks. Merozoites feed on hemoglobin; hemoglobin fragments (hemozoin), which are released during the disintegration of the erythrocytes and elicit the fever attacks.

Male and female gamonts or gametocytes develop after a few days from the merozoites. These develop to gametes only after another feeding by the *Anopheles* mosquito in the insect gut (gamogony). Fertilized, amoeboid oocytes (ookinetes) invade the intestinal wall of the terminal host and are encapsulated. In the capsule (oocyst), up to 1,000 sporozoites are formed by cell division (sporogony). The oocyst bursts open, and the sporozoites enter the salivary glands of the insect via the hemolymph, from which they can be transmitted to the human body by the next blood meal.

The so-called **sickle cell anemia** can protect against malaria and its serious consequences. Sickle cell anemia is an autosomal recessive hereditary disease occurring in Africa, which is due to a mutation of hemoglobin. Sickle cell erythrocytes can no longer transport oxygen. They are removed from the blood by phagocytosis, resulting in anemia. Homozygote carriers usually die shortly after birth; therefore disease can only be observed in people who are heterozygous carriers. Heterozygous carriers of sickle cell anemia show a stronger malaria tolerance of the immune system (Ferreira et al., 2011, p. 398). This explains the almost congruent occurrence of malaria and sickle cell anemia in Africa.

3.9 REVIEW QUESTIONS

1) Describe the two most important mechanisms of locomotion in unicellular organisms.
2) What is the function of the contractile vacuole in the Amoeba?
3) How are the two forms of sexual reproduction, isogamous and anisogamous merogamy different from each other?
4) What is the significance of symbiotic Protozoa in the intestinal tract of a ruminant?
5) How are the two trypomastigote forms of *Trypanosoma* morphologically and functionally different from each other in the blood of an animal or man?
6) How is the almost congruent occurrence of sickle cell anemia and malaria in Africa explained?

4 PHYLUM PORIFERA (SPONGES, PARAZOA)

4.1 LEARNING OBJECTIVES AND KEYWORDS

In this chapter the sponges are presented as the simplest multicellular animals, which do not yet have a stable body, and thus no true tissues or organs. Sponges live exclusively in the fresh or sea water. Many marine sponges provide humans with important drugs.

Photo 2: Marine sponges in a coral reef (Jolanta Wojcicka / Shutterstock.com).

- Reversible body, cell differentiation, adhesins
- Collagen and proteoglycanes
- Pinacoderm and pinacocytes
- Choanoderm and choanocytes
- Asconoid, syconoid, and leuconoid type
- Osculum, archaeocytes, mesogloea (mesohyl), sclerocytes, spongin
- Amphiblastula, gemmules
- Calcarea and Silicea (demosponges and glass sponges).

4.2 EVOLUTION OF METAZOA

The transition from unicellular (Protozoa) to multicellular organisms (Metazoa) probably took place through **colony-forming Protozoa** from the Flagellata et Sarcodina. Simple metazoans possess epithelial cells with flagella similar to the choanoflagellates. Thus, the choanocytes of the sponges are largely congruent with the construction of choanoflagellates. The multicellularity has probably arisen only once, thus Metazoa represent a monophyletic taxon. However, only few transitional forms are known. The oldest fossil findings of the "Ediacara fauna" are about 600 million years old.

Prerequisites for multicellularity were cell differentiation and division of labor, separation of cell strains with loss of the ability to reproduce in other than the germ cells, cell recognition and cell aggregation, signal transmission pathways from one cell to another, and the development of scaffold proteins. In multicellular organisms, cell division together with apoptosis (cell death) is found only in growth and regeneration processes. Furthermore, the formation of an extracellular matrix was important for the formation of multicellularity.

The cell-cell recognition and cell aggregation are based on interactions between membrane proteins of neighboring cells (adhesins). An important structural protein of the extracellular matrix is **collagen**. In the human body it comprises 30% of the total mass of all proteins and is found mainly in connective tissue. Of the 28 known collagen types, type 1 is most frequently found in the animal kingdom. In principle, collagen consists of single, long protein chains that form a left-handed helix (secondary structure). Three of these helices are arranged in a right-handed superhelix (tertiary structure, triple helix, tropocollagen). A staggered attachment of the triple helices by approximately one-fifth of their length leads to the formation of collagen microfibrils, collagen fibrils and collagen fibers (quaternary structure).

Collagen fibers have a high tensile strength but are hardly extensible (don't stretch). The primary structure of the protein chains is of particular importance. One in three amino acids in the primary sequence is glycine. A sequence repeating frequently in the collagen protein family is glycine-proline-hydroxyproline. In the biosynthetic pathway of collagen, procollagens are expelled from the formative cell by exocytosis. Further protein modifications take place extracellularly. Other scaffold proteins of the extracellular matrix are reticulin, fibronectin, and numerous proteoglycans.

4.3 CHARACTERISTICS OF PARAZOA

Sponges live exclusively aquatic, mostly marine (see Photo 2), and only about 120 species occur in fresh water. Freshwater sponges place high demands on water quality. The ciliated larvae of sponges are swimming; the adult animals are sessile, that is attached to a substrate. Sponges are composed of different cell types, for example reproductive cells and collar cells (choanocytes). However, the cells do not yet form any real tissues (**reversible cell body**) and some cell types have omnipotence or totipotence / pluripotence at all times, so that they can always transform to other cell types. Sense and nerve cells as well as muscle cells are not present.

The body of the sponges consists of three layers, an outer epidermis of pinacocytes (pinacoderm), an inner gastrodermis of **choanocytes** (choanoderm) lining the gastric space and an intervening **mesohyl** ("mesogloea") or mesenchyme with collagen and **archaeocytes**. Archaeocytes possess the highest omnipotence, from which all other cell types can arise. The body shape of sponges is based on their internal skeleton, which consists of calcite, silica or the scaffold protein spongin. Correspondingly, the sponges are subdivided into Calcarea (calcareous sponges) and Silicea. The latter are subdivided into glass sponges or Hexactinellidae and demosponges or Demospongiae. The skeletal elements (sclerites, spicules) are a product of the **sclerocytes**, which are found in the middle layer and can be very diverse in form (monaxone to tetraxone needles, aster, pinulus, and spheres).

Depending on the configuration of the gastric space (spongocoel), the sponges are divided into three types:

- **Asconoid type**: a tubular, thin-walled body with a central cavity as a gastric space (spongocoel) and only one central outflow opening (osculum). Sponges of this type remain very small because they have a **small inner surface** (absorption surface). The epithelium lies on the outside, and the choanocytes line the spongocoel.
- **Syconoid type**: the choanoderm is inserted into the mesohyl through radial tubes to form a large gastric space, resulting in **an enlarged inner surface**. Sponges of this type become several centimeters in size.
- **Leuconoid type**: **flagellate chambers** penetrate the mesohyl and lead to a strong enlargement of the inner surface. The body is very thick-walled, the central gastric space greatly diminished. All large sponges have this type.

4.4 PHYSIOLOGY OF SPONGES

Despite their simple morphology, the life functions of the sponges are much more complex than was assumed for a long time. Thus, many sponges react to external stimuli such as light or water current. Not only the larvae but also adult animals can slowly move forward.

Their ingestion is by means of drawing water through dermal pores and canals in the body wall into the spongocoel by means of flagellar movement of the choanocytes. The food particles are filtered out of the water and taken up by the cells through phagocytosis. The water flows out through the osculum. In sponges, numerous biomolecules were detected, which serve as neurotransmitters in the Eumetazoa, but neuropeptides have not yet been found (Jékely 2013, p. 8703).

4.5 REPRODUCTION AND DEVELOPMENT OF SPONGES

Sponges are bisexually or hermaphroditic and can reproduce asexually (for example by budding) or sexually. Sperms are derived from the choanocytes and are released into the water (**spawning**). Neighboring sponges absorb them into their choanocytes or the mesohyl, where they meet oocytes originating from archaeocytes.

A larva is formed from the fertilized egg, and a Blastula larva is found in many species of sponges. The freely floating **amphiblastula**, with its blastoporus, settles on a substrate, then gastrulates (formation of the primitive intestine usually by invagination) and develops into a sponge. Sponges can be up to 10,000 years old.

Many freshwater sponges can persist as **gemmules** when the water dries up. Gemmules contain the building material for a new sponge (archaeocytes, spicules, and spongin).

4.6 ECONOMIC IMPORTANCE OF SPONGES

The inner skeleton of the Demospongiae is free of spicules and contains spongin. After rinsing the cell material (maceration), the absorbing sponges serve as cleaning and **bath sponge**. Around the Greek island of Kalymnos, 50 tons of natural sponges are still being harvested per year.

Different types of sponges are cultivated in aquacultures, in order to obtain chemical substances which are used in medicine. In addition to medicaments for cancer, sponges' products are also used for example as medicine for herpes. Often the sponge itself is not the source of these substances, but they are rather found in stored bacteria or dinoflagellates taken up with food. A known example of this is the **okadaic acid**, a protein phosphatase 1 and 2A inhibitor. Other natural products from sponges (peptides) are added to a special paint to protect ships from epibiotic growth.

Their high water filtration rate makes sponges to good cleaners. Sponges are capable of concentrating and absorbing 15,000 times the amount of heavy metals than that present in the water of their environment.

4.7 REVIEW QUESTIONS

1) Why is the ability to synthesize collagen a prerequisite for multicellularity?
2) What makes the high tensile strength of connective tissues? Briefly describe the structure and synthesis of the most important protein involved.
3) What cell types can be found in a sponge body?
4) Why can sponges of the leuconoid type become particularly large?
5) How can freshwater sponges survive the drying out of their habitat?

5 PHYLUM CNIDARIA (EUMETAZOA)

5.1 LEARNING OBJECTIVES AND KEYWORDS

This chapter presents the first multicellular animals with a stable body, i.e. with real tissues and organs. The Cnidaria, which live exclusively in water, include, among others, hydroids, jellyfish and corals. They are characterized by their cnidocytes, which are used for capturing prey and for defense. Many Cnidaria contain light-emitting proteins that are used in biomedical research.

Photo 3: The stinging hydroid *Macrorhynchia philippina* (Keoki Stender, www.marinelifephotography.com).

- Diploblastic Eumetazoa with a stable multicellular body
- Ectoderm, mesogloea, endoderm
- Gastrocoel, gastrovascular cavity
- Epitheliomuscular cells, nutritive-muscular cells, gland cells, sensory cells, nerve cells, interstitial cells
- Cnidocytes or nematocytes
- Planula larva, polyp, medusa, metagenesis
- Symbiotic and parenteral nutrition
- Coelenterate toxins.

5.2 SYSTEMATICS AND CHARACTERISTICS OF EUMETAZOA

Eumetazoa are distinguished by the possession of specialized cell types such as muscle cells, sensory and nerve cells, which form real tissues. Epithelial cells and other cells are linked by cell-cell contacts such as **desmosomes** and **gap junctions**. During embryonic development, gastrulation occurs resulting in the formation of two germinal sheets or layers, the **ectoderm** and the **endoderm**. In the Eumetazoa, three monophyletic divisions are distinguished:

- Phylum Cnidaria
- Phylum Ctenophora (comb jellies)
- Bilateria (two-symmetrical animals, two-sided animals).

Cnidaria and Ctenophora were formerly grouped as **Coelenterata** (hollow animals with radial-symmetrical construction). Many differences in the construction plan, body size, lifestyle and reproduction confirm the differentiation into two animal phyla.

5.3 SYSTEMATICS AND CHARACTERISTICS OF CNIDARIA

The Cnidaria are subdivided into four classes, which are distinguished in particular by the position of the gonads and the arrangement of septae in the gastric space of the polyps:

- Hydrozoa (hydroids)
- Scyphozoa (jellyfish)
- Cubozoa (box jellies, formerly placed in the Scyphozoa)
- Anthozoa (corals, sea pens, sea anemones) (see Photo 3).

In recent years the stalked jellyfish (Stauromedusae) have been considered as a separate class, the Staurozoa.

Cnidaria live either planktonic or sessil in seawater and only rarely in fresh water. Sessile forms often live in colonies (coral reefs). The Cnidaria as Eumetazoa possess real tissues and organs. Its **stable body** has a radial-symmetrical structure and consists of two cell layers, the epidermis or **ectodermis** and the gastrodermis or **endodermis**. In between the two layers is the mesogloea. The gastrodermis delimits the gastrocoel (including the mouth opening or hypostome), which not only serves to absorb the food, but also to remove waste products. In addition to the mesogloea, the gastrovascular system serves as a hydrostatic skeleton. Solid skeletons occur only in the polyps of the Anthozoa (Octocorallia), which secrete calcium carbonate. The mesogloea regulates, among other things, the water and ion exchange between the animal and the environment.

The name giving cell type is the **cnidocytes** in the ectodermis. In addition, there are epithelial cells, cnidoblasts, the precursors of the cnidocytes or nematocytes, receptor cells and interstitial cells in the ectodermis. The receptor cells are connected with the nerve cells located under the ectodermis and form a simple, diffuse nervous system. Neurosecretory cells produce numerous **neuropeptides**, which are simple hormones involved in the control of development and modulation of excitements.

The **interstitial cells** are pluripotent cells, thus can develop into other cell types, e.g. sex cells, gland cells and nerve cells, but not into epithelial muscle cells and muscle cells. Interstitial cells are restricted to the Hydrozoa, where they are responsible for the high regenerative ability and potential immortality in a *Hydra*.

All Cnidaria have **cnidocytes**. They are particularly frequently found on the tentacles placed around the mouth. The cnidae capsule contains a spirally wounded thread which, when the cnidocyte is touched, is expelled in an explosive manner (acceleration up to 40,000 *g*) and toxic substance can be injected into an enemy or a prey. Cnidocytes, therefore, serve both, to capture prey and to defend against predators. Recent research suggests the explosion process takes only 700 nanoseconds, thus reaching an acceleration of up to 5,410,000 *g*. Over 30 types of cnidae or nematocysts are found in different cnidarians. They can be divided into the following groups:

- **Penetrants**: a penetrant is the largest and most complex nematocyst. When discharged, it pierces the skin or chitinous exoskeleton of the prey and injects a poisonous fluid that either paralyzes or kills the victim.
- **Glutinants**: a sticky surfactant used to trap prey is found in burrowing (tube) anemones, which also helps create the tube in which the animal lives.
- **Volvents**: a small pear-shaped nematocyst. When discharged, it tightly coils around the prey. They are the smallest nematocysts.

The endodermis is composed of nutritive-muscular cells, gland cells and basal cells. For example in a medusa, muscle fibrils are found on both sides of the mesogloea. Recent research suggests that muscle cells may have originated from cells of a third germinal layer, a **mesoderm**.

The two most important body forms of the Cnidaria are the **polyp** and the **medusa**, which can occur as different stages of life in one and the same species (secondary alternation of generation or **metagenesis** with the change of sexual and asexual reproduction). Polyps sit on a substrate with the foot disc, and the tentacles or catching arms, which are arranged around the mouth, point upwards away from the substrate. Polyps often occur as colony. Medusae (jellyfish) have a hat-shaped appearance and often swim freely (water-repulsive principle). Their tentacles hang freely downwards.

5.4 REPRODUCTION AND ALTERNATION OF GENERATIONS

Widespread among the Cnidaria is a regular alternation between sexual and asexual reproduction, a real (secondary) generation change or metagenesis. In the case of the Hydrozoa, a **Planula** larva settles on a substrate and develops into the polyp. From the adult polyp a swimming larva is separated by budding, which develops after settlement to a new polyp. Often the budding is incomplete and a polyp colony develops. Most polyps are feeding polyps. Some polyps, however, differentiate into sex polyps, from which medusae are released. Medusae live pelagic and release sperm and egg cells from their gonads into the water. A Planula larva develops from a fertilized egg. In the entire life cycle, only sperm and oocytes are haploid.

In the Scyphozoa and Cubozoa, the polyp generation is usually greatly reduced. In the Anthozoa, on the other hand, only the polyp generation is formed.

5.5 NUTRITION OF CNIDARIA

Most Cnidaria feed on prey (zooplankton), which come into contact with their cnidocytes on the tentacles. Many corals live symbiotically with photosynthesis-active protists in the ectoderm cells. These are either dinoflagellates (**Zooxanthella**) or unicellular green algae (**Zoochlorella**). These symbionts absorb carbon dioxide produced by the cnidarians and use solar energy to convert CO_2 into energy-rich carbohydrates, which provides the main food for the Cnidaria.

Another kind of nutrition for cnidarians is **parenteral** nutrition. The animals can absorb dissolved organic molecules from the water (dissolved organic matter, DOM) via the ectodermis, in the form of amino acids, monosaccharides or short-chain fatty acids.

5.6 STOCK- AND REEF FORMATION

A subgroup of the Anthozoa, the stony corals and reef corals (Madreporaria, Scleractinia) are of great ecological importance. **Coral reefs** occur in two different habitats, in cold deep water, e.g. along the European continental slopes beyond 60 m depth, and in warm tropical shallow water areas (tropical coral reefs). In the formation of reef, the above mentioned endosymbiotic protists are of great importance. They are involved in calcium carbonate formation for the exoskeleton.

Also of great ecological importance is the **ectosymbiosis** between reef corals and anemone fish. Harlequin fish live in symbiosis with sea anemones. The fish secrete mucus on the body surface, which protects them against the cnidocytes. Thus, anemone fish can live between the tentacles of the anemones and are protected from predators. On the other hand, the anemone fish attack predators of the sea anemones. The sea anemones feed parenterally from food residues and excretions of the fish.

5.7 TOXINS IN THE COELENTERATES AND CORAL FLUORESCENT PROTEINS

The poisons injected into prey and enemies through the cnidocytes are mostly polypeptides consisting of up to 49 amino acids with several intramolecular disulfide bridges, e.g. the sea anemone toxins. Furthermore, di- and **sesquiterpene**s as well as **polyketide**s are found as poisons in cnidocytes. The polyketide **palytoxin** of the crustanemone *Palythoa toxica* is one of the most toxic of all natural products. The high specificity of various coelenterate toxins makes them important tools in neurophysiology and membrane research. The sea wasp (box jellyfish; Cubozoa) and the Portuguese man o' war (Hydrozoa) also represent often fatal underwater hazards for humans.

In recent years biomedical research has made use of unique natural luminescent proteins from cnidarians (Hydrozoa and Anthozoa). For the discovery of a **green fluorescent protein** (GFP) from the jellyfish *Palythoa toxica*, and its application in biological research, two Americans and one Japanese scientist received the Nobel Prize for Chemistry in 2008. The discovery of GFP and other luminescent proteins triggered a revolution in biology. They are used in biomedical research as unique stains to make living cells and cell structures visible.

5.8 REVIEW QUESTIONS

1) Identify the most important cell types of the ectodermis and the endodermis in cnidarians and describe their functions.
2) Describe the alternation of generations (metagenesis) in the Hydrozoa.
3) What forms of nutrition are found in Cnidaria?
4) How are endosymbiotic nutrition and reef formation associated in the reef-forming Anthozoa?
5) Which generations are reduced in the metagenesis of Cubozoa and Anthozoa?
6) Which representatives of the coelenterates can become fatal to humans and why?

6 PHYLUM PLATHELMINTHES (FLATWORMS)

6.1 LEARNING OBJECTIVES AND KEYWORDS

The bilateral symmetrical flatworms are characterized by three germ layers that arise during their embryonic development (triploblastic), from which the different tissues and organs emerge. They have simple excretory organs (protonephridia) and a ladder-like nervous system with a pronounced concentration of nerve cells in the head (cephalization). The space between the body wall and the intestine is filled with parenchymatic tissue (mesenchyme). The body cavity is called a pseudocoel (acoelomates). Despite their well-developed organs, the flatworms still have a high regenerative capacity.

Many flatworms (flukes, tapeworms) live as endoparasites in domestic animals and humans, where they can often cause fatal diseases. Their metabolism shows a variety of adaptations to life without oxygen (anaerobiosis, anoxibiosis).

Photo 4: Scolex (head) with some proglottids of the pork tapeworm, *Taenia solium* (D. Kucharski, K. Kucharska / Shutterstock.com).

- Triploblastic Eumetazoa
- Histozoa, bilaterians, acoelomates
- Parenchyma (mesenchyme) and epitheliomuscular tube with longitudinal and circular muscle layers
- Protonephridia
- Ladder like nervous system with cephalization
- Regeneration
- Human endoparasites
- Monogenea and Digenea
- Metagenesis and heterogeneity
- Anaerobic energy metabolism.

6.2 ACOELOMIC BILATERIANS

The tri(plo)blastic organization level of Bilateria is characterized by three germinal layers, ectoderm, endoderm, and **mesoderm**. Derivatives of the third germinal layer include connective tissue, musculature, and a fluid-filled cavity ("coelom"). The body cavity is called a **pseudocoel** (acoelomates). The oldest known fossil animal with the basic plan of a bilaterian (*Veranimaculata*) lived 580 to 600 million years ago in the ocean.

Several phyla of the Bilateria are characterized by **spiral cleavage** during embryonic development (Spiralia). In spiral cleavage, four new cells are formed from each cell in a spindle shape, obliquely to the axis of the egg. Segmented (ringed) worms (Annelida), mollusks (Mollusca), peanut worms (Sipuncula), ribbon worms (Nemertini), and flatworms (Plathelminthes) belong to the Spiralia.

Other taxa also have spiral cleavage, but it is unclear whether this is homologous to the spiral cleavage found in the Annelida and Mollusca [jaw worms (Gnathostomulida), Entoprocta or Kamptozoa, and the "Rotifera"].

All taxa with spiral cleavage are termed protostomes (Protostomia). Their **blastopore** converts in the course of embryonic development into the mouth opening. Their mesoderm fills either the complete **blastocoel** (Acoelomata) or it only covers the external surface of the blastocoel (Pseudocoelomata). In the coelomatic, lophotrochozoan protostomes, a mesodermal band fills the blastocoel. The **coelom** (secondary body cavity) opens within the mesoderm through schicocoely (see Figure 6).

Acoelomates have only one body cavity, the digestive tract. The area between the body wall and the intestine is filled with mesoderm in the form of mesenchyme (**parenchyma**) and muscle fibers. All Acoelomata belong to the superphylum Lophotrochozoa.

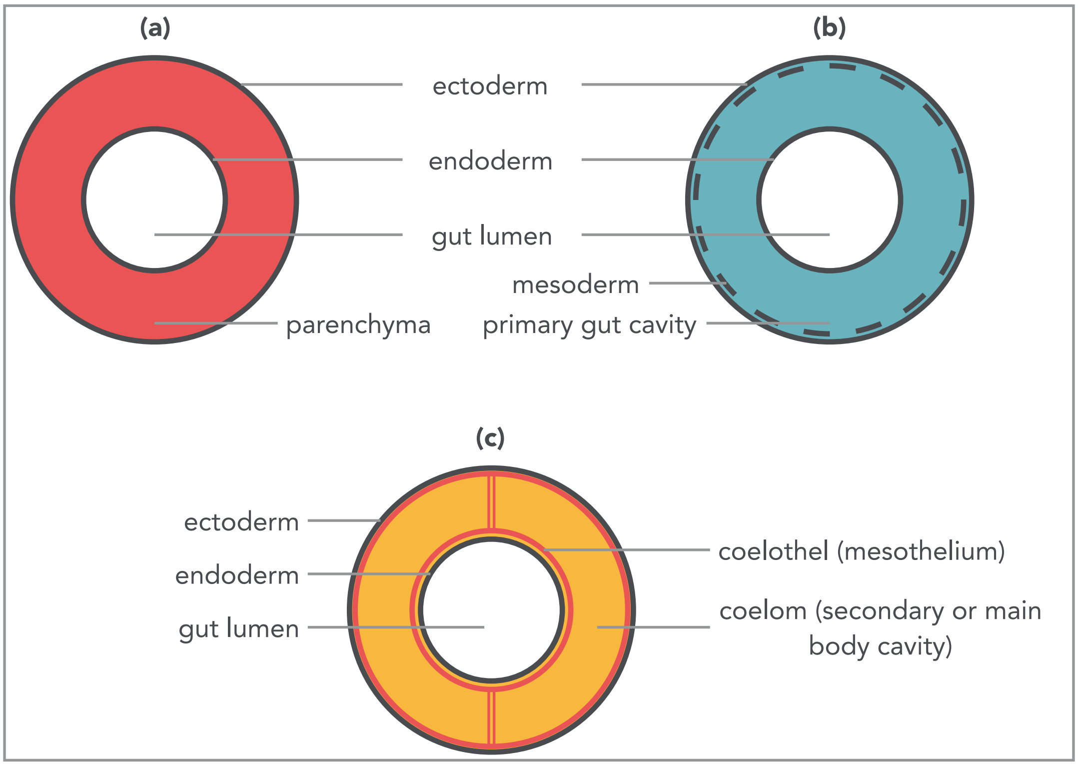

Figure 6: Schematic cross-section through an acoelomate (a), pseudocoelomate (b) and eucoelomate (c).

6.3 SYSTEMATICS AND CHARACTERISTICS OF PLATHELMINTHES

Plathelminthes or Platyhelminthes comprise four classes of bilateral symmetric, dorsoventrally flattened, worm-shaped animals. The Turbellaria or planarians live free in the fresh water or at sea coasts and are predatory. They are a few millimeters to a maximum of 50 cm in size. All representatives of the remaining three classes are exclusively parasites, most of them are endoparasites and some occur in humans. The Monogenea are ectoparasites, the Trematoda or flukes and Cestoda or tapeworms are endoparasites (see Photo 4). They are also combined as **Neodermata**.

Some cestodes can reach a body length of up to 25 m. Many species show an indirect life cycle with a change of host. The first host is often an invertebrate, the second host a vertebrate including the human beings. More recent phylogenetic studies showed that the free-living species of the Plathelminthes are not a monophyletic group but rather a paraphyletic group (Burda et al., 2008, p. 105).

Most of the planarians have a cellular, ciliated epidermis with embedded gland cells. Underneath the epidermis and the basal membrane lies a layer of circular and longitudinal muscles, which form a **musculoepithelium**. This musculoepithelium supports the shape of the body. The tegument of the parasitic flatworms is of mesodermal origin and replaces the original epidermis in the first larval stage (**neodermis**). The cells of the neodermis form a syncytium, a multinucleated cell unit.

Flatworms are also referred to as parenchymatous worms because the space between the body surface and the digestive system is filled with parenchymal tissue, in which all the organs are embedded (Figure 6). The parenchymal tissue consists of an extracellular matrix and different cell types, including parenchymal cells, muscle cells and neoblasts (undifferentiated stem cells).

In addition to the Cestoda, which do not have a digestive system, the other flatworms often have a blind-ending intestinal tract, which can be highly branched. Flatworms have neither blood or a circulatory system, nor organs for gas exchange. Except for some planarians, the excretion and osmoregulation system consists of **protonephridia** with flame cells and a filter apparatus. The beating flagella of the flame cells transport fluid through the perforated tubule cell and the associated collecting channels, thus creating a negative pressure in the protonephridium, which leads to a continuous flow of liquid. The perforations in the terminal cell are large enough for small molecules to pass, but larger proteins are retained within. Selective reabsorption of useful molecules by the canal cells occurs as the solutes pass down the tubule. The “urine” is released through nephridiopores, which are located on variable parts of the body surface. In general, protonephridia are constructed from only three monociliatic cells (terminal cell, channel cell, nephroporus cell), but fulfill all the functions of a “real” renal organ: that is filtration, secretion and reabsorption.

Flatworms have a ladder like nervous system. Longitudinal nerve cords lying on the ventral body site (Gastroneuralia) (see Figure 11) are connected by transverse cords or commissures. Together with the cerebral ganglia (**cephalization**) they form the central nervous system. The peripheral nervous system is formed by subepidermal nerve plexuses and is connected to the central nervous system. The active locomotion of the flatworms has not only favored the cephalization of the nervous system but also the evolution of sensory organs, light-sensitive eye patches or ocelli, as well as tactile (statocysts) and chemoreceptive cells.

The flatworms are protandrous, hermaphroditic animals (**hermaphroditism**), in which first the male reproductive organs are formed then the female, with mostly sexual reproduction. In all classes of flatworms, however, asexual reproduction also occurs. Planarians divide into anterior and posterior half and each half regrows the lost half by **regeneration**, in which neoblasts (adult stem cells) divide and differentiate, thus resulting in two worms.

6.4 THE ABILITY FOR REGENERATION IN TURBELLARIA

The highly developed regenerative capacity of planarians, especially in the genus *Dugesia*, provides an interesting model for developmental biologists (Reddien & Alvarado 2004, p. 737). Planarians can form complete animals from tiny body fragments. This ability is closely related to asexual reproduction by cross-division and is based on a group of cells capable of dividing, the **neoblasts** that can produce all types of tissue. Most likely, all neoblasts originate from stem cells or are stem cells themselves. This form of cell renewal probably exists in all planarians. The neoblasts have remarkable similarities to the somatic stem cells of mammals and humans.

The Tiger planarian, *Dugesia tigrina*, which was imported from North America, is used as a pollution indicator in the water industry in Europe. *D. tigrina* is assigned to a saprobic value of 2.2, that means a water quality class of II–III (critical loaded).

6.5 PARASITIC FLATWORMS IN DOMESTIC ANIMALS AND HUMANS

Numerous trematodes and cestodes live as endoparasites in millions of people and often evoke fatal diseases (Table 7).

Taxa	Disease	Way of infection (larvae)
Isthmiophora (Trematoda)	Echinostomiasis	Freshwater mollusks
Echinostoma (Trematoda)	Echinostomiasis	Freshwater mollusks
Fasciola (Trematoda)	Fasciolosis	Water- and littoral plants
Schistosoma (Trematoda)	Bilharzia (schistosomiasis)	Contaminated water
Trichobilharzia (Trematoda)	Schistosome cercarial dermatitis	Contaminated water
Dicrocoelium (Trematoda)	Dicrocoeliosis (humans rarely)	Ants
Paragonimus (Trematoda)	Paragonimiasis	Shrimps
Diphillobotrium (Cestoda)	Fish tapeworm	Raw fish
Taenia (Cestoda)	Pork and cattle flatworm, Cysticercosis	Raw meat
Echinicoccus (Cestoda)	Dog and fox tapeworm, Echinococcosis	Schmear infection (feces)
Hymenolepis (Cestoda)	Dwarf tapeworm	Infected grain

Table 7: Flatworms which are pathogenic in humans.

6.5.1 THE CATTLE TAPEWORM *TAENIA SAGINATA* AND THE PORK TAPEWORM *T. SOLIUM*

Tapeworms (Cestoda) have a head (**scolex**) with suction cups and partly with a ring of hooks. The body consists of a variable number of successive segments (**proglottids**), which form a chain (strobila). Tapeworms reach a length between 2 mm and more than 30 m. These endoparasites have no intestine and feed parenterally, that is, through the tegument. The neodermis protects the surface of the body from degradation by proteases in the digestive tract of the host.

