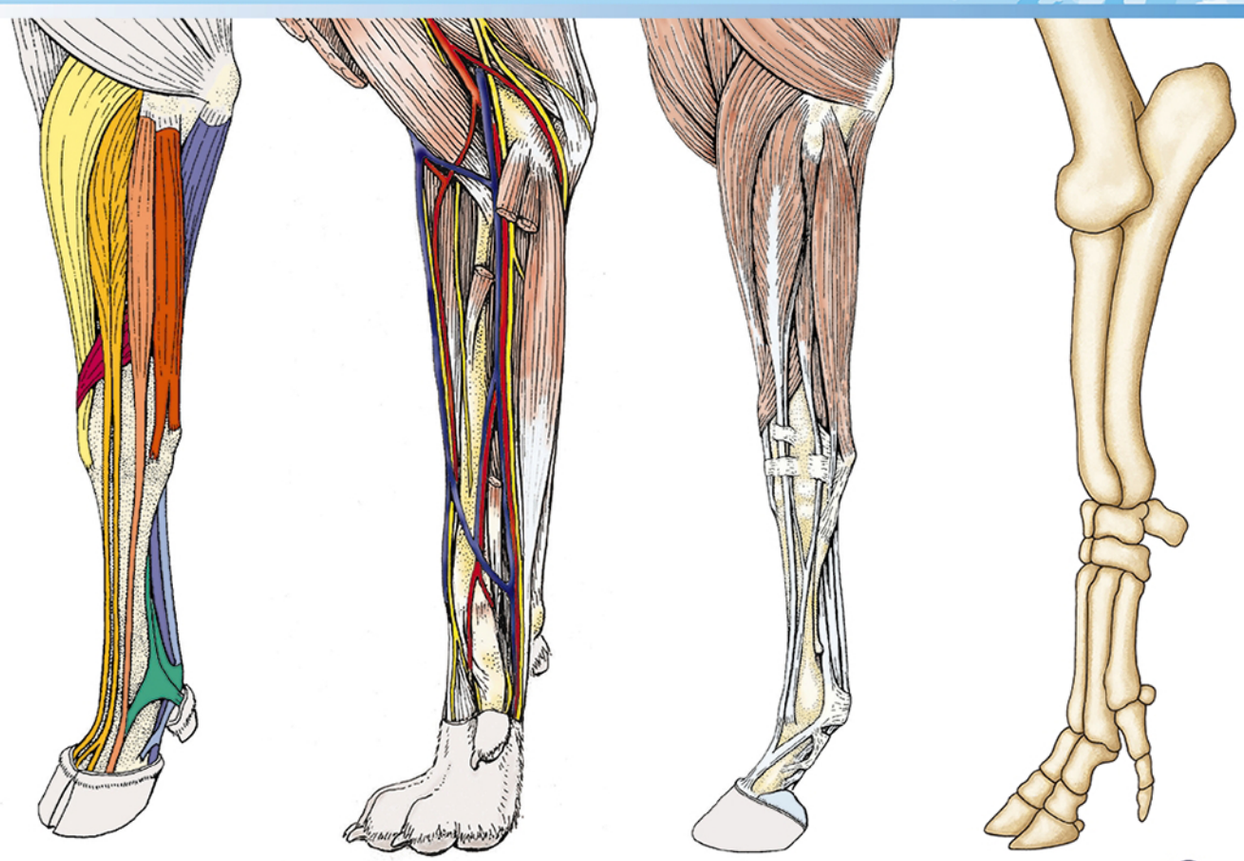
Veterinary Anatomy of Domestic Animals

Textbook and Colour Atlas

Edited by
Horst Erich König
Hans-Georg Liebich

Seventh Edition



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Veterinary Anatomy of Domestic Animals

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Horst Erich König
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7th, updated and extended edition

1147 figures

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Foreword to the 7th edition

In each of the six editions published since 1999, it has been our goal to provide readers with the latest scientific information, and to illustrate this with outstanding colour photographs of high-quality anatomical preparations, pictures derived from contemporary imaging modalities and digitally coloured schematic representations. The same approach has been rigorously pursued in this, the seventh, edition. Numerous suggestions from students and practising veterinary colleagues have been incorporated into this new version. Throughout this process, the overwhelmingly positive responses to our earlier work inspired and challenged us in equal measure to maintain our previously established standards.

The addition of a chapter on avian anatomy has transformed the book into a comprehensive volume covering the anatomy of domestic animals. Based on our colour text and atlas "Anatomie der Vögel" (2009; published in English as "Avian Anatomy" in 2016), this new chapter focuses on the anatomical features that are particular to the class Aves. More detailed descriptions and additional illustrations pertaining to the fundamental and clinical/applied anatomy of birds can be found in "Avian Anatomy".

To acknowledge the lasting contribution that our book has made to veterinary anatomy, a further priority in developing the seventh edition was to preserve its essential purpose. Thus, the newly integrated learning and teaching materials are intended not only to satisfy the increasing demands of anatomical study and clinical practice, but also, ideally, to inspire enthusiasm in our readers for a discipline that is often regarded as "dry". If we make any progress toward reaching this desired goal, we will have achieved a great deal.

The new edition covers essential aspects of systemic, topographic and clinical anatomy and aims to promote understanding of the complex relationships between anatomical structures and their associated functions. The contemporary approach of combining a veterinary anatomy textbook and colour atlas is further enhanced by the inclusion of imaging and pictures of anatomical sections. In this way, we seek to address the challenges of modern-day veterinary practice by providing practitioners with a tool for interpreting sectional representations obtained using diagnostic imaging modalities.

This edition has also been designed to facilitate modular interdisciplinary education in organ structure and function. Far more than ever before, veterinary curricula require students to acquaint themselves with the fundamentals of anatomy through independent study and critical evaluation. However, this can result in knowledge deficits that are often quite profound. This 7th edition strongly supports independent learning by organising information based on systems and topography. Presentation of fundamental anatomical content in this discipline-oriented manner facilitates understanding of applied anatomy in clinical contexts, as required in modular learning and teaching settings. To further ensure scientific rigour, anatomical terms used in the 7th edition are taken consistently from the most recent version of the Nomina Anatomica Veterinaria (2017).

Our combined text and colour atlas has in recent years been recognised internationally, earning acclaim from students and colleagues around the world. This is reflected in the appearance of licensed editions in 11 additional languages. Of particular note are the translations into Portuguese, Spanish, Italian, Polish, Turkish, Japanese and Chinese. Further translations are currently in preparation. Arguably the world's most widely translated veterinary textbook, it serves as a valuable tool for students, helping them to prepare for and successfully complete their veterinary examinations. Moreover, as a companion reference book, it has an established role in facilitating proficiency in clinical practice. These are pleasing outcomes in which we take a certain degree of pride.

Updating of the educational content in this edition would not have been possible without the assistance of numerous colleagues. We have, in the past, had opportunity to express our deep appreciation to co-authors who contributed written content and images to earlier editions, to colleagues responsible for preparing anatomical specimens and to co-workers who brought their technical expertise to bear in ensuring that the various editions have been so aesthetically pleasing. In particular, we thank Dr. Polsterer (Vienna) for the schematic illustrations and Ms Schura (Munich) for her expertise in digital colouring.

Several colleagues in the scientific community have provided helpful suggestions and contributions to this latest edition, in the form of both text and images. We acknowledge and express our thanks to Professor Latorre (Murcia, Spain) and Dr. Hartmann (Stephanskirchen) for providing clear and informative arthroscopic images and pictures of the guttural pouch of the horse. Dr. Witter (Vienna) and Dr. Schöpper (Vienna) also deserve particular thanks for their contributions to the chapter on the common integument, and to the description of the teeth. Sincere thanks are due to Professor Kneissl (Vienna) and Professor Ludewig (Vienna) for revising and updating the section on diagnostic imaging. A further debt of gratitude is owed to Associate Professor Paulsen (Vienna) for contributing recent findings to the chapter describing the lymphatic organs. Professor Budras (Berlin) supplied important suggestions regarding the common integument. Selected material relating to hoof trimming, provided by Dr. Hagen (Leipzig) for the online component of the 6th German edition, has been incorporated into this new edition. With reference to the chapter on avian anatomy, we extend our thanks to Dr. Donoso (Universidad de Concepción, Chile) for furnishing us with a valuable image of a claw on the wing of a Chilean bird.

Particular thanks are due to Dr. Corinna Klupiec for her scholarly and technically competent translation of the additional text and image labels appearing in the 7th English edition. Her profound bilingual and anatomical skills have once again been demonstrated in this publication. Our thanks also go to Professor Simoens (Ghent) for his expert suggestions and for his critical appraisal and revisions of the text and image labels.In closing, we wish to thank Dr. Schäfer, Ms Schwarz and Ms Wallstein who, on behalf of the publisher, have provided active and helpful stewardship throughout the production of this 7th edition.

Vienna and Munich, in autumn 2019

Horst Erich König and Hans-Georg Liebich

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- 2013 Guest professor at Saskatchewan University in Canada
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1 Introduction and general anatomy

H.-G. Liebich, G. Forstenpointner and H. E. König

1.1 History of veterinary anatomy

G. Forstenpointner

The doctrine of morphology as the scientific study of the form and structure of organisms was founded by **Aristotle**. He defined morphology as the search for a common construction plan for all structures, while adhering to a strict methodological process. Where similarities can be found, the relation between form and function requires further clarification. This scientific approach set Plato's best student apart from the early Greek natural philosophers and to this day is the principle method employed in all areas of basic research.

Presumably Aristotle performed anatomical research through dissections. References found in his work **Historia Animalium** indicate that he published another treatise, Parts of Animals, which sadly did not survive. This work dealt mainly with the digestive and reproductive systems. Here Aristotle recorded his impressions with schematic illustrations. Many of his observations were naturally incomplete, which often led him to erroneous conclusions. However, many of his thoughts on function remain worth reading: for example, his explanation of quadruped locomotion recorded in The Gait of Animals. Being a teacher, Aristotle's greatest motivation for research was gaining knowledge for knowledge's sake. This motivation was carried on by his student, **Theophrastos of Eresos**, and by Roman researchers in natural science such as **Plinius** and **Aelian**.

Almost two thousand years passed before the humanists of the 15th and 16th centuries renewed the Aristotelan access to comperative morphology. Especially in Italy, the study of animal and human bodies led to many new discoveries in this field. These findings were meticulously recorded in a demandingly artistic manner and are today famous works of art.

Leonardo de Vinci, by far the most famous artist of this period, embodied this new quest for knowledge and understanding, as is evidenced in his multifaceted research.

Other excellent researchers were **Fabrizio d'Acquapendente**, who completed the first work in comparative embryology (De formatu foetu, 1600), and **Marcello Malpighi**, who studied the development of the chick embryo (Opera omnia, 1687). Even though initial progress was impeded by an unstable political situation as well as by the religious establishment, these scientists were forerunners in their fields and heralded in a golden age of comparative anatomy. This trend continued until the end of the 19th century and was characterised by a period of extraordinary productivity of many notable naturalists.

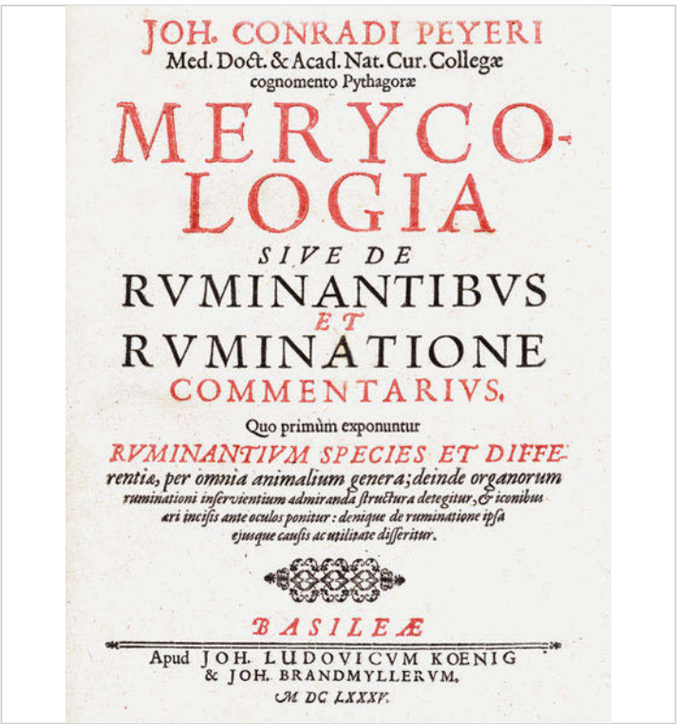
Richard Owen, a renowned English anatomist, and the Germans **Johann Friedrich Meckel** and **Caspar Friedrich Wolff** played dominant roles in the resurgence of comparative anatomy as a discipline in Europe. Since the turn of the 20th century, the field of zoological research has been subject to constant redirection. This has led to the development of new disciplines which abandoned the orginal intentions of comparative anatomy as intended by its founders.

Anatomical knowledge is not achied for its own sake, but is a prerequisite for successful medical practice. Throughout the ages, due to religious and ethical boundaries, human dissections were highly restricted or forbidden outright. Recorded exceptions were seldom, one being from the Hellenic school of Alexandria under the leadership of Herophilus and Erasistratos. These vivisections on criminal convicted contributed to a greater understanding of neuroanatomy. Furthermore, Aristotle's singular work on human anatomy was drawn from the dissection of a miscarried foetus.

Since animal dissections were the only possibility of studying the principles of form and function, these findings were extrapolated to human anatomy. **Claudius Galenus**, who served under the Emperors Marcus Aurelius and Commodus, became the most famous and influential doctor in Rome.

The results and interpretation which he gained through consequent research laid the unchallenged foundation of anatomical knowledge that lasted throughout the following 1500 years. Galen considered himself a physician by trade, however his understanding of anatomy and physiology was based upon Aristotle's publications, such as The nature of Things. He ardently pursued research in these two disciplines Aristotle's methodology. Because Galen's teachings were intelligible and rational, they endured as the unchallenged foundation of anatomical and physiological knowledge for over 1500 years.

Even though his anatomical conclusions were sound, Galen's interpretations of some systems, such as the heart and large vessels, were erroneous. Due to the lack of human autopsies, Galen's extrapolations of animal dissection results were often misguided. For example, he suspected that the Rete mirabile epidurale would


JOH. CONRADI PEYERI
Med. Doct. & Acad. Nat. Cur. Collegæ
cognomento Pythagoræ
MERYCO-
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SIVE DE
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ET
RVMINATIONE
COMMENTARIVS.
Quo primùm exponuntur
RVMINANTIVM SPECIES ET DIFFE-
rentiæ, per omnia animalium genera; deinde organorum
ruminationi inservientium admiranda structura detegitur, & iconibus
æri incisis ante oculos ponitur: denique de ruminatione ipsa
ejusque causis ac utilitate disseritur.
BASILEÆ
Apud JOH. LUDOVICVM KOENIG
& JOH. BRANDMYLLERVM,
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Fig. 1.1 Cover of Merycologia. (Johann Konrad Peyer, Basel, 1685)

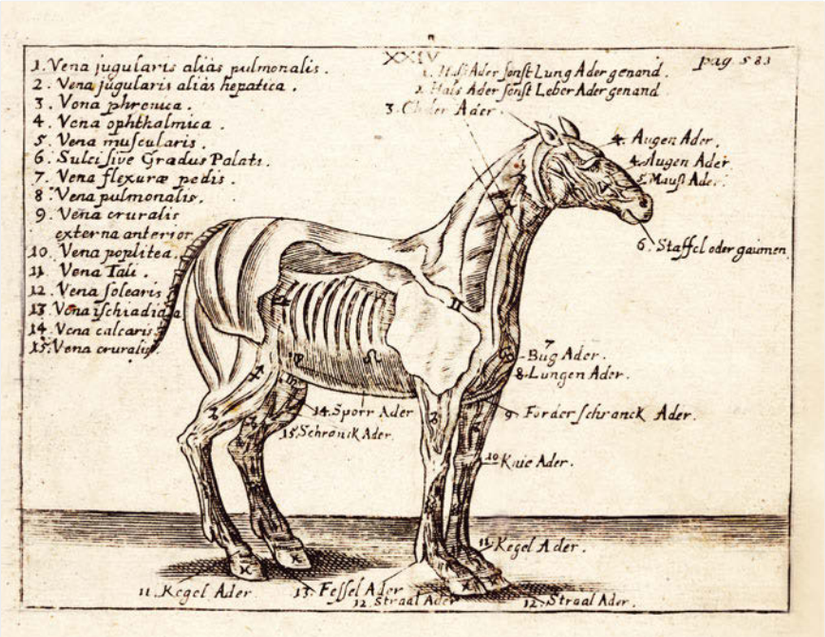

Fig. 1.2 Early illustration of the blood vessels of the horse. (Seifert von Tennecker, pseudonym Valentin Trichter, 1757)

also be found in humans even though now we know it is a typical structure of ruminants. Further, he concluded that humans must have a caecum built like that of herbivores or a uterus with cotyledons.

In the tradition of Galen, an anatomical atlas of the pig (Anatomia porci, written by Copho or Kopho) was published in Salerno around 1100–1150. This was not the first anatomy book in veterinary medicine, but rather was meant as an anatomical teaching tool for students of human medicine. The generally accepted myth then and today – that the pig resembles the human more than any other animal – relies greatly on the similar eating habits and the availability of subject material in those days.

Fig. 1.3 Illustration of the equine musculature. (Dell'Anatomia e dell' Infirmita del Cavallo; Carlo Ruini, Venice, 1598)

During the Renaissance, anatomical studies on human corpses were no longer taboo. With his monumental work on human anatomy (De humani corporis fabrica, 1543), **Andreas Vesalius** marked the hesitant beginning of a revolutionary new attitude toward the human body. Early anatomists still considered themselves naturalists, compiling many fundamental discoveries of morphology through continuing studies of animal anatomy. Vesalius was the first to realize that the Rete mirabile epidurale represented a typical structure of ruminants. Studies of ruminant digestion were advanced by **Johann Conrad Peyer** through his magnificent publication in 1685, Merycologia sive de ruminantibus et ruminatione commentarius (▶ Fig. 1.1). His discovery of lymphatic tissue (Lymphonoduli aggregati) in the intestinal mucosa resulted in the name Peyer's patches. From the beginning, the study of comparative anatomy has remained a domain for research institutes specialising in human anatomy, even more so as zoological research turned away from the study of morphology.

In the last decades of the 20th century, the use of laboratory animals led to the optimizing of therapeutic approaches. The implementation of experimental concepts has been possible only through the application of necessary basic animal morphology, which has largely been provided by physicians. Interestingly, still today animals are chosen as models, not because of their morphological comparability, but rather for their availability.

Veterinary anatomy as a prerequisite for practicing veterinary medicine has developed only in the last few centuries as an independent teaching and research subject. It is evident through ancient and medieval texts for animal caretakers that the anatomical knowledge, especially of horses, was more or less precise (▶ Fig. 1.2). However, the systematic portrayal of the basic morphological associations was nonexistent.

Equerry handbooks created in the tradition of **Jordanus Ruffus** in the late middle ages and early modern age were not systematically organised. They did contain information on equine anatomy, which was often accompanied by ineffectual illustrations. In 1598, **Carlo Ruini** published an at that time exceptional handbook, Dell' Anatomia e dell'Infirmita del Cavallo (▶ Fig. 1.3). Seem-

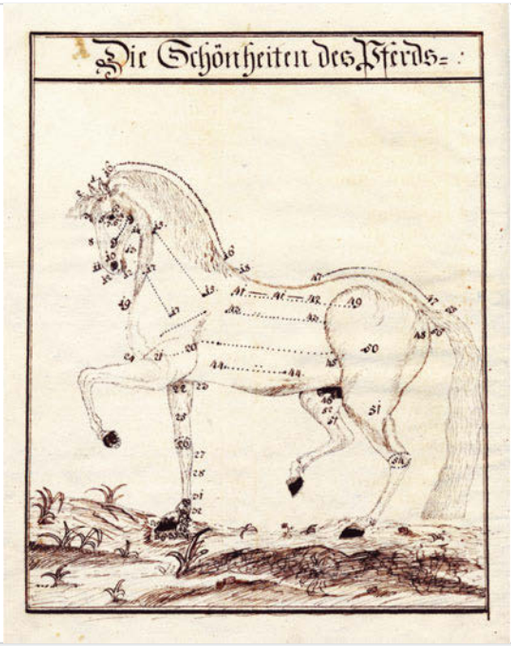

Fig. 1.4 Original drawing showing the body regions of the horse. (from the lecture notes of Ludwig Scotti, School of Horse Cures and Operations, Vienna, 1770)

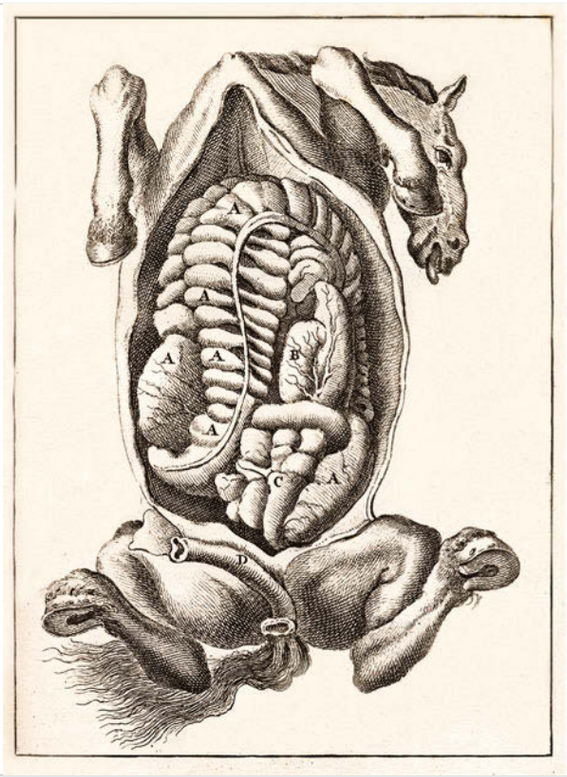

Fig. 1.5 Topography of the horse abdomen. (William Gibson, London, 1754)

ing to appear without a forerunner, this textbook was undoubtedly inspired by Vesalius.

Ruini was born into a prosperous family from Bologna and neither worked as an equerry nor was a member of the university. Through excellent private tutors, he developed a passionate interest in the natural sciences and was an enthusiastic equestrian. Although incomplete and sometimes flawed, his seminal work was nevertheless the first comprehensive and systematic portrayal of equine anatomy. The second half of the book concerning equine diseases was largely an indiscriminate recapitulation of much older literature. The magnificence of this publication lies in its illustrative quality, which rivals that of **Leonardo da Vinci** or **Vesalius**. Ruini's textbook was to be republished, plagiarised and translated many times (▶ Fig. 1.5).

At the beginning of the 17th century, veterinary anatomy was slowly beginning to enter a renaissance. However, it was not to be until about 150 years later that a veterinary academy was created where Ruini's textbook could be used to train animal doctors.

Considered to be the father of veterinary anatomy, **Philippe Etienne Lafosse** opened at his own expense a private veterinary school in Paris in 1767. This endeavour proved unsuccessful, and the school was closed in 1770. Two years later, he published his most successful work, Cours d'Hippiatrique. (A Course on Hippiatry or A Complete Treatise on the Medicine of the Horse). This work was organised according to organ systems, fundamentally resembling the form used today in modern anatomy textbooks. The clinical relevance of a topographical approach was soon integrated into the teaching of anatomy.

One of the earliest topographical illustrations of the horse (▶ Fig. 1.4) is found in the lecture notes recorded and published in 1770 by **Ludwig Scotti**, the first director of the School for Horse Cures and Operations in Vienna. The development of anatomy as an independent discipline at the newly founded European veterinary schools was tentative at best. Consequently, it was not until 1822 that the first comprehensive anatomy text- or handbook was published. The first german comprehensive veterinary anatomy reference was **Konrad Ludwig Schwab's** Anatomy Textbook of Domestic Animals of 1821 (▶ Fig. 1.6), followed closely by **Ernst Friedrich Gurlt's** Handbook of Comparative Anatomy of Domestic Mammals in 1822 (▶ Fig. 1.7). These works represented the beginning of a long German tradition of veterinary anatomical research that quickly gained international recognition and lasted far into the 20th century. Eighteen editions of Gurlt's work were published, with each new edition being revised and improved until the final one was print in 1943. **Wilhelm Ellenberger** and **Hermann Baum** were responsible for the 9th to the 17th editions, creating the style that can still be observed today in this readily available book (▶ Fig. 1.8 and ▶ Fig. 1.9). The sheer volume of publications in veterinary anatomy originating from Germany, Switzerland and Austria in the middle and late 19th century was overwhelming. This reflects the field's significance and the high esteem in which veterinary anatomy was held in those days.

A landmark decision during the modern era of veterinary anatomy was the establishment of the International Committee for Nomenclature in Veterinary Anatomy. Emulating the human medical publication, Nomina Anatomica, the first edition of Nomina Anatomica Veterinaria was published in 1968. This work standardises worldwide anatomical terminology in veterinary medicine, thus providing a useful instrument to maintain the importance of anatomy in a steadily changing medical landscape.

Anatomy is the **branch of morphology** dealing with the form, structure, topography and the functional interaction of the tissues and organs that comprise the body. The dissection of dead

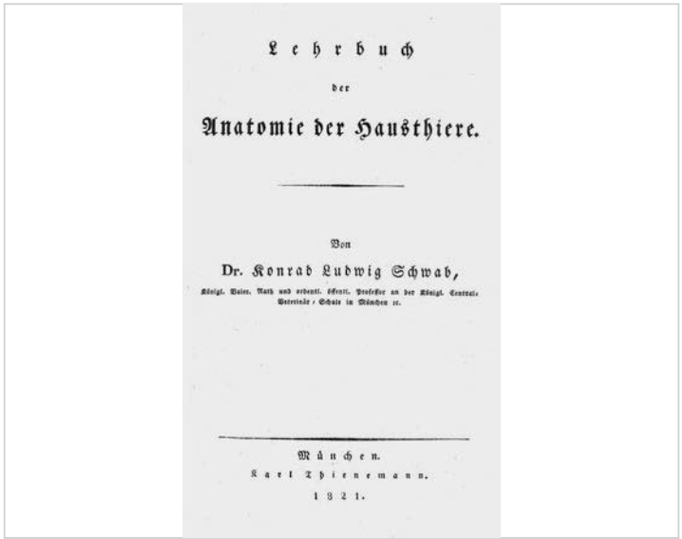
Lehrbuch
der
Anatomie der Hausthiere.
Von
Dr. Konrad Ludwig Schwab,
München.
Karl Thienemann.
1821.

Fig. 1.6 Title page of the first german language Anatomy Textbook of Domestic Animals. (Konrad Ludwig Schwab, Munich, 1821)


Handbuch
der
vergleichenden Anatomie
der
Haus-Säugethiere.
Von
Dr. E. F. Gurlt
Professor an der Königlichen Thierarzneischule in Berlin.
Erster Band.
Berlin, 1822.
Bei Friedrich Späthen.

Fig. 1.7 First edition title page of Handbook of Comparative Anatomy of Domestic Mammals. (Ernst Friedrich Gurlt, Berlin, 1822)

animals is still the most important and efficient method to study and comprehend anatomy. With the advancement of classical anatomy, **histology** including **microscopic anatomy** and **embryology** developed into independent disciplines. Although inseparable as a whole, this division facilitates a more structured and thus easier approach to gaining anatomical knowledge.

Systematic anatomy has to do with "sytem", in other words with structures and organs that fulfil a common function. The respiratory system for example is responsible for the gaseous exchange, whereas the nervous system receives, translates, transmits and responds to stimuli. Differences between the individual species can be compared, so that from an anatomical point of view "**systematic anatomy**" in teaching also represents a **comparative anatomy**, preferably limited to the domestic animals and poultry.

It is of great importance that students acquire a profound knowledge of systematic anatomy, from which they can then derive the overall connection of the structure and function of the animal body. Knowledge of **systematic anatomy** is the essential foundation for **topographical anatomy**, which describes the relative position and functional interaction of organs and structures of the various regions of the body. It presupposes a thorough working knowledge of systematic anatomy. Both systematic and topographic anatomy constitute the foundations of clinical practice.

Modern technologies, such as x-ray, ultrasound, computer tomography or magnetic resonance imaging, demand from the clinician greater knowledge of topographic anatomy, which is gained through studying sectional views of the body. **Sectional anatomy** represents a new direction in teaching and research in veterinary anatomy; a modern textbook would be incomplete without it.

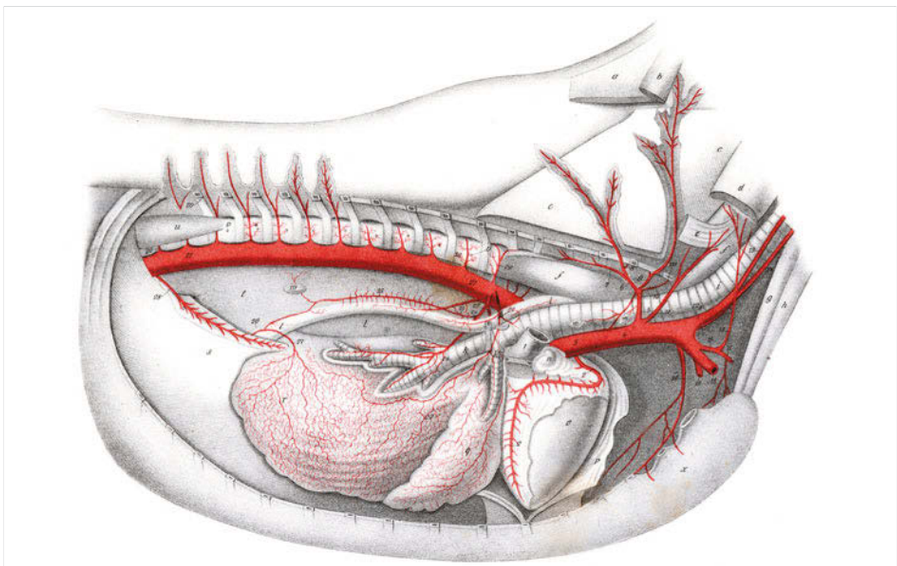

Fig. 1.8 Coloured illustration of the horse thorax. (from the Atlas to the Handbook of Comparative Anatomy of Domestic Mammals; Ernst Friedrich Gurlt, Berlin, 1860)

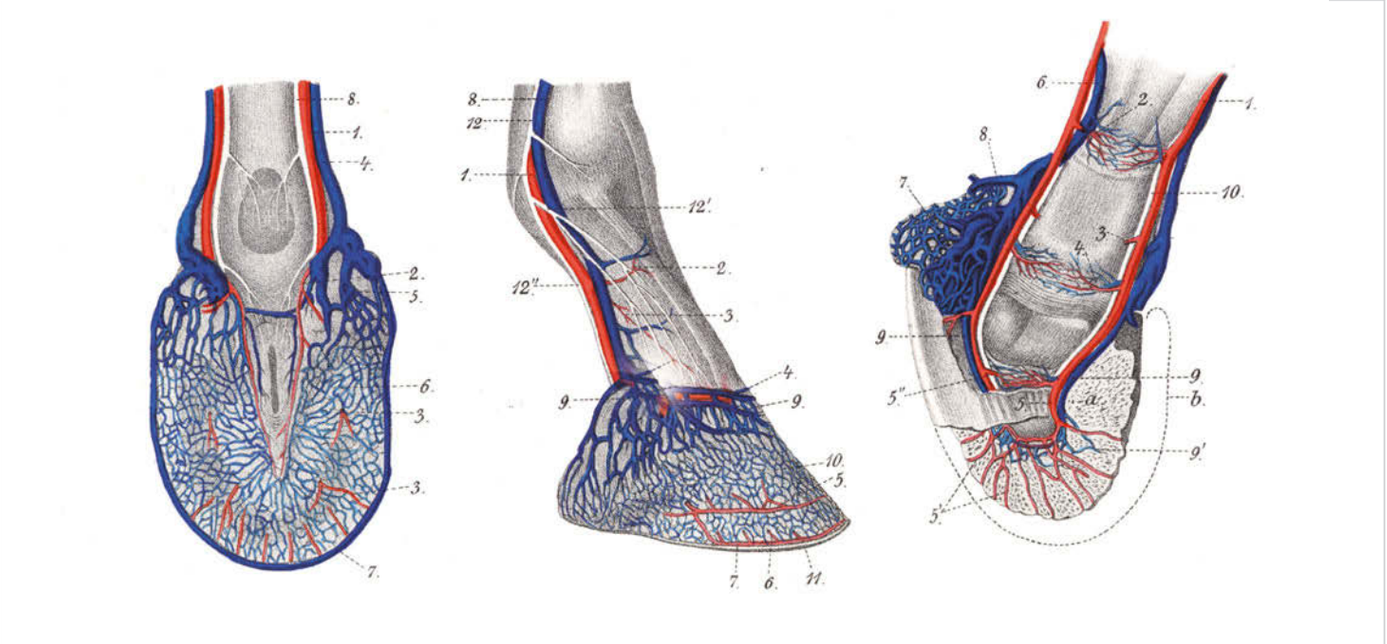

Fig. 1.9 Vascularization of the equine hoof. (from Leisering's Atlas on the Anatomy of Horses and other Domestic Animals; Wilhelm Ellenberger in cooperation with Hermann Baum, Leipzig, 1899)

1.2 Directional terms and planes of the animal body

H.-G. Liebich and H. E. König

Certain descriptive terms are employed to indicate precisely and unambiguously the position or direction of body parts. The most important anatomical terms are illustrated in ▶ Fig. 1.10 and the organ systems are listed with a short explanation in ▶ Table 1.1.

The body of an animal has major divisions which are clearly distinguishable externally: the head (caput), the neck (collum), the trunk (truncus), the tail (cauda) and the limbs (membra). Each one of these sections is in turn divided into regions, which function as descriptive motifs for the topographic anatomy; for more information see Chapter 20 "Topographical-clinical anatomy" (p. 685).

1.3 Division of the animal body in organs and organ systems

H.-G. Liebich and H. E. König

Cells and tissues similar in structure and function are joined together to form individual organs or organ systems. These act synergistically to fulfill functions that define the organism and ensure survival. The individual organ systems are composed of different types of tissue. An individual organ is made up of two types of tissue:

- parenchyma and
- interstitial tissue.

The **cells of the parenchyma** are responsible for the function of the organ (e.g. hepatic cells of the liver, renal cells of the kidneys, glandular cells of the salivary glands). The **interstitial tissue** builds the connective tissue that, for example, either encloses a small functional unit or separates larger areas of an organ into lobules (lobuli) or lobes (lobi). Connective tissue also supports metabolic transport to and from the organs, enclosing not only blood and lymph vessels but also peripheral nerves from the nervous system, all of which supply the organ. Together these structures form an overriding system that greatly influences the structural and functional character of an organ. **Systematic anatomy** examines in detail individual organ systems of the body, which are listed in ▶ Table 1.2.

Veterinary anatomy deals mainly with **domestic mammals**. These are taxonomically classified as Canis lupius f. familiaris (dog), Felis sylvestris f. catus (cat), Sus scrofa f. domestica (pig), Bos primigenius f. taurus (cattle), Ovis ammon f. aries (sheep), Capra aegagrus f. hircus (goat) and Equus przewalskii f. caballus (horse). Also included in the study of veterinary anatomy is poultry, whereby Gallus gallus f. domestica (chicken) is the most common specimen. Poultry is an important field in veterinary medicine and is therefore extensively covered in a separate textbook containing a revised and updated introduction to avian propedeutic and clinical medicine (König HE, Korbel R, Liebich H-G. Anatomie der Vögel. 2. Aufl. Stuttgart: Schattauer; 2009).

Table 1.1 Directional terms and virtual planes of the animal body.

Term	Meaning	Usage
Cranial	Towards the head, trunk and tail	Trunk and tail, limbs proximal to the carpus and tarsus
Rostral	Towards the tip of the nose	Head
Caudal	Towards the tail	Head and trunk, limbs proximal to the carpus and tarsus
Dorsal	Towards the back	Trunk, head and the front of the limbs distal of carpus and tarsus
Ventral	Towards the belly	Underside of the trunk, head
Medial	Towards the centre	Head, trunk and limbs
Lateral	Towards the side	Head, trunk and limbs
Median	In the middle	Trunk, head and limbs
Proximal	Towards the trunk	Limbs and other body parts located close to the trunk or projecting away from the trunk
Distal	Away from the trunk	Limbs and other body parts located at a distance form the trunk or projecting away from the trunk
Palmar	Towards the palm of the hand	Forelimbs distal of the carpal joint
Plantar	Towards the sole of the foot	Hindlimbs distal of the tarsal joint
Axial	Towards the axis of the digits	Digits
Abaxial	Away from the axis of the digits	Digits
External	Located outside	Body parts and organs
Internal	Located inside	Body parts and organs
Superficial	Located near the surface	Body parts and organs
Deep	Located in the depth	Body parts and organs
Temporal	Towards the temporal bone	Eye
Nasal	Towards the nose	Eye
Superior	Above	Eyelid
Inferior	Below	Eyelid
Apical	Towards the tip	Nose, digits and tail
Oral	Towards the mouth	Head
Virtual planes of the animal body		
Median plane	Plane dividing the body in two equal parts	
Paramedian plane	Any plane parallel and close to the median plane	
Sagittal plane	Any plane parallel to the median plane but located further lateral	
Dorsal plane	Any plane parallel to the dorsal surface	
Transverse plane	Any plane perpendicular to the long axis	

Table 1.2 Organ systems.