The cattle tapeworm lives as an adult worm in the human digestive tract. The juvenile form (larva) is primarily found in the intermuscular tissue of cattle. The adult worm consists of up to 2,000 proglottids and reaches a length of up to 10 m. Mature proglottids are excreted with the feces and actively creep short distances in the environment. There they can be eaten by grazing cattle. The enveloped larvae (**oncosphere** or hooked larva) hatch out and use their hooks to penetrate through the intestinal wall into blood and lymph vessels. In this way, they enter the musculature (e.g., the diaphragm, tongue, or heart) where conversion to the juvenile stage (**cysticercus** or bladder worm) takes place.

A worm infection in humans occurs by consumption of raw meat, which contains the bladder worm. The main disease symptom is a weight loss without other symptoms. For the cattle flatworm, humans are the **end host** (carrying the sexually mature adult animal), and cattle are the **intermediate host** (with larval development).

Adult *T. solium* (Photo 4) live in the small intestine of humans and become about 2 m long. On the scolex are four suction cups and a hook ring. The juvenile stages occur in the muscle tissue of pigs. *T. solium* is much more dangerous to humans than *T. saginata*, because the cysticercus larva can also develop in various organs of man (for example, the eye or the brain) (man is both end and intermediate host).

6.5.2 THE DOG TAPEWORM *ECHINICOCCUS GRANULOSUS* AND THE FOX TAPEWORM *E. MULTILOCULARIS*

Dog and fox tapeworms are both species of the genus *Echinococcus*, which have only a few proglottids and reach a body length of only a few millimeters. Adult dog tapeworms develop in dogs; juvenile forms often live in ruminants (e.g. sheep).

The fox tapeworm parasitizes mainly the red fox and other species of the genus *Vulpes*. Small rodents are usually the intermediate hosts. For both species man can act as an intermediate or "dead-end" host. The larvae (cysts) in humans are predominantly found in the liver, but also in the heart, lungs and central nervous system (Echinococcosis). The juvenile stage is a kind of cysticercus, which is called a **hydatid cyst**. In the hydatid cyst massive multiplication takes place by budding (metagenesis). This creates thousands of infectious tapeworm heads. The only treatment is the operative removal of the hydatids, without rupture of the hydatids and release of the daughter larvae. Man is infected exclusively by eating eggs.

6.5.3 DIGENIC TREMATODES

The reproductive cycle of the digenic trematodes is often very complex. The first host (intermediate host) is usually a mollusk, the end host a vertebrate including man. In some species, a second or third intermediate host may be involved. An alternation of generations (**metagenesis**) is associated with a **change of host**. Whether there is a regular alternation between heterosexual and parthenogenetic reproduction (heterogeneity) is controversial.

The adult animals usually release their eggs into water. An actively moving, ciliated larva hatches from the eggs, the **miracidium**. The miracidium penetrates into the tissue of a snail, where it transforms into a mother sporocyst. The sporocysts multiply asexually, producing daughter **sporocysts** and **rediae**. The rediae multiply asexually with the formation of daughter rediae and **cercariae**. The cercariae leave the snail host and penetrate either directly into the end host (e.g. in the case of the blood fluke *Schistosoma mansoni*) or actively or passively look for a second intermediate host (e.g. a freshwater crustacean in the lung fluke *Paragonimus westermani* or an ant of the genus *Formica* in the lancet liver fluke *Dicrocoelium lanceolatum* resp. *D. dentriticum*).

The lancet liver fluke has a developmental process optimized for an infection sequence on land. The cercariae penetrate into the subesophageal ganglion of an ant and induce a reversible behavior of the animals in the night. The ants during day cannot leave the tip of a blade of grass. This behavior increases the chances that the **metacercariae** in the ant are eaten by grazing sheep (the end host). Human infections are therefore rare.

In some species, the cercaria encysts on an aquatic plant and develops to a metacercaria (for example, in the case of the giant intestinal fluke, *Fasciolopsis buski*). After ingestion, the metacercariae excyst in the duodenum and attach to the intestinal wall. There they develop into adult flukes.

One of the most common parasitic infections in the world is **bilharzia** or schistosomiasis. The pathogens are schistosomes. Bilharzia occurs in over 70 mostly tropical countries. About 200 million people are infected and an estimated 12,000 to 100,000 people die each year. The life cycle of the flukes starts with the miracidium larva, which had hatched from the egg and must find an appropriate type of snail as an intermediate host within a few hours after hatching. In the snail, the transformation to the sporocyst occurs. The daughter sporocysts produce cercariae. The cercariae leave the snail and swim free in the water, and drill into the skin of a human being. In doing so, they throw off their fork tail and enter small blood vessels. There is no metacercaria stage.

The larvae convert into the young worm (schistosomulum) before reaching the main blood circulation and have developed a protective surface (tegument). First, the worms enter the lungs, then the liver. Schistosomes have separated sexes. The narrower female lies in the longitudinal lateral fold of the male. The worm pairs can be found in the vascular plexuses of the bladder and intestine, where they can survive for years to decades.

A female can produce up to 3,000 eggs per day, which find their way back into the water with the feces or urine. The main disease symptoms of **schistosomiasis** arise from the eggs that remain in the body on the bladder or intestinal wall. The eggs remaining in the body induce defense cells to accumulate to form so-called granulomas. When the defense cells are later replaced by connective tissue, the tissue (fibrosis) hardens. Eggs, granuloma and scarred structures can interfere with blood circulation, causing further organ damage such as bladder cancer or severe liver fibrosis.

A special form of cercarial infection is the **bathing dermatitis** or "Weiherhibbel" which occurs in Germany. It is triggered by cercaria species (e.g., *Trichobilharzia szidati*), which usually infest animals, for example, waterfowl. The human in this case represents an inappropriate host. When these cercariae penetrate into the skin of a bather, they cannot develop further and the worm dies after a few days. It comes, however, to skin itching, redness and formation of wheals.

6.6 ANAEROBIC ENERGY METABOLISM IN PARASITIC FLATWORMS

Parasitic cestodes and trematodes live in low-oxygen, but carbon dioxide-rich cavities of their final host. A further adaptation to this way of life is a special form of carbohydrate metabolism for energy production under hypoxic (oxygen-deficient) or anoxic (oxygen-free) conditions, and fixation of carbon dioxide (CO_2) (Lloyd 1986, p217). In addition to **lactate** (lactic acid) and **acetate** (acetic acid), large amounts of succinate (succinic acid) and **propionate** (propionic acid) are produced as end products of glucose metabolism. This is why the metabolic pathway is called **succinate / propionate fermentation** (Figure 7). The energy yield is up to 4 times higher than in the case of lactate fermentation (2 moles ATP per mole of lactate) because further ATP molecules (up to 8 moles) are formed during the production of succinate and propionate.

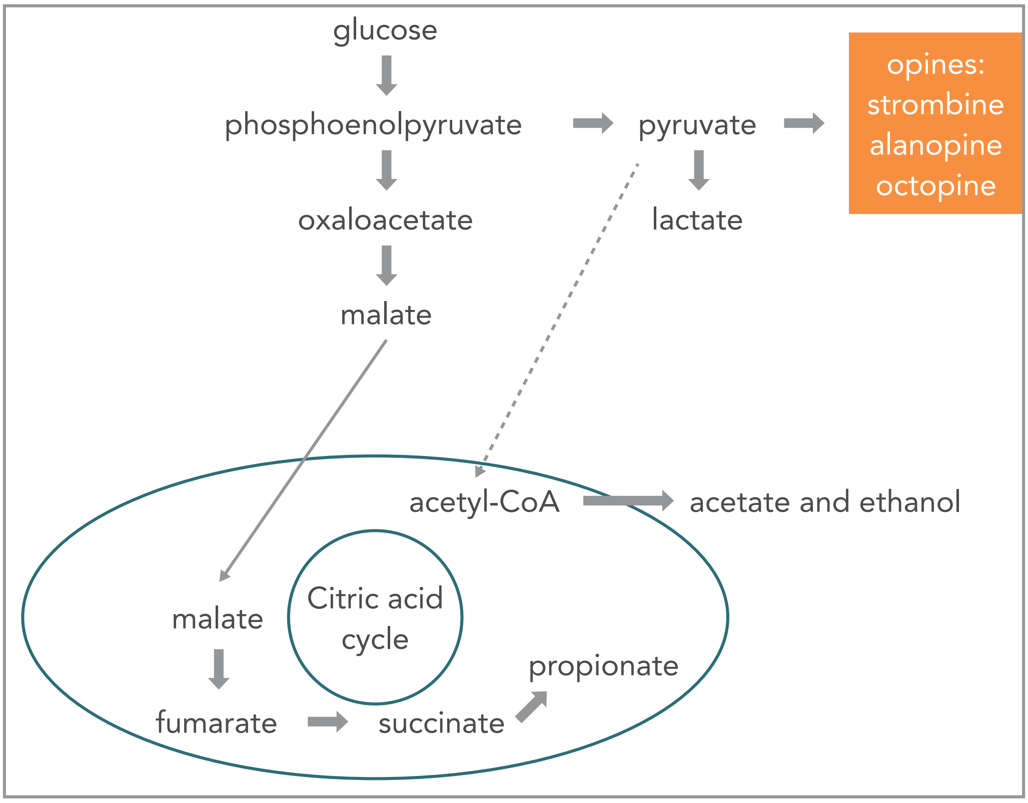

Figure 7: Scheme of anaerobic energy production in animals.

6.7 REVIEW QUESTIONS

1) Why is infection with a pork tapeworm (*Taenia solium*) more dangerous for humans than with a cattle tapeworm (*T. saginata*)?
2) Name two tapeworm species (Cestoda) for which humans may be intermediate host.
3) Explain the terms Acoelomata, Pseudocoelomata and Coelomata.
4) Why do planarians (Turbellaria) have such a high regenerative capacity?
5) Explain the term "protandry".
6) What are the benefits of anaerobic carbohydrate metabolism through succinate / propionate fermentation versus lactate fermentation?

7 PHYLUM NEMERTEA (NEMERTINI, “RIBBON WORMS“)

7.1 LEARNING OBJECTIVES AND KEYWORDS

The ribbon worms comprise a small group of marine organisms with an elongated round worm shape, whose body cavity is completely filled with parenchymal tissue. These are the simplest animals with a closed circulatory system.

Photo 5: *Baseodiscus cingulatus*, the banded ribbon worm from Hawaii (Keoki Stender, www.marinelifephotography.com).

- Proboscis and rhynchocoel
- Closed circulatory system
- Epitheliomuscular tube (skin-muscle tube)
- Pseudometamerism
- Viviparity
- Pilidium larva.

7.2 SYSTEMATICS AND CHARACTERISTICS OF NEMERTEA

Almost all ribbon worms live in the marine benthos (see Photo 5) and most are only a few centimeters long, but some reach up to 30 m (according to other statements even 60 m) length (*Lineus longissimus*). The colored body is striking. The general Nemertini body structure is largely similar to that of the Turbellaria, however, they differ from planarians by possessing a **proboscis**, as well as in their reproductive organs. From the point of evolution, the ribbon worms may have separated from a common ancestor very early.

The protuberant proboscis of the Nemertea lies free in a cavity (**rhynchocoel**) above the digestive tract. With this unique structure the predatory species capture their prey. The proboscis releases a spike-like stiletto, through which a poisonous secretion can be injected into the prey. Nicotine-like poisons were detected in several species of ribbon worms. Adult animals have a continuous intestine with an anus, in the lumen of which digestion is mainly extracellular. The body cavity is completely filled with mesodermal parenchyma, and in this sense they are typical **acoelomates**.

The ribbon worms are the simplest animals with a **closed circulatory system** consisting of two or more lateral vessels and a dorsal vessel with transverse connections. The blood is colorless. The blood flow is maintained by a combination of contraction of the vessels and general body movement. The excretory organs are protonephridia, which are closely associated with the lateral blood vessels. Their task is primarily excretion, i.e. delivery of metabolic end products, and less with osmoregulation. A respiratory system is not present. Ribbon worms have very strong layers of circular and longitudinal muscles, a **musculoepithelium**.

7.3 REPRODUCTION AND DEVELOPMENT OF NEMERTEA

The ribbon worms show a surprisingly wide range of reproductive strategies. Most species have separated sexes often with external fertilization. Some species are **hermaphroditic**, and asexual reproduction also occurs by means of cross-division and regeneration. The reproductive organs consist in both sexes of two laterally located longitudinal series of simple sacs in the parenchyma. This arrangement simulates a metamerism (segmentation of the body) (**pseudometamerism**). The animals are usually oviparous (they lay eggs), some species are viviparous (live birth).

The development of the eggs starts with spiral cleavage. Further development is mostly indirect via different types of larvae. A typical larval form is the **Pilidium** larva. This small planktonic larva is reminiscent of the trochophore larva (see Annelida) with its ciliary cords and a ciliated head. The adult animals emerge from the larvae after a complicated metamorphosis.

7.4 REVIEW QUESTIONS

1) Name at least three differences between the Nemertea and the Plathelminthes.
2) What does the term viviparity mean?
3) What are the advantages of a closed circulatory (blood) system compared to a missing or an open circulatory system?

8 PHYLUM ROTIFERA (ROTIFERS, WHEEL ANIMALS)

8.1 LEARNING OBJECTIVES AND KEYWORDS

The very small rotifers live mostly in fresh water (part of the freshwater plankton) and are characterized by a wheel organ (ciliated structure) on the head (corona), which functions for food intake and locomotion. If their habitat dries out in the summer, the otherwise separately sexually reproducing animals reproduce unisexually (virgin generation or parthenogenesis). The progeny in this case hatch from unfertilized eggs.

Photo 6: The rotifer *Floscularia* (Lebendkulturen.de / Shutterstock.com).

- Pseudocoel, Lophotrochozoa
- Cephalization, syncytial epidermis
- Cell constancy (eutely)
- Protonephridial tubules
- Parthenogenesis and heterogeneity.

8.2 SYSTEMATICS AND CHARACTERISTICS OF ROTIFERA

Wheel animals or rotifers (formerly Rotatoria) are very small multicellular animals (usually 0.1 to 2 mm) with a genetically determined, species-specific, constant number of cells (**eutely**), at least in some organs. They colonize almost all humid habitats on earth. Many species represent important members of the limnic (freshwater) zooplankton. Their average life span is only one week. Although the wheel animals are still considered today as an animal phylum, recent phylogenetic investigations have shown that the Acanthocephala, a sister group of the Bdelloidea (an Order of wheel animals, which only reproduce parthenogenetically), must be regarded as wheel animals.

In recent textbooks, the rotifers are referred to as pseudocoelomatic Lophotrochozoa. Other lophotrochozoic pseudocoelomates are the Acanthocephala (thorny-headed worms), Gastrotricha (hairybacks) and Entoprocta (formerly Kamptozoa or curved animals). The **pseudocoel** is filled with a liquid or a gelatinous substance and forms a kind of hydrostatic skeleton (see Figure 6). Mesenchymal cells are scattered in the pseudocoel. Other functions of the pseudocoel are circulation of substances and storage of waste materials.

The cylindrical body of the Rotifera can usually be divided into three sections, a head, a trunk and a foot. Located on the head is the wheel organ, consisting of ciliated rings or collars (**corona**) (see Photo 6), which serves for both food intake and locomotion. The animals usually feed on unicellular algae or detritus and only a few species are predatory. On the head is also the retrocerebral organ, a glandular structure, which is connected with the cerebral ganglion (**cephalization**).

The typical chewing pharynx of the Rotifera or **mastax** consists of a strongly muscular tube, contains chitinized or calcified structures (trophi), which are movable and serve to grind up the food. The epidermis consists not of single cells, but rather of a syncytium, which is formed by the fusion of epidermal cells. The gonads (usually only one unpaired gonad) and the excretory or osmoregulatory organs are also located in the trunk section. The mostly paired **protonephridia** (protonephridial tubules) of the Rotifera lie in the pseudocoel and consist of 3–4 multinuclear cells forming a tube system. One of the cells resembles a "flame", consisting of several beating cilia, which transport the pseudocoel fluid through a kind of filter into the lumen of the protonephridia. In the channel system of the protonephridium, electrolytes and water are reabsorbed before the hypotonic residual fluid ("urine") leaves the body via a **cloaca**. The digestive tract also ends in the cloaca.

The foot bears two toes and contains adhesive glands that open in the toes. With the aid of these glands, the wheel animals can attach to a substrate.

8.3 REPRODUCTION OF ROTIFERA

Wheel animals have separated sexes. Different taxa of the Rotifera reproduce differently. In many cases, sexual reproduction occurs under unfavorable conditions during the autumn, whereas in the summer, unisexual reproduction or **parthenogenesis** occurs.

This alternation of generations (**heterogeneity**) is especially pronounced in the class Monogononta. In response to particular environmental conditions (e.g., changes in temperature and photoperiod, or dryness), the females begin to produce haploid eggs (**mictic** females). If these eggs remain unfertilized, dwarf males are produced. The males produce sperm to fertilize further haploid eggs. These develop into diploid eggs (2n), which continue to develop under unfavorable environmental conditions in order to survive the winter in a kind of **dormancy**. In the spring, diploid **amictic** females develop, which can multiply unisexually for several generations (diploid parthenogenesis).

Some species can take up genetic material from bacteria, fungi or plants and other animals into the telomeres of the chromosomes during the dormancy, thus compensating for the disadvantages of parthenogenesis (Eugene et al., 2008, p. 1210). Some species can survive **cryptobiosis** at temperatures around -250 °C. Under these conditions, their metabolism is extremely reduced.

8.4 REVIEW QUESTIONS

1) How are metagenesis and heterogeneity differentiated and what are the differences between primary and secondary alternation of generations?
2) In what way can wheel animals endure unfavorable environmental conditions?
3) What is eutely?
4) What adaptive advantages does the possession of a pseudocoel have against the acoelomatic condition?

9 PHYLUM NEMATODA (ROUNDWORMS)

9.1 LEARNING OBJECTIVES AND KEYWORDS

With the roundworms we encounter the most numerous group of all multicellular organisms. Roundworms are found in vast numbers in the soil, but also in many other moist habitats. Especially in the tropics, many roundworms occur as endoparasites in humans and domestic animals and are often even more dangerous than the above described flukes and tapeworms. The larvae of the roundworms molt several times, which is why the animals are counted as the ecdysozoic clade of the pseudocoelomates.

Photo 7: The roundworm *Caenorhabditis elegans* (Heiti Paves / Shutterstock.com).

- Pseudocoel, Ecdysozoa
- Molting
- Cuticle and hypodermis
- Spicules
- H- or V-cells for osmoregulation
- Human pathogenic endoparasitic roundworms.

9.2 SYSTEMATICS AND CHARACTERISTICS OF NEMATODA

Nematodes or roundworms (also referred to as eelworms) are a very species-rich phylum and the probably most numerous group of all Metazoa. A fertile ground may contain up to 20 million individuals per cubic meter; in the intertidal mudflats one finds up to 4.5 million on one square meter and in a putrescent apple on ground up to 90,000 nematodes as saprobionts. As an "eelworm" one can find nematodes also in vinegar, paste or in moist beer coaster.

Characteristic for this highly successful worm type is its undulating body movement with the help of its **hydroskeleton**. They are usually small, colorless animals which generally live in moist biotopes, but also as ecto- or endoparasites in or on animals, plants (for example, beet cyst eelworm) and humans. As endoparasites they can reach a length of up to 8 m. They are triploblastic protostomes with a **pseudocoel** (see Figure 6). Their development involves four larval stages without metamorphosis. The larvae molt from one stage to the next stage of development (ecdysozoic clade of the Pseudocoelomata).

Because of their hollow, round body shape the nematodes were formerly combined in the phylum Nemathelminthes or Aschelminthes together with the acanthocephalans (spiny-headed worms), gastrotrichs (hairybacks), Kynorhyncha (mud dragons), loriciferans, horsehair worms (Gordian worms), priapulid worms (penis worms), and wheel animals.

Characteristic of nematodes is its multilayer non-cellular cuticle, which counteracts the hydrostatic pressure exerted by the pseudocoel and prevents the worm from adverse environmental conditions e.g. in dehydrated soils or in the digestive tract of a host. Some of the layers contain the polysaccharide chitin and also calcium carbonate. The cuticle is secreted by the underlying syncytial hypodermis (epidermis). The cuticle is shed from one larval stage to the next during molting.

The muscles under the epidermis consist almost exclusively of longitudinal muscles and form an epitheliomuscular tube ("skin-muscle tube") around the body. The stiff cuticle together with the longitudinal muscles allows the roundworms only an undulating kind of movement.

The digestive tract consists of an oral cavity with a muscular pharynx, followed by the non-muscular intestine with an anus. A ring of nerve tissue surrounds the pharynx, from which a dorsal and a ventral nerve cord run posterior. From each muscle cell, an extension runs to the dorsal or to the ventral nerve cord ("Kahn muscle cells"). This is quite unique in the animal kingdom, because in most animals the nerve extensions (axons) extend to the muscle cells.

The roundworms have no respiratory organs. Oxygen is absorbed over the body surface and diffuses directly to the body cells. Many nematodes live close to anoxic or sulfide-rich biotopes. A single or multicellular ventral gland in free living species and a **lateral canal system** (H-gland or V-gland) in parasitic species, whose longitudinal branches lie in the lateral epidermis, are developed as excretory or osmoregulatory organs in many nematodes. Both organs can be regarded as simple protonephridia.

9.3 REPRODUCTION AND DEVELOPMENT OF NEMATODA

Nematodes usually have separated sexes and reproduce sexually. The males are often smaller than the females and carry at the posterior end paired copulatory organs, the spicules. Fertilization takes place in the body and the eggs are stored in a uterus until oviposition. The four juvenile stages are separated from each other and grow by **molting** of the cuticle. In some species hermaphroditism occurs with self-fertilization. In free-living forms the development takes place directly, i.e. without metamorphosis. Parasitic forms often have a complicated life cycle with host changes or changes of tissue within the host.

9.4 ANAEROBIC LIVING IN NEMATODES

Many nematodes live at the limit of anoxic and sulfide-rich biotopes. As typical end products of energy metabolism, α-**methyl butyrate** and α-**methyl valerate** (Koecke 1982, p. 313, Figure 8) are found in the pseudocoel fluid. These metabolic end products are formed through the succinate / propionate fermentation pathway and are excreted with the feces (see Figure 7).

Marine roundworms of the genera *Laxus* and *Eubostrichus* have on their surface a dense coat of falciform, ectosymbiontic bacteria of unusual size. These bacteria possess the metabolic equipment to oxidize sulfur-containing substances (**chemoautotrophic sulfur bacteria**) (Ott 1993, p. 231). The symbiosis seems essential for both partners.

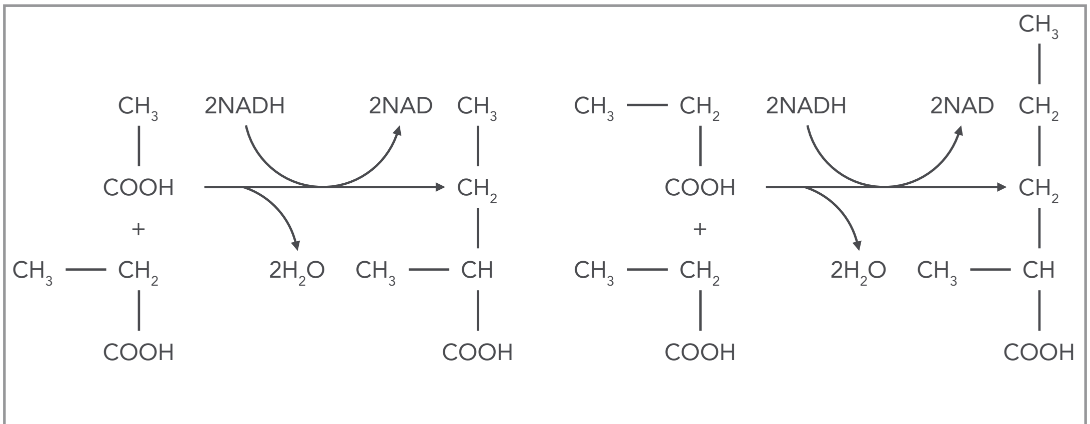

Figure 8: Formation of anaerobic end products in the energy metabolism of nematodes. After Koecke, Allgemeine Zoologie 1. Bau und Funktion tierischer Organismen, Vieweg & Sohn, Braunschweig, 1982.

9.5 PARASITIC NEMATODES IN DOMESTIC ANIMALS AND HUMANS

Particularly in the tropics, many roundworms are parasites in humans and domestic animals and are even more dangerous than flukes and tapeworms (Table 8).

Taxa	Disease	Way of infection
Ancylostoma sp. (hookworm)	Anemia, damage of the gut	Through skin (legs)
Enterobius vermicularis (pinworm)	Oxyuriasis, itchiness at anus	Fecal smear infection
Ascaris (round worm)	Ascariasis (fever, colics)	Food (field fertilization)
Dracunculus medinensis (Medina worm)	Dracontiasis (purulent traumas)	Copepods in water
Wucheria bancrofti (filarial worm)	Elephantiasis	Mosquitoes
Onchocerca volvolus (filarial worm)	Onchocerciasis (river blindness)	Black flies
Trichinella spiralis (trichina)	Inflammation of the gut, fever	Raw pork

Table 8: Human pathogenic nematodes.

An estimated 500 million people in the tropics and subtropics are carriers of the **hookworm**; the death rate is about 60,000 per year. The worm itself settles in the intestine, where it sucks blood especially in the jejunum and where the females lay their eggs. The first and second larval stages remain in the intestine, where they feed on feces. The third larvae stage burrow actively into the soil where they wait for a suitable host.

People become infected when the larvae penetrate the skin, particularly through the feet. The fourth larval stage is carried via the blood stream to the lungs and molts there to the fifth larval stage. The larvae are coughed up from the bronchia and then swallowed. In the intestine, the worm molts to the adult. The L3 larvae need a temperature of at least 18 °C in the soil for survival. Formerly, there were infections with *A. duodenale* in Central Europe in the mining district. The species was also discovered during the construction of the Gotthard tunnel in Switzerland.

500 million people around the world are affected annually by a **pinworm** that is only a few millimeters in size, *Enterobius vermicularis*. Oxyuriasis is particularly common in small children. The infection takes place directly from person to person as a result of inadequate hygiene. Oxyuriasis is a harmless disease and complications rarely occur. The infectious stage is the larvae 2. Infection can also be caused by inhalation of the eggs, e.g. while shaking bed sheets. The eggs then enter the duodenum, where the larvae hatch after 6 hours and grow in the colon to mature worms.

Ascaris lumbricoides is a 10–40 cm long colorless worm that is transmitted by ingestion of larval worms with contaminated water, vegetables or fruit (fertilization with feces). In the years after the Second World War, up to 99% of the population was infected in some parts of Germany. The incidence rate worldwide is still around 1 billion people and around 12,000 people die from **ascariasis** every year. The eggs can last for years in the soil. After oral uptake of the eggs, the larvae hatch and migrate as L3 larvae over the liver and the heart to the lung. From the lung, the larvae are expectorated and then swallowed. In the intestine they develop into an adult worm. In this type of worm, humans are therefore both intermediate and final host.

The **medina worm** occurs in the wetlands of the subtropics and tropics and has a pronounced sexual dimorphism. While the males reach only a few centimeters, females reach a length of up to 120 cm. The infection rate has drastically declined in recent years due to specific control measures by the World Health Organization (WHO). Humans take up infected copepods with the drinking water. The larvae, which are released in the stomach, enter the small intestine and then the mucous membrane. Further development occurs in the retroperitoneal space (behind abdominal membrane).

While males die shortly after copulation, the female migrates through the tissue, mostly to the extremities, and settles there in the connective tissue of the hypodermis. The head causes the formation of an ulcer by secretions. When the person comes in contact with water, the thin skin over the ulcer bursts, and at the same time also the cuticle and uterus of the worm, and as a result thousands of larvae are discharged into the water. This process can be repeated several times before the female dies. The larvae are eaten by copepods, which then drill themselves from the intestine into the body cavity. Traditionally, the removal of the female worm from an infected extremity is still done winding it up slowly with a wooden stick.

The **filarial worm** *W. bancrofti* lives parasitically in the lymphatic system of human beings and causes an inflammation there. The larvae (microfilariae) are transmitted by various species of mosquitoes. If the animals die in the lymph vessels of the terminal host, they block the lymph flow, which can lead to a congestion-induced deformation, especially of the extremities (elephantiasis). Another type of filarial worms, *O. volvolus*, causes the river blindness in wide areas of Africa and South America. Man is the only end host. In endemic areas up to 100% of the population can be infected.

Females of *Simulium damnosum*, which prefer to live in flowing water, serve as an intermediary host. In the blackfly, the microfilariae, which are taken up when the fly takes a blood meal, develop into infectious L3 larvae. After about a year they reach sexual maturity in the end host (human) and colonize the subcutaneous connective tissue. This is where balls of microfilariae are formed. When microfilariae enter the eye, they cause visual impairment to blindness.

The **trichina worm**, *T. spiralis*, is a parasitic nematode species, which is widely distributed in Central Europe. Human infections can be caused by the consumption of raw or insufficiently heated meat, however, human trichinosis is rare in Central Europe and in the United States. Basically, all mammals are susceptible to trichina; a human being is rather an error host.

9.6 THE USE OF NEMATODES IN PEST CONTROL

Nematodes can be used for the control of certain insect larvae living in the soil. Examples of this are the control of the black vine weevil (*Otiorhynchus sulcatus*) or the Garden Chafer (*Phyllopertha horticola*) with insect-pathogenic nematodes of the families Steinernematidae and Heterorhabditidae. Infected pest areas are watered with a suspension of nematodes. The standard application is 250,000 to 500,000 roundworms per square meter. The worms penetrate into larvae and pupae of the pests and kill them. All insect pathogenic nematodes live in symbiosis with bacteria that help them overcome the immune defense of the harmful insects.

9.7 THE MODEL NEMATODE CAENORHABDITIS ELEGANS

C. elegans (Photo 7) has gained great importance in the areas of developmental biology and genetics as a model organism. The worms are almost transparent and all internal organs can be easily observed with a microscope. The worm is only one millimeter in size and is characterized by **eutely**. Each adult worm has a defined number of cell nuclei; hermaphrodites 959 nuclei, and the rare males 1031 nuclei. In the hermaphroditic worms 1090 cells are produced by cell division from the egg cell. This number is reduced by programmed cell death (**apoptosis**) in the course of the development to the adult worm to 959, thus 131 cells are eliminated. Sydney Brenner, H. Robert Horvitz and John E. Sulston received the Nobel Prize in Physiology and Medicine for this discovery in 2002.

C. elegans was the first representative of Metazoa, whose genome was completely sequenced (The *C. elegans* Sequencing Consortium 1998, p. 2012). The six chromosomes and the genome of the mitochondria contain 100,281,426 base pairs and 23,217 genes. The first studies on RNA interference (RNA silencing) were carried out on *C. elegans*.

9.8 REVIEW QUESTIONS

1) Where in man is the adult form of the following human pathogenic nematodes found: *Ascaris suum*, *Enterobius vermicularis* and *Wucheria bancrofti*?
2) Explain the specificity of the connection of muscle and nerve cells in the nematodes.
3) Explain the anaerobic lifestyle of many nematodes.
4) Why can humans be intermediate and final host for the roundworm *Ascaris lumbricoides*?
5) Why are some nematode species suitable for use in biological pest control?

10 ANNELIDA (SEGMENTED WORMS)

10.1 LEARNING OBJECTIVES AND KEYWORDS

The segmented worms belong to the lophotrochozoic clade of the animal kingdom. The trochophore larva of many annelids is eponym for this group. Probably the best known segmented worm is the earthworm, *Lumbricus terrestris*. Segmented worms are characterized by their external and internal structure and possess a real secondary body cavity (coelom). Other features are their ladder like nervous system, the highly developed excretory organs (metanephridium) and a closed circulatory system with a variety of different respiratory blood pigments, which serve to transport oxygen.

Photo 8: The earthworm *Lumbricus terrestris* (https://pixabay.com).

- Coelom / schizocoely (secondary body cavity)
- Homonymous (true) and heteronomous metamery
- Teloblastic growth
- Metanephridium
- Chloragogen tissue
- Ladder nerve cord
- Respiratory blood pigments
- Parapodia
- Trochophore larva.

10.2 SYSTEMATICS AND CHARACTERISTICS OF ANNELIDA

The Annelids, with their approximately 15,000 species, belong to the lophotrochozoic-protostomic clade of the animal kingdom and exhibit spiral cleavage and a determined (mosaic-like) development. The latter properties, as well as recent molecular biological data, point to close relationship of the annelids with the mollusks. The **metameric structure** of the body is the most important innovation in the ancestry of the annelids. An even more specialized metamerism is present in the arthropods (tagmatization). Annelids have a secondary body cavity or a real coelom (**Eucoelomata**) (Figure 6). In most annelids the coelom develops in the embryo as a split in the mesoderm on both sides of the intestine (**schizocoely**) and each segment is separated by a septum. The coelomic fluid acts as a hydrostatic skeleton.

The classification of the Annelida is based on the absence or presence of **parapodia** and **setae** (chetae; chitinous bristles or hairs). Parapodia are "fleshy" paired lateral attachments on the body segments, which serve for locomotion and respiration. The Polychaeta bear numerous setae or bristles on each segment, which arise from the paired parapodia. The Oligochaeta (including the earthworms) have only a small number of setae per segment and do not have parapodia. The leeches (Hirudinea) have neither setae nor parapodia.

The segmentation represents a longitudinal division of the body into more or less identical units, each containing all essential organ systems (coelomic sacs, nephridia, ganglia of the nerve cord, lateral blood vessels). The number of segments can be as high as 1,000. On the surface of the body the segmentation is visible through small constrictions (annuli). Inside, the segments are separated by septae. Only at the anterior and posterior end of the worm is a segment without a segmental character; at the front the prostomium or **acron**, at the rear the pygidium or **telson**.

The body wall is equipped with strong circular and longitudinal muscles and covered with an epidermis and a non-chitinous cuticle (musculoepithelium). Some annelids are already capable of chitin synthesis. There, the chitin is locally incorporated into head appendages and segmental bristles.

The highly centralized nervous system consists of cerebral ganglia (brain), two mostly non-fused ventral nerve cords, which traverse the length of the body, and various ganglia with lateral branches. The complex and mostly **closed circulatory (blood) system** consists of longitudinal and circular vessels, some of which can pulsate via muscle contraction to pump the blood throughout the body. The well-developed, segmentally arranged nephridia remove wastes from the blood as well as the coelom (proto- and metanephridia).

10.3 THE LUGWORM *ARENICOLA*, A REPRESENTATIVE OF THE POLYCHAETES

Polychaetes mainly live in the ocean. They differ from the other annelids by specialized head-appendages with sensory organs, paired, limp parapodia on each segment and numerous setae. According their activity, they are subdivided into two subgroups, stationary (sessile) polychaetes or **Sedentaria** and mobile polychaetes or **Errantia**. Taxonomically, polychaetes are thought to be paraphyletic.

Sedentaria spend most of their time in permanent burrows or tubes. Errantia live pelagic, actively digging and using their tubes only for food intake and reproduction.

The lugworm *Arenicola* is living in a U- or J-shaped tube in the sandy banks of the intertidal region of the ocean. One square meter of brackish intertidal flat soil can house thousands of worms. By repeated protruding and withdrawing movements of its "proboscis", it causes a water flow. With its gills, which are located at the parapodia, it absorbs oxygen from the water and filters out its food from the sandy sediment. It ingests the sediment while in the burrow, leaving a depression on the surface sand. Once the sediment is stripped of its useful organic content it is expelled, producing the characteristic worm cast (Photo 9).

Photo 9: Worm cast of a lugworm, *Arenicola marina* (© Christian Hager/dpa; with permission).

Polychaetes do not have permanently sexual organs. They appear temporarily in the form of a pair of gonads per segment. The animals have usually separated sexes and fertilization occurs externally. The early larva is a **trochophore**. Some polychaetes live the greater part of the year as sexually immature animals (atoke). During breeding season, the posterior part of the body matures sexually (epitoke, formation of sexual segments or stolons). Each of the epitoke segments is packed with eggs and sperm.

An example of this is the **Palolo worm** (*Eunice viridis*). Its reproduction is controlled by annual as well as lunar rhythm (Hauenschild et al., 1968, p. 254). Only once a year, in one to three nights during the last quarter of the moon, between mid of October and mid of November, the epitoke (terminal part of the body) drops off and floats on the surface of the water, releasing sperm and eggs. In some polychaetes, the epitokes are formed by asexual budding from the atokes, and become complete worms.

The double conical trochophore larva of the annelids is subdivided into an anterior episphere and a posterior hyposphere by a preoral band of cilia (prototroch). While the preoral part of the larva develops into the acoelomous prostomium of the adult worm, the larval coelom divides synchronously into 3–6 segments, which then form the anterior metameric segments of the adult worm. The remaining segments are formed successively from a budding zone (teloblast; teloblastic coelom formation) located in front of the pygidium (originating from the anal area of the larva).

10.4 EARTHWORMS AS REPRESENTATIVES OF THE OLIGOCHAETES

The oligochaetes are combined with the leeches (Hirudinea) to the clitellates (Clitellata). Their **clitellum**, an epidermis region with numerous glands, surrounds the anterior half of the body during sexual maturity.

Oligochaetes include the earthworms (Photo 8) but many forms live in fresh water. They have only a few setae or “bristles” per segment and lack parapodia or gills. Breathing takes place exclusively through the moist skin (integument). Oligochaetes are hermaphrodites with reciprocal fertilization. The gonads are limited to a few segments. Juvenile worms hatch within a coccon, which had been separated from the clitellum. A layer of yellow **chloragogen tissue** is located around the intestine and the dorsal vessel of the closed circulatory system, which represents a central site of fat and glycogen synthesis and can be functionally compared with the liver of mammals.

Metamerically arranged pairs of **metanephridia**, each of which extends over two segments, serve as excretory organs. A ciliated funnel (nephrostome) opening into the body cavity absorbs the waste from the coelom. In the following ciliated tube, salts, organic compounds and water are exchanged with the capillaries of the circulatory system, before the non-recoverable wastes are excreted through nephriopores. Thus metanephridia fulfill all functions of a vertebrate kidney, namely filtration, secretion and reabsorption.

Many oligochaetes are scavengers. Earthworms usually feed on decaying organic plant material. As humus farmers, they have an important position in terrestrial ecosystems. Giant earth worms in the tropics can reach a length of 4 m.

Freshwater oligochaetes are usually smaller than earthworms. They are an important source of food for freshwater fish. *Tubifex*, which is known as an ornamental fish feed in aquaristics, is red colored and lives with its head in the mud at the bottom of stagnant or slowly flowing waters. Similar to the endoparasitic worms (see above), many oligochaetes have an anaerobic energy metabolism by succinate / propionate fermentation (Seuß et al., 1983, p. 557) (see Figure 7).

From eutrophic waters with high concentrations of dissolved organic material (DOM), oligochaetes can absorb **parenterally** low molecular weight organic compounds over the body surface (Sedlmeier & Hoffmann, 1989, p. 128). Conversely, they excrete metabolic end products, such as acetate and propionate, through the integument.

The oligochaete *Olavius algarvensis* lives in sediments of the Mediterranean Sea in a chemosynthetic endosymbiotic community with sulfur-oxidizing bacteria, which are located directly below its body surface. As a result of this symbiotic nutrition, a complete reduction of the intestine (Dubilier et al., 2001, p. 298) has occurred.

10.5 RESPIRATORY BLOOD PIGMENTS IN POLYCHAETES AND OLIGOCHAETES

Polychaetes and oligochaetes have the largest variety of respiratory blood pigments, i.e. oxygen-transporting pigments, in the animal kingdom (Table 9). Only the hemocyanin occurring in the mollusks and some arthropods is not found in annelids. Respiratory pigments support aerobic energy metabolism in environments with poor oxygen supply. The red color of *Tubifex* is caused by the high molecular weight hemoglobin (erythrocruorin) in the blood.

Name and structure	Molecular weight (Da)	O_2-capacity mL O_2 per g	Color deoxygenated / oxygenated
Hemerythrin Fe^{2+}-protein	13,000–120,000	1.67	colorless – violet
Chlorocruorin Fe^{2+}-porphyrin-protein	3 million	0.76	pale green – yellow green
Erythrocruorin Fe^{2+}-porphyrin-protein (high molecular hemoglobin)	1.5–4 million	1.29	dark red – light red
Hemoglobin Fe^{2+}-porphyrin-protein	16,000–64,000	1.29	dark red – light red

Table 9: Respiratory blood pigments in annelids.

10.6 THE MEDICAL LEECH AS REPRESENTATIVE OF THE HIRUDINEA

Leeches have a fixed number of segments (usually 34), but the outer segmentation appears to be blurred by secondary banding. In contrast to other segmented worms, the leeches lack well defined coelomic compartments. The coelomic cavity is filled with connective tissue and a system of lacunae; the blood system is reduced (**mixocoel**). Characteristic is their "looper-like" locomotion using the two suckers at the mouth and the anal end. Bristles are usually lacking.

Most of the leeches are predatory in fresh water; some are blood suckers that attack humans and other mammals or fish. Leeches are hermaphrodites, and reproduce by reciprocal fertilization. Fertilization occurs internally. After copulation, the clitellum secretes a cocoon, which contains the eggs. The development is similar to the Oligochaeta, namely directly. They can become up to 30 years old.

True blood suckers, such as the medical leech, *Hirudo medicinalis*, have three jaws with calcite teeth for cutting the host tissue. They detect potential prey with sensilla on the surface of the skin and swim with meandering movements of their muscular body to the prey. The salivary glands lying between the jaws release the anticoagulant polypeptide **hirudin** during blood sucking. Within 30 to 60 minutes, a leech can suck up to ten times its body weight in blood. The blood is preserved and digested by means of special bacteria in segmental blind sacks of the midgut. After a blood meal a leech can live without food for up to one year.

Medical leeches were used hundreds of years for "bloodletting". It was though that this would contribute to the detoxification of the body, while the hirudin would act at the same time antithrombotic and accelerate the lymph flow. Other substances from the saliva can alleviate inflammation and pain. In Germany, medical leeches can still be obtained from drugstores. For the production of ointments against pain, inflammation and swelling with hirudin as an active ingredient, the saliva of leeches is still used today. However, in the meantime, genetically engineered recombinant hirudin is available.

10.7 REVIEW QUESTIONS

1) What is the ecological significance of earthworms?
2) What are the characteristics of subdivision of the Annelida into three classes?
3) Describe the function of the clitellum in the Clitellata.
4) Discuss the great variety of respiratory blood pigments in annelids.
5) Describe the different kinds of reproduction in polychaetes.

11 MOLLUSCA (MOLLUSKS)

11.1 LEARNING OBJECTIVES AND KEYWORDS

The mollusks include the snails, mussels (clams) and squids. The most important feature is their calcium carbonate shell, which, however, can be reduced, as occurs in the case of slugs (nudibranchs). The body is divided into a head-foot and a mantle cavity that contains most of the internal organs in the visceral mass. The coelom is limited to a small area around the heart and gonads. Another characteristic structure is the radula, a rasping organ, which serves for food intake and is only absent in mussels. In snails one can very well follow the transition from life in the water (for example, breathing with gills) to the terrestrial life (pulmonates; breathing with lung).

Photo 10: Pulmonates (Gastropoda) in estivation (K.H. Hoffmann, Bayreuth).

- Gills (ctenids) and pallial lung
- Mantle (pallium) and mantle cavity, visceral mass
- Pallial complex
- Cephalopodium
- Pericardium and pericardial gland, metanephridia
- Radula
- Calcium carbonate shell with aragonite / calcite and proteins

- Hepatopancreas (digestive gland)
- Chiastoneury / streptoneury and torsion
- Hemocyanin
- Octopin fermentation.

11.2 SYSTEMATICS AND CHARACTERISTICS OF THE MOLLUSCA

The mollusks are the largest lophotrochozoic phylum with about 120,000 living and 70,000 fossil species. Their basic body parts are the head-foot (**cephalopodium**) and the internal organs in the mantle cavity (pallial complex or **visceral mass**), usually covered by a shell. The **coelom** is limited to a small cavity surrounding the heart, and in parts the gonads and excretory organs.

The body size ranges from microscopic forms to giant clams with 1.5 m diameter or giant squids with a length of up to 20 m. Their original habitat is the sea. Only the mussels (Bivalvia) and the gastropods (snails) have adapted to brackish and fresh water and only the snails adapted to the land (terrestrial gastropods). However, also some mussels, e.g. the pea clam (*Pisidium* spec.) live in moist soil.

Gas exchange takes place in specialized respiratory organs, which are designed as gills or lungs. Most classes of the Mollusca have an **open blood circulatory system** with a pumping heart consisting of two pre-chambers (auricles / atria) and a single heart chamber (ventricle) as well as some blood vessels and blood sinuses. Only the Cephalopoda have a closed circulatory system.

The hemolymph of many mollusks contains a respiratory blood pigment, **hemocyanin**, which is only found in mollusks, crustaceans and spiders. In hemocyanin, the oxygen is bound by two copper ions. The copper atoms are bound to the protein via the amino acid residues histidine. In the deoxygenated state, hemocyanin is colorless and blue-colored after oxygen binding. Hemocyanins can form extraordinarily large, extracellular molecules. Molluscan hemocyanins can reach a molar mass of up to 8 million Daltons. A few freshwater snails contain hemoglobin as respiratory blood pigment.

Another unique feature of the Mollusca is the **radula** used for feeding, which is only absent in mussels. The radula is a tongue-like rasping organ with rows of posterior directed teeth (denticles). The anterior rows of outworn teeth are continuously replaced by posterior teeth.

The skin of the mollusks is often ciliated and rich in gland cells.

A digestive gland, the **hepatopancreas** ("liver") occupies most of the intestinal sac. Digestive secretions or digestive enzymes are produced in the hepatopancreas, nutrients are stored, but also in this gland digestion and resorption takes place.

The evolution of the mollusks has not yet been completely clarified. Nowadays, three classes / subclasses without a typical mollusk shell are included in the phylum Mollusca, the Caudofoveata (Chaetodermomorpha), Solenogastres (Neomeniomorpha), and the Polyplacophora (formerly Amphineura), which are collectively designated as Aculifera, as well as the five classes of mollusks with a true shell, Monoplacophora, Gastropoda (snails), Scaphopoda (tusk shells or tooth shells), Bivalvia (mussels) and Cephalopoda ("ink-fish", octopus). These five classes probably represent a monophyletic unit.

Most mollusks have separated sexes and some are hermaphroditic. In many cases a **trochophore larva** hatches from the egg, which closely resembles the larva of the annelids. In many groups of mollusks the trochophore stage is followed by another larval stage, the **Veliger larva**, which is found only in mollusks. Some freshwater snails are ovoviviparous, in which the eggs develop in the oviduct and the young are born alive.

11.3 THE SHELL OF THE MOLLUSCA

The calcareous shell of the mollusks is secreted from mantle tissue and is covered from the inside by the mantel epithelium. It usually consists of three layers, the outer **periostracum**, the **prismatic layer** and the inner pearly, lamellar or nacreous layer. Prismatic layer and **pearly layer** form the real mineral shell. The periostracum is an organic layer containing a quinone-tanned protein, the conchiolin.

The periostracum is secreted from the periostracum fold at the mantle edge. The prismatic layer consists of densely packed calcium carbonate crystals, either in the crystalline form of aragonite or calcite. The calcium carbonate crystals are embedded in a protein matrix. The protein matrix is secreted from the mantle edge, so that the size increase of the shell always occurs from the shell edge during the growth of the animals (leading to the formation of annual rings). The pearly layer is composed of very thin layers, which make is responsible for its iridescent optical properties. The matrix between the aragonite crystals gives the pearly layer certain elasticity.

Pearl formation occurs when foreign material, e.g. a sand grain or a parasite gets under the mantle and the foreign material is gradually covered with mother-of-pearl.

Metabolic processes during shell formation are often closely related to the nitrogen metabolism of the animals (Hochachka & Somero 1980, p. 186). The urea cycle, which is already functional in the terrestrial gastropods, ensures a controlled supply of ammonia at the site of shell formation. Urea is cleaved at the mantle tissue by means of a urease into NH_3 and CO_2. The NH_3 serves to dissociate bicarbonate as a proton acceptor and provides carbonate needed for the precipitation of calcium carbonate in the shell (Figure 9).

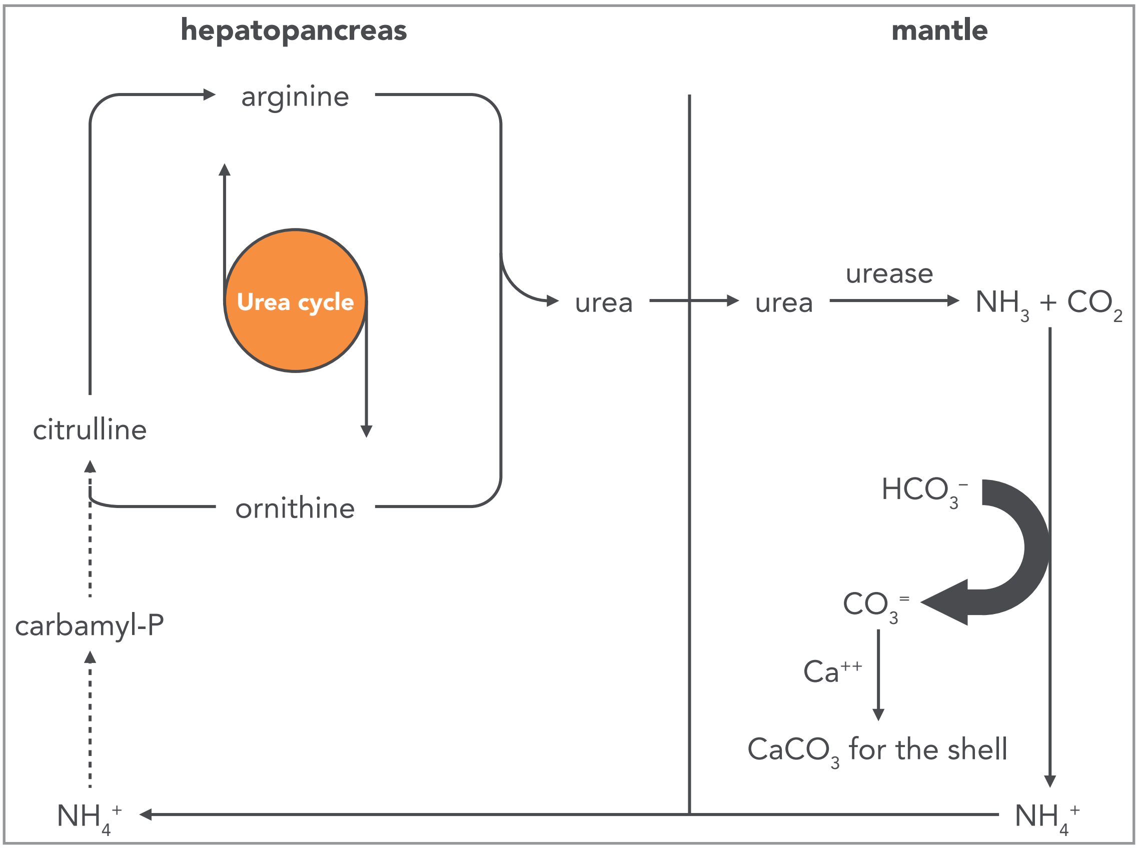

Figure 9: Controlled supply of ammonia from the urea cycle at the site of shell formation in mollusks. After Hochachka und Somero, Strategien biochemischer Anpassung, Thieme, Stuttgart, 1980.

11.4 CLASS GASTROPODA: THE SNAILS

The Gastropoda represent the largest and most diverse group of mollusks. They are basically bilaterally symmetrical. As a result of the **torsion** (a twisting of the body by 180 °, which occurs in the larval stage), its visceral mass is asymmetrical in the adult stage and often spirally rolled up. At the end of the torsion, the anus and the mantle cavity are located anteriorly and open above the head and mouth. The left gill, excretory organ, and ventricle are now on the right side of the body, and vice versa. The nerve cords are twisted to an "8" (**chiastoneury**). This torsion is especially pronounced in the Prosobranchia (gills in front of the heart). The torsion has led to a problem of accumulation of excrements in the area of the head or gills (danger of self-poisoning).

In the Opisthobranchia (gills behind the heart) and the Pulmonata (snails and slugs with a pallial lung) a varying degree of detorsion has occurred.

In snails, the foot serves as a creeping sole. The shell (missing in the nudibranchs) consists of one piece and can be rolled up or straight. With regard to the direction of rotation of the windings, the shell can be right-handed or left-handed, with right-handed shells occurring much more frequently. Left-handed snail "kings" occur with a probability of 1: 10,000 in the escargot, *Helix pomatia*. Many snails have an **operculum** (calcareous lid), with which the shell opening is closed under unfavorable environmental conditions such as drought or frost. This estivation protects the snail against dehydration and winter stagnation (see Photo 10).

In most gastropods breathing occurs via a gill, the **ctenidium** (comb or feather gill). The primary situation of two ctenidia is still found in some Prosobranchia. The ctenidia lie in the mantle cavity and are supplied with oxygen by a directed water flow. The Pulmonata have a strongly vascularized region in their mantle, which serves as a lung.

Two large blood sinuses, the **visceral sinus** and the **cephalopedal sinus** contain a large part of the hemolymph (blood). The latter also serves for the creeping movement of the snails (hydraulic mechanism).

Most gastropods have a single **(meta)nephridium**, in which the inner end (nephrostoma) opens into the coelom, in this case the **pericardium** (heart sac). The ultrafiltration of the blood takes place across the wall of the pericardium.

The feeding habits of snails are quite variable; some are herbivores, some predators and other scavengers. The **radula** is always involved in some way with food uptake. In ancient lineages of gastropods the radula was used to graze, by scraping diatoms and other microscopic algae off rock surfaces. Carnivors cut their food with the teeth of the radula. In cone snails of the genus *Conus* a gland supplies the teeth of the radula with a strong neurotoxin. When a prey is caught, a tooth is shot like a harpoon onto the victim, and the neurotoxin immediately paralyzes the prey.

Many pulmonates show complex rituals in seeking a partner. During courtship of the hermaphroditic animals, one snail shoots a "**love dart**" from a dart sac into the partner's foot. The love dart transmits a hormone-like secretion which increases peristaltic movements of the bursa copulatrix and this enhances egg production.

11.5 CLASS BIVALVIA: THE MUSSELS

Bivalvia live worldwide in salt, brackish and fresh water. They have a shell consisting of two parts, called valves. These are joined together along one edge by a flexible ligament that forms a hinge. Most mussels are filter feeders, getting their food with cilia from the water stream. The head is extremely reduced and a radula is not present. The foot is wedge-shaped and can be used for digging or jumping.

Some mussels are able to swim short distances with jerky movements of their double shell. Gas exchange takes place over the mantle and the gills. Originally simple ctenidia evolved to filter gills. Generally the gills follow the curvature of the shell margin with the maximal possible surface exposed to the water flow. Each gill is made up by numerous W- or double V--shaped lobes (filament). Each V is known as a demibranch and each lobe is called a lamella. In more primitive **lamellibranchs** the neighboring gill filaments are attached to one another through interlocking clumps of cilia (**filibranch type**). In more advanced bivalves the neighboring filaments are joined to each other at regular intervals by tissue, leaving narrow openings or ostia between them (**eulamellibranch type**). Hemolymph vessels flow through the lamellae. A counter flow of water and blood (hemolymph) results in an efficient oxygen exchange.

Pairs of nephridia are connected to the pericardium via the reno-pericardial canal.

In filter-feeding bivalves there is a cylindrical stylus-sac in the stomach, which produces a gelatinous rod, the **crystalline stylus**. At the tip of the rotating stylus, digestive enzymes, in particular amylase, are released. In the marine drilling mussel, *Teredo navalis*, the shell is converted into drilling tools, which are used to drill channels or tubes into submerged wood up to 20 cm long. The cellulosic components of the wood are converted into sugars by endogenous cellulases.

In sand or mud digging and drilling mussels, the mantle is often elongated and forms a siphon, so that the mussel can obtain oxygen and food even when submerged in the substrate. Other species, such as the common edible mussel, *Mytilus edulis*, attach themselves to the substrate by means of **byssus** threads from the byssus gland. For positional changes the byssus threads can be enzymatically resorbed. The threads of the noble pen shell, *Pinna nobilis*, were processed into the finest textiles already in the antique world (byssus silk). Bioadhesives derived from marine sources, such as the byssus silk, are regarded as promising materials for medicine, industry and nature, as they enable controllable adhesion in aqueous environments (Sure et al., 2014, p. 3392).

11.6 THE CEPHALOPODS (CEPHALOPODA)

Cephalopods are predatory marine animals. They include the squids, octopuses, and cuttlefish, nautiloids and the extinct ammonites and belemnites. The modified foot is located in the head area. The anterior portion of the foot is fused with the head and forms the arms and tentacles. The arms and tentacles are provided with suckers, the tentacles only at the ends. The number of arms is eight. The Octobrachia, e.g., *Octopus* have eight arms, the Decabrachia, e.g., *Sepia* and *Loligo* have ten. The mantle is very muscular. The shell of the nautiloids resembles a snail shell. It is subdivided by transverse walls into chambers, which can be filled with gas for buoyancy. In the other cephalopods, the shell is very reduced and is located into the body (internal shell) and enclosed by the mantle tissue. The **cuttlebone** of the cuttlefish also serves buoyancy. Gas deposits between the aragonite frameworks provide static buoyancy. Another internal shell is found as **gladius** in squids and octopuses.

Fossils of the cephalopods date back to the time of the Cambrian (about 500 million years). Giant squids from the deep sea can reach a length of 18–20 m and a weight of up to one ton. They are the largest known invertebrates.

Most cephalopods move by **jet propulsion**. With great force they eject water through a ventral siphon out of the mantle cavity. The active lifestyle is associated with a high oxygen requirement. The two gills (Dibranchiata), with the exception of the nautiloids (Tetrabranchiata), lie in the mantle cavity. The circulatory system is closed. Accessory hearts or gill hearts lie at the base of each gill and increase the blood pressure in the capillaries supplying the gills.

Nervous system and sensory organs are highly developed. Cephalopods possess the largest brain of all invertebrates with millions of nerve cells. Squids have enormous nerve fibers (giant axons). Cuttlefish are among the most intelligent of all invertebrates. With the exception of the nautiloids, the cephalopods have complex **lensed eyes** (everted retina), which are very similar to the vertebrate eye type (inverted retina). However, the structure and function of the photoreceptors have greater similarities with the photoreceptors in the complex eye of the insects than with those of the vertebrates.

Cephalopods have special skin cells, the **chromatophores**, which contain pigments or dyes. The chromatophores are surrounded by tiny muscle cells, which, by contraction and relaxation, cause different distribution of the pigments in the cells and thus enable a controlled **color change**. The color change is used in either signaling or active camouflage. An amber or black liquid (ink with melanin) can be expelled from the ink sac located at the anus. Numerous species of squids in the deep sea are capable of **bioluminescence** (production of light).

The cephalopods have separated sexes. Juvenile animals hatch from the eggs; there are no free swimming larvae. Some species, e.g. *Octopus*, provide **parental care** to their offspring and are guarding their egg clutches.

11.7 THE TRANSITION FROM WATER TO TERRESTRIAL LIFE AMONG THE MOLLUSKS

The great diversity among mollusks is reflected in the transition from aquatic to terrestrial life. The acquisition of a shell as evaporation protection and the conversion of the mantle cavity with gills to a lung allow the air-breathing snails (Stylommatophora, Eupulmonata) to live on land. If the shell is reduced, as in the nudibranchs, they can only live in very humid habitats.

Other important adaptations to terrestrial life are the direct development without larval stages and the excretion of **uric acid** (uricotelic) as the nitrogen-containing metabolic end product. Water-living mollusks generally excrete **ammonia** as an end product (ammoniotelic). The transition from ammoniotelic to uricotelic excretion can be well followed in the *Littorina* species living in the intertidal zone of rocky coasts. The uric acid concentration in the nephridia increases from 1.5 mg / g dry weight in *L. littorea* through 5 mg / g in *L. saxatilis* to 25 mg / g in *L. neritoides* (Gerlach 1994, p. 197). *L. neritoides* lives the farthest up in the splash zone.

11.8 SPECIAL METABOLIC PATHWAYS IN MOLLUSKS

In addition to the above mentioned ability to synthesize urea in the hepatopancreas for shell formation (see Figure 9), many mollusks have specific pathways of anaerobic energy production. Aquatic mussels and snails often colonize habitats with low supply of oxygen (**environmental** or **ambient anoxia** / anaerobiosis). Animals living in the tidal zone, e.g. the mussel *M. edilus*, encounter periodically dry conditions at low water for hours and cannot absorb oxygen from the water through their gills during this time. A biotope-induced (environmental) anoxia occurs. The production of chemical energy, ATP, during this time through succinate / propionate fermentation is already discussed in worms, with an ATP yield of up to 8 moles ATP per mole of consumed glucose (see Figure 7). Under aerobic conditions, 1 mole of glucose provides 36 moles of ATP.

In addition to the environmental anaerobiosis, in some mollusks, especially in the foot and mantle tissue, a **functional anoxia** can occur during intense movement. While in mammals and humans lactic acid is produced in skeletal muscles as the end product of glycolysis, anaerobic end products such as octopine, alanopine, strombine or lysopine are found in the mollusks (see Figure 7). In all cases there is a reductive condensation of pyruvate with an amino acid. As with lactate fermentation, the energy yield is 2 moles of ATP per mole of used glucose.