Name	Primary function
Outer skin	Protective covering of the animal body
Skeleton and joints	Supporting framework of the body
Musculature of the skeleton	Locomotion
Digestive system	Food intake, mastication, chemical digestion, excretion and absorption
Respiratory system	Oxygen supply, elimination of carbon dioxide and production of sound
Urogenital system	Excretion and reproduction
Circulatory system	Transport and exchange of substances
Nervous system	Regulation, transmission, reaction in response to external stimuli
Organs of sense	Reception of external stimuli
Endocrine glands	Regulation of cell functions by hormones
Immune system	Response to infection

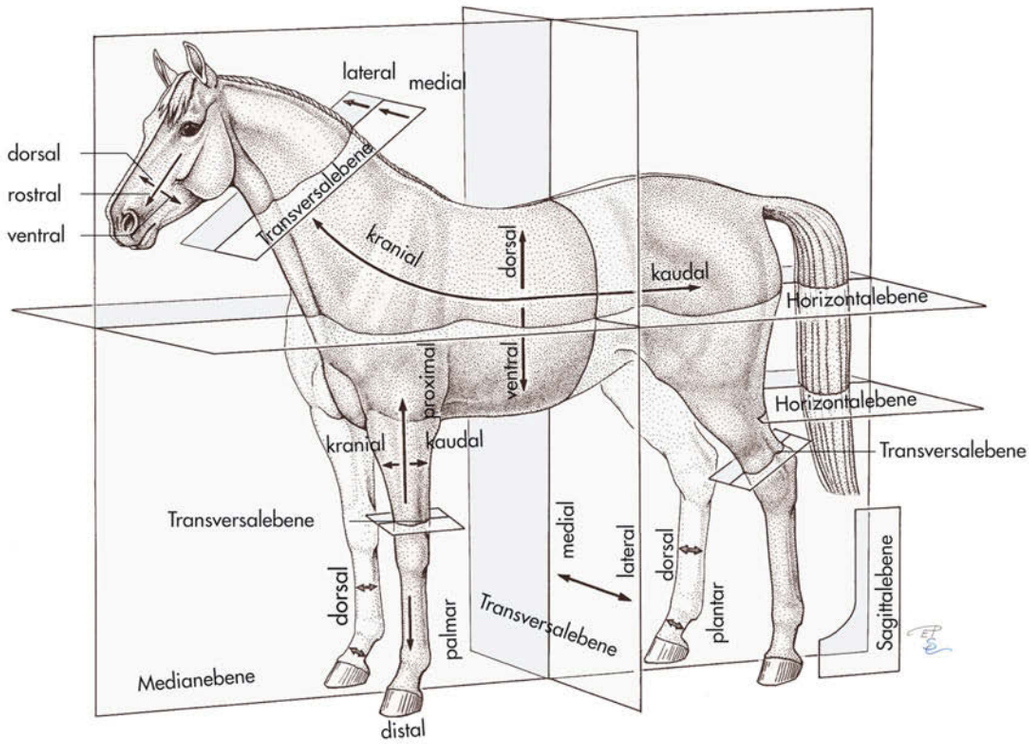

Fig. 1.10 Directional terms and planes of the animal body (schematic); fig. based on data from Dyce, Sack and Wensing, 2002.

1.4 Locomotor apparatus (apparatus locomotorius)

H.-G. Liebich and H. E. König

The locomotor apparatus is a **complex organ system** whose primary function is mechanical. The skeleton and the muscles are the major elements comprising this system, forming and maintaining the individual body shape and providing for the locomotion of body parts or the whole organism.

The **skeleton** is composed of individual elements: the **bones** (ossa), **cartilage** (cartilagines), **ligaments** (ligamenta) and the **joints** (articulationes) that together create the body's framework, the **skeletal system** (systema skeletale).

The **skeletal system** constitutes the **passive part of the locomotor system**, whereas the **musculature** (systema musculare) represents the **active part**. Both parts form a functional unit that is integrated into the body's circulatory, lymphatic and nervous systems.

The system performs many metabolic functions at a cellular level. Hormones regulate a constant process of growth, modification and breakdown. The term "**locomotor system**" does not do justice to this many-facetted system; therefore this system is more appropriately referred to as the system of motion, stability and support.

Malfunctions and diseases of this system are among the most common diagnoses made in clinical veterinary medicine. The importance of basic anatomical knowledge is often greatly underestimated.

1.4.1 Skeletal system (systema skeletale)

Osteology (osteologia)

Osteology is the study of bones (ossa) that combine to form the skeletons of diverse animal species. Bones are composed of:

- **bone tissue** which is sheathed inside and outside by the
- **endosteum** and **periosteum**, respectively, and the
- **bone marrow** (medulla ossium), as well as the
- **blood vessels** and **nerves** supplying these structures.

These components classify bone as an **organ**.

The individual form of each bone is genetically determined and remains even though forces of traction and compression subject the bone to continual adaptation processes. Because of their high **mineral content** (60–70%), bones do not undergo post-mortem changes and are thus useful objects of archaeological study. **Maceration of bone** is the process of removing **organic components** through the use of weak lye. Bones used as teaching objects have usually undergone such treatment. Treating the bones with an **acid** removes the **inorganic** or **mineralised** components.

Skeletal design

Connective tissue precursor of bone

All components of the skeletal system develop from the **middle embryonic germ layer** (**mesoderm**). Early in embryonic development, the mesoderm differentiates into three types of connective tissue: embryonic, reticular and fibrous. These tissues consist of:

- **cells** (e.g. fibrocytes),
- **fluid-filled intercellular spaces** and
- **fibrous components** (collagen and elastin).

These tissues become more abundant as development progresses, and at genetically determined locations these tissues transform into tendons, ligaments and fasciae. Developmental processes in the embryonic regions of the trunk and limbs begin early in development and lead to structural and functional specialisation of the embryonic tissue. The two elements of support tissue, **cartilage** and **bone**, develop from this primordial **loose connective tissue** (textus connecticus collagenosus laxus).

Both bone and cartilage originate from **mesenchymal precursor cells**, the **chondroblasts** and **osteoblasts**, respectively, which mature into the **chondrocytes** and **osteocytes**. These cells synthesise a matrix of collagen fibres and matrix.

Development and growth of cartilage

Cartilage is characterised by the structure of its **formless matrix**, the **intercellular substance**, which consists primarily of glycosaminoglycans. Embedded in the intercellular substance are **collagenous fibres**, the structural element of cartilage. This unique construction lends cartilage strength and flexibility. Due to their chemical structure, **glycosaminoglycans** are able to bind water, resulting in the increased elasticity and pliability of cartilage.

Blood vessels and nerves are absent in cartilage. Nutrients must diffuse through the matrix from blood vessels located in surrounding connective tissue, synovia or subchondral bone.

There are three types of cartilage classified according to the **quality of the embedded fibres**: **hyaline**, **elastic** or **fibrous cartilage**.

In adults, **hyaline cartilage** persists at the articular ends of long bones (cartilagines articulares), at the tips of the ribs (cartilago costae), and in parts of the laryngeal (cartilago laryngis), tracheal (cartilago trachealis), and bronchial (cartilago bronchialis) walls. **Elastic cartilage** forms the internal support for the epiglottis and the ear. **Fibrocartilage** forms the intervertebral discs, the menisci and the articular disc in the jaw joint. With increasing age, cartilage may ossify, to become invested with calcium salts. This occurs frequently in cats, for example, in the costal cartilage or the menisci.

The **formation of cartilage** (chondrogenesis, ▶ Fig. 1.11) originates in the **mesenchymal** (embryonal) connective tissue (see above), remnants of which still surround the cartilage in later stages of development. These remnants are the **perichondrium**, cells of which the **fibroblasts**, differentiate into **chondroblasts**, which produce the cartilage matrix containing water (70%), collagenous or elastic fibres and glycosaminoglycans.

Cartilage growth occurs through proliferation of chondroblasts in the perichondrium. This continual process leads to the **appositional expansion** of cartilage where new cartilage is created on the bone perimeter, directly beneath the surrounding perichondrium. Conversely, **interstitial growth** involves the proliferation of differentiated chondroblasts within the cartilage matrix, which continue to divide and form new matrix substance from the inside.

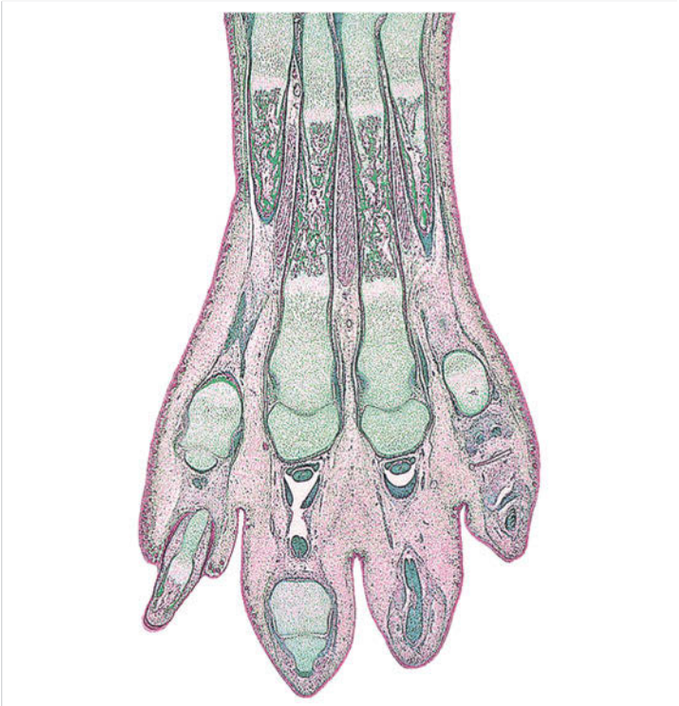

Fig. 1.11 Distal limb of a young cat during chondral ossification (histological section, Goldner staining).

Forms of bony tissues

Bones differ greatly in form, size and strength, not only between species but also within the same individual. These characteristics of bone are determined greatly through genetics, but also static-dynamic influences and structural changes due to nutrition during the juvenile and adult phases play an important role. Broad muscles or cordlike tendons create mechanical influences at their insertion points on the bone, leading to the development of a process, depression, tuberosity/protuberance, unevenness, ridge, or an edge. Blood vessels, nerves or organs (i.e. the brain, the eye, the cochlea of the inner ear) can also influence the surface structure of bone.

Despite the great variety of bones, they can be grouped according to common structural characteristics. These are as follows:

- long bones (ossa longa),
- short bones (ossa brevia),
- flat bones (ossa plana),
- pneumatic bones (ossa pneumatica) and
- irregular bones (ossa irregularia).

Long bones are characterised by a **shaft** or **diaphysis**, formed from a thick, **outer layer of compact bone** (substantia compacta), and an **inner medullary cavity** (cavum medullare, ▶ Fig. 1.12). Long bones have two ends, the **proximal epiphysis** and the **distal epiphysis**, which are covered by a thin layer of **cortical substance** (substantia corticalis). Both extremities contain **spongy bone**, which, as the name implies, resembles an ossified sponge with delicate pores (substantia spongiosa, ▶ Fig. 1.13 and ▶ Fig. 1.14).

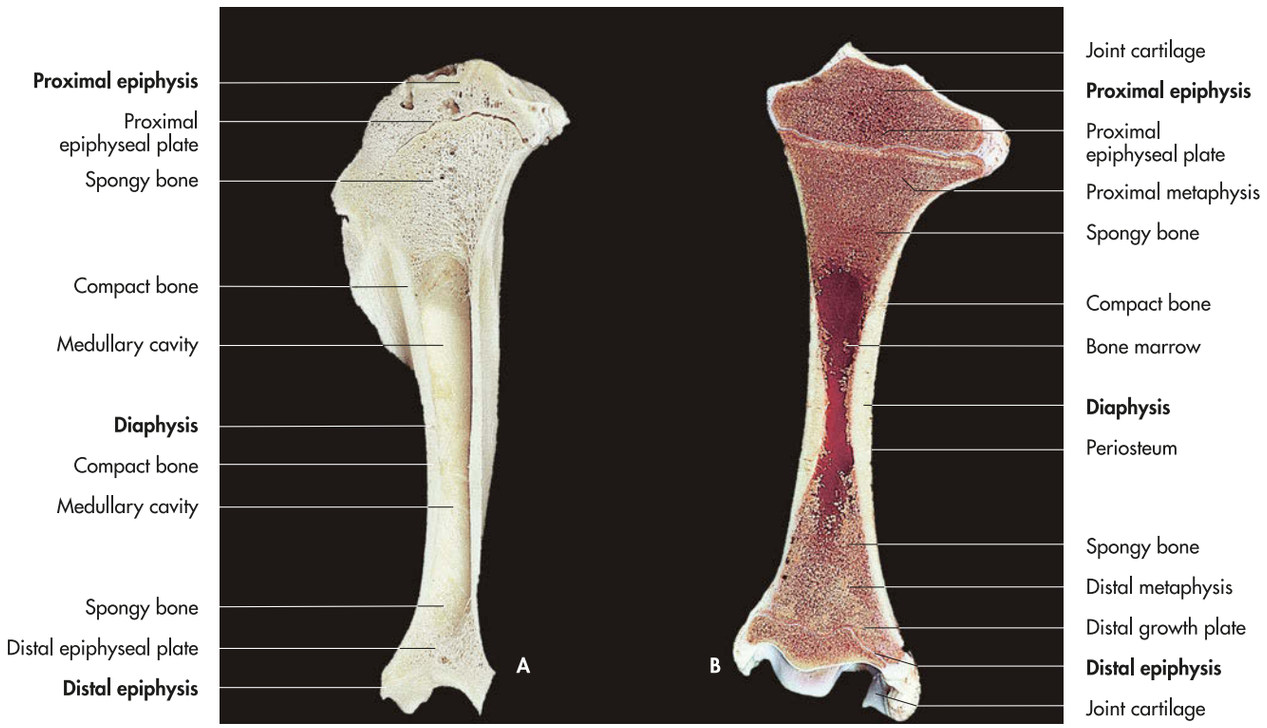

Fig. 1.12 Sagittal section of a long bone after maceration **(A)**, and sagittal section of an untreated long bone including joint cartilage and red bone marrow **(B)**.

Long bones form the basis of the limbs, i.e. upper arm (humerus), shin bone (tibia), or the metacarpal bones (ossa metacarpalia).

Short bones can have different forms: cylindrical, cubic or round. Such bones contain an extensive latticework of spongiosa in which haemoreticular tissue is present. Examples of short bones are those of the vertebral column and the hock joint.

Flat and **wide bones** consist of two layers of compact bone (tabulae) surrounding either spongy bone (diploe) or air (sinus). This group contains for example the scapula, the iliac bone or the ribs. Some bones of the skull are flat bones surrounding **cavities of air** (ossa pneumatica). These bones have formed through the subsequent resorption of bone substance and are lined with mucosa. Examples are the maxilla or the ethmoid bone.

Examples of irregular bones are the wedge-shaped bones of the skull: the sphenoid, presphenoid and basisphenoid bones. **Sesamoid bones** (ossa sesamoidea) are found close to the joints (i.e. the foot joints) and either lie beneath or are embedded in (i.e. patella) a tendon (▶ Fig. 1.33).

An **apophysis** is a bony protuberance that developed from an independent ossification centre. These structures provide attachment sites for muscles and ligaments. An example is a vertebral spinous process or the trochanter major on the femur. **Bones of the organs** are not related to the locomotor system. Such bones are found in the penis of male cats and dogs or in the bovine heart.

▶ Fig. 1.25, ▶ Fig. 1.26, ▶ Fig. 1.27, ▶ Fig. 1.28 and ▶ Fig. 1.29 schematically show the skeletons of the domestic animals covered in this textbook: cat, dog, pig, ox and horse. These illustrations provide a general overview of the topography of the bones, enabling a comparison between the species. The individual bones are described in detail in later chapters.

Architecture of bone

The high stability of bone is created through the bone tissue. Bone tissue is not massive and homogenous, but rather each individual bone has a specific architecture which is influenced by the:

- structure of the **compact bone** (substantia compacta),
- arrangement of the **spongy bone** (substantia spongiosa),
- form of the **central medullary cavity** (cavum medullare),
- **principles of tensile** (traction) and **compressive stress** (pressure),
- formation of **stress trajectories** and
- **flexure** (shear stress) demands on the entire bone.

The bone surface is constructed of **compact lamellae** which form the basis of the compact substance of bone. This solid layer surrounds the spongiosa, a delicate latticework of bone trabeculae and lamellae. Trabeculae and lamellae are arranged in a **pattern of stress lines** that have formed in response to external mechanical factors, the maximal tensile and compressive forces acting on the bone. The stress lines are either tensile or compressive trajectories. The family of curves that are tensile trajectories run parallel to one another just as the compressive trajectories run parallel to each other. These two types of stress trajectories always cross at right angles to each other **(trajectorial construction)**. One can distinguish between:

- tubules of bone (substantia tubulosa),
- trabeculae of bone (substantia trabeculosa) and
- lamellae of bone (substantia lamellosa, ▶ Fig. 1.13 and ▶ Fig. 1.14).

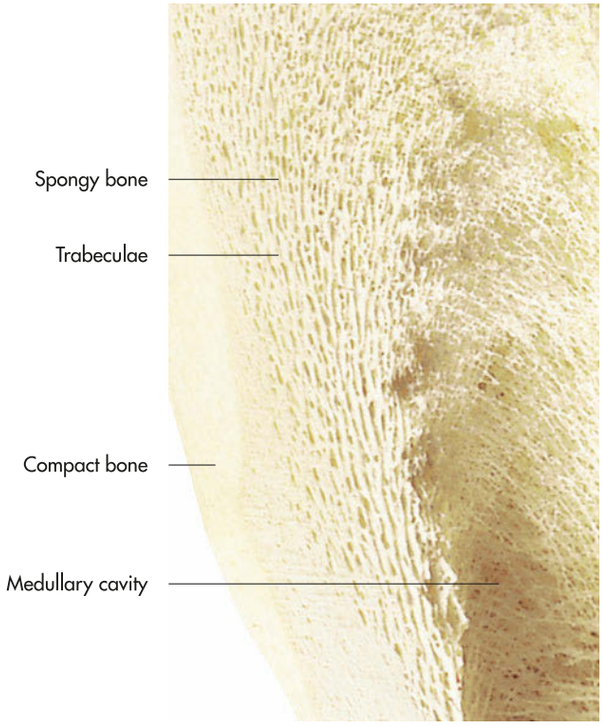

Fig. 1.13 Architecture of the wall of a long bone showing compact and trabecular bone.

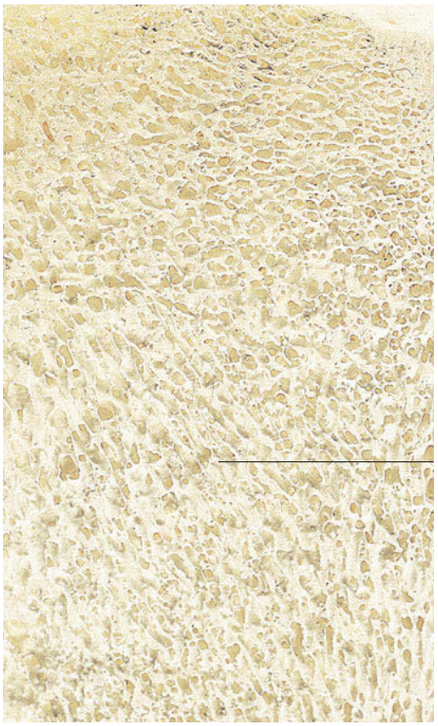

Fig. 1.14 Cross section of lamellar bone.

Stress occurring in the diaphysis of long bones does not affect stabilty but leads to tensile forces on the convex side of the bone and compressive forces on the concave side of the bone. In the centre, these two forces cancel out one another, and the net force is negligible. Thus the bone does not have to contain force-bearing structures in its centre: the ideal shape of bone is a long, hollow tube with reinforced walls, such as the diaphysis.

Instead of spongiosa as in the epiphyses, the diaphysis encloses the **medullary cavity** (cavum medullare). Here the compact substance is reinforced through thickened layers of lamellar bone (▶ Fig. 1.12). The medullary cavity is filled with **red bone marrow** where blood cells are produced (**hematopoiesis**), thus classifying bone as a **hemopoietic organ**.

Bone is built to maximise strength and stability while simultaneously minimizing material and weight. The architecture of bone creates the optimal prerequisites: the hollow tube creates strong resistance to stress, and the spongiosa economises material and is very light. The thickness of the diaphysis adapts to the maximal strain excercised on the bone. The medial walls of the limb bones carry a greater load and thus are thicker than the outer walls. Flat bones such as the scapula are denser on the edges and therefore thinner in the centre. Inorganic substances account for approximately two-thirds of a bone's dry weight. The remaining one-third is the organic substance of the bone, comprised mainly of collagen structural proteins and lipids (5–10%). Bone decalcification with acid removes the inorganic substances in bone, leaving the treated bone soft and pliable. Burning a bone destroys the organic substances; what remains are the bone ashes.

Endosteum and periosteum

Bones are sheathed on the inside and outside surfaces by a connective tissue membrane called the **endosteum** and **periosteum**, respectively. The endostium lines the medullary cavity and covers the spongiosa, thus creating a border between bone or spongiosa and bone marrow (▶ Fig. 1.17). The periosteum covers the external surface of bone, but is absent from the articular surfaces and where tendons and ligaments attach. Close to the joints, the periosteum detaches from the surface of the bone and consolidates with the **joint capsule**. On the opposite side of the joint, the periosteum leaves the capsule and attaches again to the surface of the adjacent bone. At bone/cartilage intersections, for example on the ribs, the periosteum continues over the cartilage as the perichondrium.

The **periosteum** is necessary not only for the blood supply, growth, regeneration, and fracture repair of bones, but also for the transfer of muscle power to the bone. The periosteum is composed of two layers, the:

- **inner cellular**, **osteogenic layer** (stratum osteogenicum, previously stratum cambium) and
- **outer protective fibrous layer** (stratum fibrosum).

The **stratum osteogenicum** (▶ Fig. 1.16 and ▶ Fig. 1.17) lies directly on the bone and **produces bone tissue** (i.e. is osteogenic). A great number of sensory nerve fibres as well as a network of blood and lymphatic vessels supplying the bone are enclosed in this layer. This layer also contains **progenitor cells**, the **preosteoblasts**, which can differentiate into osteoblasts, which produce bone and are responsible for **appositional growth**. This layer retains lifelong the ability to build bone tissue, which is important for physiological bone remodeling and fracture healing. The stra-

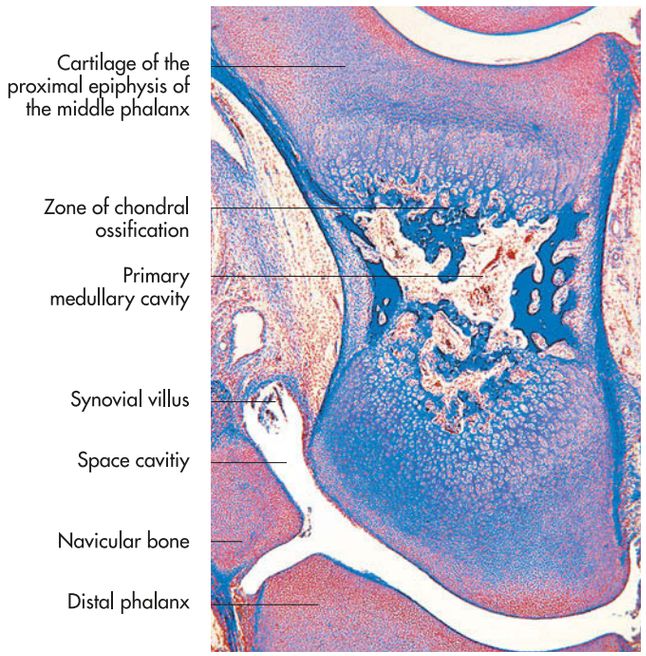

Fig. 1.15 Middle phalanx of a horse embryo (histological section, Azan staining).

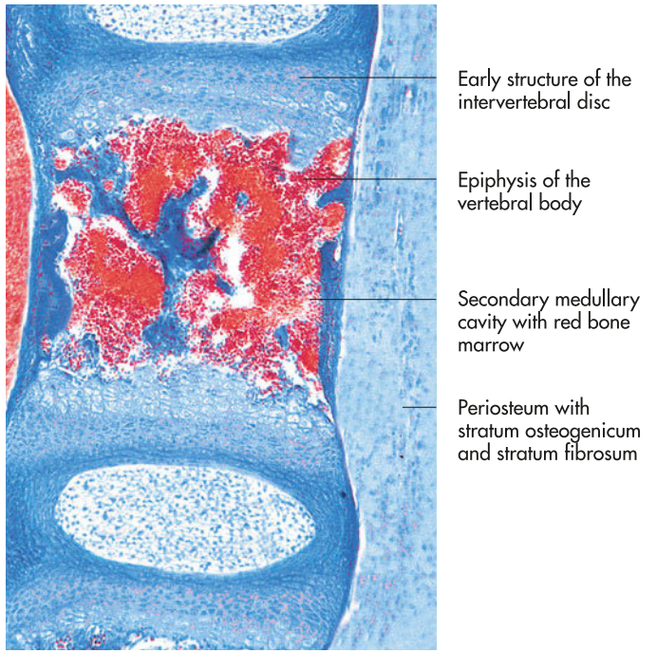

Fig. 1.16 Embryonic vertebrae (histological section, Azan staining).

tum osteogenicum forms the **cartilage callus** and **bone callus**, and prolonged mechanical stimulus of the periosteum can lead to the formation of **osseous bulges** (exostoses or splints).

Dense connective tissue interwoven with elastic fibers makes up the outer layer, the **stratum fibrosum** (▶ Fig. 1.16 and ▶ Fig. 1.17), which is very resistant to tensile forces. Collagen fibre bundles originating in this layer (**perforating fibres**) bind it to the surface lamella of the bone matrix (**Sharpey fibres**). These fibres firmly anchor the periosteum to the bone surface. The **stratum fibrosum** is also responsible for the attachment of muscles, tendons and ligaments to bone. At the site of attachment, fibres from the tendon or ligament branch out into the stratum fibrosum and, continuing as Sharpey fibres, strongly attach to the bone.

The **endosteum** (▶ Fig. 1.17) consists of a single layer of flattened, inactive osteoprogenitor (bone-lining) cells. They can differentiate into either **bone-forming cells** (osteoblasts) or **bone-resorbing cells** (osteoclasts). The endosteum borders the capillary network of the bone marrow and like the periosteum, is **capable of producing bone tissue (osteogenic potential)**.

Bone regeneration

Osteoprogenitor cells in the periosteum and endosteum are responsible for regeneration processes of the bone tissue. Regeneration is only possible when two conditions are met: 1. **mesenchyme cells** are available and 2. **osteoblast precursor cells** can proliferate. New tissue bridges the gap in the bone resulting from fracture.

Primary fracture healing occurs when motion between the two fracture pieces is negligible and they are separated by only small gaps. Lamellar bone forms directly in the fracture gap, re-uniting the two ends of the bone. When the edges are too far apart, then **secondary fracture healing** occurs. Fibrous connective tissue initially bridges the fracture gap forming a soft callus. The **callus ossifies** through mineralisation until, after a long reorganisation process, compact bone is formed.

Supply of blood vessels and nerves to the bone

Bone is an extremely well vascularised tissue, and this underscores its metabolic importance. A dense network of blood vessels supplies not only bone tissue, but also bone marrow, the periosteum and the endosteum. Bone trauma or fracture can interrupt the vascularisation, leading in extreme cases to tissue death (**bone necrosis**).

The vascularisation of bone is achieved through a unique, systematic distribution of blood vessels. **Nutrient arteries** (aa. nutriciae) branch off from the larger limb arteries and enter the long bones through openings (**foramina nutritia**) in the diaphysis. These vessels reach the medullary cavity after passing through the stratum compactum. Here they divide into several ascending and descending branches supplying the proximal and distal epi- and metaphyses (▶ Fig. 1.23). At the epiphyses, the vessels form **looped-ending arteries** that reach through the epiphyseal subchondral bone to supply the calcified zone of the joint cartilage. From the medullary cavity, the blood vessels supply the compact substance of bone through the Volkmann's canals (see below). The spongy bone does not contain blood vessels but is supplied through diffusion from the bone marrow. The venous return occurs through the axial system of the bone marrow.

Bone tissue does not contain lymphatic vessels. A dense network of lymphatic vessels is present only in the periosteum. Bone

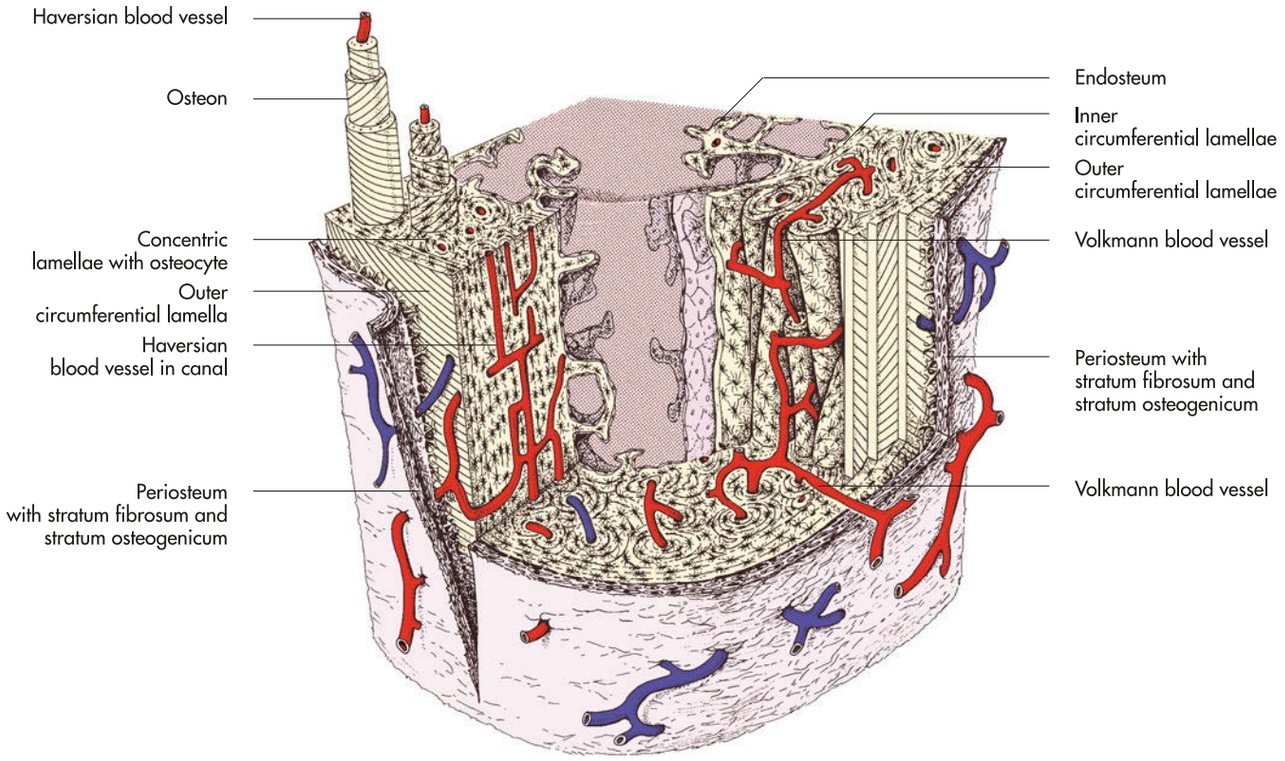

Fig. 1.17 Section of compact bone from the diaphysis (schematic).

tissue itself is not sensitive to pain. Alone vegetative nerve fibres follow the path of the blood vessels within the Haversian canals.

Bone as an organ

Bone constitutes an organ-like system composed of:
- ossified elements,
- joint cartilage (when present),
- periosteum and endosteum,
- bone marrow and
- nerve tracts.

Bone architecture and its extracellular matrix (organic and inorganic material) provide the stabilising components of the passive system of motion, stability and support. The organization of collagen I fibres, the mineralised interfibrillary matrix and the structure of bone tissue all play a large role in stabilisation.

A bone can withstand the application of mechanical stress, body weight, muscle strength or acceleration. These forces work as compression, traction, loading, torque and shear, and do not result in fracture when they are within certain limits. As opposed to the intermittent application of force, bone that experiences a continuous loading force atrophies. On the other hand, bone experiencing constant tensile force hypertrophies.

The architecture of bone tissue is governed lifelong by functional demand. Compact and spongy bone structures are continuously adapting to changes in biomechanical forces. The endosteum is responsible for inducing these structural changes which occur following the physiological principles of bone formation and resorption, for more information see Chapter "Osteogenesis" (p. 32).

Osteogenesis

During foetal development, a **precursor skeleton of cartilage** is formed, providing support and shape (**primordial skeleton**) for the growing foetus. Until ossification, this primordial skeleton undergoes quick successions of mitotic division, eventually determining the growth and form of the entire organism. In most cases, each piece of the primordial skeleton acts as a space saver for the bone tissue that will eventually replace the cartilage. Positively influencing bone tissue formation are **inductive mediators** (i.e. bone morphogenetic protein, mitogenic factors). At a certain developmental stage, the cartilage of the primordial skeleton slowly undergoes remodelling. The cartilage is slowly resorbed and eventually **replaced by bone**. This process is **chondral** or **indirect ossification**. New, foetal bone is referred to as **immature** or **woven bone** due to the random honeycomb architecture of the trabeculae. Eventually, resorbed and woven bone is replaced with **mature lamellar bone**. The majority of adult bones (i.e. the vertebrae and limb bones) are formed through **chondral ossification**.

The replacement of cartilage through bone begins during the middle foetal period at sites referred to as **primary ossification centres**. In some bones this process is completed only when the animal has reached physical maturation. Radiographs of adolescent animals often show remaining cartilage that has not yet ossified, which can lead to false diagnoses should this fact be disregarded.

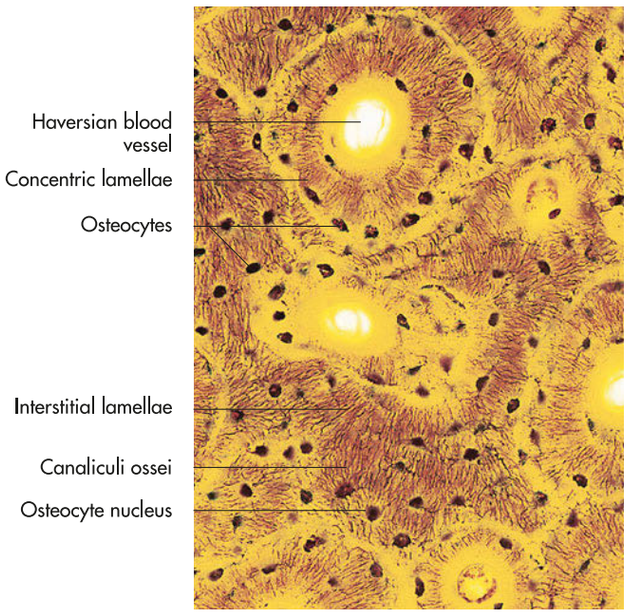

Fig. 1.18 Substantia compacta from a long bone (histological cross section, Schmorl staining).

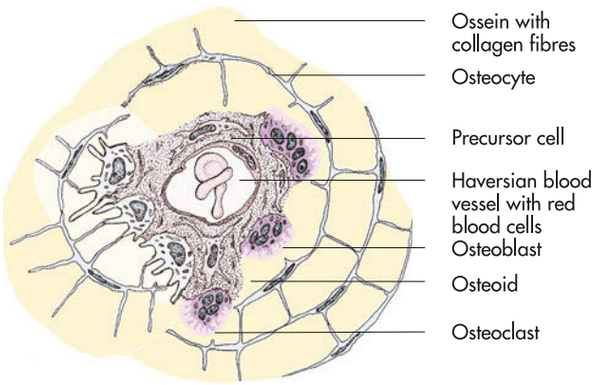

Fig. 1.19 Cross-section through a developing osteon (schematic).

Ossification

Bone can also form directly from mesenchymal tissue without a cartilage precursor; this process is referred to as intramembranous or direct ossification. The dermal bones of the skull, the periosteal collar of long bones and fracture healing are created through this process. There are two forms:

- **intramembranous** or **direct ossification** and
- **chondral** or **indirect ossification**, which can be further divided into:
  - **perichondral ossification** and
  - **endochondral ossification**.

Intramembranous ossification

Bones developing through intramembranous ossification are referred to as "**membrane bones**". Dermal bones are membrane bones arising directly from the mesenchyme tissues of the skin (i.e. most of the skull bones). Intramembranous bone development occurs when **mesenchyme cells** differentiate **directly** into cells responsible for producing bone. These cells are various and appear in many different forms (▶ Fig. 1.20 and ▶ Fig. 1.21). Non-differentiated mesenchyme cells differentiate into **osteoblast precursor cells**, which develop into **osteoblasts**, cells that build **bone**. During ossification, the osteoblasts produce an **organic, mineral-free matrix** called the **osteoid**, which completely encloses the cells. The osteoid is mainly composed of **type-I collagen fibres** (95%). The remaining 5% consists of glycosaminoglycans, proteoglycans, chondroitin-4-sulphate, chondroitin-6-sulphate, keratan sulphate and two bone proteins, osteonectin and osteocalcin. Vitamin C is required for the production of osteoid. During the subsequent mineralisation process, the collagen fibres act as scaffolding for the successive appositional deposition of **inorganic calcium** and **phosphate compounds**.

Within 8–10 days the osteoid transforms through mineralisation into a bony matrix called **ossein**. This conversion is controlled by growth hormones and vitamin D metabolites. The **inorganic bone** compounds such as calcium phosphate (85%–95%), calcium carbonate (8%–10%), magnesium phosphate (1.5%) and calcium fluoride (0.3%) are delivered by blood vessels of the circulatory system and deposited in the osteoid. Through this process, the non-calcified osteoid is transformed to **calcified ossein** (▶ Fig. 1.20 and ▶ Fig. 1.21). As the mineralisation continues, the osteoblasts become isolated in a growing field of calcified bone tissue and differentiate into **osteocytes**.

Different functional forces begin to affect the bone, leading to resorption and remodeling of the new bone tissue even as the mineralisation process continues. Cells that break down bone are called **osteoclasts** (▶ Fig. 1.20 and ▶ Fig. 1.21).

Chondral ossification

Chondral ossification involves **hyaline cartilage**, which serves as a space holder and provides the basis for the longitudinal growth of bone. The primordial skeleton consists of hyaline cartilage, until chondral ossification begins through the gradual resorption of the cartilage and its replacement with permanent bone (**replacement bone**). In this manner the vertebrae, the ribs, the sternum, the limbs and the base of the skull are formed. This process of building new bone from a hyaline cartilage precursor is the **chondral osteogenesis**. During this process one distinguishes between a perichondral and an endochondral ossification (▶ Fig. 1.15 and ▶ Fig. 1.24).