11.9 IMPORTANCE OF MOLLUSKS FOR HUMANS

In addition to afore mentioned pearl breeding, mollusks have always had a diverse influence on humans. Many species of snails, mussels and cuttlefish serve as food for humans. Due to their high filtration efficiency, they can accumulate secondary toxins e.g. from algae and dinoflagellates in their body. Consumption of these poisons can lead **to mussel intoxication** despite cooking of the food. The neurotoxin **saxitoxin** derived from dinoflagellates can be enriched in mussels, scallops or oysters, and is one of the most frequent causes of mussel poisoning.

Cone snails (genus *Conus*) also contain toxins (conotoxins) that can be fatal to humans. They are peptides of 8 to 32 amino acids. The toxin comes from a venom gland and is used for capturing fish. Some of these toxins are used in medicine as painkiller (analgesic).

From the secretion of the hypobranchial gland in the mantle of some *Murex* species (Muricidae), a **purple dye** has been obtained for textile dyeing for more than 2,000 years. The two most common Mediterranean species, *Murex brandaris* (purple dye murex or spiny dye murex) and *Truncularіopsis trunculus* (banded dye murex), served mainly as sources of purple. Chemically, purple is 6-6'-dibromoindigo ($C_{16}H_3Br_2N_2O_2$).

Cowry shells, especially *Monetaria moneta*, were used for centuries as currency. Cowry currency is mainly known from the South Pacific region, but also from Africa. North American Indians used the shells of white and reddish jackknife clams as jewelry and as currency. Shell money was especially used for buying food, but also for purchase of a bride.

11.10 REVIEW QUESTIONS

1) Which pathways of anaerobic energy production are found in the Mollusca under environmental and functional anoxia?
2) Describe the formation of a real pearl in a shell.
3) To which areas is the coelom of the mollusks restricted?
4) How can one recognize the age of a shell (mussel)?
5) What was the problem of survival with the development of torsion in gastropods?
6) Describe the manner of swimming and the mechanism of food intake in the cephalopods.
7) How can cephalopods communicate in the deep sea?

12 PHYLUM TARDIGRADA (WATER BEARS OR MOSS PIGLETS)

12.1 LEARNING OBJECTIVES AND KEYWORDS

The relatively simple tardigrades are one of the smallest phyla in the animal kingdom. They are known for their enormous resistance to extreme environmental conditions. In a kind of rigid state (decreased physiological activity; cryptobiosis), tardigrades survive long periods of complete dryness, extremely low temperatures and the vacuum in space.

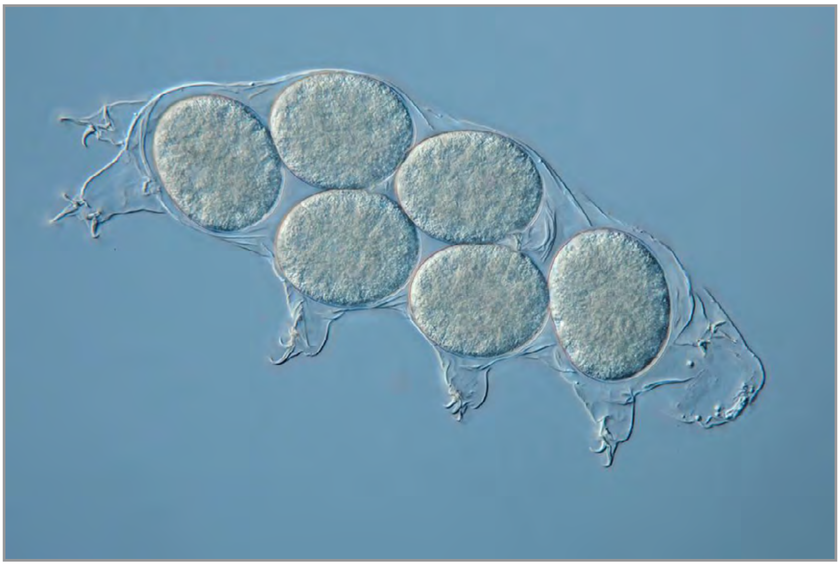

Photo 11: Moss piglet *Hypsibius dujardini* with eggs in the body (Lebendkulturen.de / Shutterstock.com).

- Molting
- Hemocoel
- Malpighian tubules
- Parthenogenesis
- Cryptobiosis.

12.2 SYSTEMATICS AND CHARACTERISTICS OF TARDIGRADA

With only about one thousand species, the tardigrades are one of the smallest phyla in the animal kingdom. The tiny animals live terrestrial in water films on mosses and lichens or in damp soil. A few species are found in the ocean. Tardigrades share features common with the arthropods, but also with the velvet worms (Onychophora).

Tardigrades have barrel-shaped bodies with four pairs of **stubby legs** carrying four to eight claws (see Photo 11). The body consists of a head, three body segments and a caudal segment, and is covered by a non-chitinous cuticle. The animals molt at least four times (Ecdysozoa) in their life cycle. With a stylet at the mouth opening, the tardigrades penetrate plant or animal cells and absorb the fluids out. Between the midgut and rectum, three glands open into the digestive tract, which probably have an excretory function and are called **Malpighian tubules**. The body cavity is a **hemocoel**. A coelom is found only around the gonads. There is neither a circulatory system nor respiratory organs.

Tardigrades are **eutelic**. Some species have as many as 40,000 cells in the adult stage, while others have far less. They usually have separated sexes, but in some species males are unknown and parthenogenesis (virgin generation) is the main form of reproduction. In other species, dwarf males are known.

12.3 CRYPTOBIOSIS IN TARDIGRADES

Cryptobiosis is a state in which the metabolic processes are extremely reduced. The oxygen consumption is decreased to very low values. In this state (dauer stage or suspended state of animation), the animals can survive prolonged periods of extreme environmental conditions. There are several types of cryptobiosis:

- Anhydrobiosis – formation of suspended state by dehydration.
- Anoxibiose – caused by low oxygen content in the environment.
- Anosmobiose – triggered by high salt concentrations in the environment.
- Cryobiose – triggered by extremely low temperatures.

Cryptobiosis is typical for Tardigrada, but it also occurs in some nematodes and in wheel animals (Wright et al., 1992, p. 1) (see above).

During stepwise desiccation, the water content of the tardigrades can drop from about 85 percent to 3 percent of body weight. The animals no longer move and the body assumes a barrel-shaped form. In the state of cryptobiosis, tardigrades can tolerate temperatures from +150 °C to -272 °C, but also ionizing radiation or withstand preservatives such as ethers and ethanol. According to recent research, tardigrades can survive in the vacuum of the space (Jönsson et al. 2008, p. R729). After years, the animals can return to normal activities if there is sufficient moisture to hydrate the body.

Protective molecules, such as the disaccharide **trehalose**, protect proteins and membranes during dehydration, which would otherwise be irreversibly damaged (Erkut et al., 2011, p. 1331). The protective effect on membranes is probably due to the formation of hydrogen bonds to the polar groups of the phospholipids in the membrane.

12.4 REVIEW QUESTIONS

1) Which environmental factors can cause cryptobiosis in some animals?
2) What is the value of cryptobiosis for the survival of tardigrades?

13 PHYLUM ONYCHOPHORA (VELVET WORMS)

13.1 LEARNING OBJECTIVES AND KEYWORDS

The velvet worms represent a very small phylum of the animal kingdom. They combine features of the Annelida with features of the Arthropoda. They belong to the clade of the Ecdysozoa.

Photo 12: The velvet worm *Peripatus* on a stamp from New Zealand (Galyamin Sergej / shutterstock.com).

- Epitheliomuscular tube (skin-muscle tube)
- Tracheal system
- Ladder nerve cord
- Chitinous cuticle
- Hemocoel
- Ovoviviparity.

13.2 SYSTEMATICS AND CHARACTERISTICS OF ONYCHOPHORA

The caterpillar-like animals comprise only about 110 species with a body length of 0.5 to 20 cm. They live terrestrially in humid habitats in tropical and subtropical latitudes, mostly in the Southern hemisphere. The velvet worms combine annelid and arthropod features. With the Tardigrada and the Arthropoda they form the taxon Panarthropoda.

The animals have between 17 and 43 pairs of parapodia-like legs with sclerotized claws (see Photo 12). The external segmentation is suppressed. The body wall is muscular and resembles the epitheliomuscular tube of the annelids. The body cavity is a **hemocoel**, which is subdivided into compartments or sinuses, similar to the arthropods. The head bears a pair of antennae, on the base of which are annelid-like eyes (ocelli). They are predatory. Each body segment with legs contains a pair of (meta)nephridia. Respiration takes place via a **tracheal system**, a tube system with many openings (spiracles). The open circulatory system has a dorsally located tubular heart with a pair of ostia in each segment. The nervous system is ladder-like and lies on the ventral side of the animals. Onychophores possess a chitin-containing cuticle, but the rigidity of the body depends on the hydrostatic pressure of the body fluid. The cuticle is periodically stripped off by molting (ecdysis).

Onychophores have separated sexes. Only a few species lay eggs in damp places. Almost all other species give birth to living young (ovoviviparous or viviparous). The development is direct, i.e. without larvae stages.

13.3 THE MOLTING HORMONE ECDYSONE IN ONYCHOPHORA

Like the tardigrades, the onychophores belong to the clade of the Ecdysozoa.

The free ecdysteroids **ecdysone** and **20-hydroxyecdysone** were found in adult females of the species *Euperipadoides leuckartii* by the chromatographic separation of the hemolymph components and a radioimmunological detection of the ecdysteroids (Hoffmann 1996, p. 27). Ecdysone and 20-hydroxyecdysone are the molting hormones of arthropods, but their function in the velvet worms is not clear.

13.4 REVIEW QUESTIONS

1) Which hormones induce molting in the Onychophora?
2) Which structures are involved in the locomotion of velvet worms?
3) What are the characteristics that velvet worms have in common with the annelids and what in common with the arthropods?

14 PHYLUM ARTHROPODA (ARTHROPODS)

14.1 LEARNING OBJECTIVES AND KEYWORDS

The arthropods (including spiders, crustaceans and insects) are represented by an estimated 10 million species by far the largest phylum of the animal kingdom. They live in almost all habitats on earth. Their segmented body appendages (arthropodia) are eponym for the phylum. Arthropods have a segmented body, whereby several segments are combined to functional units (tagmata). Their exoskeleton of chitin and protein forms a kind of armor, which must be regularly renewed during growth by molting.

The insects have conquered the air in addition to birds and some mammals. In the case of the eusocial insect species, such as in termites and some hymenopterans (e.g. bees and ants), individuals permanently live together in nest structures and show a high degree of division of labor.

Photo 13: Horseshoe crab (subphylum Chelicerata) at the Atlantic coast of North America (rozbeh / Shutterstock.com).

- Tagmata
- Segmented arthropodia
- Chitinous cuticle / exoskeleton
- Compound eye
- Coxal, antennal or maxillary glands; Malpighian tubules
- Anamorphosis and epimorphosis
- Preoral digestion
- Direct and indirect flight musculature
- Peritrophic membrane
- Trachea
- Physical gill
- Panoistic and meroistic ovarioles
- Social organization.

14.2 SYSTEMATICS AND CHARACTERISTICS OF ARTHROPODA

The arthropods represent the most species-rich phylum in the animal kingdom. To date, approximately 1.1 million arthropod species have been described, but their estimated total number may be 6 to 10 million. The arthropods include the Chelicerata (horseshoe crabs, spiders, and sea spiders; see Photos 13 and 14), the Crustacea (crayfish; Photo 15) and the Tracheata or Antennata ("Myriapoda" and insects or Hexapoda; Photo 16).

With the annelids, the arthropods have a distinct **segmentation** of the body in common. Molecular analyzes suggest, however, that annelids and arthropods developed from different precursor forms. All arthropods have a chitin-containing exoskeleton, which enabled them to colonize almost all habitats on earth. Originally, probably all body segments had paired appendages (arthropodia). In recent species, however, an aggregation or fusion of segments to functional units, the **tagmata**, is observed.

Another characteristic of all arthropods is the reduced coelom of the adults. The largest part of the body consists of **hemocoel**, filled with **hemolymph** (blood) (**mixocoel**). The circulatory system is open and has a dorsal, contractile heart. Complex mouthparts have developed from the appendages of the head segments. Cephalization is highly advanced. The **ladder-like nerve cord** is located ventrally.

The "real" arthropods (Euarthropoda) have a pair of lateral compound eyes, while the larvae possess median ocelli. In adult animals, median or lateral ocelli may still be present on the head.

Paired excretory organs are found as coxal (e.g., in Chelicerata), antennal (e.g., in Crustacea) or maxillary glands (e.g., in some crustaceans). The insects possess **Malpighian tubules** as excretory organs. Oxygen uptake occurs over the body surface, gills (Crustacea), book lung (Chelicerata) or **tracheae** (Chelicerata and Insecta).

14.3 THE EXOSKELETON OF ARTHROPODA

The exoskeleton of the arthropods consists of a three-layered **cuticle,** which is secreted from the underlying epidermis. Under the epicuticle is the procuticle, which consists of the exocuticle and the endocuticle. The also multi-layered thin epicuticle contains waxes to protect the animal against dehydration. Only the two layers of the procuticle contain chitin. Here the α-chitin is bound to proteins or embedded in the sclerotin matrix. The exocuticle is secreted before each molt, the endocuticle after molting. The complete external "skin" is called the **integument**.

Chitin is a resistant nitrogen-containing polysaccharide, the polymer of N-acetylglucosamine. It provides the high breaking strength of the exoskeleton. The sclerotization or tanning of the proteins takes place after molting by the way of **chinon sclerotization** or **ß-sclerotization** (Gewecke 1995, p. 93). The stronger the sclerotization, the harder the cuticle becomes. In the Crustacea, the procuticle is usually strengthened by the addition of calcium salts (mineralization).

The exoskeleton of the arthropods consists of individual segmental sclerites, comparable to the armor plates of a knight's armor. Between the body segments and between the segments of the body appendages, the sclerites are flexible connected, caused by the protein **resilin**. Since the exoskeleton limits growth, the animals must periodically molt, a process that the arthropods have to throw off their outer "shell" from time to time. Molting or **ecdysis** occurs between all stages (larval molts, pupal molt, and adult or imaginal molt). Molting is controlled by the interplay of molting hormones (ecdysteroids) and juvenile hormones.

14.4 THE EXTREMITIES (LIMBS) OF ARTHROPODA

The name Arthropoda derives from the segmented extremities (**arthropodia**). Their classification is specific to the individual arthropod groups, but they can be traced back to a common basic structural design. The original biramous leg consists of a protopodite linked to the body, an exopodite attached at the outer tip of the protopodite, and an endopodite attached at the inner side. In crustaceans, gills are fixed at the protopodite. The endopodite shows the typical structure of an arthropodium, the individual segments being named differently. In many cases, the terms for the individual leg segments correspond to those for the tetrapod extremities (see Table 15). Terrestrial arthropods have reduced the exopodite and the endopodite forms the walking leg.

In the head region of all arthropod groups, the extremities are converted into antennae and mouthparts.

14.5 THE COMPOUND EYE OF ARTHROPODA

Most arthropods (except Chelicerata) have highly developed compound eyes. They consist of many individual eyes (ommatidia). The number of ommatidia within a compound eye is between 300 and 30,000. The dioptric apparatus of a single eye consists of a chitin lens of the cornea, the underlying crystalline cones and the primary pigment cells (iris pigment cells). The dioptric apparatus directs the light to the retinula cells (rhabdom). The rhabdom consists of rhabdomers, the microvilli of typically six to nine (mostly eight) visual cells (photoreceptor cells). They contain the visual pigments, where the light is converted into a nervous impulse. At the inner end of the rhabdomers nerve fibers of the downstream neurons transmit the signal and pass it onto the brain.

In insects, three types of compound eyes are distinguished, which differ in structure and neural circuitry:

i) Daily active insects have an **apposition eye**; the ommatidia are optically separated from each other by shielding pigments (dark side walls). The apposition eye achieves high temporal resolution.
ii) Night-active insects have optical **superposition eyes**. In the dark, the shielding pigments move back in direction to the lens and the incident light can also fall on the rhabdom of an adjacent ommatidium. In this way, a higher light intensity is achieved, but this is at the expense of temporal and spatial resolution.
iii) Fast-flying insects, e.g. flies have **neural superposition eyes**. Here, the performance of the ommatidia is optimized by combining the retinula cells of the functionally identical peripheral rhabdomers 1–6 by neuronal interconnection with corresponding retinula cells of neighboring ommatidia to form a **neuroommatidium** extending over seven ommatidia.

14.6 SUBPHYLUM CHELICERATA

The Chelicerata (spider-like) are divided into three classes, the Merostomata (for example, horseshoe crabs), the Arachnida and the Pantopoda or Pycnogonida. Characteristic of the chelicerates is that the first limb pair (before the mouth) forms the **chelicerae** (2- or 3-segmented appendages with chelae or subchelae). The body has two tagmata. The anterior body (**prosoma**) consists of the acron and six similar segments. The posterior part or **opisthosoma** is also usually segmented (see Table 10). Horseshoe crabs have five pairs of legs on the Prosoma, and five pairs of swimming legs (paddles) with gills on the Opisthosoma. This is followed by a long tail (telson). Horseshoe crabs of the genus *Limulus* have existed morphologically unchanged since the Trias. Only three genera are still found on flat Atlantic coasts of North America. At the time of reproduction, thousands of animals arrive at the beaches in order to mate (see Photo 13). The mating rhythm is controlled by the moon phases (lunar rhythm).

14.6.1 ARACHNIDA – THE SPIDERS

The arachnids show a great deal of morphological variation. **Scorpions** have a relatively short cephalothorax (prosoma), which bears the chelicerae, pedipalps and four pairs of legs. The anterior part of the abdomen (mesosoma) consists of seven segments and the posterior part (metasoma) consists of five segments (Table 10). The metasoma ends in a sting apparatus on the telson. The **venom** of most scorpions is not dangerous to humans, but can lead to painful swelling at the injection site. The venom of some African and Mexican species can be deadly. Scorpions are viviparous. The female gives birth to living offspring after several months of development, which crawl on the mother's back after birth and remain there until after the first molt.

The spider body is very compact and consists of a **prosoma** and an **opisthosoma**, both of which are usually unsegmented. At the anterior end of the prosoma are a pair of chelicerae ("jaws") with a hollow fang (venom ejaculation) and a pair of leg-like pedipalps, and up to eight non-compound eyes. The four pairs of walking legs have claws at their ends (Table 10). The walking legs are divided into coxa, trochanter, femur, patella, tibia, metatarsus and tarsus. Spiders are predatory and often digest their food outside the body (**preoral** or extraintestinal). The intestine is often provided with large diverticula. In the opisthosoma, the **book lungs** and / or **tracheae** serve for respiration. Book lungs consist of many parallel hemolymph-filled lamellae in an air-filled invagination of the integument. The hemolymph contains **hemocyanin** as a respiratory pigment. The tracheae of the spiders are similar to those of insects, but have evolved independently. The same applies to the unique excretion system, the **Malpighian tubules**, which form a functional unit together with the rectum. In special resorption cells of the rectum, mainly water and potassium ions are recirculated. This allows the animals to live in dry habitats. Many spiders have coxal glands in the prosoma.

Segment	Horseshoe crabs		Scorpions			Spiders	
Acron							
1							
2							
3	Chelicerae		Chelicerae			Chelicerae	
4	Wl		Pedipalps			Pedipalps	
5	Wl	Prosoma	Wl		Prosoma	Wl	Prosoma
6	Wl		Wl			Wl	
7	Wl		Wl			Wl	
8	Wl		Wl			Wl	
9							
10			Genital opening			Genital opening	
11	Sl						
12	Sl			Mesosoma		Spinneret	
13	Sl	Opisthosoma				Spinneret	
14	Sl						
15	Sl				Opisthosoma		Opisthosoma
16	Telson						
17							
18				Metasoma			
19							
20							
21			Telson				

Table 10: Segmentation of the body in several classes of Chelicerata.

Wl, walking leg; Sl, swimming leg with gills.

Silk glands and **spinnerets** are located in the opisthosoma. About 38,000 spider species build a web for catching prey. The most common web forms are the spiral orb webs, canopy-like webs or a funnel web. Spider silk is a composite material mainly of proteins. In the silk gland the silk is gel-like and the formation of the silk thread is accomplished by spinning. The spider pulls the thread with the hind legs out of the spinneret; water is lost and the proteins polymerize. Threads made of spider silk are extremely resilient. Recently it has become possible to produce **spider silk** biotechnologically for industrial and medical purposes (Römer & Scheibel 2007, p. 306).

Females lay their eggs in a cocoon of spider silk. The young animals leave the egg sack after the first molt and have to molt during growth up to twelve times before the adult stage is reached. Only little is known about the hormonal control of molting in spiders.

Most spiders are harmless to humans and help in the fight against insects and other arthropod pests. In the tropical and subtropical regions of the world, however, there are some species that can be **toxic** to humans and possibly lead to death. These include the southern black widow, *Latrodectus mactans,* the brown recluse spider, *Loxosceles reclusa*, Australian funnel weavers of the genus *Atrax*, and the species of *Phoneutria* native to Central America.

14.6.2 TICKS AND MITES

Ticks and mites (Acari) are the most important group of arachnids, both medically and economically. Their body shows no segmentation or partition. Mouthparts, chelicerae, and pedipalps are merged to the **gnathosoma** or capitulum, a piercing / sucking apparatus, which is distinctly separated from the body. Adult Acari have four pairs of legs, the larvae only three. The fourth pair of legs appears during molting from the larval stage to the first nymphal stage (**anamorphosis**, see below).

Many mites and ticks are (ecto)**parasites** on domestic animals and humans and can transmit many diseases. Others are economically important plant and storage pests.

The scabies mite in humans (*Sarcoptes scabei*) penetrates and burrows into the subcutaneous tissue. Hair follicle mites of the genus *Demodex* live in the hair follicles of mammals. In honey bees, the ectoparasitic Varroa-mite, *Varroa destructor*, is known as the world's most important bee pest and the reason for the world-wide decline in honey bee populations. Some mites can transmit Protozoa, Rickettsia and other bacteria, as well as viruses and fungi to humans with their saliva when biting. Ticks can transmit viruses inducing tick-borne encephalitis (TBE), tick typhus fever (spotted fever) and **borreliosis**. Lyme borreliosis, which is transmitted by *Ixodes* species, is the most common infectious disease transmitted by arthropods in Central Europe.

14.6.3 PYCNOGONIDA – THE SEA SPIDERS

About 1,000 species of sea spiders live in marine habitats. On the North Sea coast, the pycnogonids are only a few millimeters long (*Pycnogonum litorale*), whereas in polar waters, especially the Antarctic, they reach a leg span of up to 1 meter. The body is usually very small, the generally four pairs of legs, however, are very long. The sea spiders are also called Pantopoda. In some species, segments are duplicated so that the animals can have five or six pairs of legs.

P. litorale lives together with the common littoral crab, *Carcinus maenas*, e.g. in the rocky shoreline of Helgoland (Germany). The crabs take sea spiders as potential prey to their mouth, but disgorge them immediately. The sea spiders have a chemical defense strategy. In response to mechanical contact, *Pycnogonum* excretes 1,000 to 10,000 times more molting hormones or **ecdysteroids**, than an arthropod needs for molting, through pores on the body surface (Photo 14). In the secretion eight different ecdysteroids were identified (Rehfeld & Tomaschko 1996, p. 31). The common littoral crab contains membrane-bound steroid receptors at the base of their mouthparts, with which they sense the ecdysteroids and then disgorge the prey in a reflex-like manner.

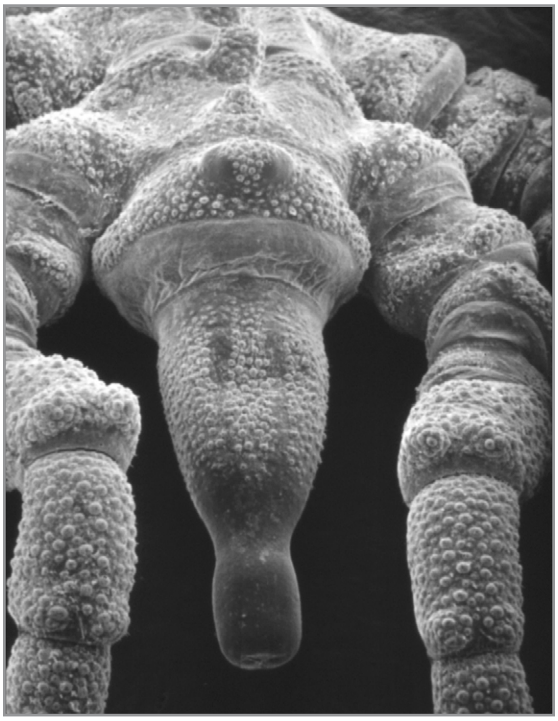

Photo 14: Pores for the secretion of ecdysteroids on the body surface of *Pycnogonum litorale* (K.H. Tomschko, Ulm).

14.7 SUBPHYLUM CRUSTACEA

In contrast to other arthropods, crustaceans possess two pairs of antennae on the head (Diantennata). The mandibles (Mandibulata) and maxillae on the head also play a role in sensory perception in addition to their primary role of crushing food and bringing it to the mouth. The number of tagmata is variable, but higher in the derived forms of the Crustacea (head, thorax, abdomen, pleon). The number of segments is 16 to 20, but some species can have up to 60 segments. Often one or more thoracic segments are fused with the head to a **cephalothorax**. Body appendages on the thorax and abdomen are mainly locomotory (running or swimming). All appendages were originally branched (biramous leg).

Most crustaceans are marine (see Photo 15), but many occur in fresh water and some are terrestrial. Respiratory organs, if present, are designed as gills. In many crustaceans, the dorsal cuticle is extended over the head and sides, forming a protective covering called a **carapace.** In the Decapoda (ten-footed crustaceans) the sides of the carapace enclose the gill cavity. A pair of tubular glands, which serve as an excretion system, end either at the base of the antennae (antennal glands) or at the base of the second maxillae (maxillary glands). The nervous system of the Crustacea is very similar to that of the annelids. Compound eyes are used as light-sensory organs.

Photo 15: Crabs on the shore of the Baltic Sea (Dirke Peschke www.kostenlos-fotos.de).

Crayfish (spiny lobster) show a direct development without larvae stages. However, most crustaceans pass through several larval stages and undergo a metamorphosis before reaching the adult stage. The most common larval form of the Crustacea is the **Nauplius** larva. Nauplius larvae bear only three pairs of body appendages, unbranched antennules, branched antennae, and mandibles, all of which serve also for swimming.

Molting is controlled hormonally. A group of neurosecretory cells in the X-organ of the brain produce a molt inhibiting hormone (MIH). The MIH is transported via axons of the X-organ to the sinus gland and there released into the hemolymph. A decrease in the MIH concentration of the hemolymph triggers the release of the molting hormone ecdysone from the Y-organ, and thus initiates the molting process. In crustaceans, in contrast to insects (see below), there is a **molt-inhibiting principle** of regulation. The role of the juvenile hormone in crustaceans is taken over by methyl farnesoate, which is produced in the mandibular organ (Laufer & Biggers 2001, p. 442). In contrast to the insects, the Crustacea continue to molt as adult animals.

The systematics of Crustacea is still controversial. Usually, six to eleven classes of Crustacea are distinguished: the Branchiopoda (with, for example, fairy shrimp, *Artemia*, *Daphnia* and other water fleas), the Copepoda, the Ostracoda and the Malacostraca (higher crustaceans). The Malacostraca include the Euphausiacea or light-emitting "shrimps" (e.g. the krill), the Decapoda or ten-footed crustaceans (e.g., crayfish and lobster) and the Isopoda (woodlice and relatives). The isopods are the only crustaceans that successfully exist in terrestrial habitats.

14.7.1 THE ORDER DECAPODA

The Decapoda comprise about 18,000 species with great diversity in their morphology (see Photo 15). However, they all have tagmata, the cephalothorax with eight thoracomeres and the abdomen or pleon. The first three thoracopod appendages have evolved into mouth parts. The following five pairs of thoracic appendages are the walking legs. All thoracopods carry gills lying in the respiratory (gill) cavity formed by the carapace. The large exopodite of the second maxilla produces the flow of water through the gill cavity necessary for respiration.

Decapods have a size between a few millimeters to about 60 cm long. In the Japanese giant crab (*Macrocheira kaempferi*), the appendages reach a span of 3.7 m. Most of the decapods live on the sea bottom or in the intertidal zone. Some species have migrated to fresh water and even onto land (e.g., coconut crab *Birgus latro*). However, for reproduction these terrestrial decapods must return to the water.

Decapods are important both ecologically and economically. Numerous species are appreciated by humans as a delicacy. Shrimp species living in warm water are cultivated in large aquacultures in India, Southeast Asia, and the USA.

A typical larval stage of decapods in addition to the Nauplius larva is the **Zoëa** larva. Appendages and new body segments are added during the life cycle through a series of moltings. This form of development is called **anamorphosis**. If the development takes place completely within the egg, and after hatching from the egg only a size increase and the formation of the gonads takes place, this is called an **epimorphosis**.

14.8 SUBPHYLUM ANTENNATA (TRACHEATA)

Antennata, the sister group of the Crustacea, are mainly terrestrial. Secondarily, numerous groups have migrated back into fresh water. Only one genus of "marine" insects, *Halobates*, lives in the ocean, or better on the surface of the sea.

Characteristic features of the Antennata are their highly branched tracheae, which extend as far as to the mitochondria of the flight muscles, and the uniramous body appendages (Uniramia). Excretion occurs via Malpighian tubules.

The term "**Myriapoda**" is used for a subphylum with four classes: the Chilopoda or centipedes, the Diplopoda or millipedes, the Pauropoda, and the Symphyla. Diplopoda and Pauropoda are grouped into the Dignatha (only two pairs of mouth parts). Together with the Symphyla, they form the Progoneata (sex opening in the anterior part of the body). While the Myriapoda still show a relatively strong homonymous segmentation, the Hexapoda (Insecta) show a heteronomous metamerism, with three tagmata, head, thorax and abdomen. An overview on important features of Myriapoda is given in Table 11.

Chilopoda	Diplopoda	Pauropoda	Symphyla
15–170 pairs of legs	>100 pairs of legs	9 pairs of legs	12 pairs of legs
First pair of legs changed to mandibles with poison claw	Diplosegments each with two pairs of ganglia and spiracles	Without tracheae and circulatory system	Tracheae end in a pair of spiracles on the head
Tracheae with spiracles in almost every segment	Calcified cuticle	Dwarfs	Without pigments and eyes
Predatory in the soil, night active	Herbivorous	Leaf litter decomposer	Leaf litter decomposer
Lithobius, Scolopendra	*Glomeris*	*Pauropus*	*Scutigerella*

Table 11: Characteristics of the Myriapoda

14.8.1 SYSTEMATICS AND CHARACTERISTICS OF INSECTA (HEXAPODA)

Insects are the most species-rich animal group on earth. The insects are divided into wingless (**Apterygota**) and winged forms (**Pterygota)**. Diplura (two-pronged bristletails), Protura (coneheads) and Collembola (springtails) are primarily wingless and the mouthparts are retracted in the head. Therefore, they are called Entognatha. In some textbooks, these three taxa are referred to as non-insect hexapods. The Thysanura (silverfish and bristle tails) are also primarily wingless, but have exposed mouthparts (Ectognatha). The Pterygota or wing-bearing insects are divided into 23 to 28 Orders or Superorders (see Photo 16). Representatives of the most recently detected Order **Mantophasmatodea** or gladiators were first described in 2002 (Klass et al., 2002, p. 1456). All known species of this Order are found in Africa.

Photo 16: The Mediterranean (two-spotted) field cricket, *Gryllus bimaculatus* (K.H. Hoffmann, Bayreuth).

Winged insects exist in all habitats on earth with the exception of the ocean. Their overall distribution is based upon their high degree of adaptability, their resistant exoskeleton and their ability to fly. The head consists of the acron and six segments; the thorax of three segments, each with a pentamerous pair of legs (coxa, trochanter, femur, tibia, and tarsus), and the abdomen of originally eleven segments plus telson. The telson often carries cerci (mechanical sensors). Larvae and nymphs have a great variety of abdominal appendages.

Insects exhibit a range of paired **mouthparts** adapted to particular modes of feeding: chewing, siphoning (sucking fluids), piercing and sucking, and sponging. The mouthparts typically consist of a labrum, a pair of mandibles and maxillae, a labium, and a tongue-shaped hypopharynx.

The cuticle of each body segment is usually formed by four **sclerites**, a dorsal tergum, a ventral sternum and two lateral sclerites. In addition to the compound eyes, there are often three ocelli found on the head. The multifunctional antennae serve as mechanical receptors, olfactory organs (pheromones) and as receptors for temperature and humidity.

In addition to the legs, the meso- and the metathorax usually bear a pair of **wings**. In the Diptera, the posterior wings are reduced to the **halteres**. In beetles, the front wings form the wing-cases or **elytra**. The wings are cuticular lateral extensions of the thoracic tergum produced by the epidermis. Ectoparasitic insects like bugs and fleas are often secondary wingless.

The nutrition of insects is highly variable and ranges from herbivory (leaf pests, plant juice suckers etc.) over predation to saprophagy, i.e. a diet of dead animals and plants. As ectoparasites, many insects suck blood from mammals. Some parasitic species are attacked by other parasites (**hyperparasitism**). A particular case of parasitism is found in numerous species of wasps. They live as larvae in the body of other insects (e.g., butterflies) and complete a large part of their larval development there. The host is consumed by the developing larvae and finally dies. Such "parasites" are referred to as **parasitoids** (lethal parasites).

As are the mouthparts, the digestive tract is well adapted to the diet. A pre-digestion of food mixed with saliva from the salivary glands can take place in the crop. The main sites of digestion are the midgut and the caeca. The excretory organs (Malpighian tubules) open into the intestinal tract at the junction between midgut and hindgut. The foregut and hindgut are lined with cuticle and are molted. The interior of the midgut contains a cylindrical membranous sheath, the **peritrophic membrane**, which encloses the solid food in the midgut and ensures a compartmentalization of the midgut lumen. The peritrophic membrane is absent in insects which feed on liquid diet.

Cells of the salivary glands in many dipteran larvae contain **polytene** (oversized) **chromosomes**. These can be prepared from the cells rather easily, stained and visualized in the microscope.

The circulatory system is an open system (hemocoel). In addition to a dorsal aorta, accessory pulsatile organs assist the hemolymph flow through the antennae, the wings and the legs. Transverse diaphragms divide the hemocoel into sinuses (pericardial sinus, perivisceral sinus, perineural sinus), which provide for a directed hemolymph flow. With the exception of some fly larvae living in water, which have hemoglobin in their blood, insects do not have respiratory pigments in the hemolymph. Oxygen transport occurs via the tracheal system. The **tracheae** and tracheoles are lined with cuticle and are molted. Gas transport in the tracheal tubes occurs through diffusion and/or convection. Many insects can open or close their respiratory openings (**spiracles**) as required, thus varying oxygen consumption in particular body regions. Many insects also regulate the release of carbon dioxide by means of controlled opening of the spiracles (**discontinuous CO2 release)**, probably a mechanism to save water when exhaling.

The number of **Malpighian tubules** varies between two and a few hundred. The tubules end blindly in the hemocoel and their anterior ends enter the intestinal tract at the junction between midgut and hindgut / rectum. Functionally, the Malpighian tubules form a unit with the rectum, which contains so-called resorption cells. The system allows a very effective absorption of salts and water, which is particularly important in insects living in dry habitats. Uric acid is excreted as the nitrogen-containing metabolic end product.

14.8.2 ADJUSTMENTS IN BREATHING TO A LIFE UNDER WATER

The tracheal system evolved basically for air breathing, but many insect larvae, nymphs and adults are, however, aquatic. The nymphs of stoneflies, mayflies, or damselflies (Zygoptera) bear tracheal gills, thin-walled cuticle extensions with rich tracheal supply. Larvae of dragonflies (Anisoptera) breathe with gills on the rectum. Mosquito larvae hang with their siphon at the abdomen on the water surface and breathe directly air.

Adult water beetles of the genus *Dytiscus* spend most of their time under water surface. They take up oxygen from an air bubble, which they carry with them underwater and which must be renewed from time to time. This is called a **volume-variable physical gill**. An incompressible, i.e. volume-constant, physical gill is a thin film of air (**plastron**), which is maintained in position by hydrofuge hairs or scales on the body surface. Insects with a plastron do not have to surface for to breathe. A plastron enables the insect to remain below water surface indefinitely, obtaining all the oxygen it requires from the surrounding water. Plastron respiration is found in stream-dwelling bugs and some beetle species.

14.8.3 INSECT FLIGHT MECHANISM

Movement of the wings is accomplished by the interaction of an assembly of muscles in the thorax. There are two types of flight muscles (Figure 10):

- **Direct flight muscles** are attached directly to the base of the wings and transfer the movement directly to the wings (mayflies, dragonflies and damselflies).
- **Indirect flight muscles** (dorsoventral muscles and longitudinal muscles) cause the thorax to vibrate. The wings as extension of the dorsal thorax are moved indirectly by these vibrations.

The movement of the wings with direct flight muscles allows only relatively low wing beat frequencies (10–40 per second), such as found in cockroaches, grasshoppers and dragonflies (restricted by the latency or refractory time of the action potential in the muscles). Even in the case of direct flight muscles, only the downstroke is direct. The upstroke is caused by the contraction of indirect muscles, which pull the tergum against the sternum. Pure indirect flight muscles (along with asynchronous control, Table 12) allow wing beat frequencies of up to 1,000 per second, as can be found in some dipterans.

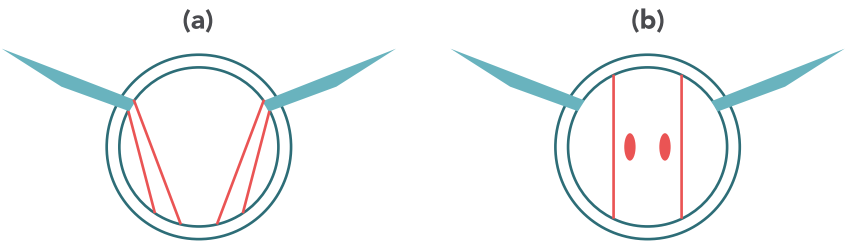

Figure 10: The direct (a) and indirect (b) flight muscles in insects.

The neuronal control of flight muscle contraction can occur in two ways, synchronously or asynchronously. Synchronous control often occurs with direct flight muscles, the asynchronous mechanism occurs only in indirect flight muscles. In the asynchronous control, the muscle contraction does not occur in phase with nervous stimulation. The types of flight-muscles also differ in their histological structure (Table 12).

<table>
<tr><th colspan="2" rowspan="2">Histology</th><th colspan="4">Physiology</th></tr>
<tr><th>Mechanics</th><th>Activation</th><th>Interlinking</th><th>Rhythm</th></tr>
<tr><td rowspan="2">”non fibrillary“</td><td>tubulary</td><td>direct</td><td rowspan="2">neurogenic</td><td rowspan="2">electro-chemical</td><td rowspan="2">synchronous</td></tr>
<tr><td>closed-packed</td><td rowspan="2">indirect</td></tr>
<tr><td colspan="2">“fibrillary” oscillatory</td><td>myogenic</td><td>mechano-chemical</td><td>asynchronous</td></tr>
</table>

Table 12: The flight muscle types in insects. After Dettner & Peters 2003, p. 248.

14.8.4 REPRODUCTION AND LIFE CYCLES IN INSECTS

Insects have separated sexes and fertilization usually occurs internal. Parthenogenesis is found in some homopterans (aphids) and hymenopterans (for example, drones of the honeybee).

In females, three different types of ovarian maturation and oogenesis occur in three different types of ovaries / ovarioles:

- **Panoistic atrophic ovaries**: in this basal type of oogenesis, the growing oocyte is supplied with yolk from the hemolymph via the oocyte-surrounding epithelial follicular cells. The yolk material (vitellogenin) usually comes from the fat body. The oocyte itself, however, also synthesizes yolk. This type of ovary is found in insects of more primitive Orders, such as in cockroaches and crickets.
- **Meroistic polytrophic ovaries**: the growing oocytes are supplied with yolk material, rRNA and cell organelles from nurse cell, which lie between the oocytes. This type occurs for example in butterflies.
- **Meroistic telotrophic ovaries**: the oocytes are supplied with material, which is transported from nurse cells in the germarium through nutritive cords. This type occurs for example in beetles.

The postembryonic development can proceed in three ways:

- **Ametabolous** (paurometabolous): direct larval development without metamorphosis. The larva resembles the sexually mature adult animal. No special larval organs can be found. This type of development is found in the Entognatha and the Archeognatha, for example in silverfish.
- **Hemimetabolous**: incomplete metamorphosis. Larva and adults differ in appearance. Special larval organs are present. The last larval stage molts to the imago. Larval stages of the Pterygota are still without wings. Imagines usually do not molt any more. This type of metamorphosis is found in cockroaches, crickets, and locusts.
- **Holometabolous**: complete metamorphosis. A pupal stage is required between the last larval stage and the imaginal stage. During complete metamorphosis, there is not only a change in he external shape, but a complete reorganization of the internal organs occurs. This type is found in dipterans, lepidopterans and beetles.

In some aphids, a life cycle with parthenogenesis alternating with sexual reproduction is found (heterogeneity), often associated with a change of the plant host. In the spring, a wingless **fundatrix** hatches from the overwintered egg on the primary host, which spreads to the secondary host and multiplies there parthenogenetically over many generations. In late summer male and female (winged) sexes appear (**sexuales**), which mate and the females deposit fertilized overwintering eggs on the primary host.

Insects in the temperate zones often undergo a **diapause** under unfavorable environmental conditions, as in the winter. This period of developmental rest can occur in all stages of the life cycle, from egg to adult stage in different insects. The most frequent type is a seasonal diapause in the pupal stage of holometabolous insects. Diapause is a prospective (preplanned) dormancy, the resting stage is preprogrammed by the brain and is triggered by environmental factors. The trigger for a winter diapause is usually not the low temperature but the decreasing photoperiod (transition to short-day conditions, critical photoperiod) in autumn.

14.8.5 THERMOREGULATION AND FREEZING RESISTANCE IN INSECTS

Insects are poikilotherms (ectotherms). Their body temperature usually corresponds to the ambient temperature. However, some species are capable of heating and maintaining their body temperature at a value far above ambient temperature (for example, about 40 °C at an outside temperature of 19 °C) under certain conditions and for a limited time. In butterflies, this occurs in the morning hours by **sunbathing**, that is heating up by a special behavior. Moths (hawk moths) heat up in the evening before flight through "**muscle shiver thermogenesis**". In doing so, they bring their flight muscles in the well isolated thorax by wing vibrations to the required operating temperature of almost 40 °C. Excess heat produced during steady flight is emitted to the environment via hemolymph through the uninsulated abdomen.

Some bumblebees produce body heat in their flight muscles by a chemical pathway (**non-shivering thermogenesis**). Honeybees regulate their stock temperature either by water evaporation (cooling) or by muscle shiver thermogenesis (heating) in summer to about 35 °C and in winter to about 20 °C. This occurs in the social union of the animals (social thermoregulation).

Many insects overwinter in protected areas, e.g. in houses or in the soil. However, some species survive outdoors at body temperatures of up to -80 °C without "freezing". Two strategies of non-freezing are observed, **freezing resistance** (tolerance) and **freezing avoidance**. In the case of freezing tolerance the hemolymph (extracellular fluid) freezes early in the winter. For this purpose, potential freezing nuclei (e.g., ice nucleating proteins) are present in the hemolymph. The ice formation in the extracellular fluid osmotically extracts water from the cells. In addition, within the cells anti-freezing compounds, e.g. polyhydroxy alcohols (glycerin) accumulate. Thereby, freezing of the cell water (intracellular water) is prevented. Intracellular freezing would destroy the cell membranes and kill the animals. In freezing avoidance, antifreezing agents (polyhydroxy alcohols and antifreeze proteins) are incorporated into intra- and extracellular fluids and the freezing point of all body fluids is greatly reduced.

14.8.6 ENDOCRINE TISSUES AND HORMONES IN INSECTS

The molting hormones or **ecdysteroids** are produced in the prothoracic glands or ventral glands of insect larvae. Adult insects synthesize ecdysteroids in epithelial cells of the abdomen and/or in the follicular cells of the ovaries. Ecdysone must be converted to 20-hydroxyecdysone, which functions as an active molting hormone. The **juvenile hormones** of insects are produced in the corpora allata at all stages of development. Most insects have only juvenile hormone III (JH III, C 16-juvenile hormone), but JH I (C 18-JH), JH II (C 17-JH) and JH III are regularly present together in the Lepidoptera. Other JH homologs (bisepoxides) were found in dipterans and homopterans. Their function is similar in all cases, the preservation of the juvenile character in larval and nymphal stages, and the promotion of yolk formation (vitellogenesis) in adult females.

The synthesis of ecdysteroids and juvenile hormones is controlled by **neuropeptides.** Prothoracicotropic hormones induce the synthesis of molting hormones (activating principle in insects) before each molt. Allatostatic and allatotropic neuropeptides inhibit or stimulate the synthesis of juvenile hormones. Many other neuropeptides are synthesized in the brain; most control the energy metabolism of the animals (for example, the adipokinetic hormone from the corpora cardiaca), the ion and water balance, muscle contractions, and many other physiological functions (Gewecke 1995, p. 132). The induction of diapause can also be controlled by a neuropeptide, the diapause hormone.

In the context of an integrated pest management (IPM, which mainly uses ecologically friendly control mechanisms to keep pests under an economically harmful level), attempts have been made to combat pest insects "with their own weapons". For example, **hormone analogues** (e.g., methoprene, hydroprene and fenoxycarb) and **anti-hormones** (e.g., precocenes) are used to interfere with growth and development of pest insects, thereby keeping the populations below a harmful threshold (Dettner & Peters, 2003, p. 355).

14.8.7 SOCIAL ORGANIZATION IN INSECTS

The degree of social organization in some insects can show a very high complexity. In the case of the **eusocial** termites (Isoptera) and some hymenopterans (ants, bees and wasps), a permanent coexistence of the individuals in nest structures with a high degree of division of labor (caste formation) is observed. The individual cannot survive by itself and must have the help of partners (Tautz & Heilmann 2007, p. 155). Other characteristics of eusocial life are cooperative brood care (including brood care of offspring from other individuals), overlapping generations within a colony, and a division of labor into reproductive and non-reproductive groups.

Other insects form only temporary and uncoordinated communities, either to withstand unfavorable weather conditions or to obtain food. They are called **presocial** or subsocial.

C**ommunication,** which is necessary in social life can be optic, acoustic (sound production, for example in grasshoppers, crickets or cicadas), or chemical (pheromones). A special form of social communication is found in bioluminescent insects. The generation of optic signals by means of bioluminescence is used in "fireflies" for sexual selection. Cave-dwelling fungus gnat larvae lure their prey with a luminous "filament" (Hoffmann 1981, p. 97).

14.8.8 IMPORTANCE OF INSECTS FOR HUMANS

Most people consider insects primarily as **pests**, but there are many more **beneficial species** as pests. Many insects provide humans with useful materials such as honey, silk or wax. The pollination of crops by insects is of existential importance to man. Predatory insects and parasitoids can destroy harmful insects and are increasingly used in biological pest control. In some countries of the world, insects (such as crickets and grasshoppers or beetle larvae) are becoming increasingly important as food for humans.

Harmful insects include those that feed on crops, fruits, or seeds and are considered collectively as agricultural or storage pests. Insects can also destroy human resources such as clothes (clothes moths) or wood (termites, house borer, bark beetles). About 10 percent of the insects are ectoparasites that attack their host without living on or inside it. Blood sucking can transmit numerous diseases in humans, e.g. Malaria (see above).

Insect **cell cultures** are used in biochemistry, pharmacy and biomedical research, for example for the production of recombinant proteins and vaccines. Typical model organisms from which cell lines are obtained for insect cell cultures are *Bombyx mori*, *Mamestra brassicae*, *Spodoptera frugiperda*, *Trichoplusia ni,* and *Drosophila melanogaster*.

14.9 REVIEW QUESTIONS

1) Discuss the contribution of the cuticle to the evolutionary success of the arthropods.
2) Which are the tagmata of the arachnids, and which tagmata bear body appendages?
3) Describe the molting process of crustaceans, including the hormones involved.
4) Describe the photoreceptor unit of a compound eye. How are compound eyes adapted to different light intensities?
5) Explain why the indirect and asynchronous flight muscles allow for higher wing beat frequencies than direct flight muscles.
6) Describe at least three types of mouthparts in insects and indicate the type of diet they are suitable for.
7) Describe four ways of communication between insects.
8) How can harmful insects be treated? What is meant by "integrated pest control"?

15 PHYLUM ECHINODERMATA (ECHINODERMS)

15.1 LEARNING OBJECTIVES AND KEYWORDS

The echinoderms represent the first branch of the Deuterostomia ("second mouth" animals). As a result of their embryonic development, the nervous system lies on the back (dorsal) and the heart on the ventral side. All echinoderms are marine. Their body shape is characterized by a pentagonal radial symmetry, but the larvae are often bilaterally symmetrical. A special feature of the echinoderms is their water vascular system, in which the ambulacral or tube feet are used for locomotion. Their numerous spines grow out of the calcareous endoskeleton and are covered by an epidermis.

Photo 17: The purple sea urchin, *Sphaerechinus granularis* (Joze Mancec / Shutterstock.com).

- Deuterostomia
- Notoneuralia
- Pentaradial symmetry
- Dipleurula larva
- Hydrocoel, axocoel and somatocoel
- Mesodermal calcareous endoskeleton
- Ambulacral or tube feet
- Acrosome reaction and cortical reaction
- Holoblastic radial cleavage
- Invagination and gastrulation.

15.2 SYSTEMATICS AND CHARACTERISTICS OF ECHINODERMATA

Echinodermata are one of the seven recent phyla or subphyla of the **Deuterostomia**. According to recent phylogenetic and comparative developmental biology studies, four phyla / subphyla of the Xenambulacraria (Axoelomorpha, Xenoturbella, Echinodermata and Hemichordata) and three phyla of the Chordata (Leptocardii, Tunicata and Craniata) are grouped within the Deuterostomia. They are primary bilaterally symmetrical animals (**Bilateria**), in which the **blastopore** (first opening) becomes the anus during embryonic development, and the mouth secondarily breaks through the **archenteron** (primary gut).

In the early stages of embryonic development, typical deuterostomes show late-determined radial cell cleavages. The coelom arises from pockets of the archenteron by enterocoely. Deuterostomes, therefore, are also known as **enterocoelomates**. During embryonic development, the nervous system comes to be located on the dorsal side (neural tube; Notoneuralia), while the heart lies on the ventral side (Figure 11).

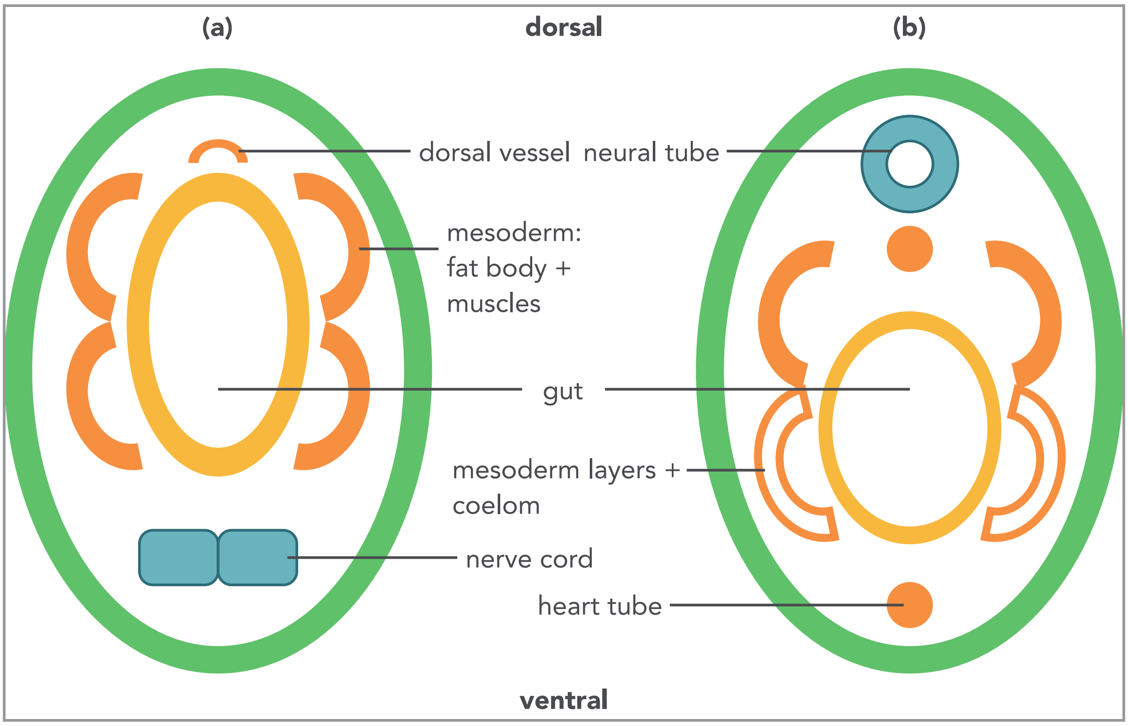

Figure 11: Body shape during inversion of the dorsoventral axis from the protostomes (Gastroneuralia, a) to the deuterostomes (Notoneuralia, b). After Wehner und Gehring, Zoologie, Thieme, Stuttgart, 2013.

The echinoderms are marine animals with a calcareous endoskeleton. Other features are their water vascular system with the ambulacral feet, a functionally hitherto unexplained hemal system, pedicellariae on the body surface, dermal branchia (papulae) or skin gills for respiration, and a trimeric coelom. Excretory organs are absent. A bilaterally symmetrical larva changes during the metamorphosis into a pentagonal radial symmetrical adult animal.

Systematically the echinoderms are divided into two subphyla with a total of six classes: the Crinoidea (crinoids; Pelmatozoa) with the "sea lilies" and feather stars, and the Eleutherozoa with the starfish (Asteroidea), the brittle stars (Ophiuroidea), the sea urchins and sand dollars (Echinoidea), and the sea cucumbers (Holothuroidea). Crinoids are primarily stalked (stem) and live sessil. They are comprised of three basic sections; the stem, the calyx, and the arms. Crinoids feed by filtering small particles of food from the sea water with their feather like arms. The tube feet can flick food particles into the ambulacral groove, where cilia transport them to the mouth.

Eleutherozoa are free moving echinoderms living on a sandy or rocky substrate. They exhibit an oral-aboral axis; the oral side is usually directed to the substrate.

15.3 ASTEROIDEA – THE STARFISH

Starfish or sea stars consist of a central disc, from which the arms radiate. Starfish have usually five arms, but there are species with up to 40 arms. The mouth is located at the center of the oral (ventral) surface. Most starfish are predators and feed on a variety of invertebrates. On the oral side of each arm, an ambulacral groove extends from the mouth to the tip of the arm, with an ambulacral channel in the middle, from which rows of tube-shaped feet or ambulacral feet arise.

On the aboral (dorsal) side of the body, minute, forceps-like, motile pedicellariae are located, which serve to clean the body surface, but sometimes also for capturing prey. The end of the intestinal tract (anus) and the circular madreporite, a calcareous sieve (the entrance to the water vascular system) are also located on the aboral side. The calcareous plates of the mesodermal endoskeleton are covered by the epidermis. The hemal system is poorly developed in the starfish. It seems to play a role in the distribution of digested food compounds in all echinoderms. Starfish do not appear to have any mechanisms for osmoregulation. The nervous system consists of three levels of ring and radial nerves. Starfish lack a centralized brain. Sensory organs are poorly developed.

15.4 ECHINOIDEA – THE SEA URCHINS

In the about 1,000 species of recently living sea urchins, the compact body is enclosed in an endoskeletal corona. The typical pentaradial symmetry is reflected in the arrangement of the skeletal plates. Five double rows of ambulacral plates (with the openings for the ambulacral feet) and interambulacral plates are located from the oral to the aboral end. Most sea urchins belong to the "regular" sea urchins (Regularia) and have a hemispherical shape, radial symmetry, and long spines (see Photo 17). The Irregularia (sand dollars, heart urchins) have become secondary bilaterally symmetrical. They have only short spines, which they mainly use for locomotion.

The pedicellariae on the body surface of sea urchins are tridentate.

Five movable teeth surround the mouth of a regular sea urchin. The teeth are attached to a complex chewing apparatus called Aristotle's lantern. The food usually consists of algae and other organic material that sea urchins graze from the substrate.

15.4.1 COELOM FORMATION IN THE ECHINODERMATA

The primarily sessile mode of life in adult echinoderms has as a consequence led to a reduced importance of coelom as a hydroskeleton. Rather, the larval left mesocoel (hydrocoel) forms the liquid-filled ambulacral system in adult animals (Table 13), which consists of a ring canal and five radial canals. The ambulacral system is connected to the axocoel via the stone canal. The right hydrocoel degenerates. A lacuna-rich axial gland surrounding the stone canal and the ciliary canals of the madreporite are formed from the left protocoel. The axial sinus, a connection of the axocoel to the aboral ring canal of the metacoel, is a remnant of the right protocoel. The left and right metacoel (somatocoel) form the genuine body cavity. It surrounds the gut and contains the gonads. The oral canal with its five radial canals lies below the mesocoel; the aboral ring canal contains the gonads in five pockets.

The larval coelom	Coelom of adult animal
Left protocoel	Axocoel
Right protocoel	Axial sinus
Left mesocoel	Hydrocoel with oral ring canal and five radial canals; center of the ambulacral system around the gut; connection to the axocoel via stone canal
Right mesocoel	degenerates
Left metacoel	Somatocoel
Right metacoel	Somatocoel

Table 13: The coelomic system of the Echinodermata.

15.4.2 SEA URCHINS – A MODEL ORGANISM FOR DEVELOPMENTAL BIOLOGIST

Sea urchins have separate sexes and release their eggs and sperm into the water for extracorporeal fertilization. Spermatozoa find the egg chemotactically. When the sperm is in contact with the plasma membrane of the egg, the vitelline membrane is elevated locally and the "**fertilization hill**" is formed. By the contact of the sperm cell with certain molecules on the jelly coat of the egg, a vesicle, the acrosome vesicle, fuses in the sperm's head with its plasma membrane, and releases its content by exocytosis.

In the following, so-called acrosomal process, a protuberance, forms at the apex of the sperm head. Hydrolytic enzymes are released during the **acrosome reaction**, which allow a rapid penetration of the sperm through the jelly coat. The tip of the acrosomal process carries numerous copies of a protein, bindin (a 30,000 mol-wt protein), which specifically binds to receptor molecules (bindin receptors) on the vitelline membrane.

After contact between sperm and vitelline membrane or plasma membrane of the egg, the so-called cortical granules discharge their content into the perivitelline space and form an extracellular envelope around the egg, the **fertilization membrane**. This membrane represents a barrier against the penetration of further sperm, thus preventing polyspermy. This cortical reaction affects the entire surface of the egg. The stimulus appears to be mediated by a wave of calcium ion influx. During the cortical reaction the sperm is absorbed into the plasma of the egg cell. This leads to the fusion of the haploid gametes to form the diploid zygote (fertilization).

Eggs of sea urchins are poor in vitellins and show a complete (total), holoblastic **radial cleavage**. The vegetative pole can be recognized by its pigmentation. During the first two cleavages, the fertilized egg cleaves along the animal-vegetal axis that means meridional (longitudinal). The third, equatorial cleavage separates the embryo into an animal and a vegetal half. The fourth cleavage is again meridional and occurs in the animal hemisphere; the vegetal hemisphere cleaves equatorial and unequal. While the eight cells in the animal hemisphere, also known as **mesomeres**, are approximately equal-sized, four large **macromeres** and four small **micromeres** are found in the vegetal hemisphere as result of the unequal cleavage.

When the embryo reaches the blastula stage (120-cell stage), a cavity is formed, the **blastocoel**, which is surrounded by a layer of equal-sized cells. The prospective cells of endoderm and mesoderm are located on the vegetal pole, while cells at the animal pole form the prospective ectoderm. During **gastrulation**, the migration of endoderm and mesoderm into the interior of the embryo begins with the transformation of the mesoderm forming cells into primary mesenchymal cells. In the following **invagination** of the endoderm cell layer, the **blastopore** ("Urmund") is formed. The following further stage of gastrulation (secondary opening of the mouth) leads to a bilaterally symmetrical **Dipleurula** larva or, for example, a **Bipinnaria** larva. This larval form transforms into other larval stages in the different taxa of echinoderms (e.g., into a **Pluteus** larva in sea urchins) (Groepler 1986, p. 186).

15.5 HOLOTHUROIDEA – THE SEA CUCUMBERS

Sea cucumbers are anatomically and physiologically one of the most curious animals on earth. In contrast to the other echinoderms the sea cucumbers are elongated in the direction of the oral-aboral axis. The calcareous endoskeleton is greatly reduced; the skin has a leathery consistency. The body is secondary bilaterally symmetrical. The opening of the mouth is surrounded by oral tentacles, 10 to 30 retractable modified ambulacral feet. The gut ends in a cloaca, into which the paired "water lungs" (respiratory trees) also open. Sea cucumbers can reach a length of up to 2.5 m. In the Asia-Pacific region, the pickled innards of sea cucumbers are eaten as delicacies.