Perichondral ossification

The perichondral ossification is similar to intramembranous ossification in that osteoid is formed and slowly mineralised. **Osteoprogenitor cells**, cells with the potential to build new bone, are located in the **stratum chondrogenicum of the perichondrium** and differentiate into **osteoblasts** (**primary ossification**). This transformation of soft tissue into bony tissue begins in the mid-

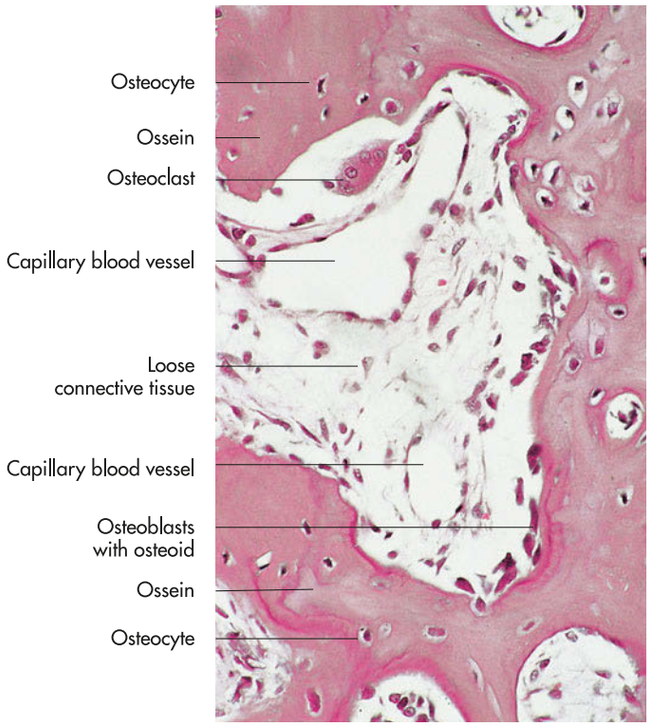

Fig. 1.20 Intramembranous ossification with central capillary in loose connective tissue including osteoblasts and osteocytes (histological section, hematoxylin and eosin staining).

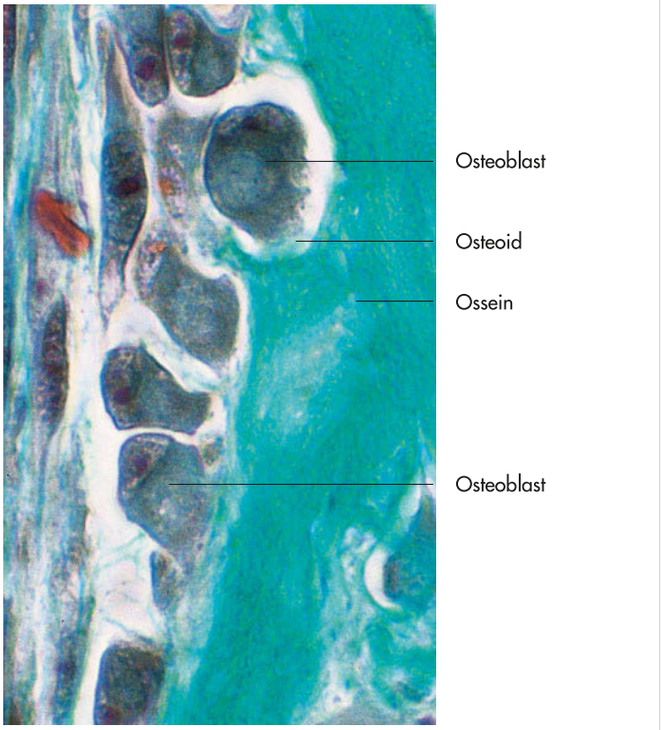

Fig. 1.21 Intramembranous ossification with osteoblasts, osteoid and ossein (histological section, Goldner staining).

dle of the diaphysis and results in the formation of a bony sheath, the **periosteal collar**. The ossification of the perichondrium progresses towards each bone extremity, the **epiphyses**. Thus, the perichondrium becomes the **periosteum**. Perichondral ossification leads to the development of the periosteum of the long bones.

The formation of the periosteum mechanically inhibits the metabolism of the hyaline cartilage, essentially forcing **calcification of the cartilage matrix**. At the same time, blood vessels burrow through the periosteal collar and invade the calcified cartilage. Cells that remove existing cartilage, the **chondroclasts**, enter the calcified matrix through the proliferating blood vessels, and resorption of the remaining cartilage follows. The chondroclasts leave behind empty spaces that soon become filled with connective tissue and capillaries, which deliver not only nutrients but also substances necessary to build new bone tissue. **Osteoblasts** also reach the medulla cavity through these blood vessels and begin from the inside to build bony tissue (**endochondral ossification**). The continuous process of bone resorption and replacement of the matrix results in the development of the primary medullary cavity, which is filled with a fine latticework resembling a partly ossified sponge (**development of the substantia spongiosa**).

The multi-chambered **secondary medullary cavity** (cellulae medullares, ▶ Fig. 1.16) is formed when connective tissue in the primary medullary cavity differentiates into hemo-reticular tissue responsible for the production of blood cells (**hematopoiesis**). This occurs during the later stages of foetal development, and the newly formed hemoreticular tissue is called **red bone marrow** (medulla ossium rubra).

The **bone marrow** (medulla ossium) located in the medullary cavities of both epiphyses and between the spongiosa trabeculae remains lifelong a **hemopoietic organ** (▶ Fig. 1.12). In adults the red bone marrow of the diaphysis is gradually replaced by **fat** (medulla ossium flava), which is again transformed into **gelatinous marrow** (medulla ossium gelatinosa) in senile animals or can prematurely form in diseased animals.

Endochondral ossification

Between the diaphysis and each epiphysis of a long bone, an area of calcified cartilage persists as the **proximal** and **distal metaphyses**. The two metaphyses border on each end of the bone an area of distinct endochondral ossification called the **epiphyseal growth plates** (cartilago epiphysialis) (▶ Fig. 1.12). The epiphyseal plates are of great importance because they are responsible for the **longitudinal growth of a bone**.

The periosteal collar encloses the bone and, in the area of the **metaphysis**, inhibits radial growth of the cartilage. The chondrocytes proliferate through mitotic division and hypertrophy, organising themselves in columns reflecting their **progressive development** (▶ Fig. 1.22 and ▶ Fig. 1.24). This organisation is the basis for the **longitudinal growth of cartilage**, which is necessary for bone growth.

The endochondral ossification of the metaphyseal cartilage occurs in **several zones** (▶ Fig. 1.22 and ▶ Fig. 1.24). The chondrocytes juxtaposed to the epiphyseal plates are diffusely located throughout the hyaline cartilage and do not divide (**zone of resting chondrocytes**) (▶ Fig. 1.22). Neighboring this zone, in the direction of the medullary cavity, is the wide **zone of proliferation**, where the chondrocytes actively divide. Mechanical influence of

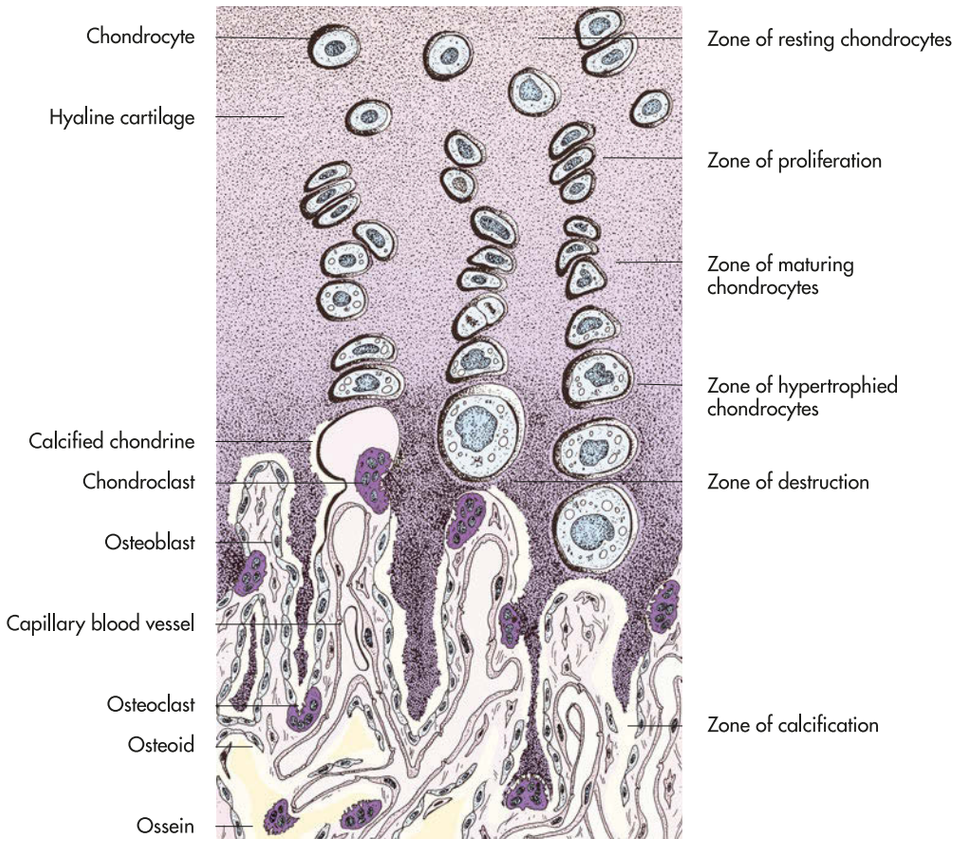

Fig. 1.22 Structural remodelling during chondral ossification in a long bone (schematic).

the periosteal collar forces the maturing chondrocytes in the following zone (**zone of maturing chondrocytes**) to form obvious columns. The chondrocytes begin to degenerate. This is a process characterised by an increase in volume due to water uptake and the calcification of the intercellular substance (**zone of hypertrophied chondrocytes**).

As calcification continues, chondroclasts enzymatically erode the remaining calcified cartilage (**zone of destruction**), (▶ Fig. 1.22 and ▶ Fig. 1.24). The chondroclasts enter this zone through capillaries and connective tissue from the medullary cavity, reaching as far as the zone of calcification. At the demarcation between the zones of destruction and calcification, the process of cartilage resorption is complete. In the final zone, the intercellular matrix becomes saturated with minerals and ossification is complete (**zone of calcification**).

Invading blood vessels also allow secondary osteoblasts to enter the zone of destruction. These cells produce new **matrix** (osteoid) through intramembranous ossification. Eventually, the young woven bone is replaced by mature lamellar bone (see below).

Types of bone tissues

There are two types of bone tissue: **woven bone** (os membranaceum reticulofibrosum) and **lamellar bone** (os membranaceum lamellosum) From an evolutionary point of view, woven (fibrous, immature) bone is regarded as the first and therefore phylogenetically oldest form of bone, often being classified as ossified connective tissue. During foetal development, each bone initially consists of woven bone, and only after birth this is bone slowly replaced by the more complex lamellar bone. However, some woven bone persists throughout life. For example the osseus labyrinth of the ear, the external acoustic meatus, and muscle attachment sites on long bones remain as woven bone.

Lamellar (mature) bone is characterised by the arrangement of strictly parallel or concentric layers of collagen fibres, called lamellae. Most bones of the adult animal consist of lamellar bone, which forms the long bones as well as the short and flat bones. The structural unit of lamellar bone is the **osteon** (**Haversian system**).

Each **osteon** (▶ Fig. 1.17) is a series of concentric rings made up of layers of bone matrix around a **central canal** (Haversian canal) through which a **blood vessel** (Haversian blood vessel), **lymphatic vessels** and **nerves** travel. The collagen fibres in the matrix of each layer are helically arranged and orientated at the opposite angle to those of the previous layer. Osteons are connected through transverse bony structures, creating a construction which enables bone to resist tensile and compression forces (▶ Fig. 1.17, ▶ Fig. 1.18 and ▶ Fig. 1.19). Bone cells (osteocytes) lie between the **concentric lamellae** (Haversian lamellae) (▶ Fig. 1.18) surrounding the Haversian canal. Cell-to-cell-contact is preserved through long, radiating processes of the cell plasma that anastomose within **bony channels** (canaliculi ossei) with processes of neighbouring cells (▶ Fig. 1.18).

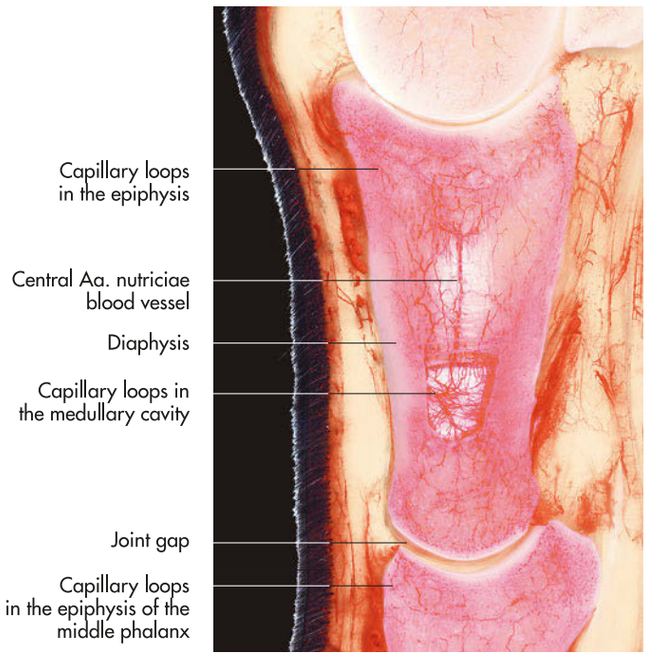

Fig. 1.23 Vascularisation of a long bone, here the first phalanx of the horse (injected plastination). (source: courtesy of H. Obermayer, Munich)

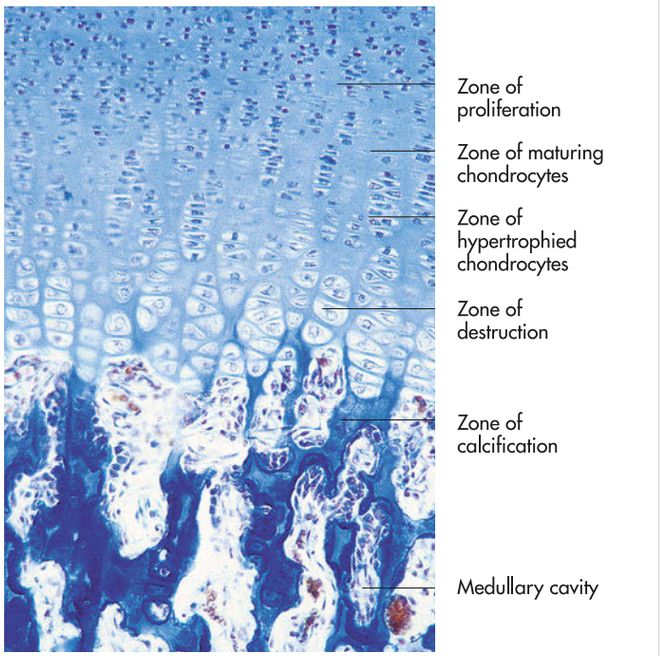

Fig. 1.24 Histological section through the epiphysis of a long bone demonstrating chondral ossification (Azan staining).

This system allows the transport of substances between the blood vessels of the Haversian canal and the bone matrix, essential for the nutrition of the osteocytes. The central blood vessels in the osteons communicate with the periosteum, the endosteum and the medullary cavity through transverse **Volkmann vessels** (▶ Fig. 1.17). By means of this dense network of blood vessels, bone becomes a heavily vascularised tissue.

Bone reacts to changes in static and mechanical forces through adaptation of its internal architecture. Superfluous osteons are destroyed and their remaining fragments form interstitial bone or lamellae (▶ Fig. 1.17).

Layers of lamellae form the outer circumference of the bone directly beneath the periosteum (**outer circumferential lamellae**). The **inner circumferential lamellae** border the medullary cavity, and the endosteum covers the innermost layer (▶ Fig. 1.17). **Collagen fibres** (**Sharpey fibres**, **fibrae perforantes**) anchor the periosteum to the outer circumferential lamellae. These collagenous fibres originate in tendons attaching muscle to bone and are essential for transmitting forces generated by the muscle to the bone.

Bone functions

Bone and cartilage form the supporting and protective framework of the body. Not only do they ensure locomotion, but also protect the soft tissue organs of the thoracic and pelvic regions and the central nervous system. Bone contains the red bone marrow responsible for building blood components (**hematopoiesis**) and stores **calcium** and **phosphate** (▶ Fig. 1.12). Thus the three major functions of the skeleton are **support**, **protection** and **metabolism**. These functions together influence the structure of every skeletal bone and thus the **architecture of the entire body**. The bone structure adapts to mechanical demands through changes in metabolism. This adaptation process involves the continuous resorption and deposition of osseous material.

Every bone is subjected to these **adaptive changes throughout life**. Changes in the physiological compressive, tensile and shear forces lead quickly to remodelling processes. The limbs, the vertebrae or the pelvic bones experience more intensive structural changes compared to, for example, the bones of the skull.

Compact bone develops in a direct relation to the amount of physiological stress it must endure. The cortex (Substantia corticalis) of long bones is thickest at the diaphysis because here the greatest forces are effective. The epiphyses are not subjected to great force and here the cortex becomes progressively thinner (▶ Fig. 1.12). Physiologically, permanent traction forces lead to thickening of the bone where they are most experienced, for example, at the point where tendons attach to bone.

Another important function of bone is to **store calcium** and **phosphate**. Spongy bone (substantia spongiosa) stores depots of calcium that can quickly be mobilised into the blood stream to maintain necessary vital functions. The metabolism of calcium and phosphorus is regulated by **endogenous** and **exogenous mechanisms**.

The **parathyroid hormone** excreted by the parathyroid gland **activates the osteoclasts**, thus increasing the amount of calcium in the blood while at the same time reducing calcium excretion by the kidneys. Together with **vitamin D_3** (**1,25-dihydroxycholecalciferol**), the parathyroid hormone enhances the **resorption of calcium** in the intestines. The **C cells of the thyroid gland** produce a hormone, **calcitonin**, that activates the osteoblasts and **antagonises parathyroid hormone**. The osteoblasts form bone, thus automatically storing calcium and reducing the amount circulating in the body. The **growth of bone** is also positively influenced by the somatotropic hormone (STH), the adrenocorticotropic hormone (ACTH) and the thyrotropic hormone (TSH), as well as by male and female sex hormones.

Arthrology (arthrologia)

The degree of mobility between two bones or cartilage structures depends entirely on the form of the gap between them. A **synarthrosis** is a continuous structure bridging two adjacent bones. It can be formed by **connective tissue**, which builds either a **fibrous union** (juncturа fibrosa) or a **fibrous joint** (articulatio fibrosa). Similarly, a synarthrosis can be formed from **cartilage**, creating a **cartilagineous union** or **joint** (articulatio cartilaginea). The range of motion between two skeletal structures can be greatly increased when a joint containing a gap **(diarthrosis)** exists between them. A **true** or **synovial joint** (juncturae seu articulationes synoviales) is characterised by a **joint gap** and a **joint cavity** (cavum articulare) filled with **joint fluid** (synovia).

Synarthroses

Fibrous unions (juncturae fibrosae) can be subdivided into three types:

- **connective tissue joints** (syndesmoses), e.g. the attachment of the dew claws to the metapodium in the ox,
- **sutures** (suturae), which unite, for example, the bones of the skull and include the:
  - **serrate suture** (sutura serrata),
  - **flat suture** (sutura plana),
  - **squamous suture** (sutura squamosa) and
  - **foliate suture** (sutura foliata), and
- **impactions** (gomphoses), e.g. the anchoring of the teeth roots in the dental alveoli by dense connective tissue, in this case the periodontal membrane.

Cartilaginous unions (juncturae cartilagineae) are:

- **hyaline cartilage unions** (synchondroses), e.g. between base of the skull and the hyoid bone, and
- **fibrocartilage unions** (symphyses), e.g. the pelvic symphysis.

A synarthrose in which bone unites two structures is referred to as a **synostosis**. A good example of a synostosis is the ossified union between the radius and the ulna in the horse.

True joints (articulationes synoviales)

Joints can be differentiated according to the number of bones involved in the joint, the degree of movement possible or the form of the joint surfaces. In spite of such variation, joints share common structural and functional features (▶ Fig. 1.30 and ▶ Fig. 1.33):

- an extensive **joint capsule** (capsula articularis),
- a **joint cavity** (cavum articulare) as well as
- hyaline **joint cartilage** (cartilago articularis), which covers the ends of the two or more bones forming the joint.

The **joint capsule** (▶ Fig. 1.33) is comprised of two layers: the outer **fibrous layer** (stratum fibrosum) and the **inner layer** (stratum synoviale, synovial membrane). The thickness and development of the outer capsule layer, the stratum fibrosum, varies greatly and is mainly determined by the mechanical load placed on the area in question. This layer may also contain capsule ligaments (see below), which strengthen the capsule on the outside of the joint. The fibres of the **stratum fibrosum** continue into the bordering periost or perichondrium (▶ Fig. 1.33). Since the blood supply to this layer is limited, injuries require a long time to heal. However, an abundance of sensory nerve fibres innervate the stratum fibrosum, which explains the pain experienced after injury to the capsule itself or through stretching of the capsule due to swelling within the joint.

The **synovial membrane** (stratum synoviale) lines the joint cavity and is replete with cells, blood vessels and nerves. The synovial membrane appears ivory in color with a slight yellow tinge and forms both **synovial villi** (villi synoviales) and **synovial folds** (plicae synoviales). Even within the same joint, these structures can differ greatly in number, size, form and location. This membrane can be further divided into the inner synoviocytes layer (intima synovialis) comprised of cover cells, the synoviocytes, and a subsynovial layer (stratum subsynoviale) (▶ Fig. 1.31 and ▶ Fig. 1.32) of tissue. Two types of synoviocytes are present in the intima synovialis:

- **type-A synoviocytes** are responsible for phagocytosis, whereas
- **type-B synoviocytes** produce and secrete proteins.

Joints are filled with a pale yellow, viscuous fluid, the **synovial fluid**, whose primary purpose is to lubricate the joint, thus reducing friction between articular surfaces. Synovial fluid is excreted by the synovial membrane into the joint cavity but also fills the tendon sheaths and is found in synovial bursa; for more information see Chapter “Accessory structures of muscles” (p. 32)). Synovial fluid is composed of hyaluronic acid, sugar, electrolytes and enzymes involved in the nutrient supply of cartilage. Hydrarthrosis occurs due to increased production of synovia.

Free joint bodies, or **“joint mice”**, are free-swimming intraarticular pieces of cartilage or bone resulting from a chip-fracture or ossification of synovial villi. Depending on their location they can be very painful.

The **joint cartilage** is firmly attached to a thin, subchondral bone layer adjacent to the epiphysis. It is not covered by perichondrium and the surface facing the joint is very smooth (▶ Fig. 1.30 and ▶ Fig. 1.35). Joint cartilage is thin in the centre of a concave surface but thick in the centre of a convex one. Some areas of the joint cartilage in hoofed animals display a reduction in cartilage, forming **synovial grooves** (fossae synoviales).

Cartilage matrix fibre bundles are arranged according to the mechanical forces of compression and tension. The hyaline cartilage matrix absorbs shock, is flexible and possesses viscoelastic properties. Similar to other types of cartilage, joint cartilage lacks nerves and, with a few exceptions, is not vascularised. The articular cartilage can be divided into the:

- superficial zone,
- intermediate zone,
- radial zone and
- calcified zone.

The **superficial zone** is comprised of tightly woven collagen fibres near the surface of the joint cartilage. These fibres arch towards the surface, where they run parallel to one another. This fibre pattern increases the stability of the surface joint cartilage. The middle layer of the cartilage, the **intermediate zone**, is structurally homogenous. The **radial zone** is comprised of cartilage fibres that partly unite to form radially organised bundles. In the **calcified zone**, collagen fibres anchor the joint cartilage to the bone and are for the most part calcified. This structure guarantees a strong attachment of joint cartilage to bone.

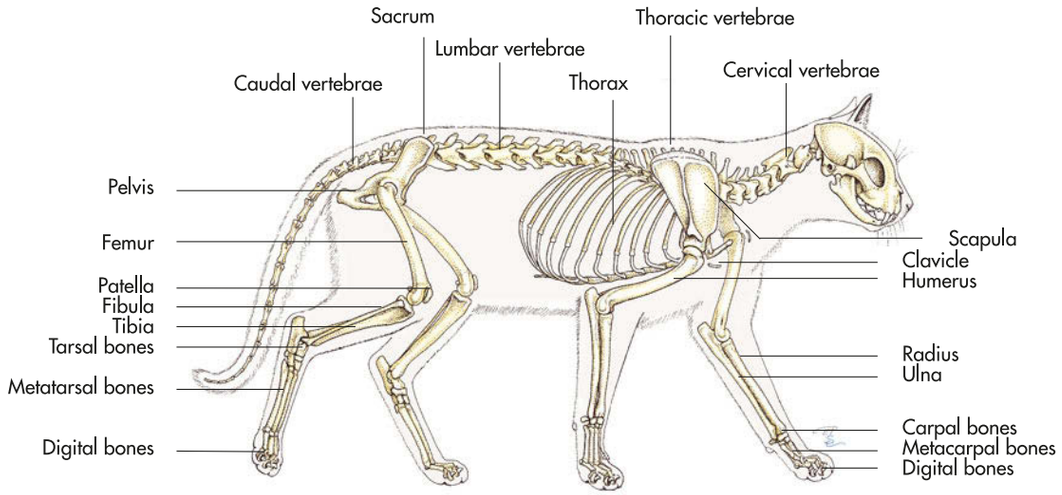

Fig. 1.25 Skeleton of the cat (schematic).

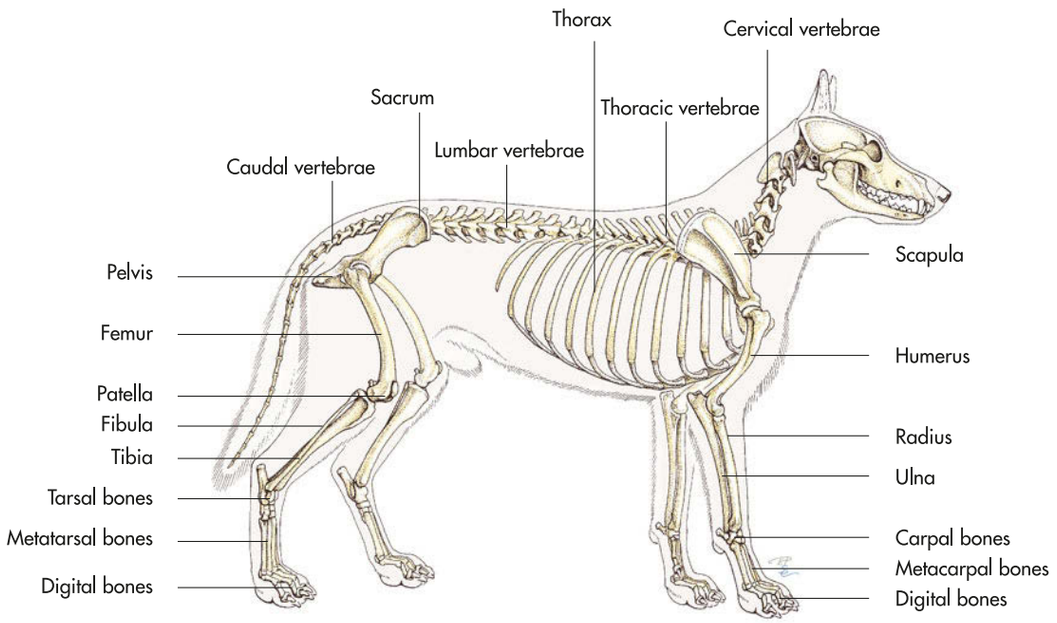

Fig. 1.26 Skeleton of the dog (schematic).

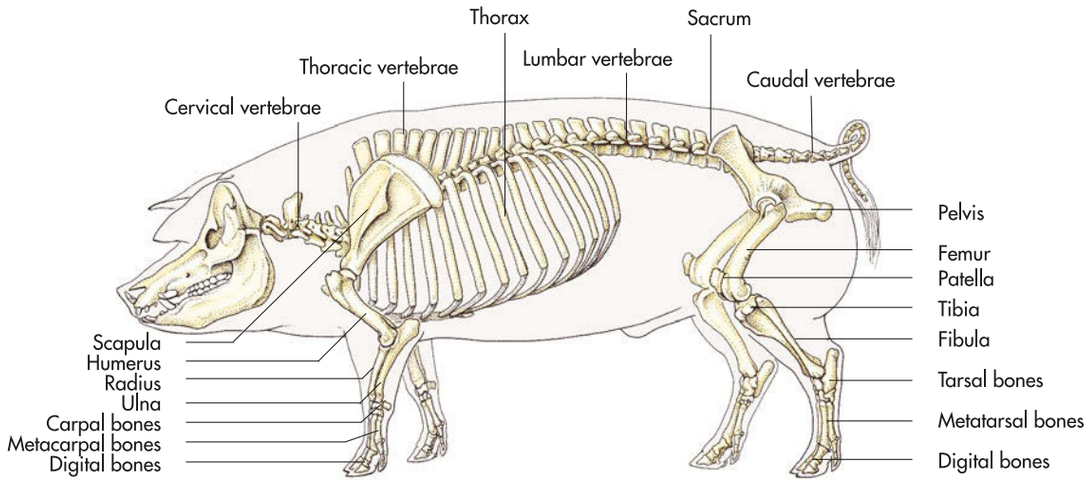

Fig. 1.27 Skeleton of the pig (schematic).

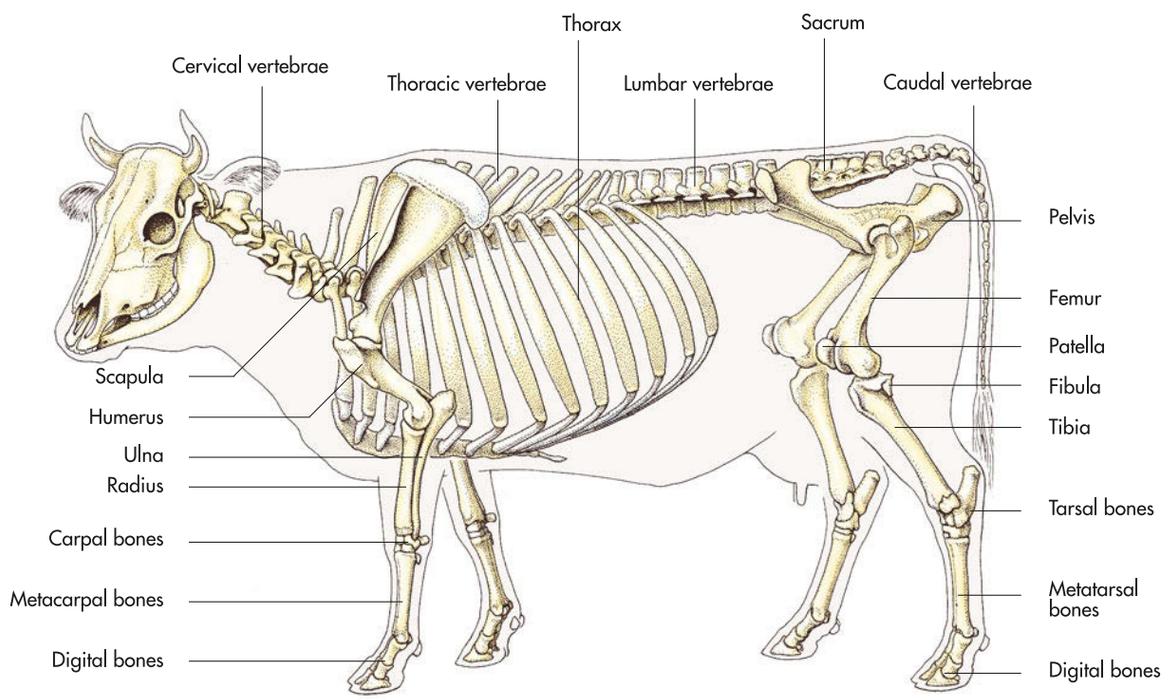

Fig. 1.28 Skeleton of the cow (schematic).

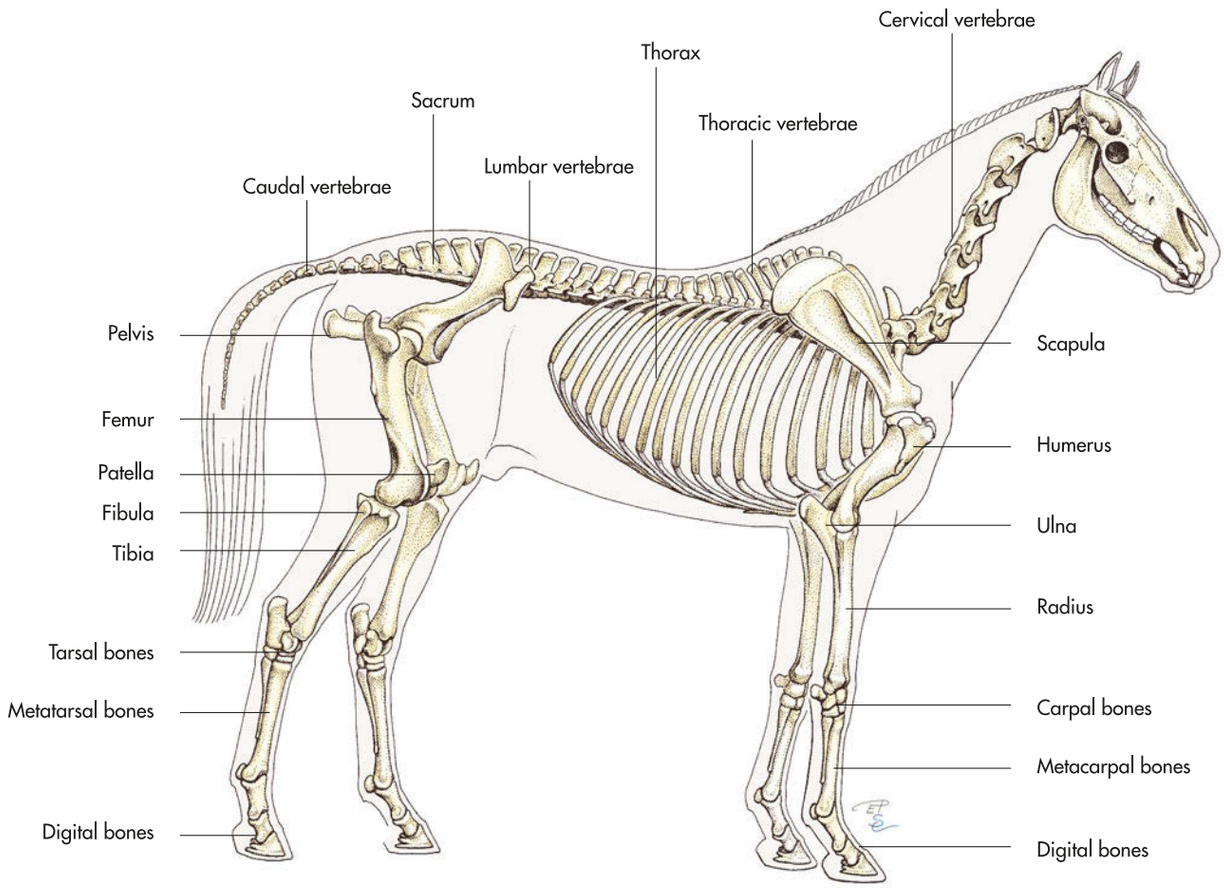

Fig. 1.29 Skeleton of the horse (schematic).

Beneath the joint cartilage is a **subchondral bone plate** that includes parts of the calcified joint cartilage as well as a layer of lamellar bone (▶ Fig. 1.33). This plate (corticalis) supports dynamic functions of the joint, acts as a cushion protecting the cartilage from axial forces and promotes the metabolic supply of the deeper layers of cartilage.

The metabolism of joint cartilage is **anaerobic**. The cartilage is supplied with nutrients, for the most part, **bradytropically** through diffusion. To a lesser degree, nutrients can also reach the cartilage from the joint synovia or through the blood vessels of the bone marrow. The high proteoglycan content lends a high capacity for binding water molecules, which facilitates the intrachondral transport of metabolites.

Joints are strengthened by intracapsular, capsular or extracapsular joint **ligaments** (ligamenta articularia). Some joints contain **fibrocartilagenous structures** (menisci articulares in the knee joint, disci articulares in the jaw joint) that serve to stabilise the joint or to compensate for **incongruent joint surfaces**. Fat tissue can also build intra-articular depots providing additional cushioning. Synovial joints can be classified according to different characteristics:

Number of bones forming the joint:
- **simple joints** (articulatio simplex), involving only two bones (e.g. shoulder joint), and
- **composite joints** (articulatio composita), involving more than two bones (e.g. the wrist joint).

Type of movement allowed by the joint (▶ Fig. 1.34):
- **uniaxial joints** with:
  - **hinge joint** (ginglymus): the joint axis is perpendicular to the long axis of the bones (e.g. elbow or tibiotarsal joint), and
  - **pivot joint** (articulatio trochoidea): the joint axis is parallel to the long axis of the bones (e.g. atlantoaxial joint between the 1st and 2nd cervical vertebrae);
- **biaxial joints** with:
  - **saddle joint** (articulatio sellaris): e.g. between the interphalangeal joints, and
  - **ellipsoidal joint** (articulatio ellipsoidea): e.g. atlanto-occipital joint between the occipital bone and the 1st cervical vertebra;
- **multiaxial joints** with:
  - **spheroidal** or **ball-and-socket joint** (articulatio sphaeroidea): e.g. shoulder joint or hip joint, and
- **tight joints** (amphiarthroses): e.g. sacroiliac joint.