15.6 REVIEW QUESTIONS

1) Describe the development of a sea urchin egg up to the Pluteus larva.
2) Explain the terms: pedicellariae, madreporite, respiratory tree, and Aristotle's lantern.
3) Describe the transformation of the larval coelom to the coelom of an adult sea urchin.

16 PHYLUM HEMICHORDATA (HEMICHORDATES)

16.1 LEARNING OBJECTIVES AND KEYWORDS

The hemichordates are the smallest group of the deuterostome animals. Characteristic are the gill pores lateral on the trunk and the gill slits or pharyngeal slits in the anterior section of the digestive tract.

Photo 18: The acorn worm *Ptychodera flava* (Enteropneusta) (Keoki Stender, www.marinelifephotography.com).

- Tricoelomatic body plan
- Proboscis
- Gill pores and gill slits
- Neurocord.

16.2 SYSTEMATICS AND CHARACTERISTICS OF HEMICHORDATA

The Hemichordata are marine, worm-shaped sea bottom inhabitants with only about 100 species worldwide. According to their name, they represent the ancestors of the Chordata (chordates). Their systematic position is, however, still controversial. The Hemichordata show the typical tricoelomatic body plan of the Deuterostomia. The anteroposterior axis is divided into three parts: the anterior prosome (**proboscis**), the intermediate mesosome (collar), and the posterior metasome (trunk). Other characteristics are the **gill pores** on the sides of the trunk and the **gill slits** in the side walls of the pharynx, as well as their so-called "chorda", which is a buccal derivate = **stomochord** in the posterior part of the proboscis, not homologous to the Chorda dorsalis of the chordates (see below).

The circulatory system includes dorsal and ventral vessels as well as a dorsally located heart. Excretory organs are absent. Hemichordates have properties in common with the Echinodermata and with the Chordata.

Hemichordata are divided into two classes, the **Enteropneusta** or acorn worms (Photo 18) and the **Pterobranchia**. The proboscis is the active part of the animals in acorn worms and it is used for foraging or food intake. There are no gills at the gill pores. Instead, the gas exchange occurs through the body surface. Swellings of their subepithelial nerve network form a dorsal and a ventral nerve cord. The dorsal nerve cord (**neurocord**) results from an invagination of the ectoderm, similar to the prototype of the dorsal nerve cord of the chordates. Larvae of the acorn worms (**Tornaria larva**) resemble in some phases of their development the Bipinnaria larva of starfish.

The Pterobranchia are sessile, often several animals life together (colonial) in tubes of collagen. They have only one pair of gill pores. The collar bears five to nine pairs of arms with ciliated tentacles, which are used for food intake. The colonies can be produced asexually by budding.

Recent molecular biology studies on the genome of two species of acorn worms confirmed the affiliation to the Deuterostomia by the detection of numerous deuterostome-specific novel genes. The hemichordate genome shows extensive synteny with the lancelet fish genome (see below) (Simakov et al., 2015, p. 459).

16.3 REVIEW QUESTIONS

1) Which findings indicate a kinship between the Hemichordata and the Echinodermata? Which indicate a kinship with the Chordata?

17 PHYLUM CHORDATA (CHORDATES)

17.1 LEARNING OBJECTIVES AND KEYWORDS

Chordates have evolved the vertebrate body plan from simple prototypes. Chordates show an enormous adaptation to almost all habitats on earth. The five characteristic features of the Chordata are the notochord (Chorda dorsalis), a dorsal hollow nerve cord (neural tube), pharyngeal slits, the endostyle, and a post-anal tail. The body segmentation is often restricted to the outer body wall, head, and tail. The tetrapod extremities (limbs) enable an efficient locomotion on land and in the air.

The phylum Chordata includes the urochordates or tunicates, the cephalochordates or Cephalochordata, and the vertebrates or Vertebrata, which include the fish, amphibians, reptiles, birds and mammals. Birds and mammals are the only warm-blooded animals in the animal kingdom (homeothermy). They maintain their body temperature between 37 and 42 °C, regardless of the outside temperature. The evolutionary success of the reptiles, birds and mammals is largely due to the evolution of the amniotic egg. Amniota can lay their eggs on land. The amniotic egg allows a rapid development of large young animals in a dry environment. In the Placentalia, the offspring develop in the female's uterus until they are mature enough for birth.

- Endoskeleton
- Chorda dorsalis (notochord)
- Pharyngeal slits
- Peribranchial cavity
- Endostyle
- Hox genes
- Ammocoete larva
- Chondral skeleton and bone skeleton
- Placoid scales and teeth
- Primitive temporomandibular joint, primary TMJ and secondary TMJ
- Genito-urinary system
- Portal vein
- Air bladder and lunge, gas gland
- Amnion
- Tetrapod limbs
- Cardio-pulmonary circulation and aortic arches
- Metanephros and loop of Henle
- Homeothermy
- Placentalia.

17.2 SYSTEMATICS AND CHARACTERISTICS OF THE CHORDATA

The phylum Chordata belongs to the deuterostomic tribe of the animal kingdom. From simple prototypes, the Chordata have evolved the vertebrate body plan, which shows an enormous adaptation to almost all habitats on earth. The body plan of the Chordata shows features of many non-chordatic invertebrates, e.g. bilateral symmetry, anterior-posterior axis, coelom, metamerism, and cephalization. In addition, the five characteristic features of the Chordata are:

- **Chorda dorsalis** (notochord): a flexible rod that traverses the whole body on the dorsal side and represents the first part of the endoskeleton. In most vertebrates the Chorda dorsalis is replaced by the spine (backbone).
- **Neural tube**: a dorsal tubular, hollow nerve cord. In vertebrates, the anterior end is enlarged to form the brain.
- **Pharyngeal slits**: in fish, the slits are modified to form gills, but in some other chordates they are part of a filter-feeding system that extracts food particles from the water. Thus, a conversion of the pharynx from a filter apparatus for feeding into a respiratory organ occurred.
- **Endostyle**: localized in the ventral wall of the pharynx, secretes mucus, in which small food particles are collected. Some cells of the endostyle secrete iodine-containing proteins. In the higher vertebrates, the thyroid gland evolved from the endostyle.
- **Postanal tail**: gives the Chordata their mobility together with the somatic muscles and the Chorda dorsalis.

The segmentation is often restricted to the external wall of the body, the head and the tail, and does not apply to the coelom. During evolution, paired body appendages have been adapted as flexible extremities (tetrapod extremities or tetrapod limbs) for efficient locomotion on land and in the air (wings). The heart lies, at least in early developmental stages, on the ventral side of the body (see Figure 11).

The phylum Chordata includes two recent groups of protochordates, the subphylum Urochordata with the Tunicata and the subphylum Cephalochordata with the lancelets, plus the subphylum Vertebrata or Craniata. The Vertebrata are divided into two superclasses, the Agnatha (jawless fish) and the Gnathostomata (jawed vertebrates).

17.3 UROCHORDATA – THE SUBPHYLUM TUNICATA

The Tunicata are traditionally subdivided into three classes, the Appendicularia or Copelata or Larvacea, the Ascidiacea or sea squirts (see Photo 19) and the Thaliacea or salps. According to recent molecular biological studies, however, the sea squirts do not constitute a monophylum. All tunicates are marine, living either sessil in the benthos (adult sea squirts) or pelagic (free-floating; salps and Appendicularia).

Photo 19: Blue sea squirt of the genus *Rhopalaea* from Indian Ocean (Jung Hsuang / Shutterstock.com).

A common feature is their tunica, a cuticle of **cellulose** (tunicine), which is secreted from the mono-layered epidermis. Often, only the tadpole-like, free-swimming larvae show the typical characteristics of the Chordata. During metamorphosis, the Chorda dorsalis, which is restricted to the tail in the larva and the tail itself, disappear. The dorsal nerve cord is reduced to a ganglion. In adult animals, the U-shaped intestine, together with the gonads, opens via a cloaca together with the outflow of the peribranchial cavity (siphon). Excretory organs are absent. The circulatory system consists of a ventral heart and two adjacent larger vessels.

Sea squirts are hermaphrodites, which means they have an ovary and testes in the same animal. Fertilization of the eggs occurs in the water. In all tunicates, asexual reproduction by budding may occur (colony formation). In the salps, a regular alteration between sexual and asexual reproduction occurs (**metagenesis**). Thus they reach high densities under favorable living conditions (phytoplankton blooming).

17.4 SUBPHYLUM CEPHALOCHORDATA – THE LANCELETS

The Cephalochordata or Acrania were an extremely successful animal group in geological history. Today only three species of lancelets exist (Photo 20). Lancelets are slender, fish-like, translucent animals that live on sandy bottom near the coast. They exhibit the five characteristic features of the Chordata in a distinct form:

- The pharynx with tentacles at the mouth, with **pharyngeal slits**, and which is surrounded by the peribranchial cavity (atrium) with an atriopore.
- A dorsal notochord, extended through the whole body (**Chorda dorsalis**).

- A **neural tube**, also traversing the entire body, on the dorsal side above the Chorda dorsalis.
- The **endostyle** in the ventral wall of the pharynx.
- **Postanal tail** with fin-like edges. The body musculature is clearly segmented (**myomers**).

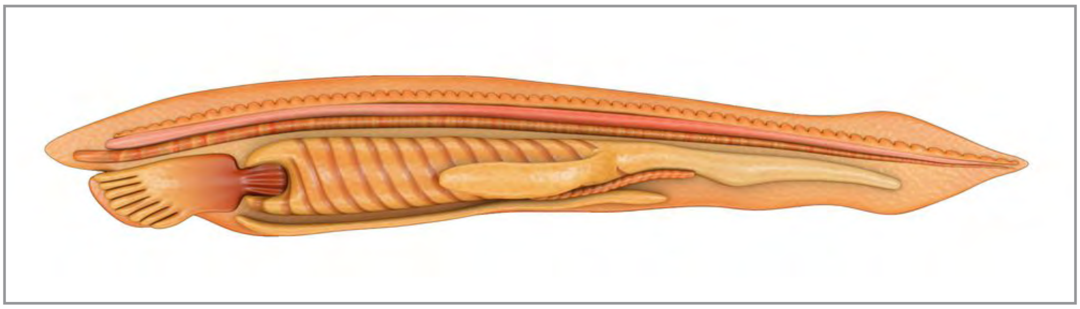

Photo 20: The lancelet *Branchiostoma* (*Amphioxus*) (sciencepics / Shutterstock.com).

The **closed circulatory system** is similar to that in primitive fish. The hepatopancreas (hepatic caecum or liver) is attached to the gut and is traversed by the **hepatic portal system**. Portal systems are venous regions of the circulatory system that specifically transport nutrients from the intestine to the liver, hormones within the brain (hypophyseal portal system) or blood within the kidney (renal portal system). Since the blood of lancelets does not contain respiratory pigments, it is more important for nutrient transport rather than gas exchange. The excretion of metabolic end products is achieved by numerous nephridia, which end individually in the peribranchial space. The sexes are separated, and fertilization takes place in the water.

17.4.1 DEVELOPMENT OF LANCELETS

For a long time lancelets were regarded as prime example for the evolution to the vertebrates. Today, however, it is known that the tunicates are genetically closer to the vertebrates than the lancelets.

The fertilized egg undergoes six **radial cleavages** up to the formation of the coeloblastula. **Gastrulation** occurs by invagination, which means tissue inversion and enveloping of the endoderm. **Neurulation** does not occur by longitudinal constriction of the neural tube, as in vertebrates, but the neural ectoderm is separated from the epidermal ectoderm and overgrown by the latter. The neural ectoderm then enfolds to form the neural tube.

The Chorda dorsalis develops from the dorsal wall of the archenteron; the mesoderm arises from several dorsolateral diverticula of the primary gut. The cavities in the pockets become the coelom (paired myotome cavity and unpaired splanchnocoel). An asymmetrical larva develops through metamorphosis into the adult animal (Holland & Onai 2012, p. 167).

So-called **Hox genes** (homeotic genes) or their gene products (transcription factors) control the body plan of an embryo along the cranio-caudal (head-tail) axis. After the embryonic segments have formed, the Hox proteins determine the type of segment structures (e.g. legs, antennae, and wings in insects) that will form on a given segment. The lancelets have ten Hox genes within one cluster. In vertebrates, the number of Hox genes is much higher (e.g., 39 in the mouse) and they can usually be divided into four clusters (Hox A to D).

17.5 REVIEW QUESTIONS

1) Give the five main characteristics of all chordates and describe the function of these features.
2) Describe the differences in structure between a larval and an adult representative of the tunicates.
3) Which characteristics are common to the three phyla of the Deuterostomia?

17.6 VERTEBRATA = CRANIATA OR VERTEBRATES

The third subphylum of the chordates shows a series of new features in addition to the basic chordate characteristics. The Craniata have a cartilaginous or bony cranium surrounding the brain. The spinal cord is surrounded by cartilaginous or bony vertebrae. The Chorda dorsalis is often found only in the embryonic stage, but it is permanently present in some fish.

Depending on the presence or absence of jaws, the vertebrates are subdivided into two classes, the Agnatha or jawless fish with the hagfish or slime eels and the lampreys (Photo 21), and the Gnathostomata (gnathostomes; jawed vertebrates) with the classes Chondrichthyes (cartilaginous fish), Actinopterygii (ray-finned fish), Sarcopterygii (lobe-finned fish), Amphibia (amphibians), Reptilia (reptiles), Aves (birds) and Mammalia (mammals).

Photo 21: The Japanese lamprey, *Lethenteron reissneri* (feathercollector / Shutterstock.com).

The marine lampreys have a larval stage living in fresh water, which is called an **ammocoete**. The segmentation of their body musculature into myomers, the presence of a Chorda dorsalis, as well as the construction of their circulatory system, strongly resemble those of the lancelets. The ammocoetes, however, also have characteristics that are lacking in lancelets and which are homologous to the characteristics of vertebrates. These include, for example, a chambered heart, a three-part brain with a pituitary gland, a pronephric kidney and a true liver with gallbladder and pancreatic tissue. The ammocoete larva is, therefore, a model for the primitive vertebrate body plan.

17.6.1 CHONDRICHTHYES- THE CARTILAGINOUS FISH

Fish are poikilothermic, gill-breathing, aquatic vertebrates with fins as body appendages. The cartilaginous fish, including the sharks, rays, and chimera, have a cartilaginous skeleton, which is a degenerative characteristic. Although the bone tissue has been lost in the cartilaginous fish, there are phosphatized mineral tissues in form of teeth, spines and scales. Almost all 850 species of cartilaginous fish are marine, only 28 species are found in fresh water.

17.6.1.1 Elasmobranchii (sharks and rays)

Sharks (Photo 22) reach swimming speeds of over 60 km per hour due to their streamline shape and strong muscles. The trunk and tail muscles are segmented in form of **myomers**. In front of the ventral mouth is a tapered snout (**rostrum**). At the posterior end, the backbone bends upwards and ends in an enlarged upper lobe of the caudal fin (heterocercal). On the ventral side are the paired pectoral, pelvic and anal fins, dorsally one or two median dorsal fins. In the males, the middle part of the pelvic fins is transformed into a copulating organ, the clasper. Two paired blind ending nostrils are located at the tip of the rostrum.

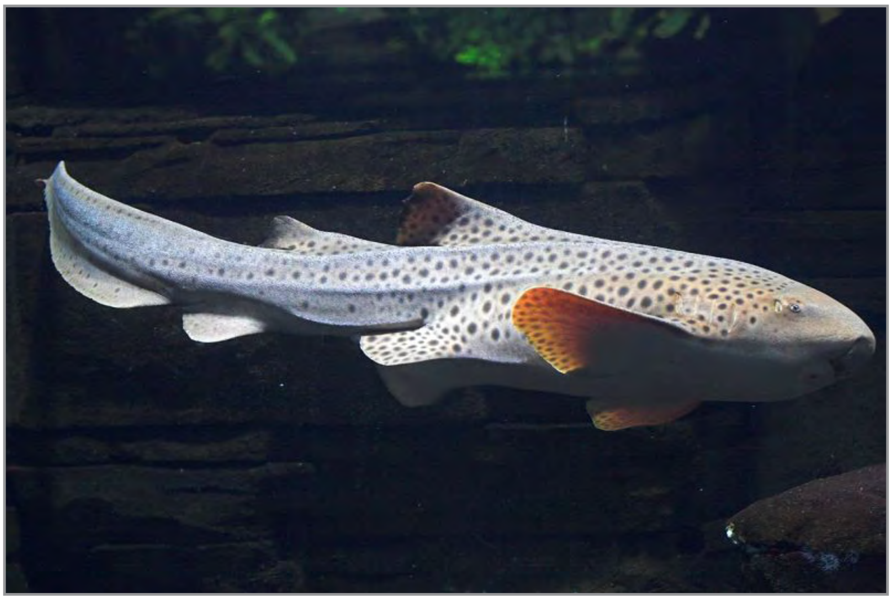

Photo 22: The polkadot catshark, *Scyliorhinus besnardi* (Dirke Peschke www.kostenlos-fotos.de).

The lateral eyes do not have eyelids. A spiracle is found posterior to the eyes, the remainder of the first gill slit. The leathery skin is covered with tooth-like, dermal denticles (**placoid scales**), which, due to their arrangement together with groove-shaped cavities in the skin (riblets), reduce turbulence when swimming. The dermal denticles of the sharks are made of dentin and enamel and are homologous to the teeth in the dentition of mammals. Modified dermal denticles are found as spines in the spiny dogfish, on the rostrum of sawfish, and as barbed stingers on the tail of stingrays.

Sharks are well equipped with very sensitive sensory organs for predatory life. They can sense their prey by means of efficient olfactory organs over miles. Prey can also be detected over long distances with mechanoreceptors (neuromasts) in the **lateral lines**. The system consists of receptor cells, which lie in the lateral line channel on both flanks and have contact with outside water through pores. Sharks also have excellent eyesight. **Ampullae of Lorenzini** are electroreceptors at the head of the shark, which can perceive extremely weak electric fields produced by the muscle contraction of prey fish (Fields et al., 2007, p. 166).

Sharks have a secondary cartilaginous endoskeleton. The Chorda dorsalis is present, but reduced. The remnants of the Chorda dorsalis are surrounded by amphicoelic, that is, anterior and posterior concave and calcified vertebrae. The cranium of the vertebrates is generally composed of three parts, the **neurocranium** or chondrocranium surrounding the brain and some sensory organs, the viscero- or **splanchnocranium**, which consists in the basic form of eight (0 to VII) consecutive branchial arches in the primary gill basket, and the **dermatocranium**, a bony coating directly under the skin, which overlies the splanchnocranium.

In the cartilaginous fish, the cartilages of the 1st branchial arch form a **primitive temporomandibular joint** consisting of the palatoquadrate cartilage (dorsal) and the mandibular cartilage (ventral). Behind the temporomandibular joint lies the hyomandible that evolved from the branchial arch II. The jaws are equipped with rows of teeth, which can be replaced at any time after loss. The dentition of the cartilaginous fish is not suitable for chewing prey.

Digestion starts in the stomach behind the branchial gut. The following midgut has an inner coiling for surface enlargement. The **rectal gland** at the end of the intestinal tract serves to regulate the ion and water balance (osmoregulation) and secretes NaCl. The blood is isoosmotic or slightly hyperosmotic compared to sea water, caused by high concentrations of **urea** (up to 600 mmoles per kg) and trimethylamine oxide (TMAO). The liver stores large amounts of oils which contribute to the buoyancy of the animals. The cartilaginous fish do not have a swim bladder.

Breathing usually occurs over five pairs of gills, which lie between the branchial arches II and VII. The circulatory system consists of a chambered heart [Sinus venosus, atrium (auricle), ventricle], and the major blood vessels are the Conus arteriosus, which pumps **oxygen-deficient** blood to the gills, the dorsal and ventral aorta, the hepatic and renal portal veins, and the anterior and posterior cardinal veins.

In all cartilaginous fish fertilization of the eggs takes place intracorporeal. Many Elasmobranchii lay large, yolk-rich eggs (oviparous), which can be surrounded by a horny shell (“Mermaid’s Purse”). Embryonic development in the egg can take up to two years. Other species are ovoviviparous or viviparous. In the latter case the embryo receives food through the maternal blood stream over a kind of placenta or by means of nutritive secretions, a uterine milk.

Types of kidney	Characteristics	Genito-urinary connections	Functional appearance
Holonephros	Kidney extends through the whole body. Many nephrotomes (one tubule in each segment) discharge excretory products into the archinephric duct or Wolffian duct	-	Larvae of hagfish
Pronephros	1–12 nephrotomes with outer glomeruli lie in the anterior part of the body. Excretory products are discharged into the Wolffian duct	-	Larvae of bony fishes (teleosts) and amphibians
Opisthonephros	Glomeruli enclosed by the Bowman's capsule (Malpighian bodies), lying in the middle and posterior part of the body. Discharge of excretory products into the Wolffian duct	Testes discharge sperm into the middle (Chondrostei) or anterior part of the opisthonephros (Pars sexualis). The Wolffian duct transports both excretory products and sperm Separation between testes and opisthonephros. Discharge of sperm through the Ductus spermaticus. The Wolffian duct serves as ureter	Elasmobranchii, Amphibia Teleostei
Metanephros	Consolidated kidney in the posterior part of the body. Discharge of the excretory products into an ureter (nephric duct)	The anterior part of the opisthonephros evolves to the epididymis. Discharge of sperm from the testes through the epididymis and the Wolffian duct, which represents a part of the spermatic duct. Discharge of excretory products through an ureter	Amniota (reptiles, birds, mammals)

Table 14: Types of kidney and the development of the genito-urinary system in male vertebrates.

The kidneys of adult cartilaginous fish are of an opisthonephros type (see Table 14). During ontogenesis, the kidneys develop through the stages of holonephros and pronephros. In males, the kidneys and ureters are closely linked to the sexual organs (**genito-urinary system**). Some cartilaginous fish already have secondary ureters (nephric duct), so that in these species the **Wolffian duct** is used only as a Vas deferens. In the females, excretory products are discharged via the Wolffian duct. A duplication of the Wolffian duct, the **Mullerian duct**, serves as oviduct. The Mullerian duct also develops in male embryos, but is later reduced. The excretory system, the sexual organs and the intestine discharge into a cloaca.

17.6.2 OSTEICHTHYES- THE BONY FISH

Bony fish are the most species-rich group of recent vertebrates, and include the two classes of ray-finned fish (Actinopterygii) and lobe-finned fish (Sarcopterygii). The latter are recently represented by only eight species, six species of lung fish and two coelacanths (crossopterygians). Characteristics of bony fishes (Photo 23) are an **operculum** of bony plates covering the gills, a gas-filled esophageal derivative, the **swim bladder**, as well as a progressive specialization of the jaw muscles and the skeletal elements of the feeding apparatus.

Photo 23: The blue discus (*Symphysodon aequifasciatus*), a bony fish (Dirke Peschke www.kostenlos-fotos.de).

17.6.2.1 Ray-finned fish

The ray-finned fish contain two main groups, the more primitive Chondrostei, which today are represented only by the sturgeon, the paddlefish, and the reedfish and bichirs, and the Neopterygii, which comprise all modern bony fish (gars, bowfins, and teleosts). The teleosts, with about 24,000 described species, represent more than 95 percent of all fish and about half of all vertebrate species. Teleosts are marine or limnic; some species periodically migrate between salt and fresh water. **Anadromous** migrating fish, such as the salmon, swim from the sea coming up rivers to spawn. **Catadromous** fish, such as the eel, swim downstream to the sea for spawning.

In bony fish, the heavy dermal armor of primitive ray-finned fish is replaced by light, thin cycloid or ctenoid scales, arranged in overlapping rows. Some teleosts (e.g., eels and catfish) do not have scales. **Cycloid scales** are nearly circular, and **ctenoid scales** are comb-shaped. All scales grow at the rate as the fish. Growth or annual rings are formed, with bright rings in summer and dark rings in winter. The annual rings can serve for age determination of the fish.

The skeleton is almost completely ossified; the caudal fin is usually homocercal, thus having equally large lobes on both sides. Fish **bones** are called connective tissue ossifications, which lie between the muscle segments and do not have any contact with the backbone.

The function of the swim bladder evolved from a primary respiratory organ (lungfish) to an organ for buoyancy. In the case of the **Physostoma** (physostomes), the swim bladder is one-chambered and connected to the intestinal tract via an air duct (e.g., in eels, pike, and salmonids). The fish swallow air to fill the swim bladder. In the **Physoclisti** (physoclists), the swim bladder is closed (Figure 12). Filling of the closed swim bladder with oxygen occurs via blood vessels (Rete mirabile, countercurrent gas exchange) and a gas gland (salting out of oxygen by means of lactic acid) (e.g., in perches, codfish, and stickleback).

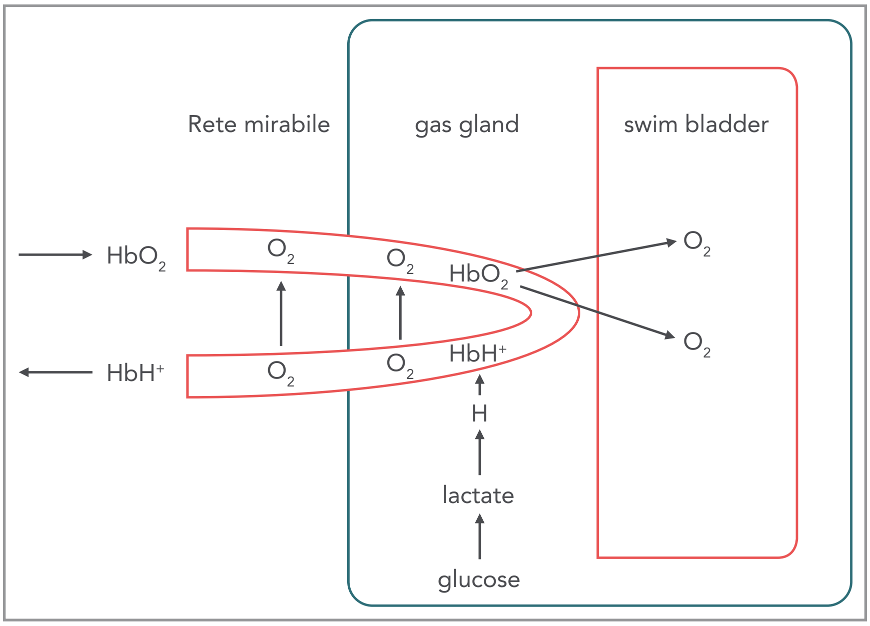

Figure 12: Gas secretion from the blood into the swim bladder of the Physoclisti. After Hochachka and Somero, Strategien biochemischer Anpassung, Thieme, Stuttgart, 1980.

The gas exchange (oxygen absorption and carbon dioxide release) in the gills is also highly efficient because of the **countercurrent principle**. The water flow through the mouth, the gill chamber and the gill filaments runs counter to the blood flow in the capillaries of the branchial lamellae.

Bony fish do not have a cloaca. Excretory organs (opisthonephros), gonads (see Table 14) (urogenital opening) and intestinal tract (anus) are discharged via separate openings.

Most fish are suitable for human consumption. However, among the bony fish as well as the cartilaginous fish, there are about 1200 species which are toxic to man. Among the most dangerous fish species are stonefish and lionfish. Both bear venomous fin rays on their back. Pufferfish have one of the most fatal nerve toxins at all, **tetrodotoxin**. The toxin is incorporated into various organs (e.g., the liver) and is probably derived from the food of the fish (e.g., poisonous blue algae, secondary toxin or poison).

In recent years, the silver-cheeked toadfish, *Lagocephalus sceleratus*, has migrated from the Red Sea across the Suez Canal into the Mediterranean Sea. Its consumption can be fatal to humans. In Japan different kinds of toxic fish are prepared by trained chefs and eaten as delicacies (fugu). During preparation, the particularly toxic ovaries and liver have to be removed without contaminating the meat.

17.6.2.2 Lobe-finned fish

The ancestors of the Tetrapoda (terrestrial vertebrates) are found in a group of extinct lobe-finned fish. Earlier lobe-finned fish had lungs as well as gills, and a heterocercal tail. The recent African lungfish, *Protopterus*, lives in streams and ponds, which dry out periodically. At the beginning of the dry season, the fish digs into the mud and secretes a large amount of mucus. Mud and mucus form a hard cocoon in which the animal survives until the next rainy season. It was for a long time thought that crossopterygians (Actinistia) became extinct 70 million years ago. However, in 1938 and 1998 two species (*Latimeria chalumne* and *L. menadoensis*) were discovered in the waters of the Comoros and Indonesia.

17.6.3 REVIEW QUESTIONS

1) How are sharks adapted to their predatory life?
2) To which external stimuli do the receptors in the lateral lines and the ampullae of Lorenzini of sharks react?
3) Describe the oxygen and carbon dioxide exchange in the gills of a bony fish.
4) Characterize the two types of swim bladders in bony fish.

17.6.4 CLASS AMPHIBIA

Amphibians are ectothermic, quadrupedal vertebrates with a **glandular skin**. Although many species have made the transition from water to land, they still depend on water for reproduction. Characteristics of terrestrial life are a strong bony skeleton, a respiration system with lungs and a pair of internal nostrils (choanae), a split circulatory system (**systemic circulation** and **pulmonary circulation**) and a modification of the sense organs for terrestrial life (e.g., ear with tympanic membrane and auditory ossicles for transmitting sound waves).

Photo 24: Common water frog or green frog (Dirke Peschke www.kostenlos-fotos.de).

The ancestors of the amphibians were crossopterygians that already possessed articulated, five-pointed limbs, but with no ability to breathe on land, as well as lungfish (Dipnoi) with lung-like excrescences of the anterior intestine (pharynx) for respiration.

The early tetrapods of the Devon era, *Acanthostega* and *Ichthyostega*, can be regarded as direct ancestors of the amphibians. While *Acanthostega* probably still lived entirely aquatic, because its limbs and the backbone were too weak to bear its weight on land, *Ichthyostega* on the other hand had fully developed tetrapod limbs and was most likely be able to walk on land. The hind limbs had seven instead of five toes. A scheme for the nomenclature of tetrapod limbs is shown in Table 15.

Forelimb		Hindlimb	
Humerus	humerus	Femur	femur (thighbone)
Radius	radius	Tibia	tibia (shinbone)
Ulna	ulna	Fibula	fibula
Carpus	carpals (wrist bones)	Tarsus	tarsals (ankle bones)
Metacarpus	metacarpals (hand bones)	Metatarsus	metatarsals (foot bones)
Phalynx	digits (fingers)	Phalynx	toes

Table 15: Nomenclature of tetrapod limbs with English and Latin names for foreleg and hind leg.