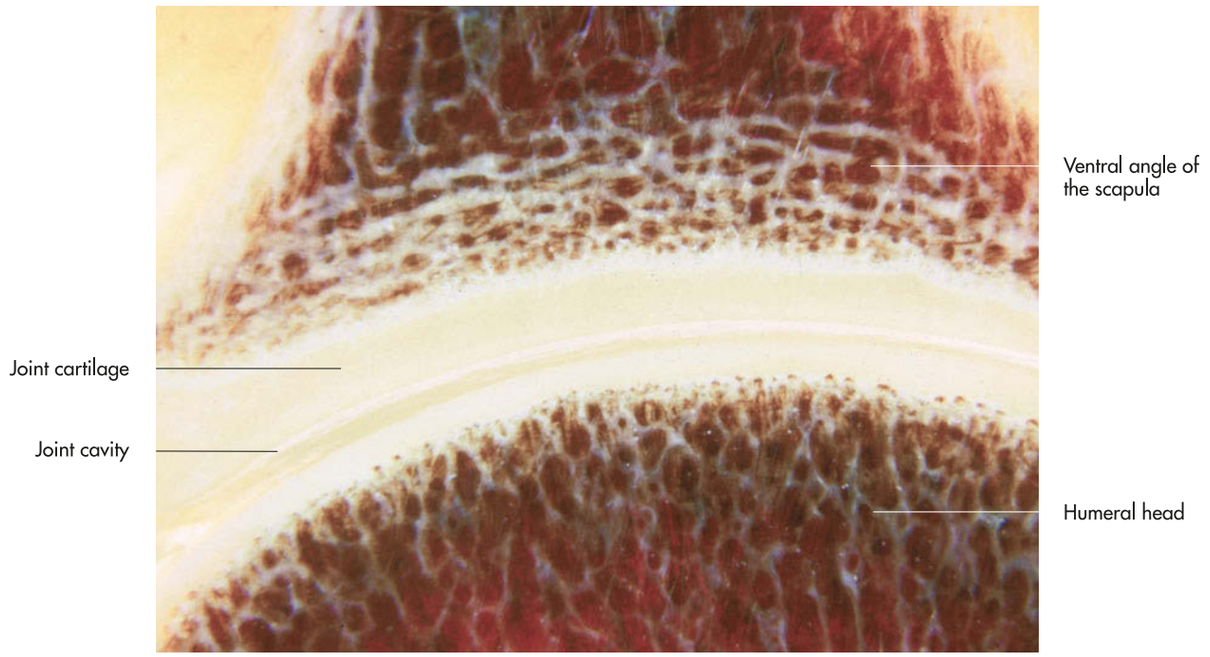

Fig. 1.30 Joint gap formed by the ends of the scapula and humerus in the dog (longitudinal section, plastination).

Form of the articular surfaces:
- **spheroidal** or **ball-and-socket joint** (articulatio sphaeroidea): e.g. shoulder joint or hip joint,
- **cotyloid joint** (articulatio cotylica): a spheroidal joint where the glenoid cavity (socket) covers more than half of the joint sphere (ball), e.g. the aviary hip joint,
- **ellipsoidal joint** (articulatio ellipsoidea), e.g. between the occipital bone and the 1st cervical vertebra,
- **saddle joint** (articulatio sellaris), e.g. the interphalangeal joints, and
- **condylar joint** (articulatio condylaris), e.g. the femorotibial joint.

Joints are also classified according to their **functional characteristics**:
- **hinge joint** (ginglymus): e.g. fetlock joint,
- **cochlear joint** (articulatio cochlearis): e.g. hock joint of the horse,
- **spring** or **snap joint**: a suspension joint as well as a hinge and cochlear joint, where the collateral ligaments attach eccentrically to the axis of rotation and proximal to the joint axis (in the neutral position of the joint, the collateral ligaments are under the greatest amount of tension; during extension or flexion, the tension in the ligaments decreases, causing the joint to spring into a position other than the neutral position, e.g. the elbow joint of the horse),
- **sledge** or **gliding joint** (articulatio delabens): e.g. femoropatellar joint,
- **spiral joint** (articulatio spiralis): the collateral ligaments attach eccentrically, distal to the axis of rotation (the ligaments are shortest in the neutral position; during extension or flexion, the tension in the ligaments increases, slowly braking the motion, e.g. the stifle joint of the horse),
- **plane joints** (articulationes planae): a gliding joint, e.g. the joints between the articular processes of the vertebrae, and
- **incongruent joints**: joints where the articular surfaces do not correspond, as seen in the femorotibial joint or in the temporomandibular joint; the joint surfaces are rendered congruent through fibrous discs, the menisci in the femorotibial joint and the articular disc in the temporomandibular joint.

Clinical note

A reduction in the passive range of movement of a joint is referred to as **joint contracture**. Causes of joint contracture include extended immobilisation or lack of use of the joint. Severe pain associated with joint effusion or free bone fragments (joint mice) can bring about a sudden decrease in joint mobility. Sprains and luxations may result in excessive stretching and rupture of ligaments, leading to joint instability.

A **marked increase in the volume of synovial fluid** (joint effusion) manifests as swelling of the joint. The associated pain is caused by stretching of the joint capsule, which stimulates pain receptors in the capsule wall.

Fig. 1.31 Filament-like synovial villi free-floating in the synovia. (source: courtesy of Dr. M. Teufel, Vienna)

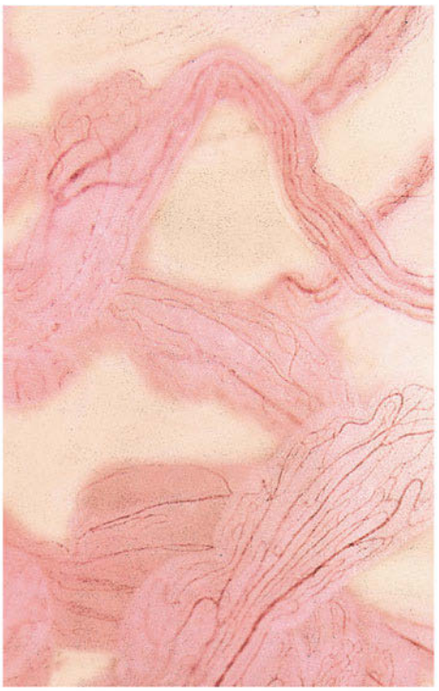

Fig. 1.32 Synovial villi within the joint cavity with injected capillaries. (source: courtesy of Dr. F. Teufel, Vienna)

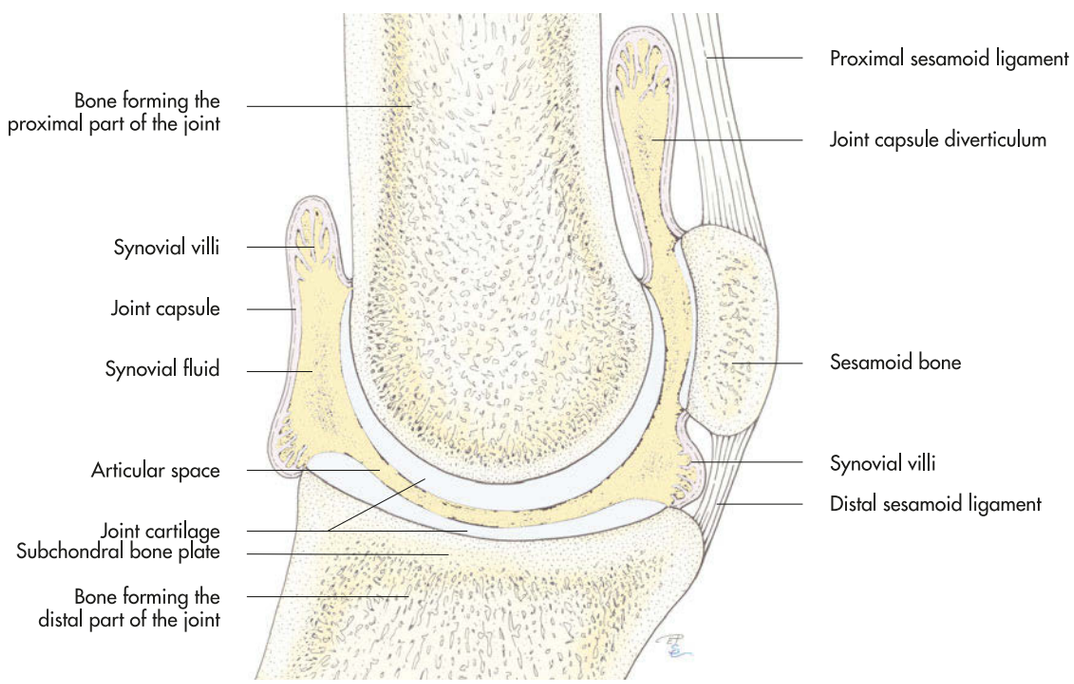

Fig. 1.33 A joint including the sesamoid bones and the suspensory apparatus (schematic).

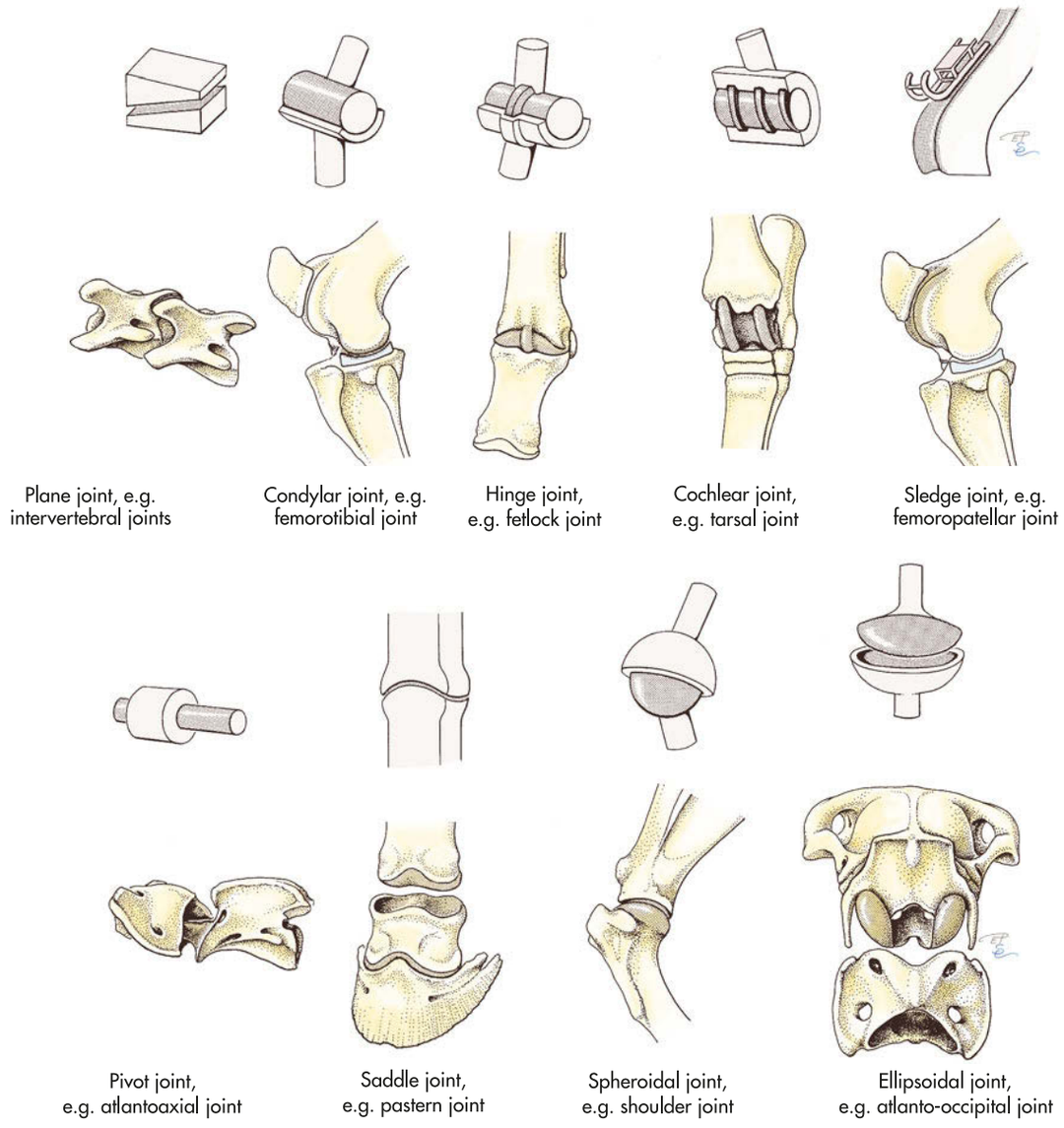

Fig. 1.34 Types of synovial joints (schematic).

1.4.2 Muscular system (systema musculare)

H.-G. Liebich and H. E. König

Myology (myologia)

In phylogenetically advanced organisms, the cells of the **middle germ layer** (**mesoderm**) develop into cells capable of contracting (somites) and their derivatives. This cell population differentiates into muscle tissue, which transforms chemical energy into mechanical energy or heat. **Two types of muscle** tissue are distinguished according to morphology and function (▶ Fig. 1.35 and ▶ Fig. 1.36):

- **smooth muscle tissue**: responsible for the contractile functions of the internal organs, lines the excretory ducts of glands, forms the blood and lymphatic vessel walls, and
- **striated muscle**: can be further divided into the **skeletal** and the **heart musculature** (see Histology textbook for further information).

The **skeletal musculature** is the active part of the locomotor system. It is generally referred to as the **musculature** or **muscles** (musculi). Skeletal muscles are highly vascularised and innervated by **cerebrospinal** (**sensible** and **motoric**) and **vegetative autonome** (**sympathetic** and **parasympathetic**) **nerves**, which together build a functional unit. Expansive sheets of connective tissue, the fasciae or aponeuroses, as well as synovial structures, such as tendon sheaths and bursae, support and protect the muscles in all of their various functions.

The muscles provide power to move the skeletal frame; the ends of the muscle always insert in bone or cartilage. They act as levers, resulting in movement of individual body parts or the entire organism; for more information see also Chapter 6 “Statics and Dynamics” (p. 309). Muscles also carry part of the body

weight, help form the walls of the thoracic and abdominal cavities, and support the activity of the internal organs (e.g. respiratory muscles, diaphragm).

Development, degeneration, regeneration and adaptation of muscle fibres

Somite cells of the middle germ layer differentiate into **mesenchymal stem cells**, thus marking the embryonal beginnings of muscle cells. The mesenchymal stem cells differentiate further into **premyoblasts** and then into **contractile myoblasts**. Myoblasts contain proteins, the **myosin** and **actin filaments**, responsible for the contractility of the cell. These proteins are specifically arranged in the cytoplasm according to muscle cell type, creating a typical striation. Neighboring cells tend to fuse together, forming long, cylindrical, multinucleated cells, also called muscle fibres, which in the adult animal can reach up to 10 cm in length and 100 µm in diameter.

A certain number of stem cells remain lifelong **satellite cells** and play an important role in **muscle regeneration**. Various factors such as local ischemia, neural atrophy, pressure damage, or toxins can cause a local degeneration of muscle. The regeneration is dependent on the activity and the number of undamaged satellite cells. The strength of an individual muscle and the percentage or bulk of muscle tissue depends almost entirely on training level. Immobility, lack of exercise, and interruption of the nerve supply cause a muscle to atrophy. Muscles gain mass (hyperplasia) through strengthening of the connective tissue sheaths, expansion of fibre thickness and increased blood flow, all of which can be accomplished with regular exercise.

Architecture of skeletal musculature and the tendons

A skeletal muscle can be divided into three general parts: the contractile **muscle belly** and the **tendons of origin** and **insertion**. The tendons attach to each end of the muscle belly and transfer the force generated by contraction of the belly to the skeleton (▶ Fig. 1.37). Viewed through a microscope, skeletal muscle appears to have **cross bands** or **striations** that result from the parallel and regular arrangement of the actin and myosin filaments. The actin and myosin filaments, along with the connective tissue sheaths and stored fat, form the **muscle tissue**.

The **muscle cells** differ according to the number and thickness of their cytoplasmic contractile myofilaments. When the cytoplasma of the muscle cell, the sarcoplasma, contains proportionately more myofilaments, then the muscle stores less myoglobin and appears pale (**white muscle type**). This type of muscle tires quickly, but its contractile strength is great. The second type of muscle (**red muscle type**) contains less myofilaments and therefore can store more myoglobin in the sarcoplasma (i.e. in older domesticated and wild animals). More explicit details of muscle contraction can be found in standard physiology and histology textbooks.

The **innervation** of the muscle occurs through neuromuscular connections. The muscle and nerve together create a functional unit. Every muscle fibre is innervated by at least one **motor nerve axon of the central nervous system** (cerebrospinal nerve). The contact between muscle and nerve is achieved through the **motor end-plate**, a special form of **synapse**. The nerve impulse is passed on to the muscle fibre by a **neurotransmitter** (**acetylcholine**).

Also located in the muscle are the **sensory nerve endings**, which are grouped as **muscle spindles** and surrounded by a capsule. These **mechanoreceptors** provide information about muscle tonus and the degree of tension in the tendons and joint capsules. In addition, the muscle spindles are responsible for **coordinating movement** and percieving the **position of body parts** relative to each other in space. Tendon organs are similar to muscle spindles and function as receptors for the tension within the muscle-tendon system.

The walls of intramuscular blood and lymphatic vessels are innervated by **sympathetic** and/or **parasympathetic branches** of the autonomic nervous system. This autonomic system ensures adequate blood supply and lymph drainage required to maintain function.

Every individual muscle belly is surrounded by an outer sheath of taut, fibrous connective tissue, the **epimysium**, which continues to sheathe the tendons as the **epitendineum**. The epimysium or epitendineum is visible with the naked eye and separates adjacent muscles from each other, creating a smooth surface allowing frictionless movement. The large vessels and nerves supplying the muscles find their way along the epimysium. A **hilus** is where vessels and nerves together enter or leave a muscle. Within a single muscle, groups of muscle cells are wrapped together in the **perimysium** composed of intramuscular connective tissue, forming more or less a network of smaller functional units (▶ Fig. 1.36). This network of collagen fibres forms a plexus, remaining in contact with one another to coordinate muscle contractions and to provide a path for smaller blood vessels and nerves. Each individual muscle cell is lightly wrapped in a delicate network of collagen fibrils, the **endomysium**. The endomysium forms a lattice enclosing connective tissue cells, the smallest blood vessels and nerve plexus (▶ Fig. 1.36). These aforementioned sheaths are classified according to the size of the bundles they enclose, into primary, secondary and tertiary bundles. They build a functional unit and combine at each end of the muscle belly, continuing into the **tendon**.

The various sheaths of connective tissue in the muscle extend beyond the ends of the muscle and unite to form the **tendon** (tendo), a white, cordlike attachment to the bone. The transfer of muscle power to the tendon occurs at the end of the muscle fibres, where small finger-like processes from the muscle fibres interlock with those of the collagenous fibrils from the tendons. This construction greatly strengthens the connection between tendon and muscle. Tendon fibres run parallel to one another and differ in radius and length (▶ Fig. 1.37).

They are also grouped into **bundles** (**primary**, **secondary** and **tertiary**) through the continuation of the muscle sheaths that are, here, referred to as the **epitendineum** and **peritendineum**. Expansive muscle plates that, because of their flat and wide form do not have a belly, attach through thin, flat sheets of connective tissue (**aponeuroses**). The fibres of both cordlike tendons and aponeuroses are oriented in the same direction as the mechanical forces they are subjected to. Compared to muscle tissue, tendons exhibit a much greater **tensile strength** due to their high collagen and low elastic content.

The long tendons of the limb distal regions exhibit a great elasticity throughout their entire length. During movement, the elas-

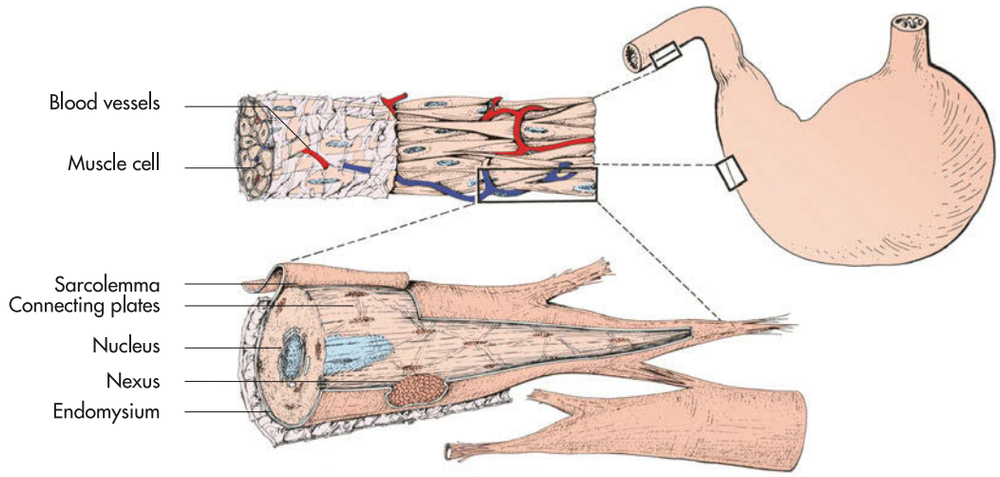

Fig. 1.35 Smooth muscle (schematic); fig. based on data from Liebich, 2004.

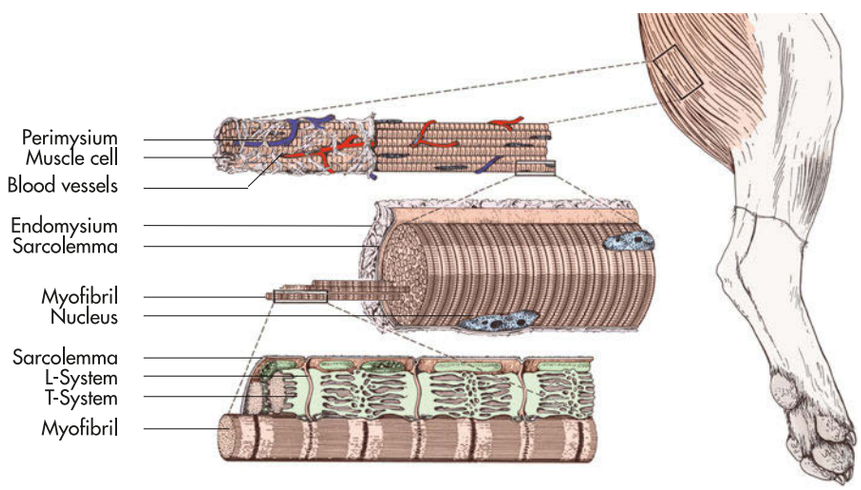

Fig. 1.36 Striated muscle (schematic); fig. based on data from Liebich, 2004.

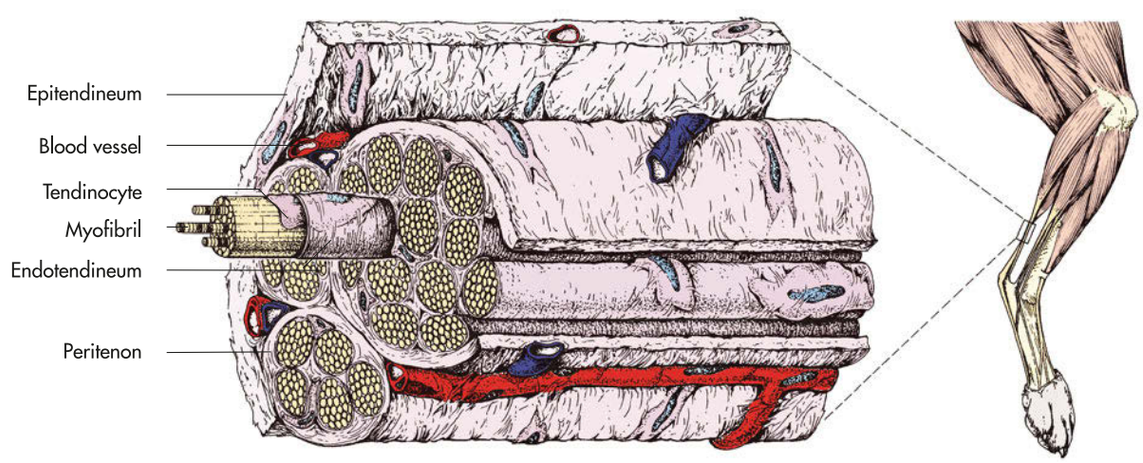

Fig. 1.37 Tendon (schematic); fig. based on data from Liebich, 2004.

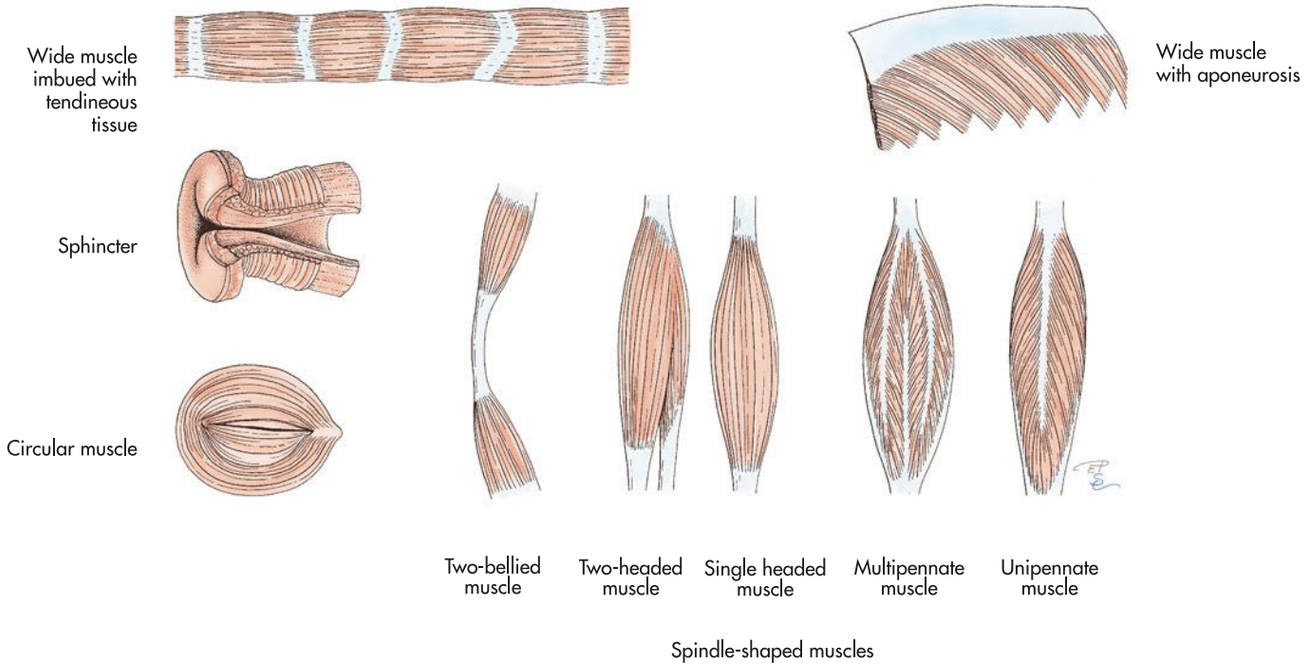

Fig. 1.38 Categories of skeletal muscles according to the arrangement of their fibers (schematic); fig. based on data from Putz and Pabst, 1993.

tic quality of the tendons store energy, absorb shock and function as a suspension mechanism. A good example of this elasticity is given by the middle interosseous muscle (M. interosseus medius) of the horse. This muscle is a long, fibrous cord greatly resembling a tendon. In fact, it hardly contains muscle tissue and functions as a tendon. When a horse is moving, this tendon is stretched by the load applied to the leg, storing energy as elastic strain energy. During the second half of the step, the body weight load on the leg decreases, and the tendon, which has stretched and shortened, releases the stored energy. When an extreme load is placed on this structure, it can stretch to the point where the fetlock joint touches the ground with each step.

At their attachment sites, the tendon fibres continue into the **periosteum** or **perichondrium** as **Sharpey fibres**. The attachment can encompass a large surface area of the bone or it can be limited to a single point, forming either a sharp or wide angle. Tendons that continue into the skin or tongue musculature contain a higher percentage of elastic fibres, thereby increasing the tension in these organs.

Macroscopically, muscle fibres appear staggered, attaching to the aponeurose at varying angle widths or to the bone with tendons of various lengths. The tendon can divide and radiate into the muscle, so that the muscle becomes imbued with tendinous tissue. The spreading of the tendon tissue in the muscles results in a pattern **(tendon sheath)** similar to a feather or a leaf. Muscles are classified according to their **structure** and **fibre orientation** (▶ Fig. 1.38):

- **unipennate muscles** (m. unipennatus) with two parallel tendon sheaths,
- **bipennate muscles** (m. bipennatus) with double tendon sheaths, and
- **multipennate muscles** (m. multipennatus) with multiple tendon sheaths.

A pennate muscle has fibres that lie oblique to the line of force generated by the muscle. The maximum force produced by a muscle is proportional to the total cross-sectional area of all its fibres. The morphological cross section is the cross-sectional area of a muscle perpendicular to its belly axis at its thickest part. The physiological cross section of a muscle represents the cross sectional area of all muscle fibres perpendicular to longitudinal axis of each fibre. Muscle strength is dependent on the number of fibres apparent on the physiological cross section. The more fibres present, the greater is the tension and the maximum force produced. The **tension** required of a muscle is dependent on the cross-section of the fibres and the distance the muscle shortens during contraction. This distance is proportional to the change in the insertion angle and the length of the muscle fibre bundles. Muscle work is the **speed of the contraction**.

Within a strong muscle belly, the muscle fibres attach to the tendon or to the bone surface at a sharp angle, allowing space for the muscle to expand when it contracts. During contraction, the attachment angle widens. This unique structural characteristic increases blood flow, thus supporting metabolism. The contraction and relaxation of muscles play an important role in the body's entire circulatory system.

Forms of muscles

Muscle vary in form, location and size. On spindle-shaped muscles, one can distinguish a passive **head** (caput) at the origin, the active muscle **belly** (venter) in the middle and the passive **tail** (cauda) at the insertion. As a result, each muscle has a designated **origin** (origo) and **insertion** (insertio). The origin and insertion are assigned by convention. Normally, the origin is the proximal end of the muscle, or the end closest to the body centre or axis.

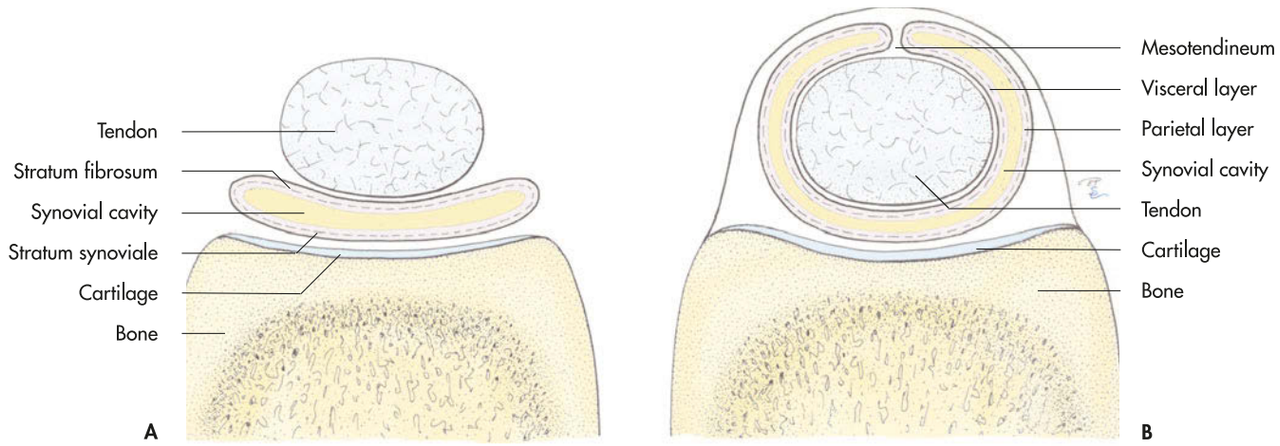

Fig. 1.39 Accessory structures of muscles: **(A)** synovial bursa and **(B)** tendon sheath (schematic).

The distal end of the muscle is the insertion. There are many different **forms of muscle** (▶ Fig. 1.38):
- spindle-shaped muscles (m. fusiformis),
- wide muscles (m. planus, whose tendon builds an aponeurosis),
- two-headed muscles (m. biceps),
- three-headed muscles (m. triceps),
- four-headed muscles (m. quadriceps),
- two-bellied muscles (m. biventer or m. digastricus),
- circular muscles (m. orbicularis) and
- sphincter muscles (m. sphincter).

Locomotion

Natural movements involve many muscles working simultaneously or one after the other. When two muscles act together, they are said to be **synergistic**. If they work against each other, they are **antagonists**. During movement, one part is the **fixed point** (punctum fixum) and the other the **moving point** (punctum mobile). The punctum fixum is every part that remains immobile due to its attachment to the trunk. The punctum mobile must be smaller and lighter than the punctum fixum. The function of a muscle can be derived on the one hand from its origin, placement and insertion and on the other hand, from its **point of rotation** (hypomochlion).

Most all natural movements, for example, breathing, walking, trotting, or galloping, are a rhythmic cycle of contractions and relaxations of antagonistic muscle groups. Even during relaxation, every muscle is under a certain amount of minimal tension, the **muscle tonus**. This state is caused by a reflectory and constant excitatory stimulus originating from the muscle spindles. Anasthesia invokes a **hypotonus**, a reduction in muscle tonus. Many muscles serve to hold a certain body part in position and therefore display a constant minimal muscle tonus. These muscles are sometimes passively supported by tendon-like tissue embedded in the muscle belly.

In order for movement to begin, both the muscle tonus of the antagonizing muscle(s) and the force of gravity must be overcome. Muscle contractions are categorised based on what happens to the length of the active muscle during movement. A continual increase in the intrinsic muscle tension without a change in muscle length is an **isometric contraction**. At a certain grade of tension, the muscle slowly begins to contract and shortens (**isotonic contraction**), resulting in movement.

A muscle exerts force on a joint according to the laws of lever systems. Depending on the **number of joints** a muscle acts upon, it can be classified as a:
- uniarticular muscle or
- biarticular muscle or
- polyarticular muscle.

From this classification scheme, it is obvious that some joints are always moved together when one muscle contracts (obligatorily linked joints). Other joints move together only under unique circumstances (facultatively linked joints).

Muscles can also be classified according to their **functional effect** on a joint as:
- extensor (m. extensor),
- flexor (m. flexor),
- adductor (m. adductor),
- abductor (m. abductor),
- sphincter (m. sphincter),
- dilator (m. dilatator),
- levator (m. levator),
- depressor (m. depressor),
- rotator (m. rotator) with:
  - supinator (m. supinator) and
  - pronator (m. pronator).

▶ Fig. 1.40, ▶ Fig. 1.41, ▶ Fig. 1.42, ▶ Fig. 1.43 and ▶ Fig. 1.44 present the superficial musculature of the domestic animals, which provide an introduction to myology. Topography, form and function of the individual muscles are described in detail in later chapters.

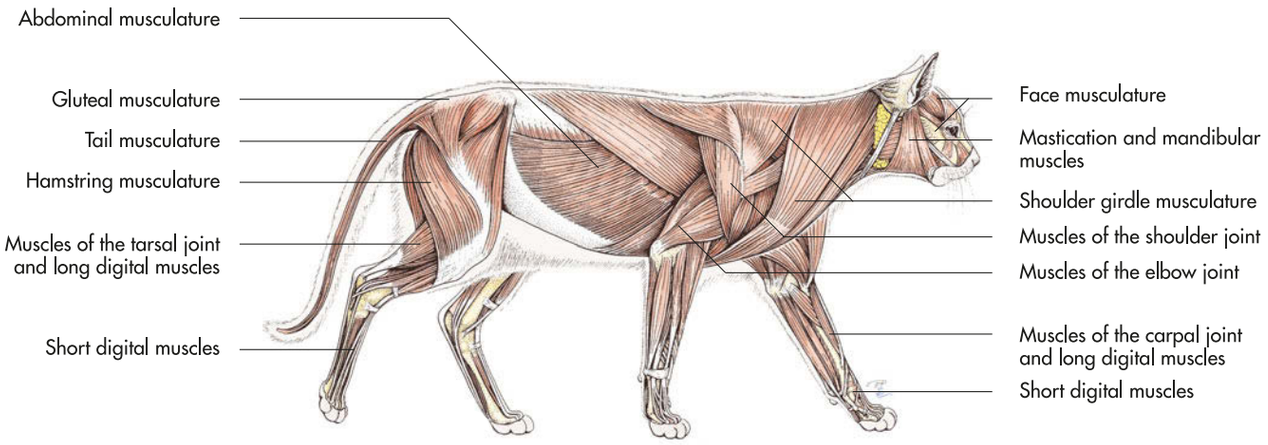

Fig. 1.40 Superficial muscle groups of the cat (schematic).

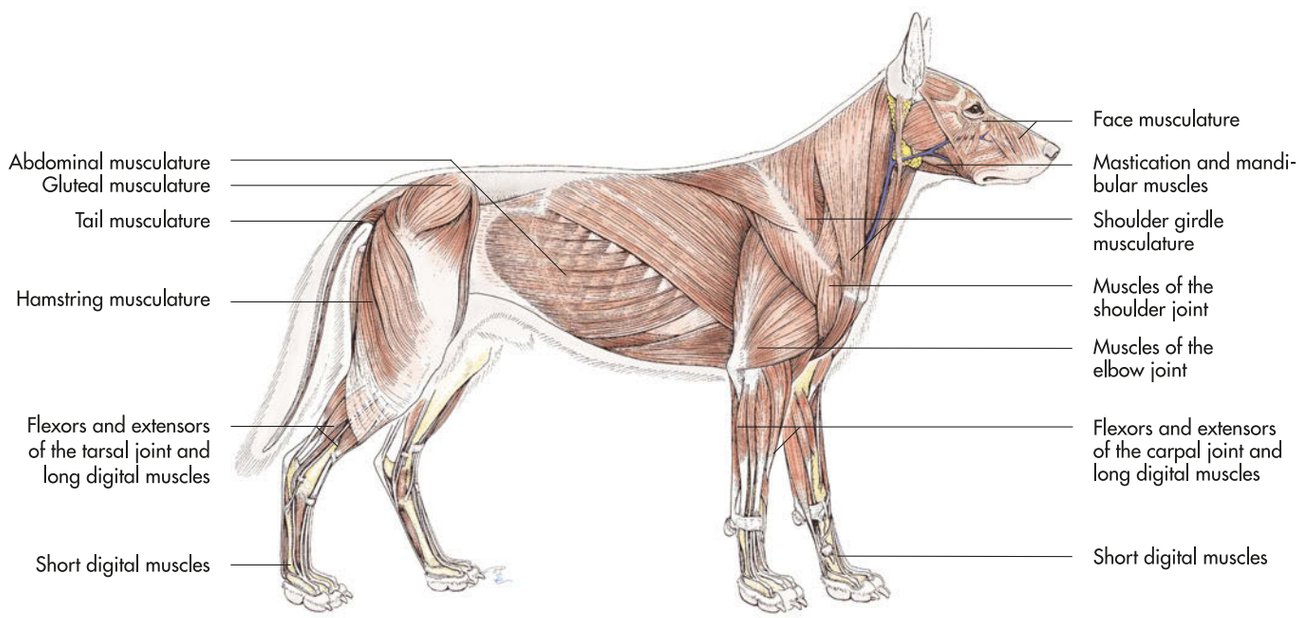

Fig. 1.41 Superficial muscle groups of the dog (schematic).

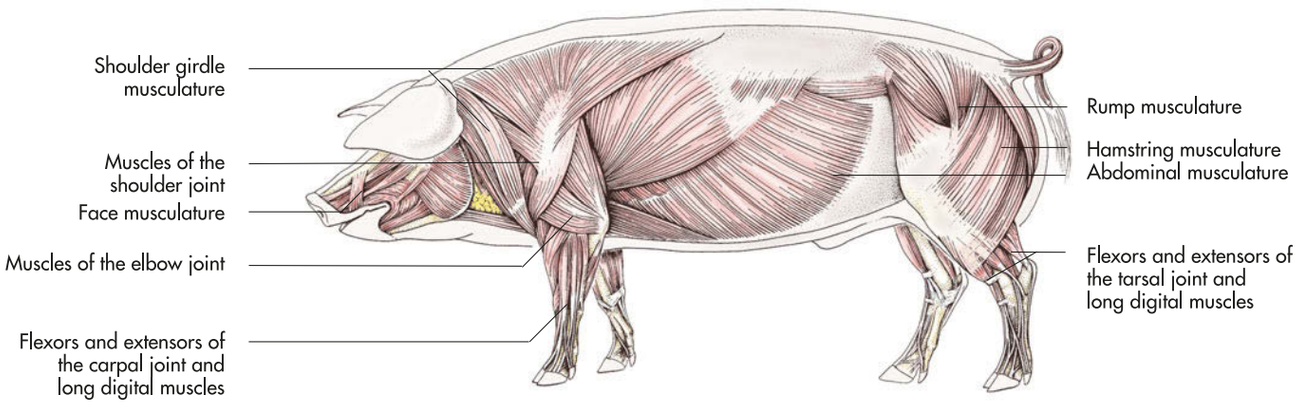

Fig. 1.42 Superficial muscle groups of the pig (schematic).

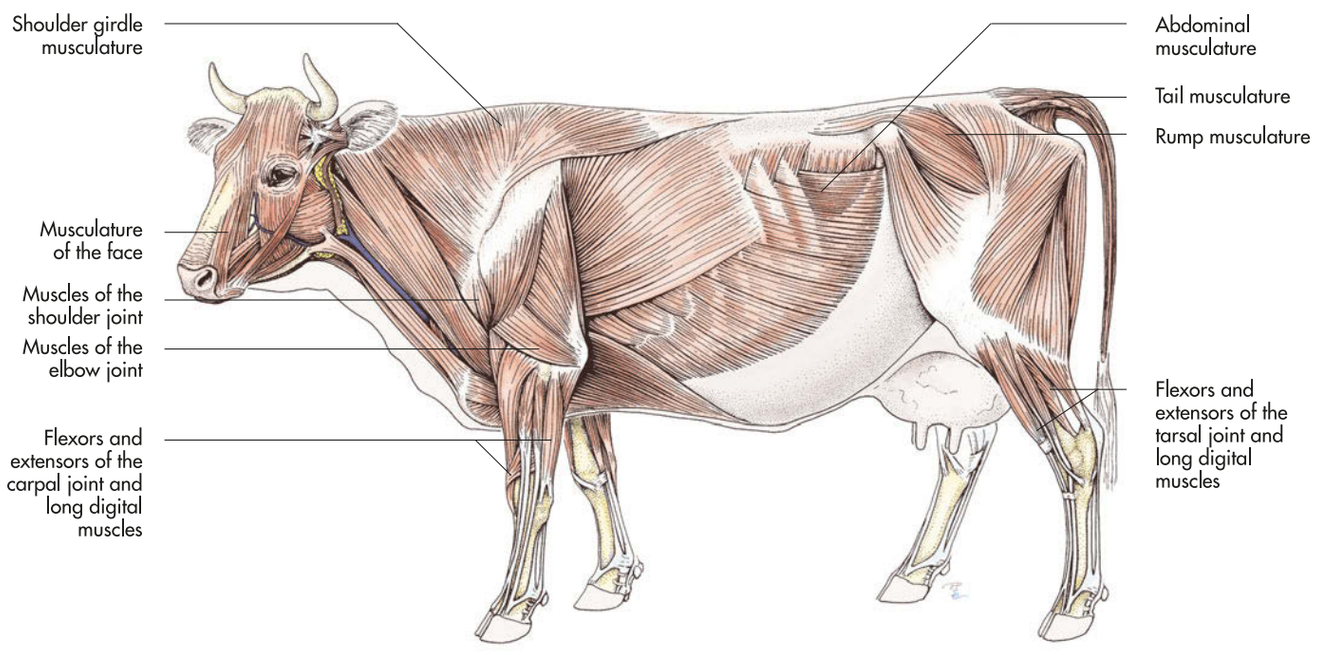

Fig. 1.43 Superficial muscle groups of the cow (schematic).

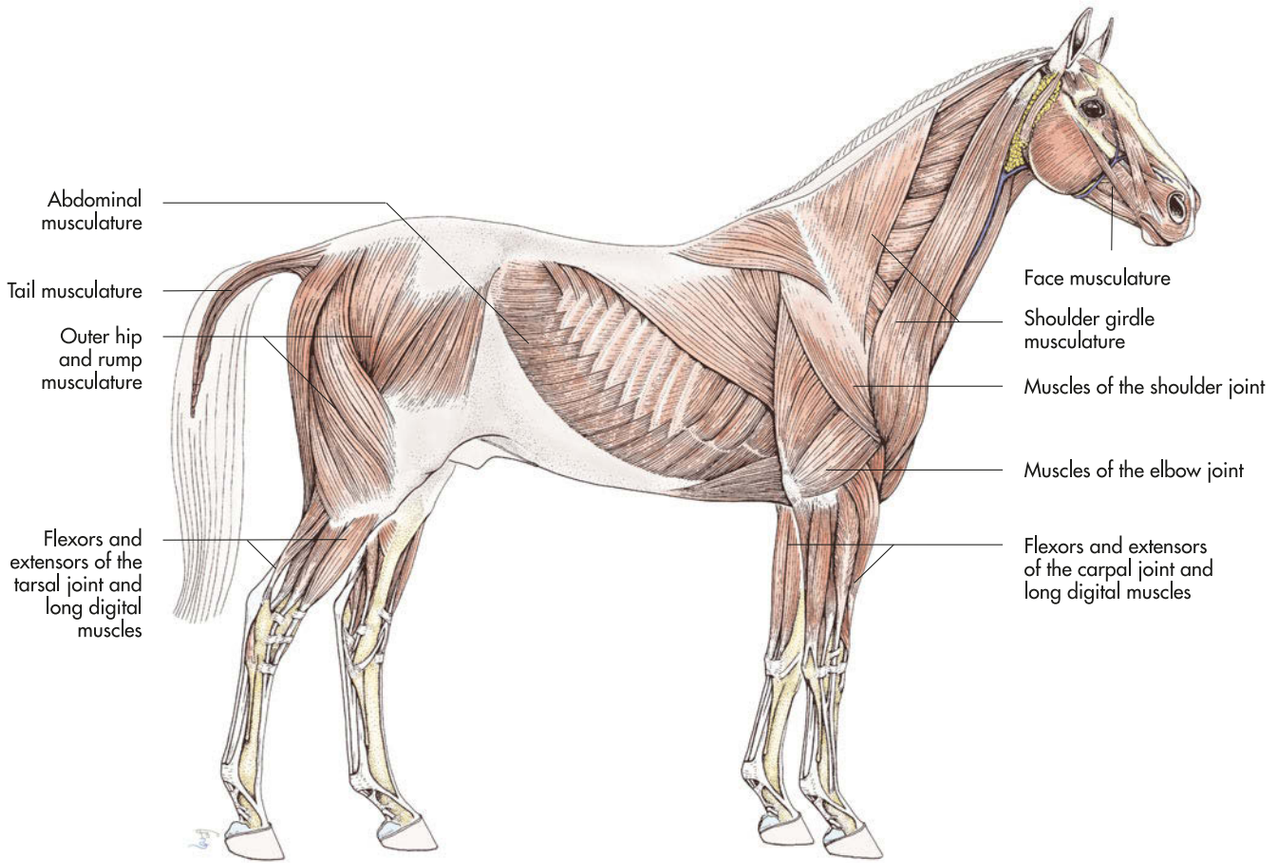

Fig. 1.44 Superficial musculature of the horse (schematic).

Accessory structures of muscles

The muscles are supported in their many functions through passive structures such as the:

- fasciae,
- bursae (bursae synovialis) or
- tendon sheaths (vaginae synovialis tendinum).

Muscles are individually sheathed in **fasciae**. The fasciae are expansive, thin and mesh-like sheets consisting of mostly collagen but also elastic fibres. These fibres are orientated in the same direction as the tension and stress forces acting upon the muscle. The mesh-like architecture of the fibres allows the fasciae to functionally adapt to changing muscle thickness resulting from muscle contraction. Fascia often serve as origin or attachment sites for muscles. By sheathing a muscle, fasciae provide a frictionless surface, allowing freedom of movement between individual muscles situated next to each other.

A unique form are the **septa intermuscularia**, independent fasciae that lie between muscles and are anchored to the periosteum. Fascia also form ringlike structures of connective tissue on extensor or flexor joint surfaces, thereby strenghthening the joint itself (retinacula tendinum).

Fasciae are located throughout the entire body and can be divided into a thinner, **superficial fascia** (fascia superficialis) and a stronger, **deeper layer** (fascia profunda). The superficial fascia enclose the superficial **skin muscles** (musculi cutanei) in most regions of the body. Especially in the horse, the deeper layers can be reinforced through elastic fibres that lend them a yellow sheen (tunica flava of the ventral abdominal wall).

Synovial bursae are enclosed in a capsule of connective tissue (▶ Fig. 1.39). They vary in size, often containing more than one compartment, and are always filled with synovia. They can be compared to small gel cushions located beneath tendons, evenly distributing pressure originating from the tendon. The structure of the bursae walls is similar to that of joints. Like the joints, the wall is comprised of two layers: the inner **stratum synoviale** and the external **stratum fibrosum**.

The synovial bursae are found everywhere in the body where muscles, tendons or ligaments glide over bone. Inconsistent or facultative bursae may develop subcutaneously at various sites subjected to constant mechanical pressure. Synovial bursae are classified according to their **location**:

- subtendinous bursae (bursae synoviales subtendinosae),
- submuscular bursae (bursae synoviales submusculares),
- subligamentous bursae (bursae synoviales subligamentosae) and
- subcutaneous bursae (bursae synoviales subcutaneae).

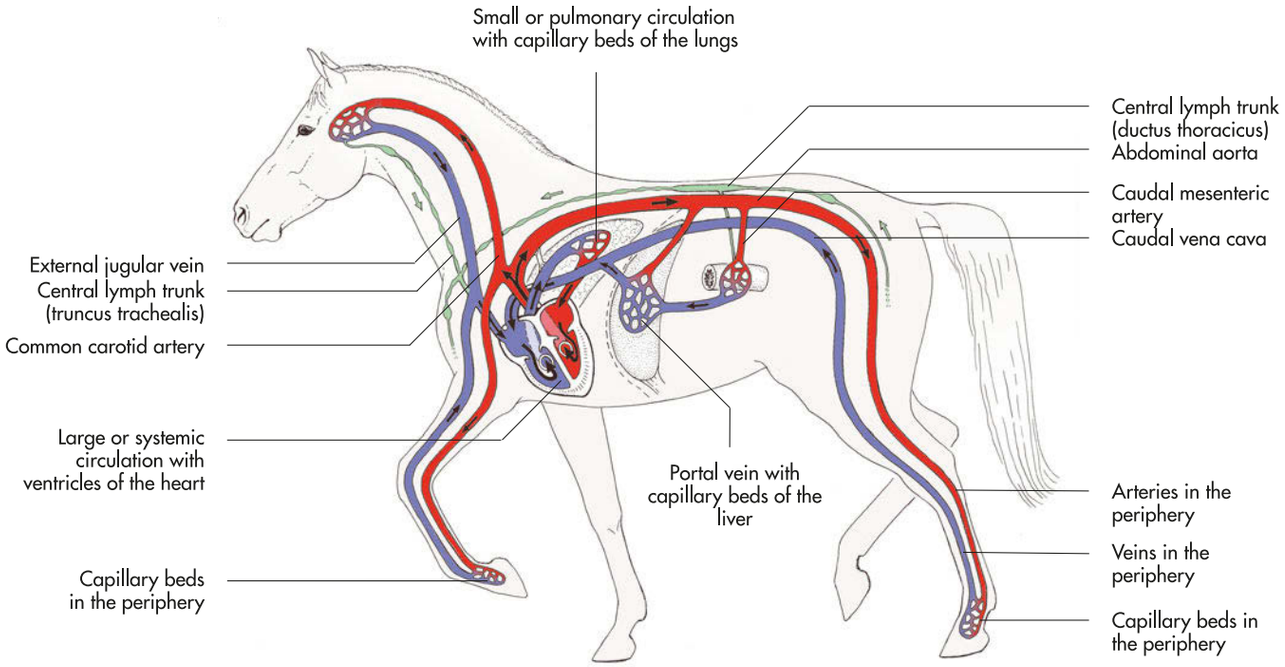

Fig. 1.45 Adult circulatory system (schematic).

Synovial tendon sheaths (▶ Fig. 1.39) are similar to the bursae, except that they completely sheathe the tendons like a tube, protecting the underlying tissues from pressure exerted by the tendon and reducing friction during movement. Tendon sheaths often form when the synovial membrane of a joint forms a **recess** (recessus), which then surrounds the tendon.

Like the bursae, tendon sheaths have **cavities** (cavum synoviale) which are also filled with **synovial fluid**. The **synovial membrane** is formed from two layers, the **visceral** and the **parietal layers**. The internal surface facing the tendon is the visceral layer of the tendon sheath. At some point, this layer doubles back and becomes the outer or parietal layer. These two layers are connected by a thin double mesentery, the **mesotendineum**, which provides passage for blood vessels and nerves. In certain places the mesotendineum is incomplete (**vincula tendinum**).

Functions of the synovial membrane

Fluid filtration, nutrient diffusion and active macromolecule transport processes occur through the synovial membrane. Among the synovial cells of the folds and villi are microscopic pores through which substances can diffuse. Hydrostatic and osmotic pressure regulate diffusion processes between the synovial cavity and the surrounding connective tissue. Located in the surrounding connective tissue are numerous blood and lymphatic vessels that considerably affect the function of the tendon sheaths. A physiological equilibrium exists when the amount of fluid entering the synovial cavity is the same as that which is reabsorbed from the cavity.

When this equilibrium is disturbed, fluid accumulates in the cavity. Clinically, this results in swelling of the tendon sheath and possibly in inflammation of the synovial membrane. The lymphatic drainage plays an important role in regulating hydrostatic pressure within the cavity. With every rhythmic contraction of the surrounding musculature, excessive fluid is drained into the lymph vessels and removed.

Clinical terminology

Examples of clinical terms derived from anatomical terms: osteopathy, osteitis, osteomyelitis, periostitis, osteosynthesis, osteoclastoma, osteoplastic, osteolysis, osteomyelography, osteoma, osteomyelofibrosis, osteonecrosis, osteoperiostitis ossificans, osteopetrosis, osteoporosis, osteochondrosis, spina bifida, osteosarcoma, abductor fracture, adductor paralysis, arthropathy, arthritis, arthrosis, arthro-scopy, arthrolysis, nucleus pulposus prolapse, hip dysplasia (HD), myopathy, myodistrophy, myofibrosis, myometritis, myocarditis, myoma, myospasm, tendopathy, tendinitis, bursitis, synovitis, synovia hernia, achillobursitis, achillotenotomy, insertion tendinosis, and many more.

1.5 General anatomy of angiology (angiologia)

H.-G. Liebich and H. E. König

The cardiovascular system can be compared to a closed system of connecting tubes, where the heart functions as the central driving pump. The heart continuously circulates blood through the arteries, capillaries, and veins, supplying the organs and peripheral body parts. This system, which also includes the lymphatic system, integrates all the various parts of the body, transporting substances to, from and between cells and tissues. These substances include nutrients, blood gases, enzymes, electrolytes, vitamins, hormones, metabolic products, heat, components of the immune system, water, and blood cells. The **blood** (hema, sanguis) is responsible for transporting these substances.

The **blood volume** in a domestic animal accounts for 6–8% of body weight. Cats are the one exception: their blood volume accounts for only 4% of their weight. This fact makes them much more susceptible to anaemia than other animals.

The **circulation time** required for a blood cell to travel from the heart, through the body and back, is approximately 30 seconds for large animals, 15 seconds for medium sized animals and 7 seconds for a cat.

1.5.1 Organisation of the cardiovascular system

The term **circulatory system** (systema cardiovasculare) refers to the **blood-filled tubular pathways** of the body. Also included is the **lymphatic system** (systema lymphaticum) that functions as a **drainage system**, draining fluid in the form of **lymph** from the interstitial tissue and returning it to the circulating blood. The red bone marrow and the spleen are also components of this system. The red bone marrow is a **hemopoetic organ** that produces various blood cells (**hematopoesis**), and the spleen acts as a filter for these cells.

Since all types of organs and tissues are supplied by blood through vessels, these vessels must be organised to accommodate very different requirements. These requirements include, for example, the digestion processes of the intestines, muscle work, and the blood supply to the heart and brain.

The **heart functions** as the **central pump of the cardiovascular system**. Blood pumped from the heart enters a **high pressure dispersion system** consisting of the large arteries and, in the periphery, the smaller arterioles. Arteries and arterioles carry **oxygen-rich (oxygenated) blood** away from the heart to the periphery of the body. The arteries branch into arterioles, which further branch into ever smaller and more abundant vessels, the **capillaries** (vasa capillaria).

Capillaries have very small diameters and extremely thin walls, both of which facilitate gas exchange and the transportation of small molecules and water between the blood and surrounding tissues. The thin capillary walls also allow some types of blood cells to exit the vessel and enter surrounding tissues.

As blood flows away from the heart, pressure within the vessels declines. This drop in pressure is the result of two factors, friction, as the blood encounters resistance from the luminal walls of vessels, and an increase in the total cross-sectional area of blood vessels. The capillaries are mainly responsible for this effect: since their lumina are small, resistance is increased. Due to the overall abundance of the capillaries, the total cross-sectional area is also increased.

Blood returning to the heart through the **veins** retains very little pressure. Veins and venules form a **low pressure collecting system**. This system carries blood containing very little **oxygen** (**deoxygenated**) and can also serve as a reservoir for blood (e.g. in the integument, subcutis, lungs, spleen), returning blood to the circulation when needed. The veins carry the blood back into the heart; for more information see Chapter 13 “Organs of the cardiovascular system” (p. 471).

Heart (cor)

The heart is the central organ of the cardiovascular system. It is a **four-chambered**, muscular sac that rhythmically contracts, acting as a pump to propel blood through the vessels. The direction of flow is pre-programmed through built-in **heart valves**, which also prevent reflux.

The heart is divided into **two main chambers** (ventriculi cordis). Each of these chambers is preceded by an **atrium** (atrium cordis), making altogether four chambers. The two atria collect blood, thus ensuring enough is present to fill each ventricle quickly.

Both ventricles have a valve located at each end. One valve prevents the blood from flowing backwards into the atria during a **contraction of the ventricles** (systole, Greek for “pull together”). The second valve prevents the blood in the arteries from returning to the ventricles during **relaxation** (diastole, Greek for “pull apart, stretch”). During diastole, blood flows into the ventricles, the following systolic and diastolic phases quickly alternate, creating a pump-like action.

Functionally, the heart is divided into a **right** and **left side**. The **right side** of the heart pumps the blood into the **capillaries of the lungs** and is referred to as the **small or pulmonary circulation**.

The **left side** pumps blood to the rest of the body and is called the **large or systemic circulation**. The right and left sides of the heart are completely separated by an **internal wall**, but both, outwardly and anatomically, the heart appears a single organ; for more details see Chapter 13 “Organs of the cardiovascular system” (p. 471).

Pulmonary and systemic circulation

The pulmonary and systemic circulations are two parts of a common circulation, where one lies ahead of the other (▶ Fig. 1.45). Both sides of the heart pump the same volume of blood, even though the path between the right side of the heart and the lungs is much shorter than that between the left side of the heart and the peripheral body parts.

The **pulmonary** or **small circulation** begins in the **right atrium**, from which deoxygenated blood flows into the **right ventricle**. During ventricle contraction, this blood is pressed into the **pulmonary trunk** (truncus pulmonalis) and the following lung arteries until it arrives in the **capillary beds of the lungs**. Here the blood becomes oxygenated and returns through the **veins of**

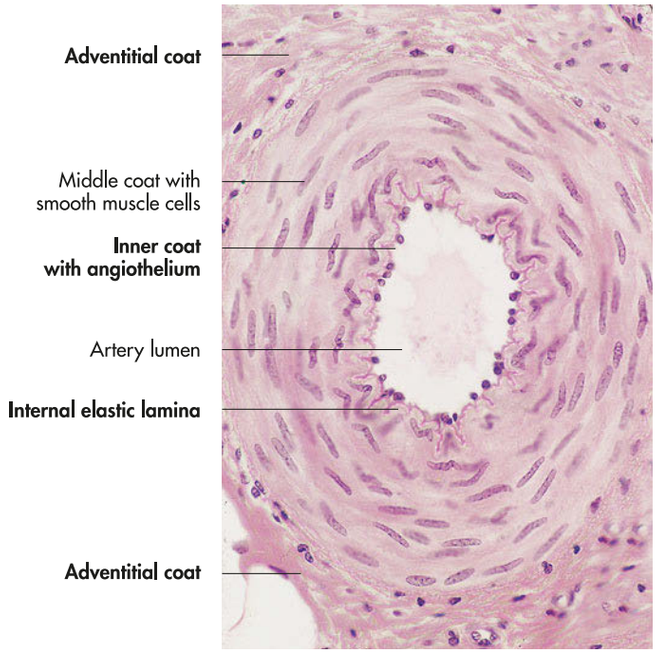

Fig. 1.46 Artery (histological section, hematoxylin and eosin staining).

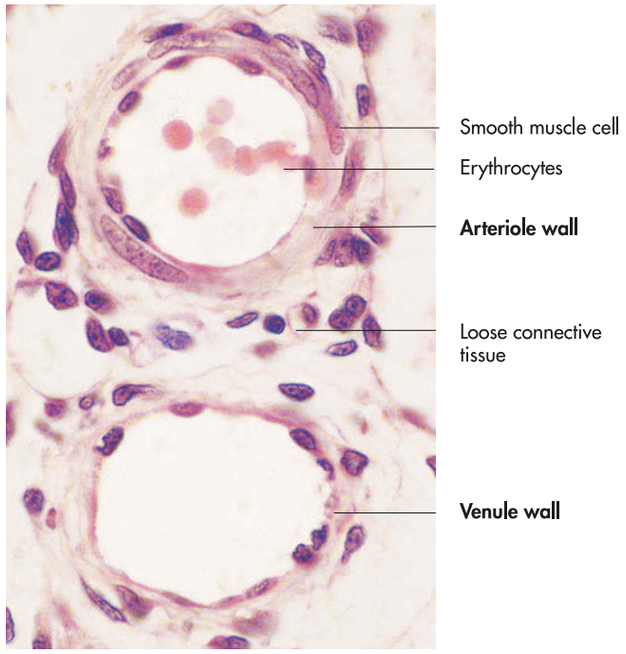

Fig. 1.47 An arteriole and a venule (histological section, hematoxylin and eosin staining).

the lungs (venae pulmonales) to the heart, flowing into the **left atrium**.

The **systemic** or **large circulation** begins in the **left atrium** of the heart. Oxygenated blood flows from the **left atrium** into the **left ventricle**. When the ventricles contract, the blood is forced into the **aorta** and is systematically dispersed throughout the **periphery of the body**, first through the arteries, then through the arterioles, until finally reaching the **capillary beds** of the tissues and organs. Deoxygenated blood returns from the hind limbs and the caudal half of the trunk through the **caudal vena cava** (v. cava caudalis) and returns from the head, front limbs and the cranial trunk through the **cranial vena cava** (v. cava cranialis). Both the cranial and caudal vena cava empty into the **right atrium**.

Portal circulation

The portal vein and its tributaries form a bypass system that begins and ends as capillary beds. The **portal vein** (v. portae) collects deoxygenated blood from the first capillary beds in the gastrointestinal tract and other unpaired organs within the abdominal cavity (spleen and pancreas). The capillaries in the abdominal viscera become confluent, eventually merging to form the portal vein. The wall of the portal vein is strengthened by muscle fibres, which rhythmically contract, increasing the portal pressure and propelling the blood towards the liver.

Within the liver, the portal vein repeatedly branches, eventually forming **capillary beds a second time**. When the blood passes through the liver and arrives in the liver's cranial side, it is collected by veins and transported into the caudal vena cava. Here the blood joins the remaining blood from the periphery to flow into the right atrium of the heart.

Another portal system of the body is located in the **pituitary gland** (hypothalamic-pituitary axis).

Peripheral circulation

The peripheral circulatory system is governed by functional adaptations which are reflected in the structures of the various vessel walls. As a rule, the organs and tissues are supplied by so-called vessel-nerve bundles, in which arteries, veins ("accompanying or concomitant veins"), lymphatic vessels and nerves mutually wind through connective tissue paths. For protection, the main vessel and nerve stems supplying the limbs are always located on the flexion surface of a joint.

Collateral arteries, terminal arteries and rete mirabile

By means of constant and continuous branching, collateral arteries break off from the main arteries and continue to accompany them, eventually reaching the same organs. Most of the collateral arteries connect to neighboring vessels, forming **peripheral anastomoses** (see below) and flow together into a common **net of blood vessels** (rete arteriosum). When this double arterial supply is missing, the single arteries are referred to as **terminal** or **end arteries**.

The occlusion of a terminal artery results in tissue ischemia and death (**necrosis**). Terminal arteries are common in the brain, heart, lungs, liver, kidneys, retina and spleen. When a terminal artery in these organs can no longer supply its area of tissue, this can result in a stroke (brain) or pulmonary embolism (lungs).

A highly modified arterial structure is the **rete mirabile**. An arterial rete mirabile forms when an artery branches into a series of parallel vessels, only to reunite into one artery again after a certain distance. These arterial structures are found mainly in the arteries at the base of the skull and on a smaller scale in the renal glomerula.

Fig. 1.48 Artery wall with elastic fibers (histological section, elastica staining).

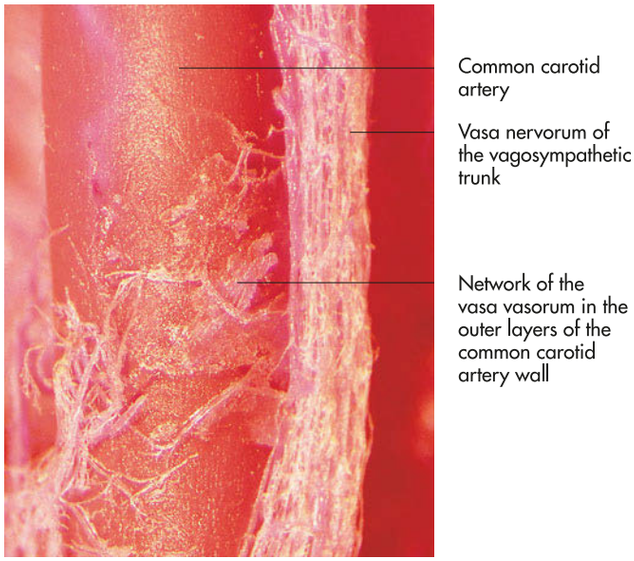

Fig. 1.49 Common carotid artery with the vasa vasorum and nerve network (corrosion cast).

The purpose of these structures has not yet been fully clarified. Since they are tightly associated with their corresponding venes, they most likely play a role in promoting the venous return (**arteriovenous junctions**). It has also been hypothesised that they slightly decrease the temperature of blood flowing to the brain. Another purpose may be to reduce pulsation of the arteries in the brain.

Anastomoses, barrier arteries and sphincter veins

Arteriovenous anastomoses are formed when a vessel branches from the arterioles before the capillary bed is reached. This vessel connects directly to venoles, thus completely bypassing the capillary bed. **Precapillary sphincters** are located at the transition of arterioles to capillary beds. These structures regulate blood flow to the capillary beds, thus controlling the peripheral circulation to the organs (e.g. integument, intestines, nasal mucosa). The arteriovenous anastomoses are the principal means of regulating temperature in the various organs. **Barrier arteries** contract to temporarily interrupt blood flow to a capillary bed. This results in an increased blood flow to the neighboring capillary bed. Venes are also equipped with **sphincters** (sphincter veins) capable of regulating the amount of blood flowing through the capillary bed located behind it. These structures are mostly found in veins of the genital organs.

1.5.2 Vessels (vasa)

A complete understanding of **angiology** (angiologia, from the Greek "angion" for vessel) can only be achieved through knowledge of structure, function, and clinical importance of different blood vessels. For the student and clinician, a basic understanding of the vessels as well as a general knowledge of the topography is more important than a comparative and detailed topographical knowledge of each vessel and their smallest branches (rami). The exact topography of every vessel down to minute detail is only of academic interest and is comprehensively portrayed in many anatomy textbooks. This textbook provides the student and practitioner with a working knowledge of the clinically important blood vessels and their paths; for more details see Chapter 13 "Organs of the cardiovascular system" (p. 471).

Structure of the blood vessels (vasa sanguinea)

The blood vessels build a **strongly branched, closed system of tubes**. In humans, were this system to be laid out in a long row, it would reach over 40 000 kilometers. The vessels are all built according to a similar design (▶ Fig. 1.46, ▶ Fig. 1.47, ▶ Fig. 1.48, ▶ Fig. 1.49, ▶ Fig. 1.50 and ▶ Fig. 1.51). The structure varies, in part greatly, according to the local functional demands. In general, the following vessel types exist, listed in the direction of blood flow:

- **arteries**, large vessels carrying blood away from the heart, without any capability of exchange with the surrounding tissues,
- **arterioles**, smaller arteries (diameter 20–100 µm),
- **capillaries**, with very thin walls participating in exchange with surrounding tissues,
- **venules**, small venes, and
- **veins**, large vessels carrying blood to the heart.

The lumen of large vessels is lined with a **tunica intima**. The tunica intima consists of a single layer of **endothelial cells** (angiothelium) resting on a **stratum subendotheliale** of connective tissue with an underlying **basement membrane**. This layer is responsible for the exchange of molecules with the surrounding tissues, allows blood cells to exit the vessel lumen and promotes the flow velocity of blood or lymph. The middle layer, the **tunica media**, consists mainly of smooth muscle cells and elastic nets. This layer contracts the vessel wall, determining the hemodynamics. The outer layer, the **tunica adventitia**, is mostly composed of loose connective tissue, which anchors the vessel to the

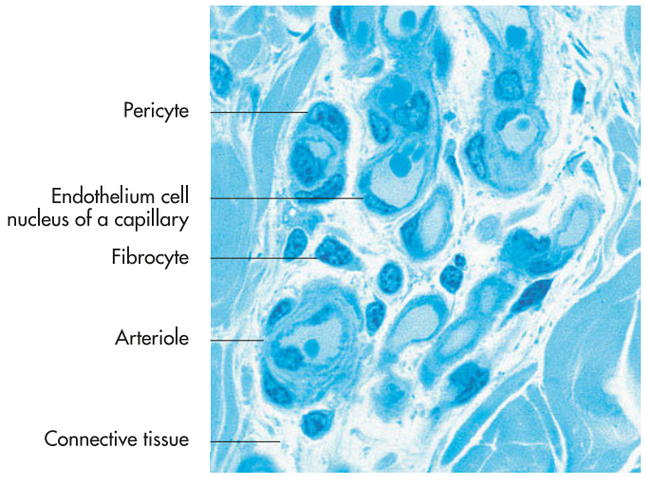

Fig. 1.50 Capillary bed with surrounding connective tissue (histological section, methylene blue staining).

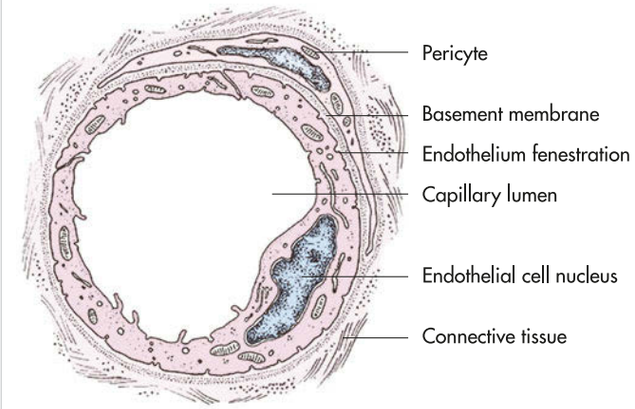

Fig. 1.51 Ultrastructure of a capillary (schematic); fig. based on data from Liebich, 2004.

surrounding tissue. The **vegetative nerve** supply to the vessels is also found in this layer, as well as in the **vasa vasorum**, which supplies nutrients to the larger vessels (see a textbook of histology for more information on vessel structure).

Arteries (arteriae)

The arteries and arterioles **carry the blood away** from the heart and into the periphery to all the organs. There are two types of arteries: those of the **elastic type** and those of the **muscular type** (▶ Fig. 1.46, ▶ Fig. 1.47 and ▶ Fig. 1.48). The tunica media in the **aorta** and **arteries located near to the heart** contains mainly **elastic fibres**. These elastic fibres are responsible for the **typical expansion** of the vessels during **systole**. Arteries can regulate their calibre by contraction of the muscular layer, which conducts the blood further into the periphery. With a contraction of the left ventricle (systole), a blood stream is forced into the aorta and the arteries closest to the heart. The aorta and the arteries expand to receive the blood, due to the elastic nature of their walls, thus absorbing the energy of the blood stream. When the left ventricle relaxes (**diastole**), the aorta and arteries closest to the heart passively narrow to their former diameter, pressing the blood together and forcing it further along. The absorbed energy in the walls is transferred back to the flowing blood. The elastic aorta and arteries functionally transform the **discontinual pump action** of the heart into a **continual flow of blood** to the body. Examples of elastic arteries are as mentioned above, the aorta, the aortic arch, the brachiocephalic trunk, and the pulmonary arteries.

Arteries situated further from the heart have **smooth muscle fibres** in the tunica media and are arteries of the **muscular type** (▶ Fig. 1.48). These peripheral arteries, along with the arterioles, can change their lumen diameter, thus regulating blood pressure and blood flow. The **tunica media** is greatly strengthened by the smooth muscle fibres, which sometimes are reinforced with elastic fibres. The outer layer, the **tunica adventitia**, consists of connective tissue and elastic fibres. This layer anchors the blood vessels in the surrounding tissues.

Blood and nerve supply to the vessels

Blood vessel walls are partly supplied with nutrients that diffuse from the blood flowing in the lumen (transendothelial). The thick tunica media in large vessels prohibits transendothelial diffusion. Larger blood vessels require their own supply, which is provided by small blood vessels (**vessels of the vasculature**, **vasa vasorum**) which form capillary beds in the vessel walls.

The vessel wall is abundant in **vegetative nerve networks**. These nerves signal the smooth muscles to constrict (**vasoconstriction**, **adrenergic**) or to dilate (**vasodilation**, **cholinergic**). Located in specific vessel sections are **pressoreceptors**, unique nerve structures that measure the pressure in the vessel wall and acting on the vessel wall (i.e. in the carotid sinus). Such sensors have a **regulatory function on the blood pressure**.

A cat's blood pressure is measured on the upper arm and a dog's on his forearm or shank. The blood pressure in dogs can also be measured at the base of the tail.

Arterioles

Arterioles play an important role in regulating not only **arterial blood pressure** but also **blood flow velocity** in the periphery. Compared to the arteries, arterioles have a much thinner muscle layer and a smaller lumen diameter. The precapillary sphincters, the **metarterioles**, are also functionally important in **regulating blood pressure** (▶ Fig. 1.47). Through contraction of the ring muscle, the lumen of the arteriole can be completely occluded. These sphincters are usually located at the **transition of arterioles to capillary beds**, thus reducing the blood flow into the capillary beds. **Arteriovenous anastomoses** exist in the precapillary region to restrict blood transport to the capillary region in order to, for example, avoid the breakdown of a metabolic product.

Blood capillaries (vasa capillaria)

Capillaries (hair vessels) are responsible for the **gas** and **molecule exchange** between the blood and the tissues. For this to occur, **blood flow velocity** is reduced from 400–900 mm/sec in the aorta to approx. 0.3 mm/sec in the capillaries. **Blood pressure** is also greatly reduced in the capillaries. A capillary has an average diameter of 5–15 µm. Capillaries result from the **repeated divisions of the arterioles** and build three-dimensional nets before their transition into venules. Some structures do not contain capillaries, such as the cornea, the lens, cartilage, and dentin.

The **capillary wall** consists of only two layers, an **endothelial layer** lining the lumen and an outer **basement membrane** (▶ Fig. 1.50 and ▶ Fig. 1.51). The endothelium is usually continuous, however, the endothelium of some capillaries contains pores between the cells. Similarly, pores are also sometimes found in the basement membrane.

Sinusoid capillaries (vasa capillaria sinusoidea) are found in the liver, in red bone marrow, and in the spleen. These capillaries are characterised by a large diameter (approx. 40 µm), intercellular pores, and a discontinuous basement membrane. The cells of the lumen wall are capable of phagocytosis. Capillaries exhibit structural characteristics that are specific to the organ they supply. Organs and tissues may differ in the number of capillaries, or the amount of vascularisation, or in the rate of blood flow. For example, the heart muscle and the brain are very dependent on oxygen and are therefore vascularised quite extensively. On the other hand, a large percentage of cartilage or of the cornea remains free of vessels (bradytrophic tissue).

Capillaries are biologically effective for transport and barrier, for example, in the lungs, the kidneys, and the brain (blood-brain barrier). They play a role in filtration and reabsorption, or they can build a blood-clot-inhibiting layer. Tissues vascularised by arteries with anastomoses are not endangered by the occlusion of a single artery. Tissues vascularised by a single **terminal artery** are destined to become necrotic if the artery occludes. This process is called an **infarction**. The capillary density is very high in some organs like the heart muscle, in the grey substance of the central nervous system and in the endocrine glands. In other organs, the capillary density is dependent on the activity level. For example, in the ovaries, capillary beds develop during functional phases and are resorbed during resting phases.