The three recent Orders of amphibians (Gymnophiona or caecilians, Urodela = Caudata or salamanders, Anura = Salientia or frogs, Photo 24) comprise about 5,400 species. During ontogenesis, most species change from aquatic to terrestrial life (**metamorphosis**). Aquatic larvae (for example, tadpoles), which breathe with gills and have a tail for swimming, hatch from the eggs, which had been deposited in the water. As aquatic animals, they excrete ammonia as nitrogen-containing metabolic end product (ammoniotelism). During metamorphosis, gills and tails are reduced and lungs as well as the tetrapod limbs are formed. As terrestrial animals, they excrete urea (ureotelism). Some salamanders retain their aquatic, larval morphology in adult life. Other salamanders and some caecilians no longer have aquatic larvae and live completely on land.

In many parts of the world, amphibian populations are currently declining. The reasons for this are climatic changes and mycosis (fungus disease).

17.6.4.1 Caecilians

Caecilians have a long, curving shape with many vertebrae, long ribs, but no limbs. Light sensory organs are very small or completely absent. They usually live burrowed in the soil. The approximately 200 species are found in the tropical rainforests of South America, Africa and Southeast Asia. Many caecilians are specialized earthworm hunters. Females lay their eggs in the damp soil; some species are viviparous. Larger species can reach an amazing age of up to 80 years.

17.6.4.2 Salamanders

The Order of Urodela comprises about 500 species of salamanders and newts. In the aquatic species, larvae hatch from the eggs with outer gills and a fin-like tail. During metamorphosis the forelegs appear first. After metamorphosis, the adults are usually terrestrial.

The real terrestrial species have a direct development without metamorphosis. Some salamanders practice **parental care** of the eggs. Depending on their different life cycles their respiration modes are variable. Salamanders can have external gills, lungs and cutaneous respiration. Some species reach sexual maturity still in the larval stage, which means they retain gills and other larval features (pedogenesis, **neoteny**). The axolotl (*Ambystoma mexicanum*) can permanently maintain gills or, in the case of drying out of its habitat, it can reduce the gills and breathe with lungs. A tympanic membrane and a middle ear are missing in the Urodela.

Salamanders live predominantly in the moderate to subtropical regions of the northern hemisphere and are exclusively carnivorous.

17.6.4.3 Frogs

The nearly 5,000 species of frogs (Photo 24) and toads live in a wide range of habitats. Their aquatic reproduction and water permeable skin prevent them from living far away from water. The eggs of the Anura are usually covered by a water-absorbing gelatin layer and are often laid onto aquatic plants. Females of the hourglass tree frog (*Dendropsophus ebraccatus*) spawn on land even during drought.

Tadpoles with gills and with a long, fin-like tail but no legs hatch from the eggs, which are all herbivorous. In young tadpoles, the gills lie outside, in older larvae inside. The metamorphosis is controlled by the thyroid hormone **triiodothyronine**. During metamorphosis the hind legs appear first, and the tail is gradually resorbed (apoptosis). As the lungs develop, the gills are also resorbed. The aortic arch VI of the larva is converted to the pulmonary artery. Lung veins transport the oxygen-rich blood to the heart.

The division into systemic and pulmonary blood circulation is still incomplete in amphibians (and also in most reptiles). Adult amphibians have only one ventricle, in which oxygen-rich and oxygen-poor blood is still mixed. Frogs are carnivorous, like most other adult amphibians.

The skin of frogs is thin and moist. Mucous glands secrete a protective mucus layer to reduce evaporation. All amphibians produce toxins in special granular skin glands, which have very different effects on humans and other mammals. The extremely poisonous toxins of South American **poison dart frogs** are used by Indians to prepare their blowpipe darts. Usually these toxins are of secondary origin (poison); the precursors of the poison are absorbed by the frogs from their food. Maintained in a terrarium the poison dart frogs are completely safe, if they are not fed their natural food (for example oribatid mites).

One of the best known amphibian poisons is the neurotoxically acting **batrachotoxin,** a steroid-alkaloid of the South and Central American poison dart frogs (Dendrobatidae). Numerous frog toxins are currently being tested in medicine as pain killers, antibiotics or cytostatics.

In all amphibians, coloration of the skin is caused by special pigment cells, the **chromatophores**. Chromatophores are highly branched skin cells containing pigments, e.g. melanin. Color change is caused by migration of pigments within the chromatophores (physiological color change). The bright coloration of dart frogs is a warning signal against potential enemies (aposematic coloration).

In terrestrial vertebrates, the backbone functions as a support for the body, to which the limbs are fixed. The Anura show a strong shortening of the body. A frog has only nine sacral vertebrae and a rod-shaped urostyle, which is formed from several mutually fused caudal vertebrae. The cranium consists of relatively few bones. Quadrate and articular bone form a **primary temporomandibular joint**. The middle ear contains a first auditory ossicle for the transmission of sound, the **columella** (homologous to the stapes or stirrup of mammals), which evolved from the hyomandible cartilage of fish (see Table 16).

The lungs of adult frogs are sack-shaped structures with a small inner surface area. To the oral cavity, the lung opening can be closed by means of the glottis. Breathing is performed by laryngeal oscillation with open nostrils and closed glottis, followed by lung ventilation with closed nostrils and open glottis. **Cutaneous respiration** plays an important role especially in winter.

Both male and female frogs have vocal cords, but they are much better developed in males. Sounds arise by air flow between the lungs and a pair of large air bags (**vocal sacs**). In the males, the vocal sacs serve as resonator.

The transition from water to terrestrial life necessitated numerous adaptations in the light-sensory organs (eyes) for their use in air. Lacrimal glands and eyelids prevent the eyes from desiccation. Accommodation is achieved by movement of the lens. In the resting state, the eyes are set on remote objects. To focus on a near object, the lens is pushed forward. The retina contains rods and cones, which allow color vision. The lower eyelid is folded into a transparent nictitating membrane, which can slide over the eye.

Some frog species exhibit a high degree of parental care. In the strawberry poison dart frog (*Dendrobates pumilio*), the hatched tadpoles are carried individually on the back of the female to the water, e.g. in a bromeliad axil. The female regularly visits her tadpoles and feeds the offspring with unfertilized eggs. The tadpoles live exclusively from these eggs.

17.6.5 REVIEW QUESTIONS

1) Describe the bloodstream in amphibians for the larval stage and for an adult animal.
2) What forms of breathing (respiration) are found in amphibians?
3) Describe the structure of the integument (skin) of a frog. Which structures are responsible for skin coloring?
4) Compare the course of metamorphosis for a salamander and a frog. Which hormone controls metamorphosis?

17.6.6 CLASS REPTILIA

The evolutionary success of the reptiles as terrestrial vertebrates is to a large extent due to the evolution of the amniotic egg. **Amniota** (reptiles, birds and mammals) can lay their eggs on land. The amniotic egg allows a relatively rapid development of large young in a terrestrial environment. This is also the case for sea turtles (Photo 25), which come on land for egg laying.

Photo 25: Sea turtle (Dirke Peschke www.kostenlos-fotos.de).

Characteristics of the amniotic egg are a calcified or leathery shell, which protects the embryo against dehydration, membranous sheaths, which are formed by the germ layers during development (**amnion**), as well as sac-like skin formations (chorion and **allantois**), which take over the gas exchange. In later development the allantois stores waste products from metabolism. The embryo itself develops within the amnion. Nutrient supply of the embryo takes place by yolk proteins from the yolk sac (Sauropsida; reptiles and birds) or via the placenta (mammals). There are no aquatic larvae stages such as in amphibians.

The reptiles, with approximately 9,000 species, represent a paraphyletic group within the terrestrial vertebrates, since some representatives (Crocodylia) are closer related to the birds than to other reptiles. Characteristic features of the Reptilia are, besides the amniotic egg, a robust, dry and strongly keratinized skin (**epidermal scales**), two-pair limbs with five toes each, a strongly ossified skeleton with ribs and sternum (breast bone), a keel-based autostyle cranium, which allows head rotation, respiration with lungs, blood circulation divided into pulmonary and systemic circulation (left and right ventricles), and **metanephric kidneys** (see Table 14), usually with uric acid as the most important nitrogen excretion product (for water conservation).

Strong jaw muscles allow a powerful jaw closure. Reptiles are ectothermic; many regulate their body temperature by behavior (e.g., sunbathing). Intracorporeal fertilization is a prerequisite for a shell-borne egg because the sperm must reach the ovum before it is closed by the shell.

Present day reptiles *sensu stricto* include the turtles (subclass Anapsida; Order Testudines or Chelonia), the tuatara (subclass Diapsida; Order Sphenodonta) and the worm lizards, snakes and lizards (subclass Diapsida, Order Squamata). The ichthyosaurs, the Sauropterygia (lizard flippers), and the Plesiosauria are extinct. The crocodiles (Crocodylia) represent a sibling group to the birds (subclass Diapsida; Suborder Archosauria). Within this Suborder, the Pterosauria (winged lizards) and the Thecodontia (socket-teeth) are also extinct. Also extinct is the Suborder Sauropodomorpha (lizard-footed dinosaurs).

17.6.6.1 Turtles

Turtles have adapted to various biotopes, ranging from desert turtles to the sea turtles (Photo 25). The leatherback sea turtles (*Dermochelys coriacea*) are the largest sea turtles with a length of 2 m and a mass of over 700 kg. The giant tortoises on Galapagos also reach a weight of several hundred kilograms and can become up to 150 years old. The oldest known turtle died in 2006 with 256 years in the Zoo of Calcutta, India. In Europe there are four species of terrestrial and five aquatic turtles; in Germany only the European freshwater turtle, *Emys orbicularis orbicularis* is native.

The turtle **shell** is unique. It consists of two layers, an outer keratinized layer and an inner layer of bones. This largely rigid armor requires adaptation for respiration and locomotion. Turtles have solved this problem by moving the extremities by means of strong abdominal and pectoral muscles.

Turtles are mostly omnivorous, but usually either herbivore or carnivore feeding predominates. Turtles are oviparous. They bury their eggs (including sea turtles) in the soil, whereby the female migrates over long distances to a suitable egg laying place and exercises great care in the selection of the nest site. Eggs are brooded by the sun. In some species the sex of the incubating young can be determined by the nesting temperature. Low temperatures lead to male animals, high temperatures to female offspring.

17.6.6.2 Lizards, snakes and anguids

The Squamata, with almost 10,000 species, represent a large part of the terrestrial vertebrate fauna, considerably more than the mammals with about 5,500 species. They colonize almost all terrestrial habitats except the Antarctic. Most of the scaled reptiles live in the subtropics and tropics; their number decreases rapidly towards the poles. The viviparous lizard (*Zootoca vivipara*) and the European adder (*Vipera berus*) are the two reptilian species that spread farthest north.

The squamation of the multilayer epidermis is highly variable. The top layer of the epidermis does not grow and is regularly shed. The skulls of Squamata are distinguished from the original diapsid skull by a reduction of the dermal bones. This resulted in a skull with relative movement between the upper jaw and the braincase (kinetic skull). The mobility of the skull is most pronounced in snakes. This modification allows the Squamata to capture and swallow very large prey. In addition, they increase the effective closing force of the jaw muscles.

The skeleton of the Squamata is often greatly modified, having developed over eons to quite different ways of life. The number of thoracic vertebrae depends on the length of the body. It is 23 to 29 in the geckos, while snakes have up to 400 vertebrae, of which 300 are thoracic vertebrae. All thoracic vertebrae bear ribs. With the exception of the iguanas, a reduction of the extremities occurs in all subgroups of the Squamata. Thus the limbs are missing in some anguids and all worm lizards, and of course all snakes.

The eyes are very large in some geckos, but are almost completely reduced in the blind snakes (Typhlopidae). Olfactory (chemical) perception takes place through the nostrils via an olfactory epithelium on the roof of the nasal cavity.

Another organ for olfactory perception is the **Jacobson's organ** (vomeronasal organ) of the snakes, a pair of cavern-like organs in the palate area, which are stimulated by odor molecules captured by the forked tongue. Recently, it was shown that the Gecko *Cyrtodactylus philippinicus* can determine its position relative to the magnetic field of the Earth (Marek et al., 2010, p. 93).

Geckos seem to be able to overcome gravity. They run along the ceiling and creep up vertical surfaces. This is possible by means of millions of so-called **spatulae** (200 nm wide and long structures) on the sole of a Gecko foot, which create a powerful cohesive force.

Xeric spiny-tailed agama and marine iguanas secrete waste salts via enlarged nasal glands (osmoregulation).

Squamata are inseminated internally and usually lay eggs. In some taxa ovoviviparity and viviparity developed independently from each other (e.g. in skinks, night lizards, some anguids, boas, sea snakes and some vipers). A surprisingly high number of Squamata shows **parthenogenesis** (e.g., four genera of geckos).

Brood care occurs only in some snakes. Pythons lie in loops around their eggs and warm the eggs by means of **muscle shiver thermogenesis**. As with turtles and crocodiles, the sex of some lizards is determined by the temperature during the last third of the egg incubation period.

Less than one-fifth of all snakes are toxic. Only in Australia, four times more venomous snakes than non-toxic species occur. **Snake toxins** are divided into two categories. The neurotoxic type acts on the nervous system and can lead to respiratory paralysis. Chemically, they are usually toxic peptides. The hemorrhagic type causes a destruction of the red blood cells and blood vessels by enzymes (e.g., hydrolases). Other toxic components interfere with blood coagulation. As a rule, snake toxins contain several components.

The venomous snakes are divided into five families or subfamilies, the vipers (Viperidae) with the true vipers (e.g. the European adder) and the rattlesnakes, the elapids (Elapidae) with the taipans, death adders, mambas and cobras, and the sea snakes (Hydrophiinae), and the mole vipers (Atractaspididae). Species differentiation is partly based on different types of fang, for example either folding or fixed. In Germany there are only two species of venomous snakes, the European adder and the aspic viper.

Snake venoms are also used in medical therapy, mainly in treatment of hypertension or pain. The snake venom is obtained by "milking" the venom glands.

Pitvipers have their name of a heat-sensitive (infrared sensing) organ on the head, the **pit organ**. The free nerve endings in the pit organ react to thermal radiation energy in the long-wave infrared range (5,000 to 15,000 nm). Pitvipers use the organ to hunt on warm-blooded small mammals (predator detection).

The European blindworm (slowworm) (*Anguis fragilis*) belongs to the worm lizards or legless lizards. Blindworms live in moist soils with covering vegetation, have no extremities and feed on slugs and earthworms.

17.6.6.3 Tuatara

Tuataras are represented by only two species of the genus *Sphenodon*, which live on 30 smaller islands of New Zealand. They are considered "living fossils", the only survivors of the sphenodontid line, which had reached their peak of success in the early Mesozoic era. In contrast to most other poikilothermic reptiles, they are mobile even at low outside temperatures and have a body temperature of only 10–12 °C. The low body temperature corresponds to a slow metabolism. The animals grow very slowly and can reach an age of more than 100 years.

17.6.6.4 Crocodiles and alligators (Crocodilia)

The modern crocodiles are the only survivors of the lineage of archosaurs, from which the dinosaurs and their relatives, including the birds, evolved. They are divided into three families, the alligators and caimans, mostly living in the New World (eight species), the world-wide real crocodiles including the saltwater crocodiles (15 species) and the two species of gavials (gharials) in India, Myanmar and Indonesia.

Crocodiles have an elongated, massive skull and strong jaw muscles. The secondary palate allows them to breathe even with water or food stuffed mouth. The four-chambered heart exhibits a complete separation of the atria and ventricles.

The largest crocodile is found in South Asia, *Crocodylus porosus,* with a weight of up to 1,000 kg and a length of more than 6 m. Crocodiles and alligators can be distinguished by their skull shape. Crocodiles have a relatively narrow snout and the fourth tooth of the lower jaw protrudes when the mouth is closed. Alligators have a wider snout; when the mouth is closed, no teeth can be seen. Alligators are usually less aggressive and, therefore, less dangerous to humans than crocodiles. In the mating season, male alligators draw attention to themselves by sound. Some species squeak before hatching from the egg and the mother then helps the offspring to leave the breeding ground and find water. Gavials are characterized by a very narrow snout. They usually feed on fish.

Unlike in turtles, low temperatures in the nest of crocodiles and alligators lead exclusively to female animals; a high temperature in the nest favors the development of males.

17.6.7 REVIEW QUESTIONS

1) Which changes in the structure of the eggs have allowed reptiles to lay their eggs on land?
2) Describe the function of the Jacobson's organ of snakes.
3) From which lineage of the diapsids did the crocodiles evolve?
4) How do turtles and crocodiles differ in terms of sex determination in response to different temperatures?

17.6.8 CLASS AVES (BIRDS)

The birds represent a lineage of endothermic (warm-blooded), diapsid amniotes, which have acquired the ability to fly about 150 million years ago in the Jura era. Their phylogenetic history can be demonstrated by fossils. *Archeopteryx lithographica* and *A. bavarica* were found as fossils in the approximately 145 million-year-old Solnhofen plate limes (Late Jurassic). In common with the reptiles they had teeth on the jaws, non-fused metacarpal bones, three fingers with claws, a large number of tail vertebrae, and they possessed neck ribs. A ridge (carina) was missing.

In the 120 million-year-old clay strata (Lower Cretaceous) of Liaoning (northeast China*),* *Confuciusornis* spec. was found. These animals still had claws, but a clearly reduced tail and for the first time a hornbill.

The living birds are divided into two clades: the Ratitae or Paleognathae (paleognaths) with the flightless ostriches, emus, rheas and kiwis; and the Carinatae or Neognathae with about 8,600 mostly flying species in 24 Orders (see Photo 26). Among the Neognathae, the sparrows are the largest group with approximately 4,500 species. A secondary loss of flight capacity developed independently in several bird taxa, mainly when the animals lived on islands without enemies. Though penguins are unable to fly, but they can use their short wings to “fly” in the water.

Photo 26: The black stork (*Ciconia nigra*)
(Dirke Peschke www.kostenlos-fotos.de).

A characteristic feature of birds is their **feathers**, which led to the ability to fly. Further adaptations to flight are (i) the transformation of the anterior extremities into wings, (ii) hollow bones (**pneumatization** of bones), (iii) a keratinized bill rather than heavy jaws with teeth, (iv) endothermia (homeothermy), combined with a highly increased metabolic rate, compared to the reptiles, (v) a large, powerful heart with a high-pressure circulatory system, (vi) a highly efficient breathing system with **parabronchial lungs** and **air sacs**, (vii) excellent optical senses, and (viii) a high neuromuscular coordination. The aorta of the circulatory system (original branchial arch IV) lies on the **right** side of the body.

Their high mobility enables birds to colonize different habitats during the year, for example, to breed in Central Europe and to overwinter in Africa. About half of our native bird species are truly migratory (see Photo 26). Birds use the geomagnetic field for navigation in addition to the sun and stars.

17.6.8.1 Feathering of birds

Feathers are epidermal formations formed of keratin. The feathers of birds are homologous to the scales of reptiles, which means that they evolved from the latter. Genuine scales are still found in birds, e.g. on the legs. Two types of feathers are distinguished, the **vaned feathers** or **contour feathers** in the plumage, which give the bird its external shape and are essential for flight, and **down feathers** primarily serving for insulation.

Contour feathers typically consist of a hollow shaft (calamus) with a subsequent vane. The rachis carries the numerous barbs. Each barb consists of up to 500 barbules with hooklets (barbicles). Thus, a contour feather can have more than a million hooklets. The distal barbule of one barb interlocks with the proximal barbule of the next barb, forming a “herringbone pattern”.

Birds cast their feathers at least once a year. While penguins **molt** their entire plumage at once, most birds gradually shed their feathers over time to avoid bear areas and thus still maintain their ability to flight. Many water birds, however, lose all their primary feathers at the same time and are thus unable to fly during molting.

17.6.8.2 The bird skeleton

The hollow pneumatized bones result in a light bone system without loss of their mechanical strength. Thus, the skeleton of a frigate bird with a wing span of two meters weighs only 114 g. This lightweight construction is mainly found in the skull and the wing bone, while the leg bones are relatively heavy. The backbone of the birds is almost inflexible. Most vertebrae are fused together. Except in the Ratidae, the sternum carries a large, thin keel, the **carina**, which functions as insertion for the flight muscles.

The anterior and posterior extremities of the birds correspond to the basic construction of the tetrapod appendages, but the number of bones is reduced and several are fused together. Thus in the modern birds the tibia and upper tarsal bones are fused into a tibiotarsus. Other tarsal bones fuse to the tarsometatarsus. As a result, the heel "ankle" lies between these two metatarsal bones.

The cranial bones are also largely fused, which increases the stability of the skull. Quadratum and Articulare form a **primary temporomandibular joint** in birds. Birds, like the lizards, possess a kinetic skull.

17.6.8.3 Bird beaks

The keratinized (horny) beak (bill) of the birds is formed around a bony core (jaws). The beak is highly adapted to different feeding methods. Thus the beak of a woodpecker is a very hard, chisel-like structure and also its skull is particularly robust, in order to absorb the shocks of the hammering. Corvids (crows) have a powerful, attenuated beak, parrots a hooked beak, which is well suited for cracking nuts. Insectivores have a pointed, narrow, tweezers-like beak, and granivores (seed-eaters) possess a conical beak. Wading birds have a particularly long beak to be able to pick their food out of the intertidal mudflat. Sensors for food detection are located on the beak. Flamingos use their beak as a sieve to filter their food from the water.

Toucans are birds with the most extravagant beaks. In the channel-billed toucan (*Ramphastos vitellinus*) with a body length of about 50 cm, the massive, colored beak reaches a length of 15 to 20 cm. Marine birds have an anatomical specialty, a **salt gland** in the skull between the eyes with an outflow channel to the beak tip. The salt gland serves for the secretion of salts taken up with their food (osmoregulation).

17.6.8.4 The bird lung

Birds possess a **parabronchial lung**, through which air flows continuously and unidirectional. Also unique are the seven to eleven **air-sacs** in the thorax (anterior air sacs) and abdomen (posterior air sacs), which extend with their diverticula into the cavities of the bones. There is no gas exchange in the air sacs. They serve as storage space for air (a kind of ventilator), but are also important for thermoregulation (water evaporation) and phonation.

Two inhalation and exhalation cycles are necessary for a complete flow through the parabronchi, as well as the anterior and posterior air sacs. The breathing rate is much lower in birds than in mammals. In all birds, except the penguins, a so called "**neopulmonic parabronchi**" occurs, an additional mass of lung tissue, which creates a connection from the main bronchus to the posterior air sacs, and air flows alternatively in both directions.

Birds have the most efficient respiratory apparatus of all terrestrial vertebrates. The cross-current exchange of respiratory gases between the lung and the blood enhances the efficiency of breathing in the birds. For example, the bar-headed goose (*Anser indicus*) routinely crosses the Himalayan and temporarily reaches an altitude of 9,000 m and the snow grouses breed at an altitude of 5,800 m.

17.6.8.5 Thermoregulation in birds

Birds are endothermic homeothermic. That is they maintain their body temperature at values of 40–42 °C by their own heat production. The plumage is used for insulation and reduces heat dissipation. At night, many birds fluff their plumage up for better insulation.

Extremely small birds such as hummingbirds reduce their metabolic rate when they do not forage, especially at night. This so-called **torpor,** an energy-saving mode, is a kind of cold rigor in which the body temperature can drop below 10 °C. Small birds, such as the wren, require up to two weeks after hatching from the egg before reaching their full ability to regulate the body temperature (nidicolous birds). Nidifugous birds, on the other side, quickly reach their "normal" body temperature and can leave the nest earlier.

Ducks and other water birds can stand on an ice surface in winter without freezing. They use a **countercurrent heat exchanger** in the feet. In the feet and legs, the veins run parallel and closely interwoven with the arteries. Thus the cold blood flowing back from the feet into the body is heated and the warm blood from the body is cooled. The feet reach temperatures near 0 °C at their tip.

17.6.8.6 Excretion in birds

Urine is produced in the paired metanephric kidneys by glomerular filtration and reabsorption. Birds, as also the reptiles, excrete waste nitrogen in the form of uric acid (uricotel). Due to the low solubility of uric acid in water, birds save immense amounts of water during excretion. The concentration of the uric acid takes place in the **cloaca**, where the excreta are mixed with the feces. The excrement of fish-eating birds is called guano. Guano has been used since the 19th century as fertilizer in agriculture.

17.6.8.7 Bird reproduction

More than 90 percent of all bird species are monogamous; they have only one mating partner during a breeding season. Males and females alternate in parental care, both during breeding and when feeding. Brood parasites like the cuckoo (*Cuculus canorus*) lay their eggs in the nests of smaller bird species. When the offspring hatch, they are cared for by the stepparents. The young cuckoo grows faster and often shoves the other offspring out of the nest.

Nidifugous birds (for example, chicken, ducks, and other water-birds) hatch from the egg already covered with down feathers, so they are immediately capable of thermoregulation and can run and swim. **Nidicolous birds**, on the other side, are naked and blind at the time of hatching. Parthenogenesis is also present in birds. For example, turkeys can reproduce without males. Their offspring are, however, all cocks.

17.6.9 REVIEW QUESTIONS

1) Marine birds secrete excess salt via the salt gland. Does a seagull take up larger amounts of salt after eating a marine fish or an equal portion of mussels?
2) Why did the discovery of *Archaeopteryx* prove that the birds possess a common ancestor with some reptiles?
3) What is the difference between nidicolous birds and nidifugous birds?
4) What are the characteristics of the birds' respiration system?
5) Why does a penguin not freeze on the ice surface?

17.6.10 CLASS MAMMALIA (MAMMALS)

Mammals diverged from the line of synapsid amniotes (reptilian-like therapsids) during the late Permian about 250 million years ago. Mammals are dispersed over the entire earth and have settled in almost all habitats. This is reflected in the diversity of their body shape. There are considerable differences in body size. For example, the smallest mammals are the Etruscan shrew and the Kitti's hog-nosed bat with a body weight of 2 g and the largest mammal, the blue whale, has a weight of up to 150 tons.

Along with the birds, mammals have **homeothermy** (warm-blooded) in common (convergent development with birds). A **hair pelage** provides protection of the body from heat loss. The hairs of the mammals are analogous to the feathers of the birds. The epidermis (upper skin layer) is multi-layered and rich in glands, such as sweat glands, sebaceous glands and scent glands. On the surface it is often keratinized. The underlying true skin (dermis) merges into a fat-rich subcutaneous connective tissue. This layer serves as an energy reserve and heat pad, and it protects bones, muscles and organs from pressure, shock and heat loss.

The placenta of the placental mammals allows the development and feeding of the embryos in the protected environment of the maternal body. After birth, the offspring feed on their mother's milk, produced by the mammary glands, via the female teats. Through the mother's milk, the young mammals are supplied with all the necessary nutrients and immune defenses. The sucking of the offspring on the teats requires a separation of the nasal cavity and the oral cavity (secondary palate) in order to develop the necessary suction force.

Photo 27: The grazing antelope *Addax nasomaculatus* (Dirke Peschke www.kostenlos-fotos.de).

The **secondary temporomandibular joint** of the mammals is formed from the Squamosum (upper) and the Dentale (below). The cartilaginous components of the primary temporomandibular joint (Quadratum and Articulare) migrate into the inner ear as further auditory ossicles (Table 16).

Mammals	Other tetrapods		Fish
Stapes (stirrup)	Columella		Hyomandibulare
Incus (anvil)		Quadratum	
Malleus (hammer)		Articulare	
Tympanicum (tympanic)		Angulare	

Table 16: Homology of the auditory ossicles of mammals with elements in the visceral skeleton of fish and other tetrapods.

The upper and lower jaws have two tooth generations per individual, the primary dentition (milk teeth) and the permanent dentition. The teeth are heterodont in most species, which means a different structure and function adapted to the food of the animals. The permanent dentition includes a maximum of 44 (Placentalia) to 52 (Marsupialia) teeth (see below).

The spinal column consists of 33 vertebrae in humans. Five are fused into the sacrum, and four form the coccyx. The first and second cervical vertebrae are modified in all mammals in such a way that they enable movements of the head in all directions. The number of cervical vertebrae is seven in all mammals, regardless of the length of the neck.

The circulatory system with the four-chambered heart (two atria and two ventricles) shows a strict separation into systemic and pulmonary circulation immediately after birth. In contrast to birds, the aorta of the systemic circulation is on the **left** side of the body. The excretory system (metanephric kidneys) has secondary ureters, usually opening into a bladder. A cloaca is only present in the Monotremata and has a very flat design in the Marsupialia.

Urine formation proceeds in five sections of the basic unit of the kidney (nephron):

i) Ultrafiltration of the blood in **Bowman's capsule**.
ii) Reabsorption of low molecular weight organic molecules, e.g. glucose, salts (mostly NaCl) and water from the primary urine in the proximal tubule, in the **Henle's loop** (only present in birds and mammals) and in the distal tubule.
iii) Secretion of protons in the distal tubule (pH regulation).
iv) Reabsorption of water and urea in the collecting tube.
v) Excretion of the urine.

The length of the Henle's loop determines the ability for urine concentration. The human kidney contains about 2 million nephrons (100 km in length) and has a filtration area of 1.5 square meters. The filtration rate is 175 liters per day.

Only mammals possess a **diaphragm**, a flat muscle sheet, which separates the pectoral (pulmonary) cavity from the abdominal cavity.

The highly evolved **brain** with its approximately 35 billion nerve cells and the particularly large forebrain or neocortex (cerebral cortex) allows mammals to have a greater capacity for memory and learning than other vertebrates. The five parts of the brain, Telencephalon (forebrain or Cerebrum), Diencephalon, Mesencephalon (mid brain), Metencephalon (Cerebellum) and Myelencephalon, develop from five embryonic (primary) brain lobes. The development of the brain is accompanied by highly developed sensory perception, in particular for hearing, smelling and touch.

17.6.10.1 Systematics of Mammalia

The class Mammalia is divided into two subclasses, the Protheria with the egg-laying Monotremata and the viviparous Theria with the Marsupialia (Metatheria) and the Eutheria (true mammals, Placentalia).

The three recent species of the **Monotremata** (duck-billed platypus and spiny anteater) live exclusively in Australia / New Guinea. Characteristics are their still poorly developed homeothermy and in females the mammary glands.

About 200 species of **Marsupialia** occur in Australia and about 65 species in South and Central America. Only one species is found in North America, the Northern Opossum. The most species-rich Order is the Diprotodontia with the koalas, wombats, phalangerids, wallabies and kangaroos (131 species). All species have a very short gestation period of up to 36 days in the uterus of the female.

In the **Eutheria** the gestation period in the uterus is up to 660 days. Characteristics are the mammary glands with teats and an unpaired vagina. Of the 28 known Orders of true mammals, 20 recent Orders with about 4,400 species are currently extant (Table 17).

In the Marsupialia and Placentalia there was a parallel evolution of species. The species pairs resemble each other in their appearance and habitat selection, and partly in their way of life. Examples of this are Tasmanian tiger and wolf, quoll and ocelot, wombat and marmot, and Marsupial mole and mole.