Venules

Venules are the smallest veins, and differ from veins in that they have a miniscule lumen, a thinner wall and no elastic fibres (▶ Fig. 1.47). Venules connect the capillary beds with the veins and can be divided into three types. The **postcapillary venules** are similar to the capillaries with their pores in the vessel walls. These pores allow blood cells to diffuse into the tissues (**diapedesis**). Next are the collection venules, followed by the muscular venules, which are characterised by a muscle layer reaching up to 100 µm in thickness. A **venous sinus** (sinus venosus) is a **postcapillary vessel** that is present, for example, in the spleen.

Veins (venae)

From the capillary beds, blood returns to the heart by way of the postcapillary venules, then the smaller veins and finally, by way of the veins (Greek “phleb”, Latin “vena”). After the blood passes through the capillaries, the blood pressure in the veins measures approximately one/eight of the pressure measured in the precapillary arteries. This dramatic decrease in blood pressure results from the maximal increase of the total cross-sectional area of the capillaries and from the presence of unique **venous structures**. These structures (sinus venosi) are located mainly in the liver and spleen and together can store up to three times more blood than that which is present at any one time in the entire arterial system. Structural distinctions between the arteries and veins reflect an adaptation of the vessels to blood pressure: veins have a much larger diameter than arteries, and their walls are much thinner.

Vein architecture

Veins are built similarly to arteries except that the tunica media is much thinner, due to the **low pressure in the venous system**. Most often the tunica adventitia, the outer layer of the vessel, is the thickest. Collagen fibre nets located in the wall of the veins anchor them in the surrounding tissues, and strengthen the wall, preventing its collapse. In the limbs, each artery is located in a fold of connective tissue and is usually accompanied by two veins. The pulsation of the artery, in addition to muscle contractions, helps pump the venous blood back to the heart (see below). The distal limb veins are equipped with a much thicker tunica media in relation to the hydrostatic pressure.

Venous return of blood

Unique pump mechanisms are required to carry venous blood over long distances back to the heart.

Valves of the veins

The tunica interna forms **valves** to prevent blood flowing backwards into the capillary beds when circulation stagnates. These passive valves normally lie flat on the lumen wall when blood flows towards the heart. When blood flows backwards, the valves extend into the lumen, thus closing the vessel. The valves are double-sided endothelial extensions of the tunica interna and are normally found in groups of two to three. Their purpose is to ensure unidirectional blood flow.

The veins of the skull and veins in the vertebral canal **do not have valves**. Blood flows into duplicates of the dura matter (**sinus durae matris**), which are not independent vessels but rather empty spaces lined with endothelial cells.

Muscle pumps

The walls of veins contain few muscle fibres, and the pressure present in the venous system is very low. For these reasons, veins require pressure from the surrounding tissues to aid them in conveying blood back to the heart. The lack of pressure in the veins is compensated for by contractions in the surrounding muscles. The term **muscle pump** summarises the function of the skeletal muscles and their contribution to venous blood flow. During muscle contraction, the veins in and around the muscle are pressed flat. When the muscle relaxes, the veins open again, creating a vacuum, and blood from the periphery is pulled in the direction of the heart. The valves prevent the backward flow of blood. Every body movement affects the return flow of venous blood to the heart. With each step, the terminal vessels in the

toes undergo this functional process. Through the pulse, the arteries of the limbs also compress the neighboring veins. The heart itself also acts as a **pressure pump**.

Composition of venous blood

The composition of the venous blood depends upon where the **main root of the vein** in question originates. Venous blood from the intestines carries energy-rich molecules, white blood cells from the spleen, and hormones from the endocrine glands. Blood returning from the kidneys contains very little metabolic products. Veins transport tissue hormones such as prostaglandins, which in the female animal are produced in the uterus. In the cow, prostaglandins are delivered transmurrally to the ovaries via arteriovenous coupling between the vein draining the uterus and the artery supplying the ovaries (a. ovarica). Thus, the prostaglandins are delivered by the shortest and quickest path to the ovaries, where they induce luteolysis of the corpus luteum. The veins of the muscles and the liver carry blood that has been warmed, thus contributing to a constant body temperature.

Nomenclature of veins

Veins are normally named after the artery that they accompany. **Retrograde** (against the direction of blood flow) names are found in the older literature and tend to be misleading. Veins have **root origins**, combine to form larger veins, and eventually open into the **right atrium of the heart**. The retrograde description of veins makes its impossible to understand correctly the functions of blood flow, arteriovenous coupling, the orientation of the valves, and the effect of an intravenous injection.

Other organs beside the liver and the hypophysis are supplied not only from arteries, but also from veins. Therefore, veins contribute to the **supply of the organism**, similar to arteries. This fact is often not recognised in many textbooks.

1.5.3 Lymphatic system (systema lymphaticum)

A second vessel system exists in the body, which is designated the lymphatic system since its vessels carry lymph instead of blood. These **lymph vessels** are responsible for the integrity of the body. It functions within the **non-specific** and **specific immune systems**; for more information see Chapter 14 “Immune system and lymphatic organs” (p. 501).

Lymphatic organs

The lymphatic organs are responsible for many functions, most of which are executed by the cells of the lymphatic system. There are two classes of cells: the specific immune cells and the non-specific immune cells.

The **lymphocytes** (**T and B lymphocytes**) are the most important functional cells. They are produced in the bone marrow and in the lymphatic organs and travel with the lymph through the lymphatic vessels into the blood. Lymphocytes have surface receptors enabling them to recognise foreign material (antigens) in the body and, by triggering a **specific chain reaction**, to induce an **immune response**. The macrophages support this immune response but are non-specific in their function. They possess the ability to incorporate (phagocytise) antigens, break them down (histocompatibility reaction) and display the antigens (antigen presentation) on their cell surface (for more information, see physiology and immunology textbooks).

The nonspecific immunity cells belong to the extensive mononuclear phagocytosis system (MPS), previously termed the reticuloendothelial system (RES). Included in this system are the tissue macrophages, the endothelium of the liver, the spleen and marrow sinusoids, the alveolar macrophages in the lungs, the Langerhans cells in the skin, and the microglia. Lymphatic tissue is found in the body as:

- single cells (diffuse lymphatic tissue, lymph nodules),
- aggregates of cells (tonsils) or
- complex organs (thymus, lymph nodes and spleen).

Collections of **lymph nodules** (**not** lymph nodes) are found for example, in the intestinal wall as gut-associated lymphatic tissue (GALT). Similar to GALT are the reaction centers of the lungs (BALT: bronchus-associated lymphatic tissue). Such lymph nodules found in the mucosa are referred to as MALT (mucosa-associated lymphatic tissue).

The **thymus** consists of primary lymphatic tissue necessary for the development of cellular immunity. This organ coordinates the active immunity and the the growth of secondary lymphatic organs (lymph nodes, tonsils) during development.

Functions of the lymphatic system

The lymphatic system transports substances to the local lymph nodes that require filtration before they can enter the blood stream. Among such substances are particles, especially dust (lungs) and bacteria (skin, intestinal system, respiratory system). Lymph is also responsible for transporting fats absorbed through the intestines. In all cases, the lymph functions as the carrier.

Lymph is comprised mainly of **proteins** and similar in composition to the blood plasma. Also present in lymph are the **lymphatic cells** that are picked up in the lymph nodes. The lymph originating in the intestines shows a milky-white color due to its high fat content (**intestinal lymph** or **chylus**). Of great physiological importance is the fact that some of the body fluids cannot be transported by the blood vessels and are removed instead by the drainage system of the lymphatic vessels. This drainage system is very flexible and is capable of quickly increasing the amount of transported body fluid as much as ten fold. Interruptions in this drainage system can lead to lymphatic edema.

Architecture of the lymphatic vessels (vasa lymphatica)

The lymphatic vessels begin in the body’s periphery as a system of blind ending, capillary-like tubes that opens in the so called venous angle to the venous circulation.

The following vessels are distinguishable:

- lymphatic capillaries (vasa lymphocapillaria),
- lymphatic vessels,
- transport vessels,
- central lymph trunks and
- lymphatic ducts.

The **lymphatic capillaries** are similar in structure to the blood capillaries. However, the wall of the lymphatic capillaries is much

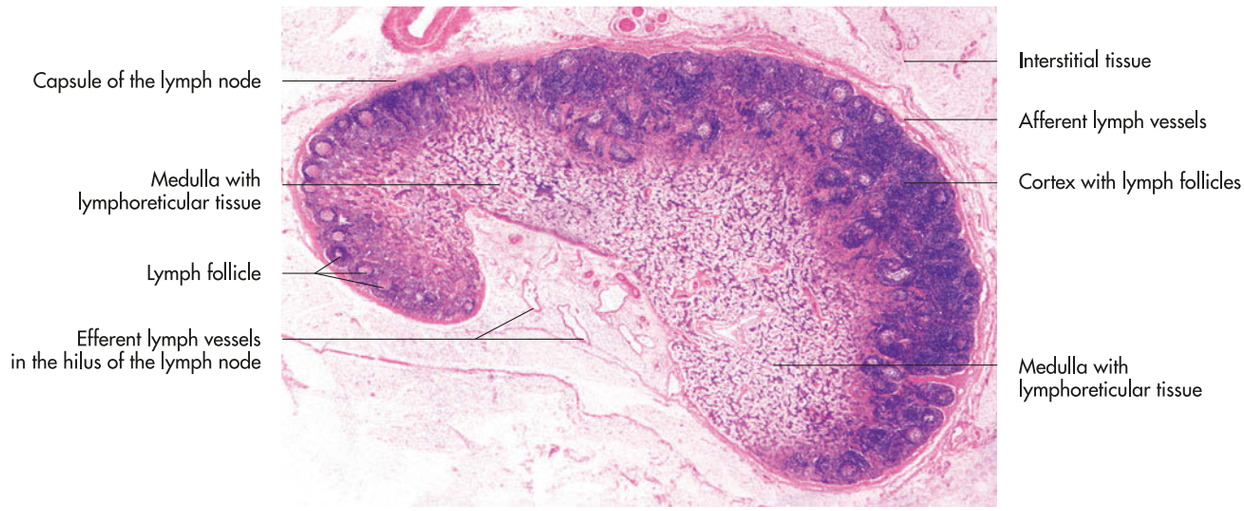

Fig. 1.52 Lymph node of a sheep (longitudinal section).

thinner and they do not possess valves. Close to the blood capillaries, the lymph capillaries form vessel nets (**retia lymphocapillaria**) within most body tissues. The capillaries merge to form the **lymphatic vessels** that collect the lymph from the plexuses. The lymphatic vessels have valves (valvulae lymphaticae) and thin walls, and they can build plexuses (plexus lymphaticus).

Transport vessels are able to contract due to the presence of a middle muscular layer. The contractions occur in the vessel segments between the valves, transporting the lymph in the proximal direction. The transport vessels run parallel to the veins and carry the lymph to the nearest **tributary (regional) lymph node**, thus referred to as the afferent lymph vessels (vas afferens) (▶ Fig. 1.52). The lymph enters the cortex of the lymph node through the afferent vessels, flows through the organ, and exits at the hilus through the efferent lymph vessel (vas efferens). One exception to this flow direction is found in the pig, where the vasa afferentia reach the lymph node at the hilus, and the vasa efferentia leave the cortex. Usually a second lymph node is found directly after the first to provide additional filtration and collection of lymph from numerous vessels. Multiple lymph nodes filtering lymph from the same area or tributary territory form **lymph centres**. **Central lymph vessels** collect the lymph from lymph centres in the abdomen and thorax. Lymph from the abdominal region initially flows through the **chyle cistern** (cisterna chyli) and finally into the **thoracic duct** (ductus thoracicus), where it is further transported.

The **ductus thoracicus** passes through the diaphragm alongside the aorta and continues dorsally through the thorax, entering the venous system at the left venous angle. The venous angle is formed by the convergence of the internal jugular and the left subclavian veins. The lymph drainage from the head and throat occurs through the two branches of the **tracheal trunk**, which unite and empty into the venous angle as well. Lymph vessels are not present in epithelial tissue, in the central nervous system, in the dental pulp, in bone, in cartilage or in the placenta.

1.6 General anatomy of the nervous system (systema nervosum)

H.-G. Liebich and H. E. König

The nervous system, along with the endocrine and immune systems and the sensory organs, is responsible for receiving various stimuli and coordinating the reactions of the organism. The nervous system receives stimuli that affect the body surface and/or the insides. The stimuli cause impulses that are registered, transmitted, processed and answered in the form of passive or active reactions. Thus, the nervous sytem enables the body to interact, adapt and react to the environment.

In simple organisms, this function is completely realised by individual sensory cells. These cells are stimulated by the environment and send the resulting impulse through a cell process directly to a muscle or gland cell. Sensory cells with processes that are responsible only for impulse transmission can still be found in domestic animals, – for example in the olfactory epithelium. In the rest of the body, **neurons** and their accompanying **glial structures** (glia cells, gliocytes) transmit the impulse, sometimes over quite a distance, from the **sensory cell (receptor cell)** to an **organ of response** (e.g. muscle cell or gland cell).

A **network of nerves** connects all organs of the body. This network is comprised of nerve tissue, which can be classified according to function or morphology. This classification is purely didactic; in fact the nervous system builds a **single functional unit**.

Morphological classification divides the nervous system according to location into a **central** (systema nervosum centrale) and a **peripheral system** (systema nervosum periphericum). The **central nervous system** (CNS) includes the brain (encephalon) and the spinal cord (medulla spinalis). The spinal cord connects the CNS to the remaining parts of the organism or to the **peripheral nervous system** (PNS).

Functional classification differentiates between the **somatic (cerebrospinal) nervous system**, which innervates structures under conscious control (e.g. locomotor system), and the **auto-**

nomic (vegetative) nervous system. The autonomic nervous system functions involuntarily and remains beyond the conscious control of the organism. This system innervates the internal organs, the blood vessels, and the glands. This system assumes the control and coordination of the internal organs; for more details see Chapter 15 "Nervous system" (p. 515).

1.6.1 Functions of the nervous system

The functions of the nervous system are divided as follows:

Sensory functions:

- **exteroceptive sensibility** (exteroceptors register stimuli from the environment as in hearing, sight, taste, heat, cold, pressure, pains, etc.),
- **proprioceptive sensibility** (proprioceptors are concerned with stance and position of the joints and muscles),
- **enteroceptors** react to stretch stimuli in hollow organs, blood pressure (baroreceptors) or the blood pH (chemoreceptors), and
- **vegetative (visceral) sensibility**.

Motor functions:

- **somatomotorics** (body motorics) and
- **visceromotorics** (motorics of the internal organs).

The **sensory functions** of the nervous system register and react to various types of stimuli. Sensory receptors monitor the external and internal environments. **Exteroceptive sensibility** involves stimuli from the surrounding environment that are registered through the skin, mucosa or sense organs. Information on the stance and position of the body is elicited by the **proprioceptive sensibility**. The organs responsible for receiving and transmitting this information are receptors found in the tendons and muscles. In this case, the receptor and effector organs are identical, for example the stretch mechanism of the muscle spindle. The system that transmits stimuli originating in the blood vessels or the internal organs to vegetative centers is referred to as the **vegetative (visceral) sensibility**.

The **motoric functions** of the nervous system are responsible for coordinating movement. **Somatomotorics** include all movements of the striated muscles that are under **conscious control**, and these movements are usually the result of environmental stimuli. Conversely, **visceromotorics** include all movements of the smooth muscles that are controlled **autonomously (subconsciously)**.

These **functions of the nervous system** are intricately linked. For example, a stimulus from the environment (exteroceptive stimulus) is translated by a **sensory receptor** into a nerve impulse. This impulse is carried by afferent sensory nerves to the central nervous system (CNS) and coordinated in the central nuclei. The stimulus is processed and answered in the form of a nerve impulse, which travels over **efferent motor nerves** to the musculature. The muscular reaction is controlled and regulated through feedback (**proprioceptive stimulus**) to the CNS in the form of a nerve impulse carried by sensory nerves.

The individual not only reacts to the environment but also interacts spontaneously with it. A spontaneous movement originating as an idea in the CNS is sent as a nerve impulse through efferent nerves and is registered by sensory organs. The sensory organs send a feedback signal to the CNS reporting if the movement was successfully completed or not. This feedback is referred to as a **reference**. If the movement was accomplished, then the CNS sends inhibiting impulses stopping the movement. If the reference is unsatisfactory, the CNS sends signals to enhance the movement. Countless excitatory circuits in the body build the foundation of the nervous system.

1.6.2 Architecture and structure of the nervous system

Understanding the architecture of the nervous system is difficult without the knowledge of some basic terminology. Further detailed information can be found in histology, neurophysiology, or neuroanatomy textbooks.

The nervous system follows a common structural design, which can be classified functionally and structurally into different sections:

- signal registration (sensory receptors),
- signal transmission (afferent nerve fibres),
- central processing of information,
- stimulus response (efferent nerve fibres) and
- reaction of the effector organ (muscle, gland).

Sensory receptors are macromolecules on the surface of receptor cells. Sensory receptor excitation occurs through mechanical, chemical, or thermal stimuli, as well as light and electrochemical stimuli (**receptorpotential**). The receptors are classified as **mechano-**, **chemo-**, **or photoreceptors**. Stimuli occur in countless forms and qualities and are received by a wide **spectrum of sensory cells**. Two types of sensory cells can be distinguished:

- **primary sensory cells**: the receptor is located on the surface of the **nerve cell**, and
- **secondary sensory cells**: the receptor is located on **modified epithelial cells** (e.g. hair cells of the inner ear and sensory cells in the taste buds).

Primary cells are found in the olfactory epithelium, as rods and cones in the retina, and as free nerve endings. Other examples of primary sensory cells are the encapsulated nerve endings, which are ends of sensory processes enclosed in specialised structures. For example, Meissner's corpuscle is a nerve ending wrapped in mesodermal cells located in the dermis of the skin. It responds to touch. The corpuscle of Ruffini, responsive to warmth, and the end bulb of Krause, responsive to cold, are other encapsulated receptors located in the dermis. Pacinian corpuscles (corpuscles of Vater-Pacini) are located in the skin, joints, and deep tissues of the body. They respond to pressure.

Receptors of deep sensibility, located in the tendons, the muscles or ligaments, and the internal organs are always **primary sensory cells**. Receptor or sensory cells can combine with other such cells to form an **organ**, in this case, a **sensory organ** (e.g. eye, ear, vestibular apparatus for balance, taste and olfactory organs).

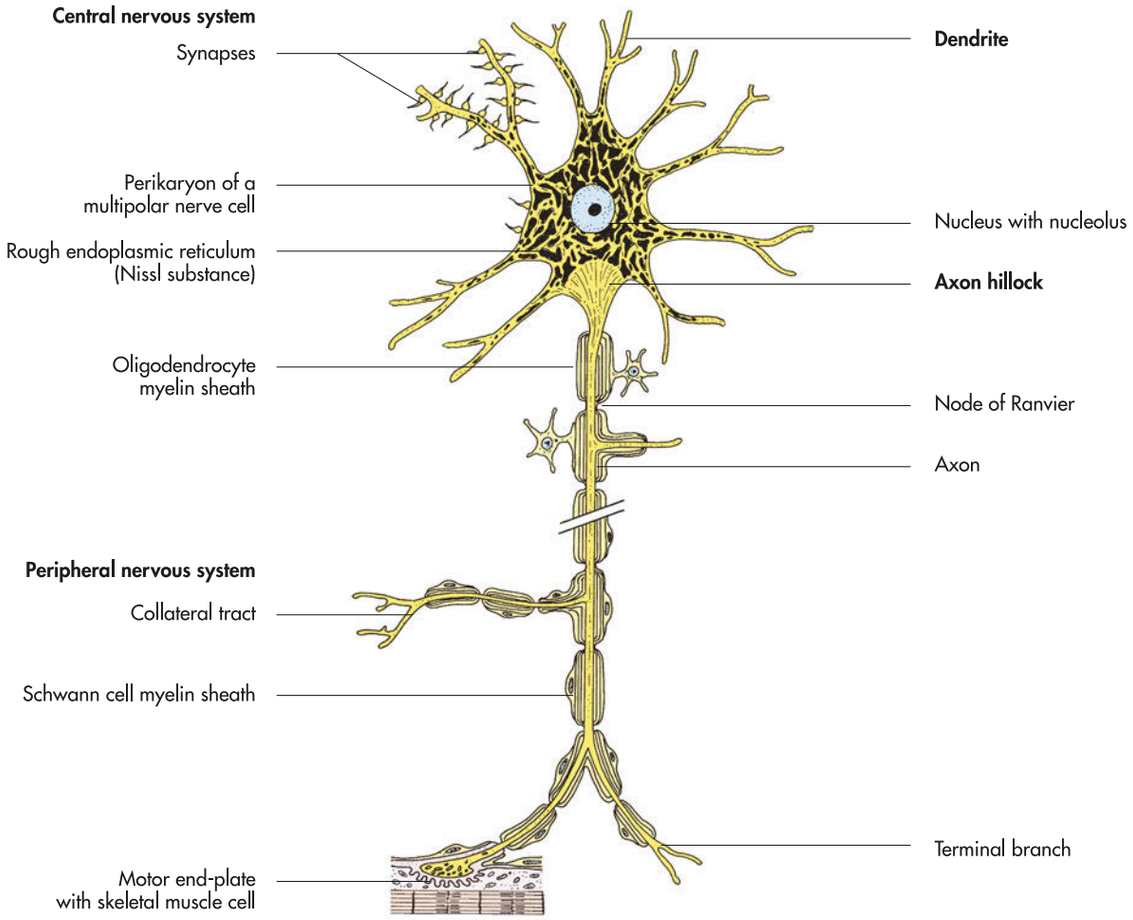

Fig. 1.53 Motor neuron (Nissl staining) with the central perikaryon, a peripheral nerve fibre and a motor end-plate on a muscle cell (schematic).

1.6.3 Nerve tissue (textus nervosus)

The nerve tissue is the basic element that forms the various parts of the nerve system previously mentioned. Nerve tissue originates from the **neuroectodermis**. Cells found in nerve tissue are:

- **nerve cells** (**ganglion cells**, **neurocytes**, **neurons**) as sensory or receptor cells and
- **glial cells** (**gliocytes**) as protectors and suppliers of nerve cells.

Neurons

Neurons vary greatly in function and structure. There is a distinction between:

- **multipolar neurons**, which send impulses to non-neuronal effector cells (**muscle or gland cells**) and induce activity (**efferent**, **motor neurons**),
- **pseudo-unipolar neurons**, which receive stimuli and send them on to higher centers, (**afferent**, **sensible neurons**) and
- **bipolar neurons**, which form a network to connect neurons over short and long distances (**interneurons**).

The **neuron** is the smallest functional unit of the nerve system. Structurally, it contains a **cell body** (neuroplasma, soma, perikaryon) and **various numbers of processes** (dendrites and axons) of different lengths and degrees of branching. Dendrites conduct a nerve impulse towards the cell body (afferent stimuli transmission), and **axons** conduct the nerve impulse towards the periphery (efferent stimuli transmission) (▶ Fig. 1.53 and ▶ Fig. 1.54). In the central nervous system, **interneurons** make up a large percentage of the total nervous tissue. The brain consists of a great variety of nerve cells. One example is the **Purkinje cells** of the cerebellum. A greater distance separates the neurons in the brain than those in the periphery due to the intricate neuron network. The **neuropil** is the area between the perikaryons of the neurons containing the dendrites and axons.

Neurons are seldom individually found; rather, they usually form bunched networks of many cells. A **ganglion** is such a network of neurons located in the periphery. Each ganglion is responsible for innervating a certain section of the periphery and for communicating with higher centres of nerve control. Phylogenetically, vertebrates developed a **complex centralisation of ganglions**, which led to the formation of the central nervous system as the conduction and coordination system of the body.

Glial cells (gliocytes, neuroglia)

Neurons require other cells for nourishment, support and insulation. All types of **glial cells** or **neuroglia** bind together nervous tissue, but are usually specialiced for certain functions. Glial cells do not transmit impulses, but rather assume trophic functions in the central nervous system for the neurons. They form the blood-brain barrier and are situated between the capillaries and the neurons.

In the brain, **macroglia cells** (**astrocytes**) (▶ Fig. 1.55) nourish the neurons by exchanging metabolic substances between capillaries and neurons. These cells also aid nerve impulse conduction by building an insulating layer around the neurons. Other glial cells, the microglia, engulf foreign material, thus providing a non-specific cellular immune defence mechanism to protect the neurons. Specialised **microglia cells** in the spinal cord, the **oligodendroglia**, compose the myelin sheath that provides insulation for the neurons. The **ependymal cells** line the ventricles of the brain and the central canal (canalis centralis) of the spinal cord.

The **Schwann cells** assume the functions of the oligodendroglia cells in the peripheral nervous system. Peripheral nerve fibres are metabolically supported by the Schwann cells and are protected by connective tissue sheaths.

1.6.4 Central nervous system (systema nervosum centrale, CNS)

The central nervous system primarily coordinates voluntary and autonomic functions of the organs that enable an organism to survive in its environment. It includes theis **spinal cord** (medulla spinalis) and the **brain** (encephalon). Both structures arise from the embryonic neural tube; see Chapter 15 “Nervous system” (p. 515).

Within the anterior neural tube, three embryonic regions of the brain differentiate into the **prosencephalon**, **mesencephalon** and **rhombencephalon**.

These give rise to three regions of the adult brain, the forebrain, midbrain and hindbrain. In further embryonic development, the **prosencephalon** differentiates to form the rostral **endbrain** (telencephalon) with two rostrolateral ventricles and the caudal diencephalon. The **rhombencephalon** differentiates into the **myelencephalon** (medulla oblongata) and the **metencephalon**, which includes the cerebellum. The brain is bilaterally symmetric and is protected by a bony skeleton, namely the skull and the vertebrae.

The brain encloses a system of connected cavities consisting of **four ventricles** and **a central canal**. These cavities within the brain are filled with cerebrospinal fluid (liquor cerebrospinalis).

Approximately 100 billion neurons are present in the CNS, including the interneurons and the perikaryons of the motor neurons from the body’s cerebrospinal (somatic) nerve system. The neurons are highly specialised structurally and functionally and have **lost their ability to divide**. New neurons develop from precursor cells, the neuroblasts. Once a neuron is no longer functional, it cannot be replaced. With intensive training, the loss of neuronal function due to small injuries can partly be regained by the neogenesis of neuron network.

The **interneurons** synapse partly with the perikaryon (soma) of a neuron and partly with dendrites. It is estimated that one neuron can have as many as 10 000 interneuronal connections with other neurons. The interneurons form a net, connecting practically all regions of the brain to one another. The assumption that each part of the brain (nucleus) is solely responsible for a single function has been revised in light of the extreme interconnectivity of the neurons. These parts of the brain or nuclei are also controlled by higher functional circuits.

The central nervous system is comprised of **various types of nerve tissue**:

- all **interneurons**,
- the **motor neurons** of the cerebrospinal, voluntary nerve system,
- the central part of the **axons of sensory neurons** and
- **preganglionic motor neurons** of the autonomic, vegetative nervous system.

Clusters of perikaryons with similar functions are grouped in **complexes called nuclei**, where the perikaryons are connected to afferent dendrites through many synapses. These clusters are seen as grey-rose coloured areas in a cross section of the freshly prepared brain or spinal cord. For this reason, this type of nerve tissue is referred to as **grey matter** (substantia grisea). Between these centres in the CNS axons are communicating that are sheathed in **myelin** (myelinated nerves). The myelin tends to be white and this type of nervous tissue is referred to as the **white matter** (substantia alba).

Grey matter (substantia grisea)

The grey matter forms the nuclei in the brain, as well as the cortex of the cerebrum and cerebellum, where it is connected to the ventricles through an expansive layer of ependymal cells. It is also located in the middle of the spinal cord, where in cross section it resembles the form of a butterfly or an “H”. The nuclei in the grey matter can be classified according to the:

- **form of the neurons** (e.g. multipolar pyramidal cells or granular cells and Purkinje cells in the cerebellum),
- **intrinsic neurons** (short, unmyelinated axons within a nucleus),
- **projection neurons** (long, myelinated axons of the white substance tracts),
- **type of nerve impulse** (excitatory or inhibitory neurons) and
- **type of neurotransmitter** or **neuromodulator** (e.g. cholinergic neurons, noradrenergic neurons).

The term nucleus for a cluster of neurons with similar function can be replaced by other terms such as **substantia** (e.g. substantia nigra), **formatio** (e.g. formatio reticularis) and **corpus** (e.g. corpus mammillare). The CNS is comprised of far more glial cells than neurons. It is estimated that glial cells are ten times more abundant, so they are the dominant cell type in the CNS, also making them the most common cell in the CNS. Glial cells retain their ability to divide lifelong, making them the most likely cell type to form tumours.

Protoplasmatic astrocytes are star-like in appearance due to their many filament-like, branched processes. They form cytoplasmic connections between neurons and capillaries, transporting metabolic substrates to the neurons. Additionally, they store transmitter precursors and control the extravasal ion concentrations. Astrocytes also build the outer layer of the cortex (glia limitans).

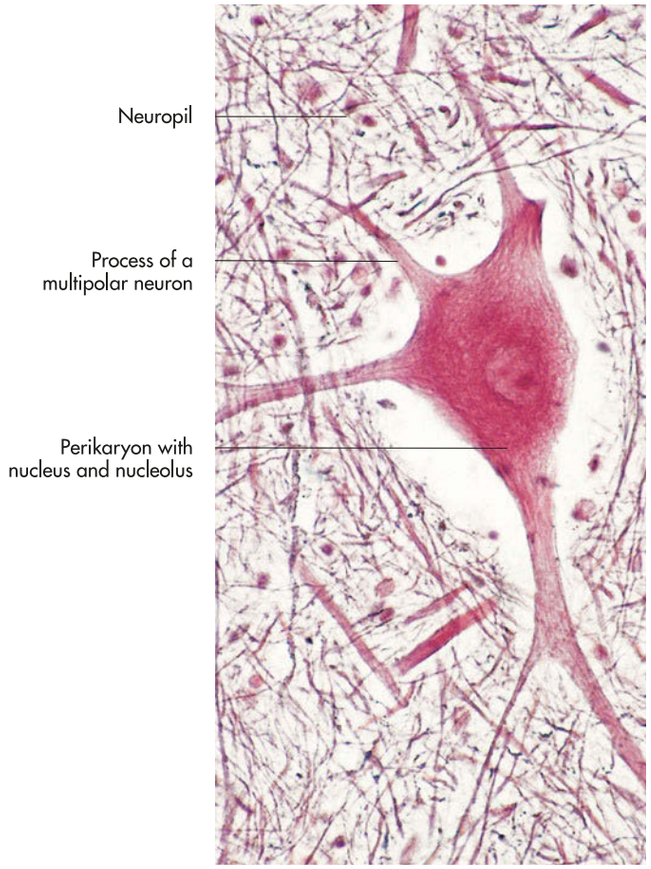

Fig. 1.54 Multipolar neuron in the spinal cord with neurofibrillary inclusions (histological section, Bodian staining).

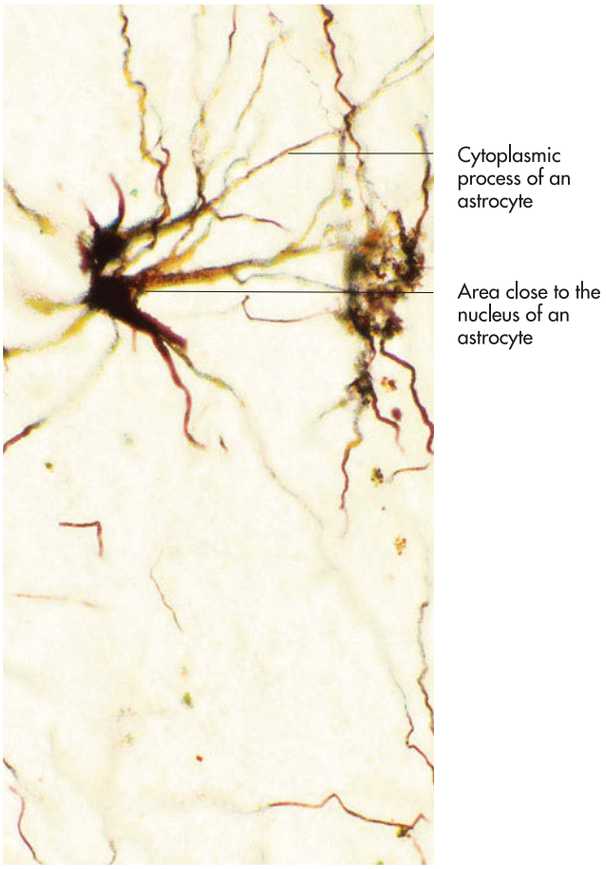

Fig. 1.55 Microglia of the spinal cord (histological section, silver staining).

White matter (substantia alba)

The white matter includes nerve tracts that not only connect central nuclei within the CNS, but also connect parts of the CNS with the periphery. It consists mostly of interneuronal axons, but also sensory nerves. The **white appearance** is due to the presence of the **myelin sheaths** around the nerve processes formed from the **oligodendroglia**. Also found in the white matter are the **fibrillary astrocytes** that not only form supportive tissue in the CNS but also connect neurons and capillaries with their multiple, mostly unbranched processes. The forms of various central nerve fibres are designated as follows:

- **tract**, a central nerve fibre with a definite beginning and end (tractus corticospinalis),
- **lemniscus**, a tract following a spiral course,
- **decussatio (crossing)**, a tract that switches to the other side of the body,
- **radiatio**, a tract spreading radially,
- **funiculus**, a compact tract,
- **fasciculus**, a narrow tract, and
- **commissura**, a tract connecting the right and left sides of the CNS.

The white matter surrounds the grey matter in the spinal cord and is made up of tracts from and to the brain.

1.6.5 Peripheral nervous system (systema nervosum peripheric um, PNS)

The peripheral nervous system connects the CNS to the organs of the body. It includes the **paired cranial** and **spinal nerves**. The spinal nerves sequentially arise from the spinal cord and are named according to their association with regions of the vertebral column (cervical, thoracic, lumbar, sacral). The PNS is comprised of neurons and ganglions. Like the nuclei in the CNS, ganglions are clusters of perkaryons. The tracts of the **peripheral nervous system are the nerves**.

Nerves (nervi, neurons)

The nerves are the nerve processes or fibres of the neurons whose perikaryons (soma) lie in the CNS (brain or spinal cord) or in the spinal ganglions; see Chapter 15 “Nervous system” (p. 515). Nerve fibres differ in diameter, in the thickness of the myelin sheath, and in the interval length of the nodes of Ranvier. Bundles of nerve fibres are enclosed in connective tissue sheaths (endo-, peri- and epineurium) that also provide scaffolding for the blood vessels (vasa nervorum) (▶ Fig. 1.56).

Every nerve fibre is in its entirety the process of a **single neuron**. With the process, a neuron can reach up to 2 meters in length (e.g. the left n. laryngeus recurrens of the horse). Nerves

connect the organs and the CNS to one another. The term peripheral nerves comprises of:
- efferent (axonal, motor) nerves,
- afferent (dendritic, sensory) nerves and
- peripheral glial cells (Schwann cells), which form the myelin sheaths.

The nerve fibres always transmit an impulse in **only one direction**. An **efferent** (Latin: carrying away) **nerve** conducts impulses from the CNS to the PNS (centrifugal direction, towards the periphery). These neurons are also referred to as **motor neurons**, because they carry the impulse to an effector organ, namely the muscles. The motor neuron nuclei of the peripheral nerves lie in the ventral horn of the grey matter in the spinal cord (spinal nerve) and in the grey matter within the brain stem (cranial nerves). Each muscle fibre (cell) is innervated by a single motor neuron.

Afferent (Latin: carrying towards) **nerves** conduct impulses from the **nerve endings** or **sensory cells** (receptor cells) of the PNS to the CNS (in a centripetal direction or towards the centre). As in the central nervous system the impulse or nerve stimulus is registered as a conscious perception or sensation, the neuron is classified as a **sensory neuron**.

Most nerves are so-called **mixed nerves** because they include not only motor and sensory fibre qualities, but also nerve fibres of the vegetative, autonomic (sympathetic and parasympathetic) nervous system.

Motor and sensory roots

The motor output roots are the efferent nerve fibres that leave the spinal cord through the ventral roots of the spinal cord grey matter. Their nerve stimuli are carried to the skeletal musculature. Conversely, sensory input originating on the body surface or from the organs enters the CNS through the dorsal roots of the spinal nerves. These nerve bundles always pass through a sensory, dorsal root ganglion (ganglion spinale) and enter the CNS as a sensory root.

In a reflex arc, the impulse is directly transmitted from a sensory neuron to a motor neuron without first travelling to the brain. Reflex arcs exist as mono- or polysynaptic loops.

Ganglions (ganglia)

A ganglion (▶ Fig. 1.57) is a cluster of nerve cell bodies (perikaryons) with similar functions located outside of the CNS. There are two types of ganglions:
- **sensory ganglia**, which include the perikaryon of the sensory nerves, and
- **vegetative ganglia**, which include the postganglionic motor neurons of the vegetative nervous system.

All **spinal ganglia** contain only **sensory neurons** and can be located as a swelling within the **sensory dorsal roots** (radices dorsales). These sensory ganglia are found on both sides of the spinal cord close to the intervertebral foramen. The cranial nerves (V and VII–X) also contain sensory ganglia that are equivalent to the spinal ganglia. Most of the neurons tend to be pseudounipolar and are sheathed in myelin by Schwann cells.

Vegetative ganglia are part of the autonomic nervous system and are postganglionic motor neurons. They can be classified as:
- **sympathetic chain ganglia** (truncus sympathicus),
- **prevertebral ganglia** (2nd neuron of the sympathetic tract for the abdominal organs),
- **parasympathetic ganglia** in the area of the head and
- **intramural ganglia** in the wall of the alimentary canal (plexus nervorum submucosus, plexus nervorum myentericus).

The vegetative ganglia are nerve networks whose multipolar neurons synapse with motor neurons or collateral tracts of the afferent fibres and the internal organs. The motor neurons of the vegetative ganglia innervate the smooth muscle cells of the organs, blood vessels, and organ-specific glands.

Somatic (voluntary) nervous system

The somatic nervous system is also referred to as the voluntary or animalistic nervous system. This system transmits nerve impulses over sensory neurons from the body surface or from the locomotor system to the CNS. The responses to these stimuli can vary greatly in type or quality and include the:
- innate reflex and
- acquired reflex.

A **reflex** exhibits the simplest level of control within the nervous system. The nerve impulse of an **innate reflex** is triggered by a stimulus (e.g. muscle or tendon stretching) and carried by an afferent, sensory nerve fibre. The response to this stimulus occurs through a simple reflex arc (stretch or tendon reflex) ending in an efferent motor neuron. This type of reflex is a **monosynaptic reflex** which occurs unconsciously and quickly, and the response is always the same (e.g. patellar reflex, achilles tendon reflex). **Polysynaptic reflex arcs** occur when more than two neurons are involved in the response to the stimulus, meaning the impulse is transmitted over more than two synapses. **Acquired reflexes** are learned reflexes, such as the salivation reflex in Pavlov's dogs.

Vegetative (autonomic) nervous system

The vegetative nervous system regulates the internal environment of the body. It presides over the visceral activity of the organs – for example, respiration, digestion, circulation of the blood and sexual functions. In addition, pressure or temperature changes as well as oxygen levels in the blood are registered by the viscerosensory ganglia (glomus caroticum, glomus aorticum), for further information see Chapter 15 "Nervous system" (p. 515). The vegetative nervous system is divided into the:
- sympathetic nervous system (pars sympathica, sympathicus),
- parasympathetic nervous system (pars parasympathica, parasympathicus) and
- enteric nervous system.

The sympathicus and parasympathicus are two contrasting, **antagonistic systems** of control over visceral activity.

The **nuclei of the sympathicus** are present only in the thoracic and lumbar regions of the **spinal cord** (thoracolumbar outflow). The sympathic axons leave the ventral horn of the spinal cord together with motor neurons and continue to the sympathetic chain. The **sympathetic chain** (truncus sympathicus, paired para-

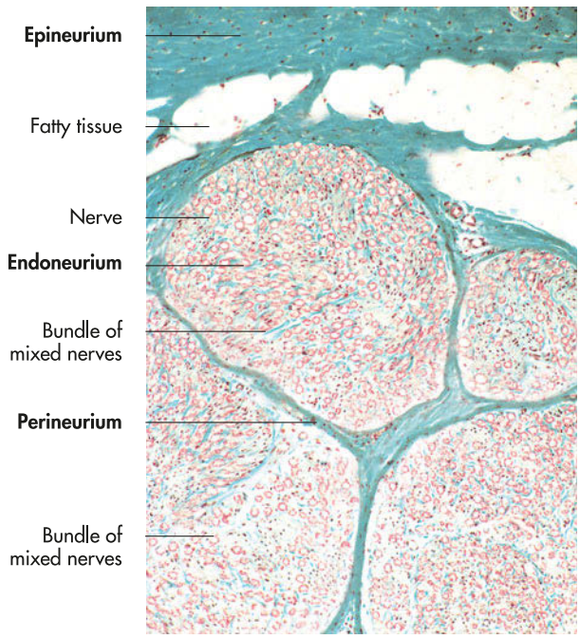

Fig. 1.56 Bundles of mixed nerves enclosed in connective tissue sheaths (endo-, peri- and epineurium) (histological section, Goldner staining).

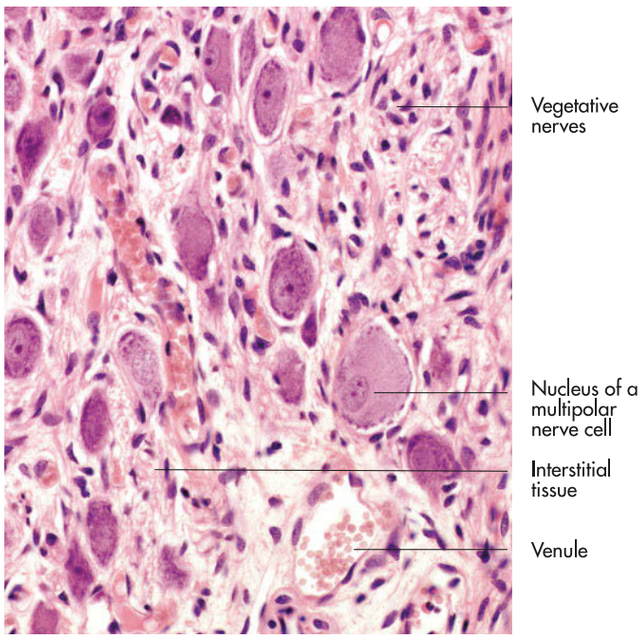

Fig. 1.57 Vegetative ganglion (histological section, hematoxylin and eosin staining).

vertebral sympathetic chain ganglia) is a series of linked sympathetic ganglia adjacent and parallel to each side of the **vertebral column in the thoracolumbar region**. From here, the sympathetic nerve fibre bundles pass through unpaired ganglions to the organs.

The **sympathicus activates vital functions** (catabolic function):
- increases blood pressure,
- increases heart and respiratory rates,
- constricts the blood vessels (vasoconstriction, without heart),
- mobilises glucose (glycolysis),
- increases perspiration, raises hair, dilates the pupils and
- inhibits activity of the alimentary canal.

The sympathicus is said to be adrenergic because the neurotransmitters released during stimulation are noradrenaline and neuropeptide Y. Pharmacologically, the sympathicus can be stimulated by sympathomimetic drugs and inhibited by sympatholytic drugs; β-blockers decrease the heart rate and lower blood pressure through vasodilation.

The **parasympathicus** antagonises the sympathicus in that it restores the body to a restful or idle state. It contains two separate nuclei: cranial nuclei in the **brain stem** (cranial parasympathicus) and caudal nuclei in the **sacral region of the spinal cord** (pelvic parasympathicus). The majority of parasympathetic nerve fibres are contained in the **cranial nerve X** (n. vagus).

The postganglionic neurons are located in the parasympathetic ganglia in the head region as well as in the prevertebral and enteric ganglia of the organs. The **parasympathicus** inhibits the body's use of energy (**trophotropic functions**) by:
- decreasing heart and respiratory rates to their basal values,
- constricting the bronchies,
- constricting the pupils,
- stimulating digestion and
- increasing metabolism.

The parasympathicus is said to be cholinergic because the main neurotransmitter released is acetylcholine. One cotransmitter is vasoactive intestinal peptide, or VIP. The most commonly known parasympatholytic agent, an inhibitor of the parasympathicus, is atropin. Locally applied to the eyes, atropin causes dilatation of the pupils. The **enteric system** is located in the wall of the alimentary canal. It is independent of but can be modified by the sympathetic and parasympathetic nervous systems. This system contains two nerve networks:
- submucosal nerve plexus (plexus nervorum submucosus, Meissner plexus) in the tela submucosa and
- myenteric nerve plexus (plexus nervorum myentericus, Auerbach plexus) in the tunica muscularis.

In these nerve networks, the multipolar neurons interconnect and mingle to form woven patches of nerve processes, termed plexuses (plexus entericus). The Meissner plexus controls resorption and secretion in the wall of the alimentary canal along with the sympathetic and parasympathetic plexus. The Auerbach plexus regulates intestinal motility. The nonmyelinated nerve fibres synapse with as many as 107 or 108 interneurons. The neurotransmitters of the enteric system are the substances noradrenaline, serotonin and acetylcholine.

1.6.6 Nerve transmission of information

Synapses

Complex systems of neurons are dependent on junctions capable of transmitting nerve impulses between neurons, muscle cells and glandular cells. These gaps between the various cells involved in nerve signalling are termed **synapses** and play an extremely important role in the transmission of impulses. One neuron can be equipped with only a few hundred synapses or with far more than a thousand. Synapses break up a network of neurons into functional units responsible for processing information. Without synapses, a nerve impulse could spread throughout an entire network of interconnected neurons, inevitably causing an overload of information or signals. Neighboring cells exchange information through synapses functioning as inhibitors or enhancers (inhibitory/excitatory synapses).

Information travelling through the nervous system is transmitted in the form of electrical and chemical signals. An electrical signal is propagated by decreasing the membrane potential in the neurons (electrical synapse). A chemical signal is propagated through the release of neurotransmitters at the synapse (e.g. acetylcholine, noradrenalin, dopamin, serotonin). A synapse is comprised of the following structures:

- **presynaptic neuron** (with the bulbous corpuscle) with the presynaptic membrane,
- **synaptic gap** and
- **postsynaptic neuron** with the postsynaptic membrane.

The synaptic bulbous corpuscle varies according to the type of tissue in which it is found:

- neurosensory synapses (e.g. sensory nerves of the ears or tongue),
- neuroglandular synapses (e.g. endocrine and exocrine organs),
- interneuronal synapses between the perikarya, dendrites or axons of neurons and
- neuromuscular synapses (motor end plate).

Neuroglandular synapses are also called neuroepithelial synapses. Together with hormones, these synapses enhance or inhibit glandular secretion. For example, parasympathetic nerve fibres promote salivation, whereas sympathetic fibres inhibit it.

Neuromuscular synapses are responsible for the transmission of nerve impulses to skeletal muscle. Acetylcholine functions as the neurotransmitter, which binds to postsynaptic receptors, causing depolarisation of the cell membrane (**excitatory synapse**). The axon of the motor neuron diverges into many smaller, collateral branches, forming bulbous corpuscles or **boutons at their ends**. The neurotransmitter is stored in vesicles located at the ends of the presynaptic neurons. Upon arrival of an electrical nerve impulse, the neurotransmitter is released into the synapse through exocytosis. The transport vesicle fuses with the postsynaptic membrane of the muscle cell. This reaction is high dependent on the presence of calcium. Specific toxins inhibit this specific interaction (e.g. tetanus toxin and botulin neurotoxin).

The most important **neurotransmitters** are **acetylcholin (cholinergic receptors)** and **noradrenalin (adrenergic receptors)**. **Cholinergic receptors** are found in the motor end-plates, in all parasympathetic synapses, in the postganglionic synapses of the sweat glands, in the arteriovenous anastomoses and in the CNS. Blocking the cholinergic receptors, for example with curare, causes total relaxation of the skeletal muscle. This mechanism is taken advantage of in anaesthetics.

Adrenergic receptors are divided into α- and β-receptors. The stimulation of α1-receptors leads to vasoconstriction and the stimulation of α2-receptors to vasodilatation. Activation of β1-receptors increases heart rate and intestinal motility whereas activation of β2-receptors inhibits the bronchus and smooth muscle. It is possible to block receptors with a substance (receptor blockers) that renders the neurotransmitters ineffective. So called β-receptor blockers inhibit the positive chronotropic effect of β1-receptors on the heart and are prescribed to treat high blood pressure.

Neuromodulators (cotransmitters, e.g. substance P, endorphine, neuropeptide Y, and somatostatin) influence the excitability of nerves over a longer time period. After stimulation, the neurotransmitter must be inactivated as quickly as possible to prevent an uncontrolled, permanent depolarisation of the postsynaptic neuron. Otherwise, the neurotransmitter accumulates in the synapse, and, in the case of a neuromuscular end plate, paralysis of the musculature can result. Inactivation of synaptic excitation occurs through one of three mechanisms: enzymes (e.g. acetylcholinase) break down the neurotransmitter in the synaptic gap; the transport vesicle is recycled; or the neighboring glial cells break down or inactivate the transmitter.

1.6.7 Barriers in the nervous system

Biological barriers exist in the nervous system to control the access of blood components to nerve tissue. Nerve tissue functions only within a well-controlled environment separate from the milieu of the periphery. However, a selective exchange of substances serving nutritional and detoxification purposes is indispensable to maintain nerve function. The barriers of the nervous system include the:

- blood-brain barrier,
- blood-liquor barrier and
- blood-nerve barrier.

The mechanisms that control the unique environment of the brain are collectively referred to as the **blood-brain barrier**. The blood-brain barrier strictly limits transport into the brain with both physical (tight junctions) and metabolic (enzymes) barriers. This barrier consists of endothelial cells of the capillaries, which allow the unhindered passage of certain (e.g. fat-soluble) substances only. Other substances are actively carried through this barrier by receptor-mediated transport (e.g. glucose or amino acids).

The **blood-liquor barrier** is formed by the epithelial cells of the choroid plexus (plexus choroideus) in the ventricles of the brain (ventriculi cerebri) and functions much like the blood-brain barrier. The ependymal cells, which line the ventricles, form a continuous sheet around the choroid plexus. The ependymal cells fold over onto themselves, forming the double-layered arachnoid membrane. Within this double layer is the subarachnoid space, which participates in liquor drainage.

A barrier present in the peripheral nervous system is referred to as the **blood-nerve barrier**. It is a semipermeable, diffusion barrier between the endoneurium and the capillaries of the vasa

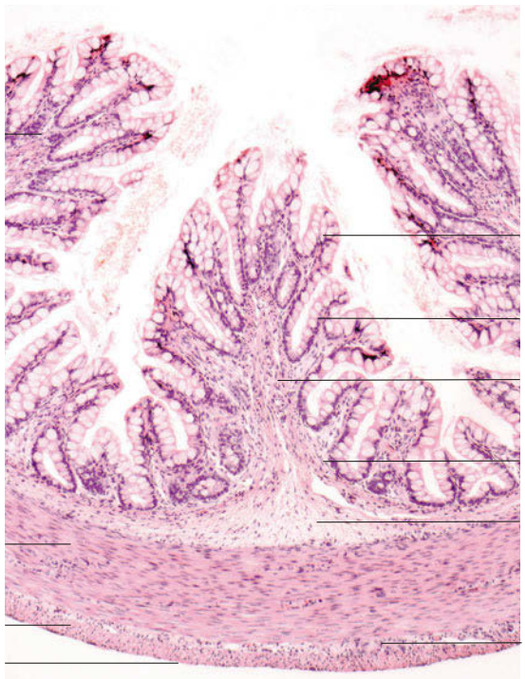

Fig. 1.58 Histological section of the colon of a swine.

nervorum, whose endothelial cells form tight junctions that establish the barrier. This barrier has been found to be relatively less effective within nerve roots, dorsal root ganglia, and autonomic ganglia than along the rest of the nerve.

1.7 General anatomy of the viscera

H.-G. Liebich and H. E. König

The **viscera** denotes the internal organs of the thoracic, abdominal and pelvic cavities, as well as the digestive and respiratory organs located in the head and neck regions. The viscera can be divided into the organs of the head (caput), neck (collum), thorax, abdomen and pelvis. **Splanchnology** (splanchnologia) is the study of the internal organs and is usually taught according to organ system. In contrast, topographical anatomy is concerned with a body region and the functions and interactions of the organs within that region. This fundamental knowledge is the basis for clinical anatomy; for more information see Chapter 20 "Topographical-clinical anatomy" (p. 685).

The digestive, respiratory and urogenital organs are basically canal systems that are referred to in the body as tracts (e.g. digestive tract). These organs are open to the body's surface through the mouth, nose, anus, vagina or urethra. These openings provide the possibility of non-invasive examinations of the internal organs (endoscopy). The individual organs differ in their location and structure and are responsible for a multitude of various functions. Despite these differences, the organs also display structural and functional similarities that justify a general overview of the different systems (▶ Fig. 1.58). In this respect, **basic anatomical terms** must be clarified, such as:

- visceral mucosa (tunica mucosa),
- visceral connective tissue (interstitium),
- visceral motility (tunica muscularis) and
- body cavities and their serous lining (tunica serosa).

1.7.1 Visceral mucosa

The lumen of most hollow organs is in one way or another connected to the external environment. The internal lining of such organs is a layer of muscosa (tunica mucosa, Latin "tunica" = tunic) that normally produces mucus (mucus). The linings of the circulatory and nervous systems are two exceptions, in that they do not produce mucus. Every mucosa is comprised of two layers:

- an epithelial lining on the internal surface of the organ (**epithelium**, epithelium mucosae) and
- an underlying layer of **loose connective tissue** (lamina propria mucosae, Latin "lamina" = sheet, plate and "proprius" = own).

Certain sections of organs also display a third, thin **layer of muscle cells** (lamina muscularis mucosae) beneath the lamina propria mucosae. One example is the alimentary canal.

Epithelium

Functions of the mucosa epithelium are protection and the absorption, resorption and secretion of substances. The **protective functions** include:

- protection against mechanical, chemical, thermal, or osmotic influences (e.g. in the digestive or urinary systems),
- protection against inhaled dust particles or suspended particles in the air, and
- protection against infectious agents (e.g. viruses, bacteria, parasites) and immune defense.

The mucosa is responsible for the **absorption** of substances. To increase the surface area capable of absorption, the mucosa forms villi, crypts, folds, or crests (e.g. longitudinal and tranverse folds of the intestinal mucosa, intestinal villi, ruminal papilla, reticulum crests). In addition to these structures, the apical cells on the free surface facing the lumen contain tiny, finger-like projections, the microvilli (e.g. in the small intestine and in the gallbladder). The microvilli are responsible for the resorption of water, small molecules, and ions.

The mucosa epithelium also secretes substances. It builds, stores, and secretes, for example, mucus and digestive enzymes into the lumen of the gastrointestinal tract. The epithelium is to a degree specialised, in that it contains organ-specific, differentiated, single epithelial cells called goblet cells, and gastric (glandulae gastricae) or intestinal (glandulae intestinales) glands. Multicellular glands (buccal, labial, pharyngeal, nasal, or tracheal glands) can produce large amounts of mucus when necessary, for example, for predigestion in the oral cavity. These glands are always located in connective tissue outside of the epithelium (exoepithelial), but are connected to the organ lumen through single or branched excretory ducts.

Exocrine secretion is the **release of substances** into an organ lumen or onto the surface of the body (Greek "éxo" = outside, "krínein" = to excrete). If the substance is secreted into a capillary network or locally into the surrounding connective tissue, then it is an **endocrine** (Greek "éndon" = inside) **secretion**. The substance internally secreted is a hormone (Greek "hormán" = to stimulate).

The gland cells are categorised on the basis of their structure, method of substance release, or the **composition of their secretion**. Different structures include (▶ Fig. 1.60):

- **tubular glands** with:
  - simple tubular glands (e.g. intestinal glands),
  - simple, coiled, tubular glands (e.g. sweat glands),
  - simple, branched glands with secretion ducts (e.g. stomach glands) and
  - composite, tubular glands with secretion ducts (e.g. glands of the small intestines);
- **acinous glands** (grapelike glands with a small lumen, Latin "acinus" = grape) with:
  - simple, branched acinous glands (e.g. sebaceous glands) and
  - composite acinous glands (e.g. pancreas, parotid salivary gland);
- **alveolar glands** (round glands with a wide lumen) with:
  - composite tubuloalveolar glands (e.g. mammary glands, accessory sex glands).

Glands are also grouped according to secretion composition:

- **mucous glands** produce a mucous substance (e.g. buccal glands),
- **serous glands** produce a watery substance (e.g. parotid salivary gland, lacrimal glands) and
- **mixed glands** contain both serous and mucous secretory units (e.g. sublingual glands).

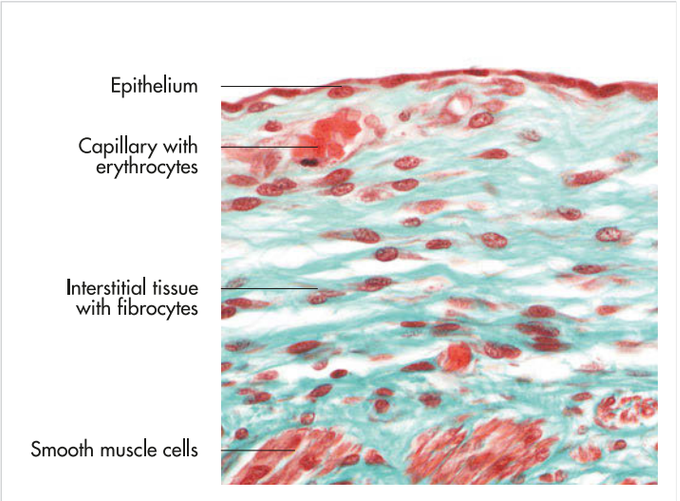

Fig. 1.59 Monocellular layer of the epithelium (Lamina epithelialis serosae) and the interstitial tissue (Lamina propria serosae).

Transport of the secreted substance is achieved through hydrostatic pressure, through the contractile myoepithelial (basket) cells, and through neighbouring smooth muscle cells, as well as through the mechanical power of the skeletal muscle (e.g. mastication muscles for transport of saliva).

Connective tissue layer of the epithelium

Every glandular epithelium rests upon a layer of connective tissue, the **mucous membrane proper** (lamina propria mucosae), which basically has three functions:

- transport of substances
- mechanical protection and
- specific and non-specific immune defense.

The mucous membrane proper contains vessels supplying the mucosa (blood and lymphatic vessels) as well as the nerve tracts innervating the mucosa (sensory and vegetative nerves). This layer is comprised of loose connective tissue containing delicate fibres of collagen bundles with elastic properties. Between the fibres, the spaces are filled with formless intercellular substance. The epithelium is free of blood vessels (except parts of the inner ear wall), so the capillaries of the mucous membrane proper are responsible for the metabolic supply of the epithelial cells. The capillaries also transport substances resorbed in the intestine (amino acids, carbohydrates). The lymphatic capillaries transfer the long-chain fatty acids resorbed in the intestine. Sensory nerve receptors are located in this layer and are responsible for tactile and taste sensations. The mucous membrane proper anchors the epithelium to underlying structures, for example on the palate or the tongue.

This layer can also contains immune cells (lymphocytes, macrophages), which play an important role in the non-specific and specific immune defence mechanisms (MALT, mucosa-associated lymphatic tissue). The immune cells are found as diffused single cells or as collections of cells that form solitary lymph nodules. Aggregates of such cells form the tonsils in the pharynx or the **Peyer's patches** in the intestine.

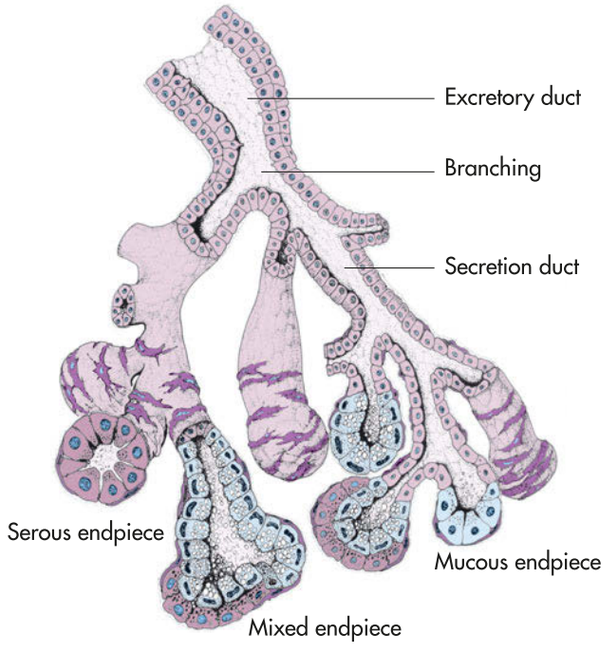

Fig. 1.60 Structure of composite tubuloalveolar glands with different forms of endpieces (schematic).

Muscle layer of the epithelium

In certain sections of the organ walls (e.g. in the alimentary canal), the epithelium (epithelium mucosae and lamina propria mucosae) includes a third layer, the **lamina muscularis mucosae**. This layer is comprised of smooth muscle cells responsible for the motility of the epithelium.

1.7.2 Visceral connective tissue

The connective tissue of the viscera fulfills a wide spectrum of functions. It forms an outer capsule that surrounds the organs, stabilises the form of the organs, and provides connective tissue paths for vessels and nerves. The high degree of flexibility provided by the connective tissue allows organs to adapt to changing amounts of content and permits frictionless movement between the organs. The sheer amount of connective tissue present in the viscera underscores its important functional and structural role. Usually, the importance of the connective tissue is first realised when function is reduced due to weakness or sickness. Two types of connective tissue can be found in one organ:

- the **non-specific connective tissue**, also referred to as the **stroma** (organ stroma) or **interstitial connective tissue** (interstitium), and
- the **organ-specific tissue**, called the **parenchyme** (organ parenchyme), which defines the function of an organ (liver parenchyme, kidney parenchyme).

Such organs are also referred to as **parenchymatous organs**. The **stroma** surrounds the parenchymal parts of the organ (single cells, cell clusters, epithelial bundles or cords, cell groups, cell trabeculae or cell plates, etc.) and encloses the vessels and nerves. It builds the lamina propria mucosae in the epithelium, the tunica adventitia on the outside of the organ as well as the **organ capsule** (kidney capsule, testicular capsule, liver and spleen capsule). The capsule is taut and often contains elastic fibres. Connecting tissue fibres originating in the capsule enter the parenchyme of the organs (i.e. spleen trabeculae, connective tissue septum in the testicles).

Vessels and nerve tracts enter an organ together at a certain point (**hilus**). At this point, the stroma of the organ becomes the **mesenterium**, which provides support for the continuation of the vessels and nerves.

Visceral motility

Visceral motility is responsible for transporting the contents of the different organs. Thus, it controls the amount of contents found in the organ at any time. Through contraction and dilatation mechanisms, the food bolus passes through the intestinal tract, the gallbladder secrets bile, urine is excreted, semen is transported and the uterus wall contracts during birth.

This motility is also responsible for the closing of sphincters, for example at the stomach exit (pylorus) or in the bladder. The diastole and systole of the heart can be understood as the motility of the circulatory system.

The muscle of the internal organs is usually smooth muscle tissue (visceral musculature) (▶ Fig. 1.58). This musculature is innervated by sympathetic and parasympathetic (vegetative-autonomous) nerves. The motility of the internal organs is peristaltic motion, which is controlled by vegetative autonomic nerve impulses. These nerve impulses can have stimulatory or inhibitory effects on the motility. Two exceptions are the heart muscle and the tongue, both of which are composed of striated muscle. The smooth muscle of the hollow, visceral organs is characteristically arranged. One differentiates a **tunica muscularis** with:

- an inner, circular layer of muscle cells (stratum circulare) and
- an outer, longitudinal layer of muscle cells (stratum longitudinale).

1.7.3 Functions of the viscera

The majority of the internal organs (viscera) are situated in the body cavities, in which very little free space remains. The flexible mesenteries and small, fluid-filled spaces between the organs reduce friction to a minimum, thus allowing the organs to glide freely against each other, for example, during breathing or the digestive process. The mesenteries secure the integrity of cavities, define spaces in which active organs operate more freely, and help sequester organs with conflicting activities. The freedom of movement of the visceral organs is essential for their function.

1.7.4 Body cavities and their serous lining

The body cavities are contained in the body trunk and, similar to the vertebrae, can be divided into three **different zones**:

- thorax,
- abdomen and
- pelvis.

At an early embryonic stage, the diaphragm develops from the perpendicular **septum transversum** and the neighboring, predisposed, **mesenchymal muscle**. The diaphragm separates the primary, single body cavity into the:

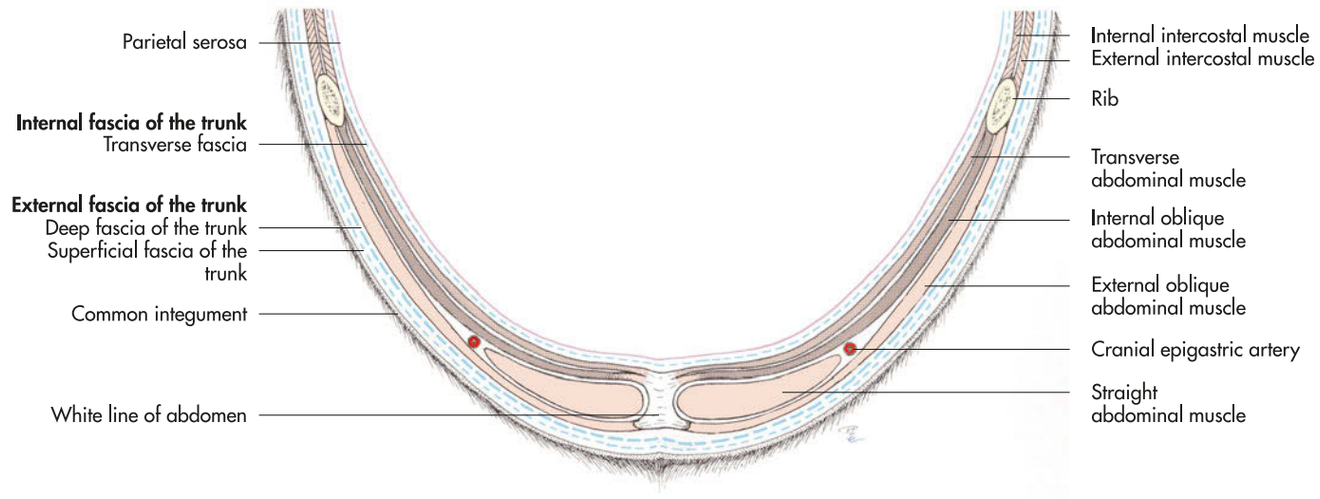

Fig. 1.61 Transverse cross section of the abdominal wall layers (schematic).

- **thoracic cavity** (cavum pectoris) and
- **abdominal cavity** (cavum abdominis), which remains connected to the
- **pelvic cavity** (cavum pelvis).

The thoracic and abdominal cavities communicate through **three openings**, the **caval foramen** (foramen venae cavae), the **oesophagal hiatus** (hiatus oesophageus), through which the oesophagus, the vagal nerve trunks and the oesophagal vessels pass, and the **aortic hiatus** (hiatus aorticus), through which the aorta, the thoracic duct and the azygos and hemiazygos veins pass. Between the dorsal edge of the diaphragmatic crus muscles and the psoas musculature, a small area remains filled with connective tissue, the **lumbocostal arch** (arcus lumbocostalis), through which the sympathetic trunk and splanchnic nerves pass on each side.

This area is a weak spot between the thoracic and abdominal cavities.

The **pelvic cavity** (cavum pelvis) is the caudal continuation of the abdominal cavity. Dividing these two cavities is the terminal line of the pelvis (linea terminalis), which extends from the sacral promontory, runs laterally through both arcuate lines of the ilia to unite on the cranial edge of the pubis.

The internal walls of the body cavities are structurally similar even though modifications occur according to region. The **layers of the walls** are as follows, beginning externally:

- superficial trunk fascia (fascia trunci externa),
- skeletal muscles,
- internal trunk fascia (fascia trunci interna) and the
- serous membrane (tunica serosa with tela subserosa).

Serous membranes line almost completely the body or serous cavities. There are **four serosal cavities**:

- the **left** and **right pleural cavities** (cavum pleurae sinistrum et dextrum),
- the **peritoneal cavity** (cavum peritonei) and
- the **pericardial cavity** (cavum pericardii) with the pericardium.

A serous membrane (tunica serosa) is comprised of a single layer of pavement epithelium (mesothelium = lamina epithelialis serosae) and an underlying (subepithelial) layer of connective tissue, the lamina propria serosae (▶ Fig. 1.59). The serous membrane is capable of **excreting** and **resorbing watery-serous fluids** and of **resorbing air** or **gaseous substances** (e.g. carbon dioxide after a laparoscopy). The serous membrane covers the outside of the organs and lines the inner walls of the body cavities (▶ Fig. 1.61), physiologically appearing **transparent**, **moist**, **smooth** and **shiny**.

The serous fluids contain not only a physiological buffer system, but also mesothelial cells and non-specific immune cells (pleural or peritoneal macrophages) that engulf foreign particles. The serous fluids, together with the mesothelial cells of the inner wall of the body cavities, function as a barrier. This function is extremely important clinically.

The **tela subserosa**, a layer of loose connective tissue, underlies the tunica serosa. This layer contains fat, blood and lymphatic vessels. A delicate network of nerve plexuses in the subepithelial layer (serosa parietalis) is sensitive to tactile, mechanical, thermal and chemical stimuli acting on the serous surfaces.

Between the serous membranes and the wall of the body cavities are narrow, fissure-like spaces formed by the tela subserosa. At the dorsal abdominal wall and at the floor of the pelvic cavity, this **retroserosal space** widens into the **retroperitoneal space**. Located in this space are the kidneys and both ureters (▶ Fig. 1.61). **Retroperitoneal** (behind the peritoneum) describes the location of organs situated in the retroperitoneal space and, therefore, covered only on one side with peritoneum. These organs can be surgically reached without opening the peritoneal cavity. **Peritoneal organs** that are completely covered by serous membranes are located intraperitoneally. The visceral organs located in the thorax that are covered by serous membranes on all sides are described as **intrapleural**.

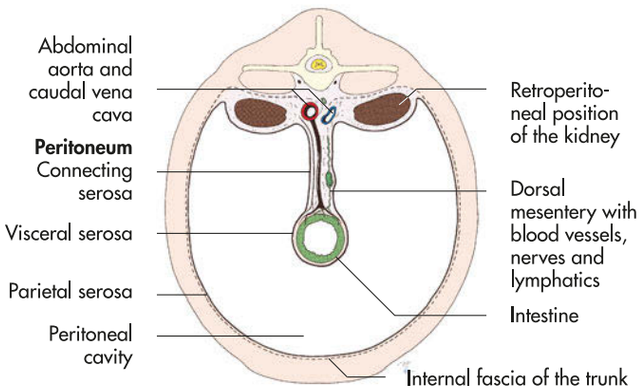

Fig. 1.62 Schematic illustration of the serous membranes as exemplified in the perineal cavity.

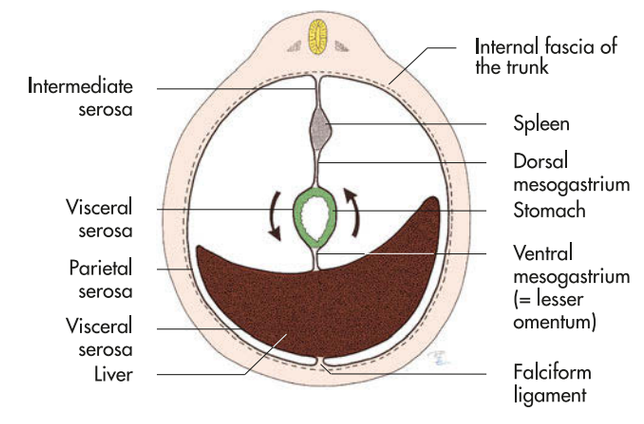

Fig. 1.63 Schematic illustration of the dorsal and ventral mesenteries in early embryonic development.

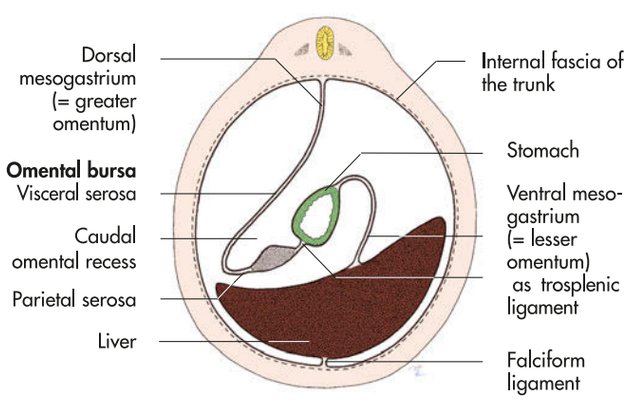

Fig. 1.64 Schematic illustration of the dorsal and ventral gastric mesenteries at an early embryonic stage with the development of the greater and lesser omentum.

The wall of the **serous cavities** (▶ Fig. 1.61 and ▶ Fig. 1.62) are divided into **three general sections**:

- **parietal serosa** (serosa or lamina parietalis) (= serosa of the wall),
- **connecting serosa** (serosa or lamina intermedia) (= mesentery, intermediate serosa) and
- **visceral serosa** (serosa or lamina visceralis) (= serosa of the organs).

The **parietal serosa** is the section of serous membrane that lines the inner wall of the body cavities. Sections covering the organs are named with the prefix "peri" and the Greek name of the organ, for example pericardium or periorchium. In contrast to the other serous membranes, the parietal serosa is extremely sensitive to pain. For surgical procedures, local anaesthesia must be applied to the body wall to render the serosa insensitive to pain. The parietal serosa is divided into sections and named depending on location:

- parietal pleura in the thorax and
- parietal peritoneum in the abdomen and pelvis.

The parietal serosa rests upon and is strongly attached to the **internal fascia** (fascia trunci interna) of the body trunk (▶ Fig. 1.62, ▶ Fig. 1.63 and ▶ Fig. 1.64). The section of this fascia located in the thorax wall is the **endothoracic fascia** (fascia endothoracica); in the lateral and ventral abdominal walls it is called the **transverse fascia** (fascia transversalis, ▶ Fig. 1.61), and in the wall of the processus vaginalis it is the **internal spermatic fascia** (fascia spermatica interna).

The **intermediate serosa** (serosa intermedia) are the serous membranes which form the **mesenteries** (▶ Fig. 1.62). The serosa intermedia is a continuation of the serosa parietalis from the left and right sides in each body cavity. These two sides unite and form a double-layered serosa stemming from the wall of the cavity. This occurs both at the top and bottom of the body cavity, creating dorsal and ventral mesenteries. In some cases, the mesentery is referred to as a **ligament** or **plica**. The individual mesentery sections are named with the prefix "**meso-**" and the Greek name of the organ it reaches, for example mesogastrium (▶ Fig. 1.63). The mesogastrium is the mesentery which leads to the stomach and suspends it in the abdominal cavity.

The **primary mesenteries** also provide a way for the arteries, veins, nerves and lymphatic vessels to reach the organs they supply. The lymph nodes are often located in the mesentery of the organ. The secondary mesenteries support and stabilize the **positions of the organs** (e.g. plica duodenocolica, ligamentum triangulare). A mesentery consists of connective tissue and fat deposits. The mesenteries of cats additionally contain **mechanoreceptors**, most often corpuscles of Vater-Pacini, which respond to pressure.

Mesenteries begin dorsally as double-layered sheets and continue ventrally, where the sheets separate to surround a specific organ of the thoracic, abdominal or pelvic cavity. The part of the mesentery covering the organ is referred to as the visceral serosa. They are more aptly named with the prefix **"epi-"** in combination with the Greek name of the organ, for example epicardium or epiorchium.

Once the other side of the organ is reached, the **visceral serosa** unite again to form a double sheet which attaches to the ventral thoracic wall or to the cranial section of the ventral abdominal

wall. The middle and caudal sections of the intestines **do not have a ventral mesentery** due to the embryonic developmental process.

The dorsal and ventral mesenteries of the stomach and the cranial section of the duodenum build a unique structure in respect to their involvement of the liver (▶ Fig. 1.63 and ▶ Fig. 1.64). The **greater omentum** (omentum majus) develops from the **dorsal mesentery of the stomach** (mesogastrium dorsale), which extends and doubles back, thus forming the pouch-like **omental bursa** (bursa omentalis). The deep, visceral part and the superficial, parietal part of the omental bursa form a **recess**, the recessus caudalis omentalis.