Superorder	Order	Some representatives
Afrotheria	Tenrec-like (Afrosoricida)	45 species of tenrecs and golden moles; formerly merged with the insectivores
	Elephant shrews (Macroscelidea)	15 species in Africa
	Aardvarks (Tubulidentata)	One species, the aardvark (*Orycteropus afer*)
	Hyraxes, dassies (Hyracoidea)	Five families with seven species; most closely related to elephants and manatees
	Elephants (Proboscidea)	One family, the Elephantidae with two species
	Manatees (Sirenia)	Four recent species in two families
Xenarthra "strange joints" (29 species)	Armored New World placental mammals (Cingulata)	Only two recent families (*Dasypodidae*, *Chlamyphoridae*)
	Pilosa "hairy"	Anteaters and sloths
Euarchontoglires	Treeshrews (Scandentia)	Treeshrews in Southeast Asia; 20 species; in some classifications merged with the primates

Superorder	Order	Some representatives
	Flying lemurs or colugos (Dermoptera)	Only one recent family with two species, the Philippine flying lemur and the Sunda flying lemur
	Primates	Strepsirrhines (wet-nosed primates) and haplorhines (dry-nosed primates) with apes (Hominidae) und humans (*Homo sapiens*); 279 species
	Gnawing mammals (Rodentia)	2,100 species (42 percent of all mammals)
	Pikas, hares and rabbits (Lagomorpha)	About 80 species
Laurasiatheria	Insect-eaters (Eulipothyphia / Insectivora)	Moles, shrews and hedgehogs
	Bats (Chiroptera)	Flying foxes and bats with about 1,000 species
	Pangilins (Pholidota)	Three recent genre with 8 species in Southeast Asia and Southern Africa
	Meat-eaters (Carnivora)	About 280 species of dog-like carnivores and cat-like carnivores, including seals
	Odd-toed hoofed animals (Perissodactyla)	Three recent families (horses, rhinoceroses and tapirs) with 17 species
	Even-toed hoofed animals (Artiodactyla)	Four Suborders (pigs, hippopotamuses, camels and ruminants (Ruminantia) with 221 species
	Whales (Cetacea)	About 80 aquatic species. Baleen whales and toothed whales including dolphins

Table 17: The Orders of recent true mammals (Placentalia).

17.6.10.2 Some morphological and functional adaptations in mammals

Mammals have several types of horns and horny structures. The true **horns** of the Bovidae (see photo 27) are hollow structures with a keratinized epidermis surrounding a bony core, which protrudes from the skull. True horns are not branched and are not discarded. The **antlers** of the Cervidae (deer) are branched and consist of solid bones. They are re-formed every year and discarded after the reproductive period. With the exception of the reindeer, only the males form antlers.

Mammals use a wide range of food sources. Usually the teeth reflect the food habits of a mammal better than all other physical features. The **heterodont dentition** consists of four types of teeth, which differ in structure and function, the incisors, canines, anterior (premolar) and posterior molars. The total number of teeth in the primary mammalian set of teeth is 44 (some insectivores), and in humans 32. The deciduous dentition (milk teeth) comprises only 20 teeth in humans.

Special adaptations to the handling of food are found in the **Herbivora** (herbivores). No mammal secretes an endogenous (body's own) cellulase to degrade cellulose. Instead, plant-eating vertebrates generally harbor bacteria and Protozoa in special fermentation chambers in their digestive tract. In horses and many rodents, an ample sacculation of the intestine (appendix or caecum) represents the fermentation chamber for cellulose digestion; in the **ruminants** the rumen of the four-chambered stomach digests cellulose. Cellulose degradation is hardly possible below 10 °C body temperature. This is the reason for the fact that there are plant-eating mammals (endotherms) in arctic regions, but no plant-eating ectotherms (neither invertebrates nor vertebrates).

In mammals there is an exponential relationship between metabolic rate and body mass or body surface. Small shrews with about 2 g body weight eat more per day than their own body mass and starve within hours without food, whereas a large predator can get along with only one meal every few days.

17.6.10.3 Migration in mammals

In contrast to fish and birds, there are only a few species in mammals with regular seasonal **migration**. In Canada and Alaska, reindeer (*Rangifer tarandus*) migrate twice a year over distances of up to 1,000 km, from the boreal coniferous forest (taiga) into the treeless tundra to calve and back. In August millions of hoofed ungulates migrate through the Serengeti in Tanzania and Kenya in search of new feeding places, covering a distance of about 3,000 km each year. The farthest migration in mammals is found in seals and whales, with distances of up to 18,000 km.

17.6.10.4 Thermoregulation in mammals

The regulation of body temperature to about 37 °C is multifactorial also in the mammals and consists of behavioral (e.g. shade search, selective consumption of water-containing food), morphological (e.g. coloration of the skin) and physiological adaptations (e.g. reduction of water evaporation, sweat secretion).

Whereas the body core temperature is kept rather constant, temperature on the periphery (extremities, nasal tip) can drop to values of 0-10 °C. Within the so-called environmental **thermal neutral zone**, the core temperature is kept constant without great energy expenditure. This thermal neutral zone is very narrow in tropical animals, but very wide in Arctic and Antarctic animals (for example in polar bears between -50 °C and + 30 °C ambient temperature).

Small mammals (e.g. bats, hedgehogs, marmots) often fail to maintain their body temperature at a high level during the winter. They go into a **winter sleep** (hibernation, prospective dormancy) in late autumn. The metabolic rate is strongly reduced and their body temperature is kept at a low value between 5 °C and 20 °C (adaptive hypothermia). Hibernation periods range from a few weeks to seven months. The awakening process in spring is very rapid, and the energy comes from brown adipose tissue (**chemical thermogenesis**). Entrance into hibernation as well as the awakening process is controlled by hormones.

Some larger mammals spend the winter in a **winter rest** (consecutive dormancy, denning). For example, badgers and brown bears sleep for weeks in a cave, but without a lowering of the body's core temperature.

17.6.10.5 Functions of the blood

In animals with a closed circulatory system such as in the vertebrates, two types of extracellular fluid, tissue fluid or interstitial fluid and **blood plasma** are distinguished. The tissue fluid fills the interspaces between the cells of the body; blood plasma is restricted to the blood vessels. The blood consists of the blood plasma (in mammals approx. 55%) and the cellular components, the blood cells (in mammals approx. 45%). The blood plasma consists of 90% water, in which non-volatile substances such as plasma proteins, hormones, metabolic waste products as well as small amounts of other organic and inorganic substances are dissolved.

The cellular components of the blood consist of the red blood cells (**erythrocytes**), white blood cells (**leukocytes**), and cell fragments (platelets, **thrombocytes**). Erythrocytes contain hemoglobin for oxygen and carbon dioxide transport, leukocytes function as defense cells (immune system) and platelets play a role in blood clotting. The red blood cells of the mammals lack a nucleus.

Each component of the blood has a specific function in the body: (i) transport of nutrients, excreta, hormones and respiratory gases (oxygen and carbon dioxide); (ii) buffer system (homeostasis); (iii) wound closure; (iv) immune function (blood groups, antibodies, etc.) and (v) thermoregulation.

17.6.10.6 Learning behavior in mammals

The behavioral spectrum is broader and more flexible in mammals than in any other animal group. The behavior of mammals is often modified by experience. Learning and understanding contribute significantly to mammalian behavior. Two examples of the learning process are **habituation**, which can lead to the complete disappearance of a behavioral reaction in the absence of reward or punishment, and sensitization, in which a repetitive stimulus increases the strength of a behavioral reaction. Another form of learning is **imprinting**. In mammals, olfactory imprinting, i.e. sensitization to different odors, is more important than in other vertebrate groups.

17.6.10.7 Fluctuations in mammalian populations

A population comprises all individuals of a single species occurring in a specific habitat. Changes in the size of a population are triggered either by environmental factors such as weather and natural disasters (**density-independent factors**) or they are related to the density of a given species (**density-dependent factors**). In many rodents, cyclic outbreaks occur with strong population fluctuations. The best-known example are the lemmings of Northern Scandinavia, where mass migrations occur at time of high population densities and many animals perish by drowning in lakes, rivers and the sea. In the case of predators and parasites, periodic fluctuations in the density can be observed, which are phase shifted to fluctuations in the density of their prey or hosts (Figure 13).

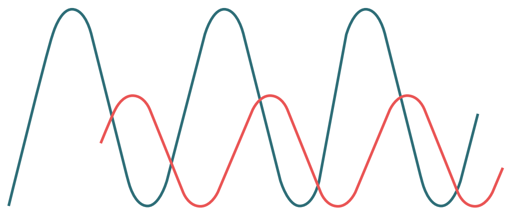

Figure 13: Temporal, phase shifted changes in the population density of a predator (red) and its prey (blue).

7.6.10.8 Humans and mammals

Mammals have decisively influenced human history. Humans have always eaten the flesh of mammals and processed their fur and their bones. Mammals are also used as milk suppliers or as working animals. Some mammals have dramatically increased their distribution area as a result of human attendance or have been naturalized as **neozoans** in foreign regions. Numerous species of mammals have disappeared from the earth forever as a result of human predation (hunting). According to WWF (World Wildlife Fund) statistics, 73 species of mammals became extinct on the Earth in recent years, and a further 188 species are considered highly endangered (IUCN World Nature Conservation Press release of October, 6, 2008).

For animal experimentation, mammals, mostly primates and rodents are used, e.g. as test organisms in the development of drugs and cosmetics. Dogs and cats are mainly used as guard dogs and pets. Domesticated animals are called livestock or farm animals. The **domestication** of these mammals, mostly hoofed animals, probably began 100,000 years ago.

A number of mammals are considered to be agricultural and food pests, especially numerous species of rodents. For the livestock industry some species of predators are considered as food competitors, for example seals and other fish-eating mammals for the fish industry. Some predators (e.g., wolves and tigers) were at one time a direct threat to humans. However, there are now only few threats, for example bears.

A much greater danger to humans is posed by some mammals as **disease vectors**. More than 50,000 people die from rabies, transmitted by dogs, cats, foxes, raccoons and bats, every year, especially in underdeveloped countries. Another menacing disease is the plague transmitted by fleas, which are ectoparasites of house rats and other rodents.

17.6.11 REVIEW QUESTIONS

1) What properties of the mammals were particularly important for their successful development and spread on the earth?
2) How do the horns of the bovids differ from the antlers of the deer? In which species does the female wear an antler and why?
3) How is cellulose digestion different between horses and cattle?
4) What factors can be responsible for fluctuations in a mammalian population?

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19 ANSWERS TO REVIEW QUESTIONS

In the following, answers are given to the review questions concerning knowledge verification in the respective chapters.

2.7 EVOLUTION, SYSTEMATIC ZOOLOGY AND THE ANIMAL CELL

1) Point mutation, segment mutation, genomic mutation, horizontal gene transfer, sexuality, heterozygosity and gene coupling, chromosomal crossing over in the meiosis, environmental influences such as UV radiation or mutagenic substances.
2) The first term refers to a genus; the second term defines the species, and often represents a characteristic feature of the species. The scientific name is derived from Latin or Greek, and the species names are often followed by the name of the first author and the year of the initial description, sometimes abbreviated as e.g. (L.) for Linné (Linnaeus).
3) Monophyletic: taxa go back to a common ancestor (parent type) and all descendants of this parent type are contained within this group. Paraphyletic: Not all taxa of a group go back to a parent type. Polyphyletic: Taxa of a group are from different ancestral species.
4) Biomolecules: proteins, ribonucleic acids. Function: protein biosynthesis.
5) Active transport, cytosis.

3.9 PROTOZOA / PROTISTA

1) Amoeboid movement: displacement of cytoplasm and contraction of actin and myosin filaments. Locomotion with cilia and flagella: 9 × 2 + 2 arrangement of microtubules in cilia and flagella; radial spokes and nexin bridges; interactions between the outer double structures by means of dynein arms (motor protein).
2) Regulation of the water balance, in particular in freshwater forms.
3) Isogamous: sex cells arising by division of gamonts (gamogony) are of the same size. Anisogamous: sex cells are of different size.
4) Supply the cellulases for the degradation of cellulose in the rumen of a ruminant.
5) "Slender form" (long slender) represents the dispersal and multiplication form. As the infection progresses, the slender trypomastigotes partly transform into compact "short stumpy" trypomastigotes. Only this form can develop further after uptake by a tsetse fly in their intestine.

6) Mutation of the erythrocytes, the so-called sickle cell anemia, can protect against malaria and its serious consequences. Homozygote carriers usually die shortly after birth, while heterozygous carriers of sickle cell anemia show a stronger malaria tolerance of the immune system.

4.7 PHYLUM PORIFERA (SPONGES, PARAZOA)

1) Collagen is a prerequisite for the formation of extracellular matrix. It represents an important structural protein in connective tissue; prerequisite for tissue formation.
2) High tensile strength of the collagen fibers is due to their special construction (triple helix). A staggered attachment of the triple helices by about one-fifth of their length leads to the formation of collagen microfibrils, collagen fibrils, and collagen fibers.
3) Pinacocytes, choanocytes, sclerocytes, archaeocytes.
4) Flagellate chambers penetrate the mesohyl and lead to a strong enlargement of the inner surface for better gas and mass transfer. The body is thick-walled.
5) Formation of gemmules as a permanent state. Gemmules contain the necessary building material for the creation of a new sponge.

5.8 PHYLUM CNIDARIA (EUMETAZOA)

1) Ectodermis: cnidocytes (defend against predators, capture prey), epitheliomuscular cells (locomotion), cnidoblasts (precursors of cnidocytes), receptor cells (stimulus perception) and interstitial cells (regeneration ability). Endodermis: nutritive muscular cells (nutrition and digestion), gland cells (hormone production and secretion) and basal cells (tissue formation).
2) Metagenesis: a Planula larva settles on a substrate and develops into a polyp after metamorphosis. From the adult polyp a swimming larva is separated by budding, which develops after settlement to a new polyp. Often, the budding is incomplete and a polyp colony develops. Most polyps are “feeding polyps”. Some polyps differentiate into sex polyps, from which medusae are released. Medusae live pelagic and discharge from their gonads sperm and egg cells into the water. A Planula larva again develops from a fertilized egg.
3) Prey uptake of zooplankton; symbiotic nutrition by means of Zoochlorella and Zooxanthella and their photosynthesis products; absorption of dissolved organic material (DOM) via the ectodermis.
4) Through the carbon dioxide metabolism (calcium carbonate formation).
5) In the case of Cubozoa, the polyp generation is greatly reduced. In the Anthozoa, only the polyp generation is formed, that means, the medusa generation is reduced.
6) The sea wasp (box jellyfish; Cubozoa) and the Portuguese man o’ war (Hydrozoa; allergic shock) represent often fatal underwater hazards for humans.

6.7 PHYLUM PLATHELMINTHES (FLATWORMS)

1) Man is always the end host for the cattle tapeworm; adult, sexually mature worm lives in the intestine. For the pork tapeworm, man can also be an intermediary host; cysticercus larva can develop in different organs of humans.
2) In addition to the pork tapeworm, humans can be intermediate hosts for fox and dog tapeworms.
3) Acoelomates: bilaterians without a coelom, that means without a true body cavity; parenchymatic tissue fills the spaces between the organs. Pseudocoelomata: coelomatic Bilateria with a distinct, fluid-filled body cavity, which, however, is not enclosed by a typical coelom wall (coelothel). Coelomata: animals have a true secondary body cavity lined by a coelothel.
4) Regenerative capacity is based on a group of cells capable of division, the neoblasts, which can produce all tissue types.
5) Hermaphroditic animals, which are first male and later female (usually after further growth).
6) Up to four times higher energy yield in ATP equivalents per glucose molecule.

7.4 PHYLUM NEMERTEA (NEMERTINI, "RIBBON WORMS")

1) Nemertea: worms with a protuberant proboscis and a closed circulatory (blood) system. They are rarely parasitic.
2) Live birth.
3) More efficient distribution / transport of nutrients, hormones and excreta.

8.4 PHYLUM ROTIFERA (ROTIFERS, WHEEL ANIMALS)

1) Primary alternation of generations: alternation of gamogony and agamogony (in Protozoa). Metagenesis and heterogeneity are forms of a secondary alternation of generations in Metazoa. Metagenesis: alternation between (bi)sexual (gamogony) and asexual reproduction; heterogeneity: alternation between bisexual and unisexual (parthenogenesis) reproduction.
2) Dormancy in winter; dry stiffness in dried-up pools in summer. Then often multiplication by parthenogenesis occurs.
3) Cell constancy; organisms or organs have a fixed number of cells.
4) Pseudocoel forms a hydroskeleton; efficient distribution of substances in the body and storage of waste materials.

9.8 PHYLUM NEMATODA (ROUNDWORMS)

1) *Ascaris suum*: adult worm in the intestine; humans are intermediate and final host. *Enterobius vermicularis*: Large intestine (colon). *Wucheria bancrofti*: Lymph vessels, especially in the extremities.
2) An extension runs from each muscle cell either to the dorsal or to the ventral nerve cord ("Kahn muscle cells"). In most animals the nerve extensions (axons) extend to the muscle cells.
3) Many nematodes live at the limit of anoxic and sulfide-rich biotopes. Typical end products of the energy metabolism are α-methyl butyrate and α-methyl valerate. Marine nematodes often live in ectosymbiosis with sulfur-oxidizing bacteria.
4) Eggs may last for years in the soil. After oral uptake of the eggs, the larvae hatch and migrate as L3 larvae over the liver and the heart to the lungs (humans as intermediate host). From the lung, the larvae are coughed up and then swallowed. In the intestine, they develop into an adult worm (humans as final host).
5) Numerous soil nematodes are entomopathogenic (insect pathogenic); they attack insect larvae and kill them.

10.7 PHYLUM ANNELIDA (SEGMENTED WORMS)

1) Scavengers and humus formers (decomposer).
2) Absence or presence of parapodia and setae.
3) The clitellum is an epidermis region with numerous glands, which surrounds the anterior half of the body during sexual maturity. The eggs of the Clitellata develop in a cocoon, which is secreted from the clitellum.
4) Respiratory pigments (hemerythrin, chlorocruorin, erythrocruorin and hemoglobin) support the aerobic energy metabolism in annelids with poor oxygen supply.
5) Polychaetes usually have separated sexes. Fertilization occurs externally. The early larva is a trochophore. Some polychaetes live the greater part of the year as sexually immature animals (atoke). During breeding season, the posterior part of the body matures sexually (epitoke, with the formation of sexual segments or stolons).

11.10 PHYLUM MOLLUSCA (MOLLUSKS)

1) Ambient anoxia: succinate / propionate fermentation; functional anoxia: lactate fermentation and octopine fermentation (octopine, alanopine, strombine etc. as end products).
2) A foreign body (sand grain, parasite) gets under the mantle and induces "shell formation", that means it is gradually covered with mother-of-pearl.
3) Coelom around heart and gonads.
4) Annual rings of growth on the shell.
5) Torsion has led to a problem of accumulation of excrements in the area of the head and the gills (danger of self-poisoning).
6) Swimming by jet propulsion. They eject water out of the mantle cavity with great force. Predatory lifestyle; capture of prey with tentacles, which are provided with suckers.
7) Communication by means of bioluminescence.

12.4 PHYLUM TARDIGRADA (WATER BEARS OR MOSS PIGLETS)

1) Anhydrobiosis (dehydration); anoxibiosis (low oxygen content in the environment); anosmobiosis (high salt concentrations in the environment); cryobiosis (extremely low temperatures).
2) Survival at temperatures from -272 °C to + 150 °C in almost all biotopes on Earth; survival also in the vacuum of the outer space.

13.4 PHYLUM ONYCHOPHORA (VELVET WORMS)

1) Free ecdysteroids (ecdysone, 20-hydroxyecdysone).
2) Parapodia-like legs, skin-muscle tube and hydrostatic pressure in the hemocoel.
3) Annelids: parapodia-like legs, body wall, eyes (beaker cells), metanephridia, ladder-like nervous system. Arthropods: hemocoel with blood sinuses and open circulatory system, tracheal system, chitinous cuticle with molting, ladder-like nervous system.

14.9 PHYLUM ARTHROPODA (ARTHROPODS)

1) Arthropods have conquered almost all habitats on Earth. Mechanical protection of the body: protection against predators and invaders (parasites). Protection against water evaporation.
2) Body split into two parts: prosoma and opisthosoma. Body attachments are on the prosoma.
3) A group of neurosecretory cells in the X-organ of the brain produces a molt inhibiting hormone (MIH). The MIH is transported via axons of the X-organ to the sinus gland and released into the hemolymph. A drop in the MIH concentration in the hemolymph triggers the release of the ovulation hormone ecdysone from the Y-organ, and thus the molting process. In crustaceans, in contrast to insects, there is a molt-inhibiting principle of regulation.

4) The dioptric apparatus of a single eye consists of a chitin lens of the cornea, the underlying crystalline cones and the primary pigment cells. The crystal cone directs the light to the retinula cells (rhabdom). The rhabdom consists of rhabdomers, the microvilli of typically six to nine (mostly eight) visual cells (photoreceptor cells). They contain the visual pigments, where the light is converted into a nervous impulse. At the inner end of the rhabdomers nerve fibers of the downstream neurons transmit the signal and pass it onto the brain. Daily active insects have an apposition eye; night-active species have a superposition eye. Fast-flying insects have neural superposition eyes.
5) In the case of direct flight muscles there is a 1:1 ratio between nerve impulse, muscle contraction and wing beat frequency. The latency during nerve impulses / muscle contraction does not allow a higher wing beat frequency than approx. 40–100 per second. Contraction of asynchronous (indirect) flight muscles occur independent of membrane potentials. The flight muscles form a kind of mechanical resonance system that builds itself up to reach wing beat frequencies of 1,000 and more per second.
6) Biting chewing (predatory life, leaf eater), piercing-sucking (e.g., phloem sap in aphids or blood in mosquitoes), leaking-sucking (e.g., sugar intake in flies), sucking (e.g., nectar uptake in butterflies).
7) Optical (e.g., colors and bioluminescence), acoustic (e.g., stridulation), chemical (pheromones).
8) Insecticides; biological pest control by predators and parasites / parasitoids; hormones and hormonal analogues or antihormones; mechanical (e.g., pick-up) and physical control (e.g., sound). Integrated pest management (IPM) uses mainly ecologically friendly control mechanisms to keep pest insects below an economically harmful threshold.

15.6 PHYLUM ECHINODERMATA (ECHINODERMS)

1) Sea urchins eggs are poor in vitelline and show holoblastic radial cleavage. During the first two cleavages, the fertilized egg cleaves along the animal-vegetal axis that means meridional. The third, equatorial cleavage separates the embryo into an animal and a vegetal half. The fourth cleavage is again meridional and occurs in the animal hemisphere; the vegetal hemisphere cleaves equatorial and is unequal. When the embryo reaches the blastula stage, the blastocoel is formed, which is surrounded by a layer of equal-sized cells. Gastrulation, the migration of endoderm and mesoderm into the interior of the embryo, begins with the transformation of the mesoderm forming cells into primary mesenchymal cells. In the following invagination of the endoderm cell layer, the blastopore is formed. The further stages of gastrulation lead to a bilaterally symmetrical Dipleurula or, for example, Bipinnaria larva, which is specifically transformed in different taxa (e.g., sea urchins with Pluteus larva).

2) Pedicellariae: serve to clean the body surface, but sometimes also for capturing prey; found in sea urchins and starfish. Madreporite: sieve-like perforated calcareous plate; connects the axocoel (ambulatory vascular system) with the sea water (especially in sea urchins and starfish). Respiratory tree: pairs of water lungs in sea cucumbers. Aristotle's lantern: complex chewing apparatus in sea urchins.
3) The larval left mesocoel (hydrocoel) forms the fluid-filled ambulacral system in the adult animal. It is connected to the axocoel via the stone canal. The right hydrocoel degenerates. From the left protocoel, a lacuna-rich axial gland surrounding the stone canal as well as the ciliated canals of the madreporite is formed. The axial sinus, a connection of the axial coelom to the aboral ring-cannel of the metacoel, is a remnant of the right protocoel. The left and right metacoel (somatocoel) form the genuine body cavity.

16.3 PHYLUM HEMICHORDATA (HEMICHORDATES)

1) Echinodermata: tricoelomatic construction of the coelom; Tornaria larva. Chordata: "Chorda" (stomochord), dorsal nerve cord (neurocord).

17.5 PHYLUM CHORDATA: UROCHORDATA AND CEPHALOCHORDATA

1) Chorda dorsalis; neural tube (central nervous system); pharyngeal slits (filter apparatus, food uptake and respiration); endostyle (mucus secretion, food transport); postanal tail (locomotion).
2) Larval tunicates have typical chordate characteristics, which can be greatly reduced in adult tunicates.
3) During embryonic development the blastopore becomes the anus and the mouth secondarily breaks through the archenteron. Nervous system during embryonic development displaced downwards; tubular central nervous system dorsally located; Notoneuralia. Heart ventrally located; pharyngeal slits partially existing; possess an inner skeleton.

17.6.3 VERTEBRATA = CRANIATA OR VERTEBRATES (FISH)

1) Streamline shape, strong muscles, placoid scales prevent turbulence on the body surface, sensitive sense organs (olfactory organs, mechanoreceptors, ampullae of Lorenzini), temporomandibular joint and growth of additional tooth rows.
2) Lateral lines: wave motions, water pressure; ampullae of Lorenzini: weak electric fields.
3) The gas exchange (oxygen absorption and carbon dioxide release) is highly efficient and based on the countercurrent principle. Water flows through the mouth, the gill chamber and the gill filaments, which runs in the opposite direction to the blood flow in the capillaries of the branchial lamellae.

4) In the case of the Physostoma, the swim bladder is one-chambered and connected to the intestinal tract via an air duct (e.g., in eels, pike, and salmonids). The fish swallow air to fill the swim bladder. In the Physoclisti, the swim bladder is closed. Filling of the swim bladder with oxygen occurs via blood vessels (Rete mirabile, countercurrent gas exchange) and a gas gland (salting out of oxygen by means of lactic acid) (e.g., in perches, codfish, and stickleback).

17.6.5 AMPHIBIA (AMPHIBIANS)

1) Larval stage: blood circulation similar to that in fish; oxygen supply via gills. Adult stage: The aortic arch VI of the larva is converted to the pulmonary artery. Lung veins transport the oxygen-rich blood to the heart. The separation of the systemic and pulmonary circulation is still incomplete in the amphibians (and also in most reptiles). Adult amphibians have only one ventricle, in which oxygen-rich and oxygen-poor blood is still largely mixed in the heart.
2) Branchial (gill) respiration in the larvae, pulmonary respiration in adult animals; cutaneous respiration in adult animals, especially in winter.

3) The skin of frogs is thin and moist. Mucous glands secrete a protective mucus layer. All amphibians produce toxins in specific granular skin glands, which have very different effects on humans and other mammals. In all amphibians, the coloration of the skin is caused by special pigment cells, the chromatophores. Chromatophores are highly branched skin cells containing pigments, e.g. melanin. Color changes are caused by migration of pigments within the chromatophores (physiological color change).
4) Salamander: in aquatic species larvae with outer gills and a fin-like tail hatch from the eggs. During metamorphosis the forelegs appear first. Lungs develop and gills are reduced, as is the tail. After metamorphosis, the adults are usually terrestrial. Terrestrial species show a direct development, that means no metamorphosis. Frog: from the spawn, tadpoles with gills and a long fin-like tail hatch, without legs and with special adaptations for herbivore nutrition. In young tadpoles the gills lie outside, in older larvae inside. Metamorphosis is controlled by the thyroid hormone triiodothyronine. During metamorphosis the hind legs appear first and the tail is reduced (apoptosis). The lungs develop and the gills are resorbed.

17.6.7 REPTILIA (REPTILES)

1) Amniotic egg allows a relatively rapid development of large young in a terrestrial environment. Characteristic features are a calcified or leathery shell, which protects the embryo against dehydration, membranous sheaths, which are formed by the germ layers during the development (amnion), as well as sac-like skin formations (chorion, allantois), which take over the gas exchange. In the later development the allantois contains waste products from metabolism. The embryo itself develops within the amnion. The embryo is supplied with yolk proteins from the yolk sac (reptiles and birds) or via the placenta (mammals).
2) The Jacobson's organ is an organ for olfactory perception (vomeronasal organ) in snakes and consists of a pair of cavern-like organs in the palate area.
3) The modern crocodiles are the only survivors of the lineage of archosaurs, from which the dinosaurs and their relatives, including the birds, evolved.
4) In turtles, high temperatures in the nest lead to female offspring. In the nest of crocodiles and alligators low temperatures lead to female animals; a high temperature in the nest favors the development of males.

17.6.9 AVES (BIRDS)

1) The seagull secretes a larger quantity of salt after feeding on mussels because they are poikilosmotic, the fish are homeosmotic. The mussels, therefore, contain more salt in their body fluids than fish.

2) *Archeopteryx lithographica* and *A. bavarica* were found as fossils in the 145 million-year-old Solnhofen plate limes (Late Jurassic). In common with reptiles they had teeth on the jaws, non-fused metacarpal bones, three fingers with claws, a large number of tail vertebrae, and they possessed neck ribs. A ridge (carina) was missing.
3) After hatching from the egg, nidicolous birds have hardly any thermoregulation mechanisms and must be warmed by the parents. They reach their "normal" body temperature only after a few weeks. Nidifugous birds are capable of thermoregulation shortly after hatching and can immediately leave the nest.
4) Birds possess a parabronchial lung, through which air flows continuously and unidirectional. Also unique are the seven to eleven air-sacs in the thorax (anterior air sacs) and abdomen (posterior air sacs), which extend with their diverticula into the cavities of the bones. There is no gas exchange in the air sacs. They serve as storage space for air (a kind of ventilator), but are also important for thermoregulation (water evaporation) and phonation. In all birds except the penguins so called "neopulmonic parabronchi" occur, an additional mass of lung tissue, which creates a connection from the main bronchus to the posterior air sacs. This forms a bidirectional channel through which air flows in both directions.
5) Countercurrent heat exchange in the blood vessels of the legs. The tips of the feet can have a surface temperature of 0 °C.

17.6.11 MAMMALIA (MAMMALS)

1) Homeothermy, hair pelage, brood care, complete separation of body and pulmonary circulation with high blood hemoglobin content, ability to concentrate urine, high muscular performance during exercise, sensitive sense organs, learning behavior, heterodont dentition, ability to digest cellulose, adaptive immune system.
2) The true horns of the Bovidae are hollow structures with a keratinized epidermis surrounding a bony core, which protrudes from the skull. True horns are not branched and are not discarded. The antlers of the Cervidae are branched and consist of solid bones. They are re-formed every year and discarded after the reproductive period. With the exception of the reindeer, only the males form antlers.
3) In horses and many rodents, an ample sacculation of the intestine (appendix or caecum) represents the fermentation chamber for cellulose digestion; in the ruminants the rumen of the four-chambered stomach. In both cases, cellulose degradation occurs through bacteria and Protozoa.
4) Changes in the size of a population are triggered either by environmental factors such as weather and natural disasters (density-independent factors) or they are related to population density (density-dependent factors).

INDEX