The **greater omentum** originates from the dorsal abdominal wall and extends caudally, in carnivores and ruminants as far as the pelvic inlet, and reverses direction, continuing cranially until attaching to the major curvature of the stomach. Extension folds of the greater omentum bind to other organs, constricting their mobility but also forming niches where displaced organs can become trapped, such as in the nephrosplenic space in the horse; for more information see Chapter 8 "Digestive system" (p. 327).

The **ventral mesogastrium** (▶ Fig. 1.63) is divided into two sections by one of the associated glands of digestion, the **liver**. The proximal section of the mesogastrium ventrale, the **hepatogastric ligament**, extends between the minor curvature of the stomach and the portal fissure. On the parietal facies of the liver, the mesogastrium ventrale continues as the **falciform ligament**, eventually attaching to the linea alba of the ventral abdominal wall. Together, the **hepatogastric ligament** and the only ventral intestinal mesentery, the **hepatoduodenal ligament**, form the **lesser omentum**; for more information see Chapter 8 "Digestive system" (p. 327).

Organs located close to the dorsal wall of the body cavities are only covered on one side by the serous membrane. This position is described in general as **"retroserous"**. In the abdominal cavity, the organs would be located **"retroperitoneal"** (e.g. the location of the kidneys and the ureters) and in the thoracic cavity **"retropleural"** (e.g. the location of the sympathetic trunk). The organs of the caudal pelvic cavity lie **"extraperitoneal"**.

Clinical note

The serosal lining of the body cavities is absorptive, enabling the **intraperitoneal administration of pharmacological agents**. Substances absorbed by the parietal peritoneum reach their target organs **without passing through the liver**.

Inflammation of the peritoneum (**peritonitis**) can result in uptake of bacterial toxins, leading to serious disease. Increased pressure in the venous system, due to cardiac insufficiency or liver disease, may cause **peritoneal fluid** to accumulate within the peritoneal cavity (**ascites**). Abdominocentesis (abdominal paracentesis) is required for removal of excess fluid.

When performed for diagnostic purposes, abdominocentesis is carried out in the **umbilical region** (regio umbilicalis). Removal of pleural fluid is referred to as **thoracocentesis**. This is performed at the level of the costal cartilages.

Surgery conducted within the body cavities can result in **adhesions** of the pleura or peritoneum. Adhesions can be painful and may limit the mobility and motility of organs.

In the case of the peritoneum, this phenomenon can also be exploited for prophylactic purposes. For example, following surgical correction of gastric volvulus, gastropexy is used to bring about fusion of the stomach wall with the parietal peritoneum, thus reducing the risk of further gastric displacement.

2 Axial skeleton (skeleton axiale)

H.-G. Liebich and H. E. König

The axial skeleton comprises the:

- **skeleton of the head** with:
  - skull,
  - neural part (cranium, neurocranium),
  - facial part (facies, viscerocranium),
  - mandible,
  - hyoid apparatus and
  - ossicles of the middle ear,
- **vertebral column** and
- **skeleton of the thorax**.

2.1 Overview of the skull

The skull forms a rigid construction composed of many bones, which are mostly paired. It encompasses and protects the brain and the sensory organs of sight, smell, sound, balance and taste. It also lodges part of the upper respiratory and alimentary tracts. Bony projections form attachments for the facial and masticatory musculature.

The individual bones of the skull are firmly united by **sutures** (suturae), whereas the **lower jaw** (mandible) and the **hyoid apparatus** (apparatus hyoideus) are attached to the skull by articular joints (▶ Fig. 2.1, ▶ Fig. 2.2 and ▶ Fig. 2.23).

Few bones of the head have their embryological origins in the **axial skeleton**, the majority are ossified structures of a **dermal skeleton**. The bones derived from the dermal skeleton develop by membranous ossification and cover the lateral and dorsal aspects of the brain, whereas the bones of the axial skeleton develop by endochondral ossification and form the base of the skull and parts of the facial skull.

The **individual bones** develop from **separate centres of ossification**. In young animals they are divided by strips of fibrous, or less often, cartilagenous tissue. This form of development provides the adaptability of the skull for postnatal growth. In the newborn, the facial part of the skull is comparatively small, due to the disproportionate small size of the masticatory apparatus, the nasal cavities and the paranasal sinuses. In the post-natal period, the proportions of the skull change.

This is due to the species-specific development of the roof of the skull and the individual bones and also the enlargement of the skull as a whole, which is significantly influenced by the growth of the teeth, the formation of the paranasal sinuses and the elongation of the base of the skull. This remodelling is a long process, which continues for some structures of the skull throughout the whole life.

2.2 Overview of the vertebral column or spine

The bony components of the vertebral bodies are derived from the axial, perichondral mesenchymal of the sclerotomes. The **intervertebral discs** (disci intervertebrales) are considered to be remnants of this original tissue. The embryological precursor of the vertebral body forms a bony arch dorsally, thus completing the central **foramen of the vertebra** (foramen vertebrae), which encloses the spinal cord.

The individual vertebrae are joined together by articular processes and ligaments. The vertebral column as a whole consists of a series of separate bones, the vertebrae, which extend from the skull to the tip of the tail. Starting with the **foramen magnum** at the skull and ending with the **sacral canal** (canalis sacralis), the vertebral foramina of the single vertebrae sum up to constitute the **vertebral canal** (canalis vertebralis), which encompasses the spinal cord (medulla spinalis), its meninges, the spinal nerves (nervi spinales), blood vessels and connective tissue. The separate vertebrae are not joined rigidly together, but have spaces between them (spatia intervertebralia) for the passage of the spinal nerves.

Along the long axis of the vertebral column **three major curvatures** are recognised:

- the dorsal convex curvature between the head and neck,
- the dorsal-concave curvature between the cervical and thoracic spine, and
- the dorsal-convex curvature between the thoracic lumbar spine.

The vertebral column serves to support the body and takes over a central function as part of the locomotor system by forming a bridge between the thoracic and pelvic limbs. The cranial thoracic vertebrae of the vertebral column are supported by the ribs, which are linked to the thorax by muscles and tendons. This anatomical arrangement provides stability and mobility for the vertebral column. In the region of the pelvis the vertebral column is firmly joined to the pelvic limb by the articulation of the **sacral wings** to the **ilia**. Thus the propelling force of the hindlimb, generated by the muscles and the hip joint, is transmitted directly to the rest of the body.

The vertebral column fulfills various additional functions. As movement between the individual vertebrae is limited, it contributes to the maintenance of posture. However, the degree of movability of the individual vertebrae forms the basis for dynamic functions, including the transmission and reduction of forces during walking, running and jumping. The smallest functional unit consists of two successive vertebrae, the intervertebral disc, their articulations, ligaments and muscles. Even small anatomical changes of one of the components will result in a significant disturbance of the locomotory system. The movability of the vertebral column varies in the different segments; for example, it is very rigid in the region of the sacrum, while the caudal vertebrae remain quite flexible.

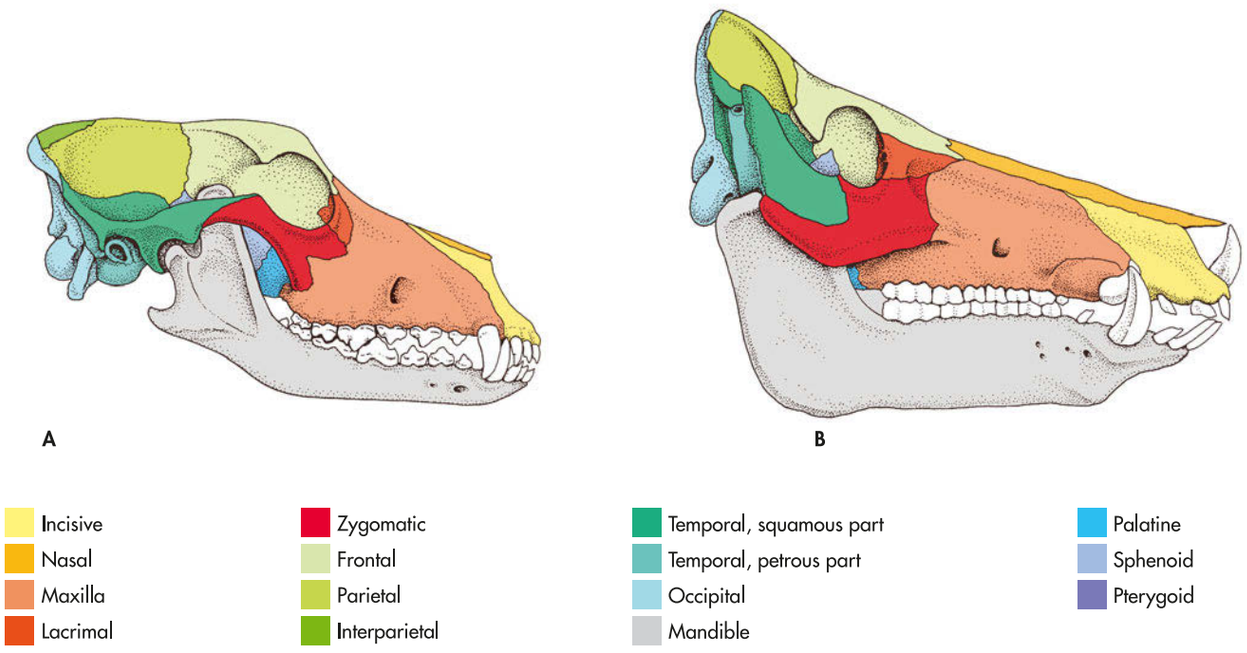

Fig. 2.1 Bones of the skull and mandible of the dog **(A)** and pig **(B)** (schematic, lateral aspect); fig. based on data from Ellenberger and Baum, 1943.

The vertebral column in the thoracic and lumbar region allows movement in three directions. Small movements of the individual intervertebral joints cause dorsal, ventral and lateral flexion of the whole column. Considerable lateral, dorsal and ventral movements are possible in the neck.

2.3 Overview of the thorax

The rib cage is composed of the **thoracic vertebrae** (vertebrae thoracicae) dorsally, the **ribs** (costae) laterally and the **sternum** ventrally. They form the bony components of the thoracic wall and are joined functionally by a variety of ligaments, chondral junctions and true articulations. The rib cage encloses the **thoracic cavity** (cavum thoracis) and is kept under tension by its surrounding muscles. The thorax of the domestic mammals has the shape of a laterally compressed, truncated cone, with its apex pointing cranially and its base caudally. It has a **cranial** and a **caudal aperture** (apertura thoracis cranialis et caudalis).

2.4 Skeleton of the head

2.4.1 Skull, neural part (cranium, neurocranium)

The bones of the neural or cranial part of the skull enclose the **cranial cavity** (cavum cranii), including the brain, its meninges and blood vessels. The structure of the cranium is a collection of many smaller bones, that fit together in a species specific construction. Skulls differ largely, not only between different species and breeds, but also between individuals of the same breed, age and sex. The basic anatomical architecture of the neural part of the skull will be described, with species specific variations emphasised. The cranium is formed by the same bones in all domestic mammals:

- **the floor is composed of the**:
  - unpaired basioccipital bone (pars basilaris ossis occipitalis) and
  - unpaired basisphenoid and presphenoid bones (os basisphenoidale et os presphenoidale),
- **the nuchal wall is composed of the**:
  - unpaired supraoccipital bone (squamous part, squama occipitalis) and
  - exoccipital bones (lateral parts, partes laterales),
- **the lateral walls are composed of the:**
  - paired temporal bone (os temporale),
- **the roof is composed of the:**
  - paired frontal bone (os frontale),
  - paired parietal bone (os parietale) and
  - unpaired interparietal bone (os interparietale), and
- **the nasal wall is composed of the:**
  - unpaired ethmoid bone (os ethmoidale).

Occipital bone (os occipitale)

The occipital bone forms the nuchal wall of the skull and can be divided into the **basilar part**, the **squamous part** and the **lateral parts** (▶ Fig. 2.1, ▶ Fig. 2.2, ▶ Fig. 2.3 and ▶ Fig. 2.4). These bones form a ring surrounding the spinal cord, the **foramen magnum**.

The **basilar part** (pars basilaris, basioccipital bone) constitutes the caudal part of the base of the cranium. It is situated rostral to the foramen magnum, where it is joined to the basisphenoid by a cartilagenous suture (▶ Fig. 2.4). On the ventral surface are the paired **muscular tubercles** (tubercula muscularia) for the attachment of the flexors of the head and neck. The surface of this bone is concave, forming the **caudal cranial fossa** (fossa cranii caudalis)

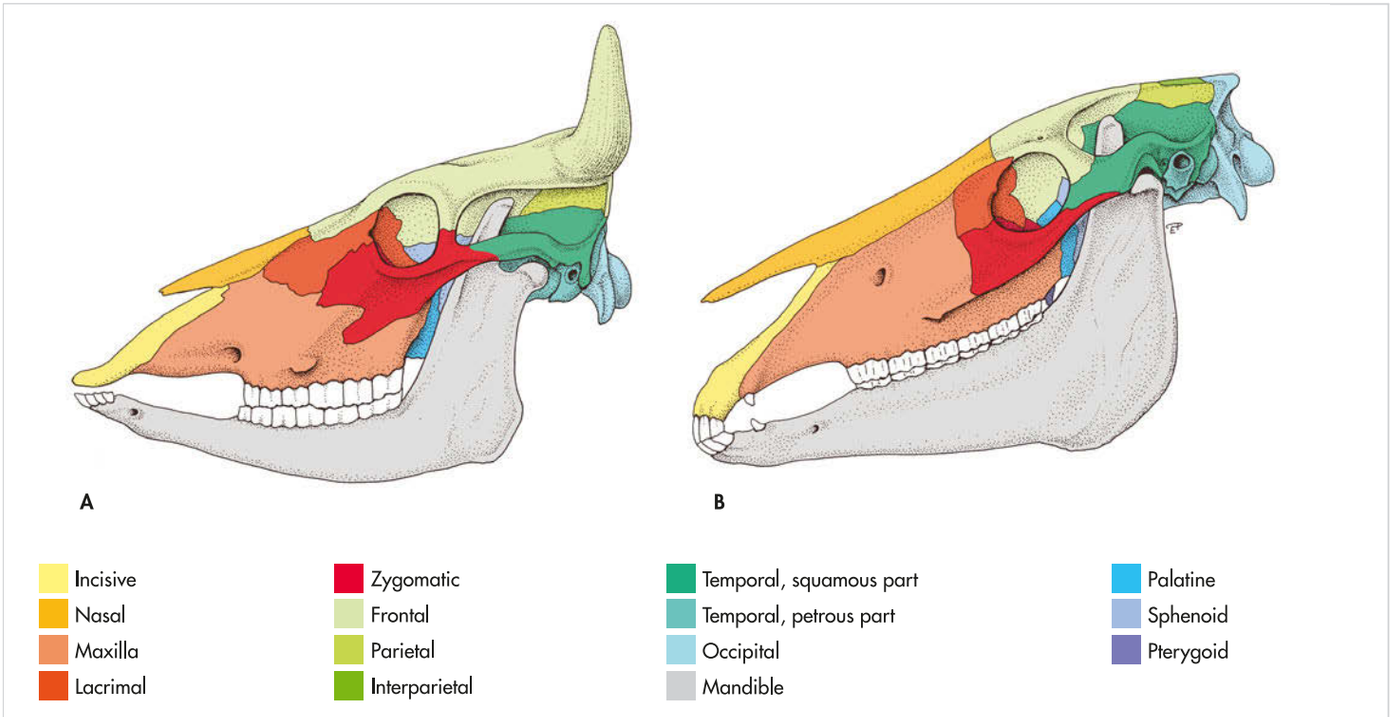

Fig. 2.2 Bones of the skull and mandible of the ox **(A)** and horse **(B)** (schematic, lateral aspect); fig. based on data from Ellenberger and Baum, 1943.

(▶ Fig. 2.5), which is subdivided into rostral and caudal depressions. The rostral depression encompasses the pons (impressio pontina) and the caudal depression encompasses the medulla oblongata (impressio medullaris).

The **jugular foramen** (foramen jugulare) is located on either side of the basilar part, adjacent to the tympanic bullae. In the pig and the horse the sharp and thin lateral borders of the basilar part form the deep **petro-occipital fissure** (fissura petro-occipitalis) together with the petrosal part (pars petrosa) of the temporal bone where the foramen lacerum is built (▶ Fig. 2.40 and ▶ Fig. 2.41).

The **squamous part** (**squamous part**, supraoccipital bone) is situated dorsal to the **lateral parts** (partes laterales ossis occipitalis) and the **occipital condyles** (condyli occipitales), completing the foramen magnum dorsally (▶ Fig. 2.3 and ▶ Fig. 2.4). Its **external surface** (lamina externa) is demarcated by a sharp-edged ridge, the **nuchal crest** (crista nuchae) (▶ Fig. 2.4, ▶ Fig. 2.9 and ▶ Fig. 2.11). In ruminants, the nuchal crest is reduced to the prominant **nuchal line** (linea nuchae). The nuchal crest is easily palpable and can be used as a landmark, together with the wings of the atlas, for the collection of cerebrospinal fluid.

The well-defined median ridge, the **external sagittal crest** (crista sagittalis externa), arises from the nuchal crest in carnivores and the horse (▶ Fig. 2.4, ▶ Fig. 2.9 and ▶ Fig. 2.11). The **external occipital protuberance** (protuberantia occipitalis externa) (▶ Fig. 2.13 and ▶ Fig. 2.92) are median triangular projections with the base pointing towards the base of the cranium, and provides attachments for the **nuchal ligament** (ligamentum nuchae). In carnivores, the poorly defined external occipital crest extends from the external occipital protuberance to the foramen magnum (▶ Fig. 2.4).

The **internal surface of the cranium** (lamina interna) has many shallow depressions, which conform to the surface of the cerebellum (impressiones vermiales) and the basal blood vessels (sulci sinus transversi). The internal surface is marked by the **internal occipital protuberance** (protuberantia occipitalis interna). Carnivores and horses have an additional process, the tentorial process (processus tentoricus), which forms the tentorium cerebelli osseum (▶ Fig. 2.5 and ▶ Fig. 2.10), together with like-named processes of the parietal and interparietal bones.

The **lateral parts of the occipital bone** (partes laterales, exoccipital bones) form the lateral borders of the foramen magnum. They include the **occipital condyles** (condyli occipitales), which articulate with the atlas to form the atlanto-occipital joint (▶ Fig. 2.4 and ▶ Fig. 2.6). Lateral to the condyli process, the **paracondylar processes** (processus paracondylares), provide attachment to the specific muscles of the head (as described in Chapter 2).

These processes are elongated in the pig, shorter in ruminants and the horse and bulb-shaped in carnivores (▶ Fig. 2.4, ▶ Fig. 2.6, ▶ Fig. 2.7 and ▶ Fig. 2.9). They are thought to be rudimentary transverse processes analogous with those of the cervical vertebrae. The ventral **condyloid fossa** (fossa condylaris ventralis) (▶ Fig. 2.6 and ▶ Fig. 2.12), which forms the end of the **hypoglossal canal** (canalis nervi hypoglossi), through which the hypoglossal nerve passes, is located between the paracondylar and the condyli process. This fossa is continuous with the **dorsal condylar fossa** (fossa condylaris dorsalis).

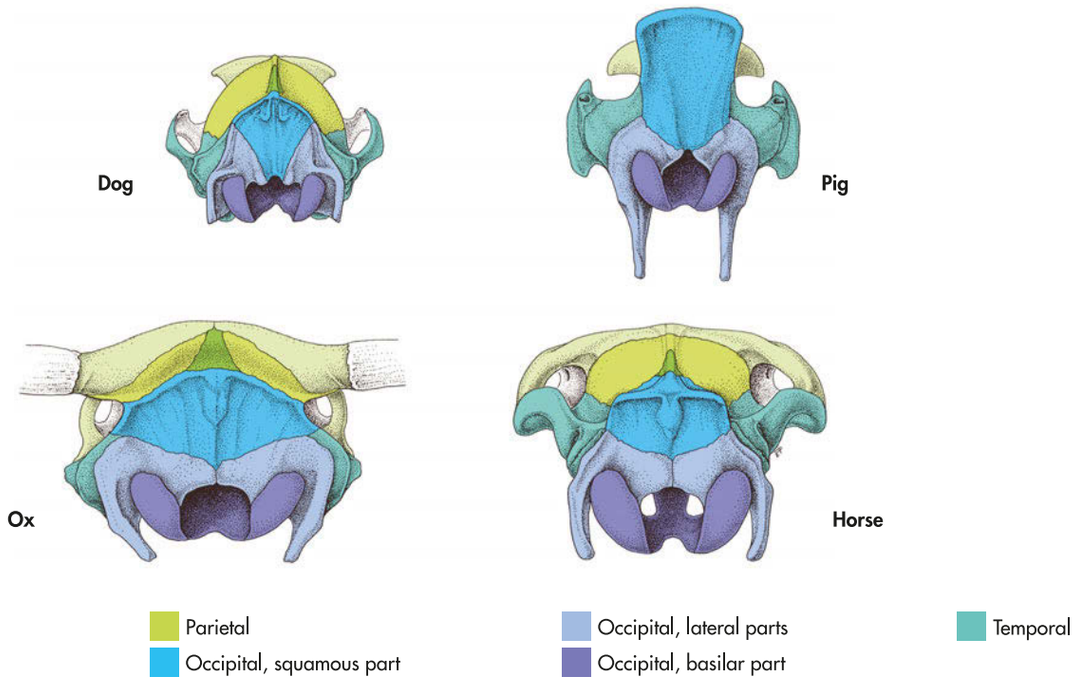

Fig. 2.3 Nuchal aspect of the canine, porcine, bovine and equine skull (schematic); fig. based on data from Ellenberger and Baum, 1943.

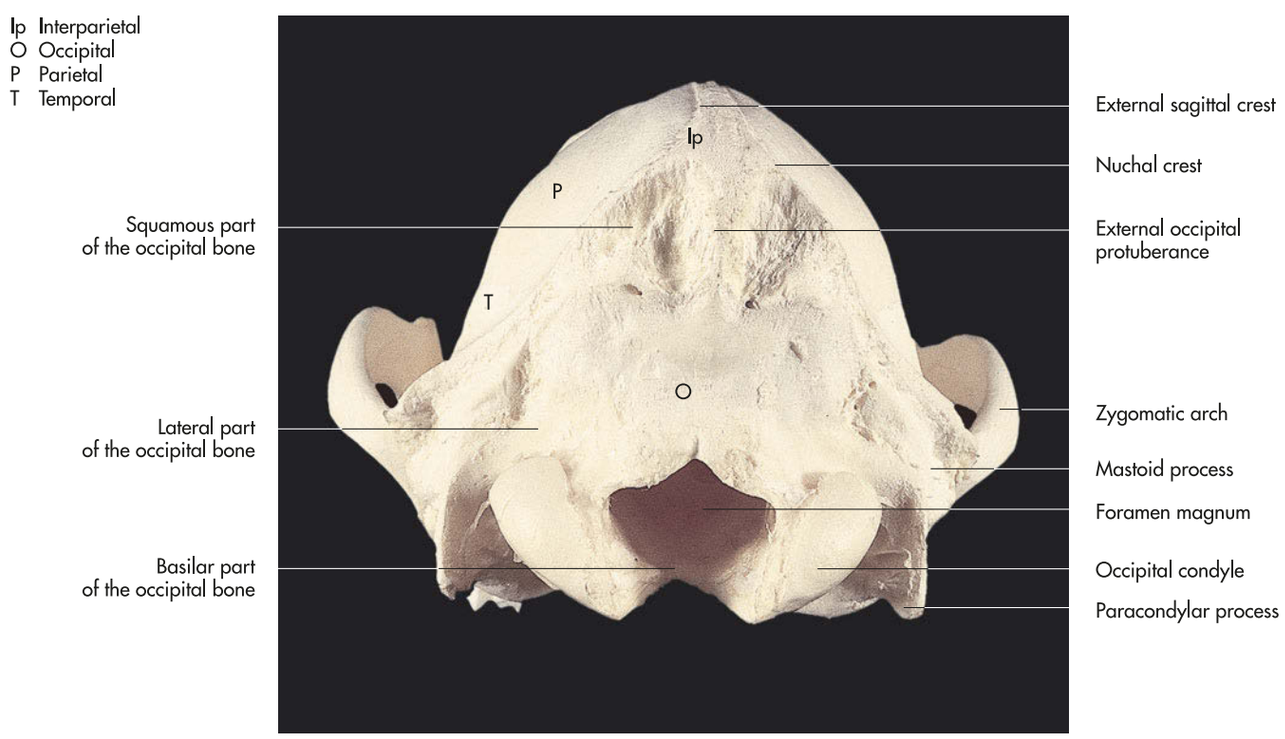

Fig. 2.4 Nuchal aspect of a canine skull.

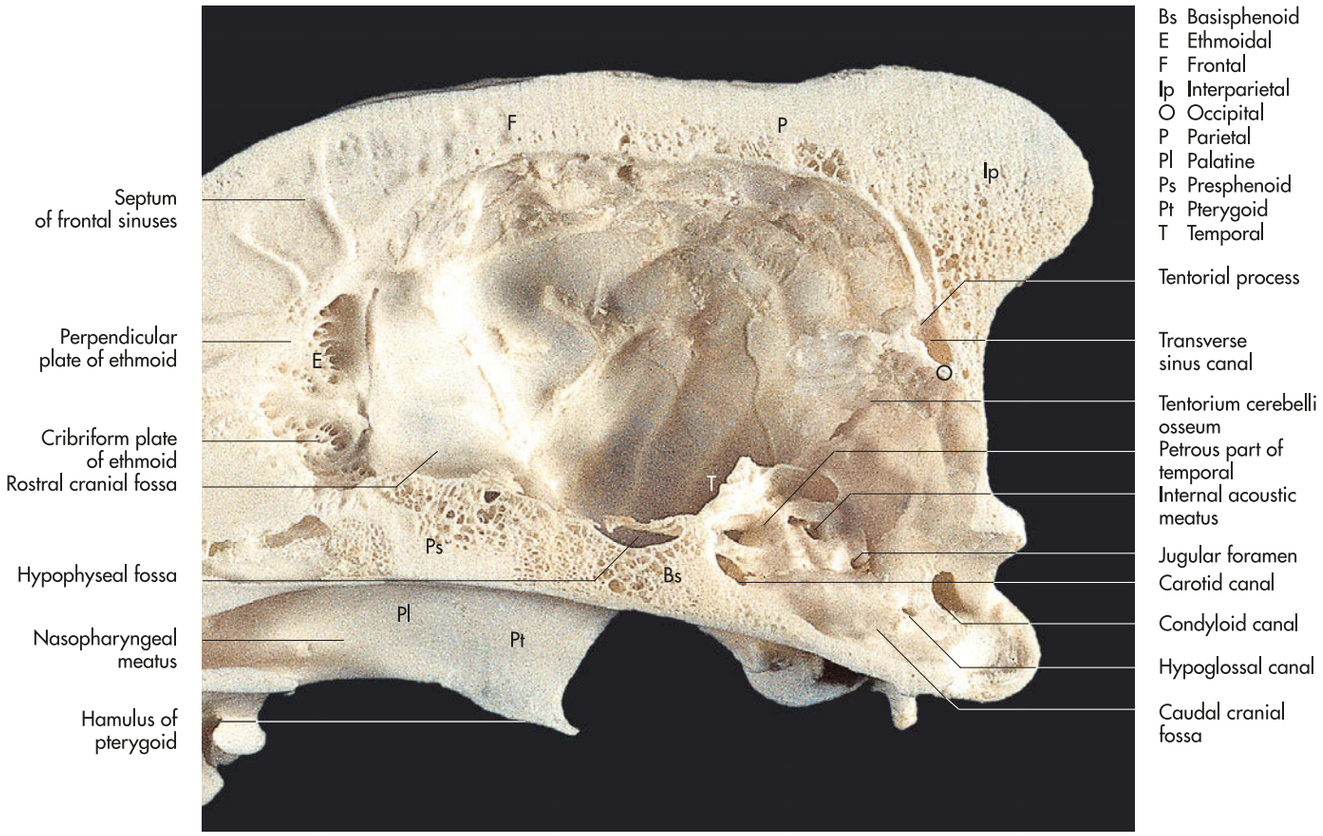

Fig. 2.5 Bones of the cranial part of a canine skull (medial aspect of sagittal section).

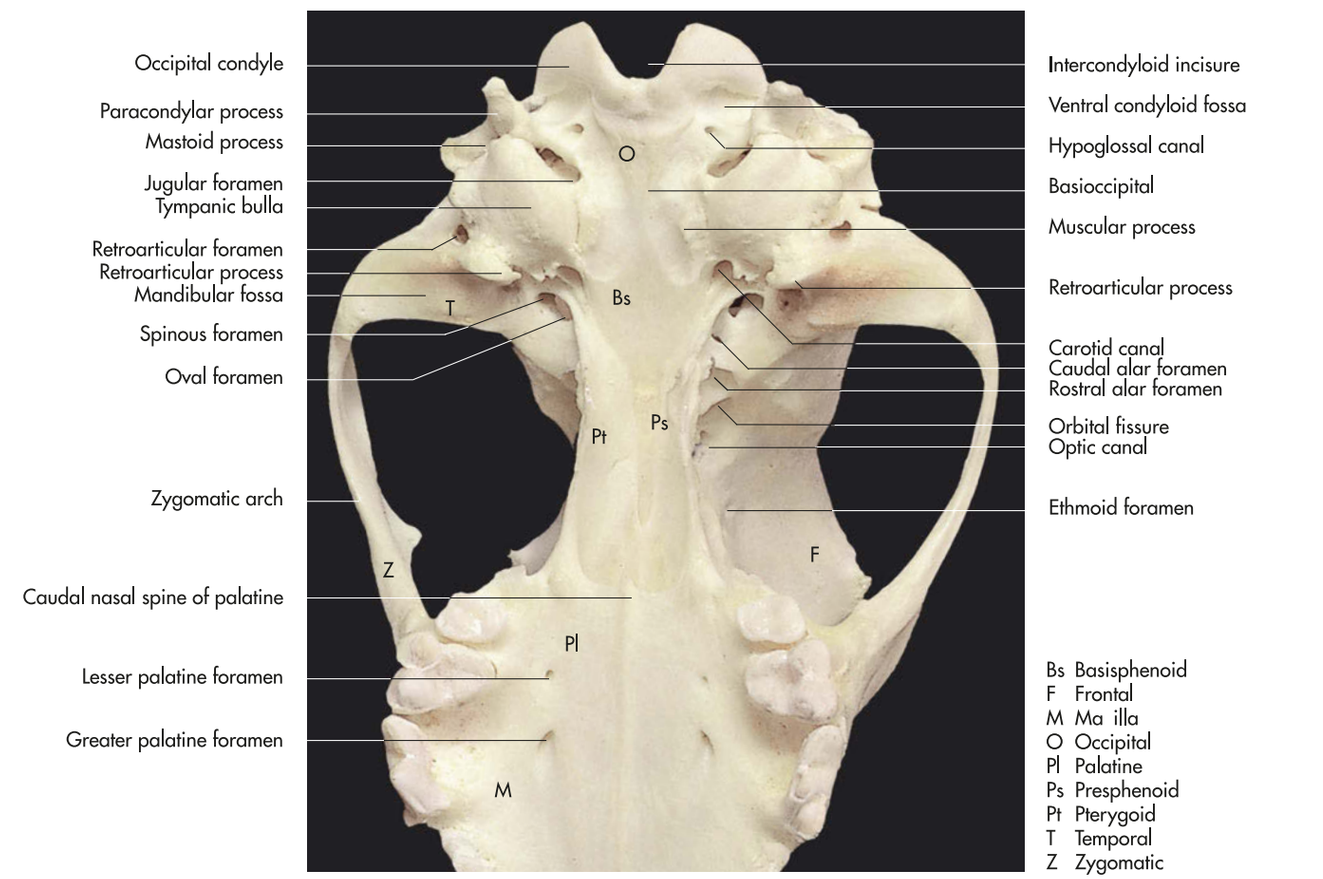

Fig. 2.6 Bones of the cranial part of a canine skull (ventral aspect).

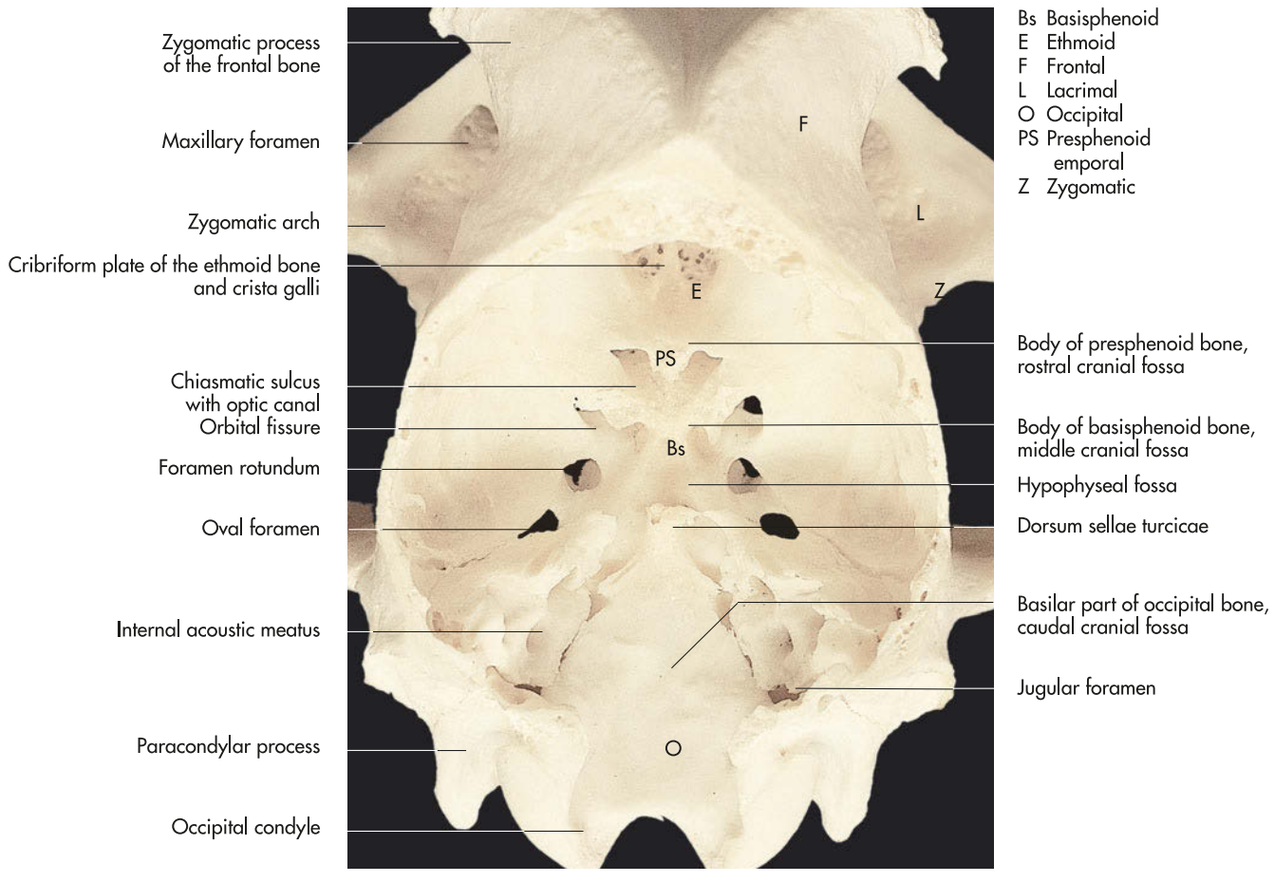

Fig. 2.7 Cranial cavity of a dog with calvaria removed (dorsocaudal aspect).

Sphenoid bone (os sphenoidale)

The **sphenoid bone** forms the rostral part of the base of the neurocranium and consists of two similar segments, the **presphenoid** (os praesphenoidale) rostrally and the **basisphenoid** (os basisphenoidale) caudally (▶ Fig. 2.2, ▶ Fig. 2.5 and ▶ Fig. 2.6).

Each bone is composed of a **median body** (corpus ossis sphenoidalis) and **wings** (alae ossis sphenoidalis) laterally. In humans these bones fuse firmly in early life, while in adolescent domestic mammals they are separated by a cartilagenous suture, which ossifies in the adult. Therefore they are considered as individual bones in veterinary anatomy.

Presphenoid (os praesphenoidale)

The **body** and **wings of the presphenoid** (corpus et alae ossis praesphenoidalis) constitute the bony parts of the **rostral cranial fossa** (fossa cranii rostralis) and articulate with the basisphenoid caudally (▶ Fig. 2.7). The body of the presphenoid is hollow and encloses the paired **sphenoid sinuses** (sinus sphenoidales), which are separated by an incomplete septum (▶ Fig. 2.10). The beak-shaped **sphenoidal rostrum** (rostrum sphenoidale) projects from the body rostrally towards the ethmoid. Just caudal to this, there is a transverse depression (sulcus chiasmatis) on which the **optic chiasm** (chiasma opticum) rests. The bony **optic canal** (canalis opticus) extends from each end of this groove over the wings of the presphenoid through which the optic nerve passes (▶ Fig. 2.7).

The external surface of the **wings of the presphenoid** (alae ossis praesphenoidales) contribute to the formation of the orbit and the optic canal, whereas the internal surface forms part of the cranial cavity.

Basisphenoid (os basisphenoidale)

The **body** and **wings of the basisphenoid** (corpus et alae ossis basisphenoidalis) consitute the bony parts of the **medial cranial fossa** (fossa cranii medialis), which includes the **tuberculum sellae** (sella turcica) rostrally, the **hypophyseal fossa** (fossa hypophysialis) in the middle and the **dorsum sellae** (dorsum sellae turcicae) (with the exception of the horse) caudally (▶ Fig. 2.7). The surfaces of the **wings of the basisphenoid** (alae ossis basisphenoidalis) oppose the brain (facies cerebralis), the temporal bone (facies temporalis), the maxilla (facies maxillaris) and the orbit (facies orbitalis). The piriform fossae are located lateral to the optic groove and encompass the **piriform lobes** (lobi piriformes) of the brain. Each wing contributes to the formation of various foramina and notches for the passage of nerves and blood vessels with species-specific variations.

In the horse, the caudal border of each wing forms the rostral border of the **foramen lacerum**. It forms three notches, the **carotid notch** (incisura carotica) for the passage of the internal carotid artery medially, the **oval notch** (incisura ovalis) for the passage of the mandibular nerve and the **spinous notch** (incisura spinosa) for the middle meningeal artery laterally (▶ Fig. 2.41). The foramen lacerum is absent in carnivores and ruminants and

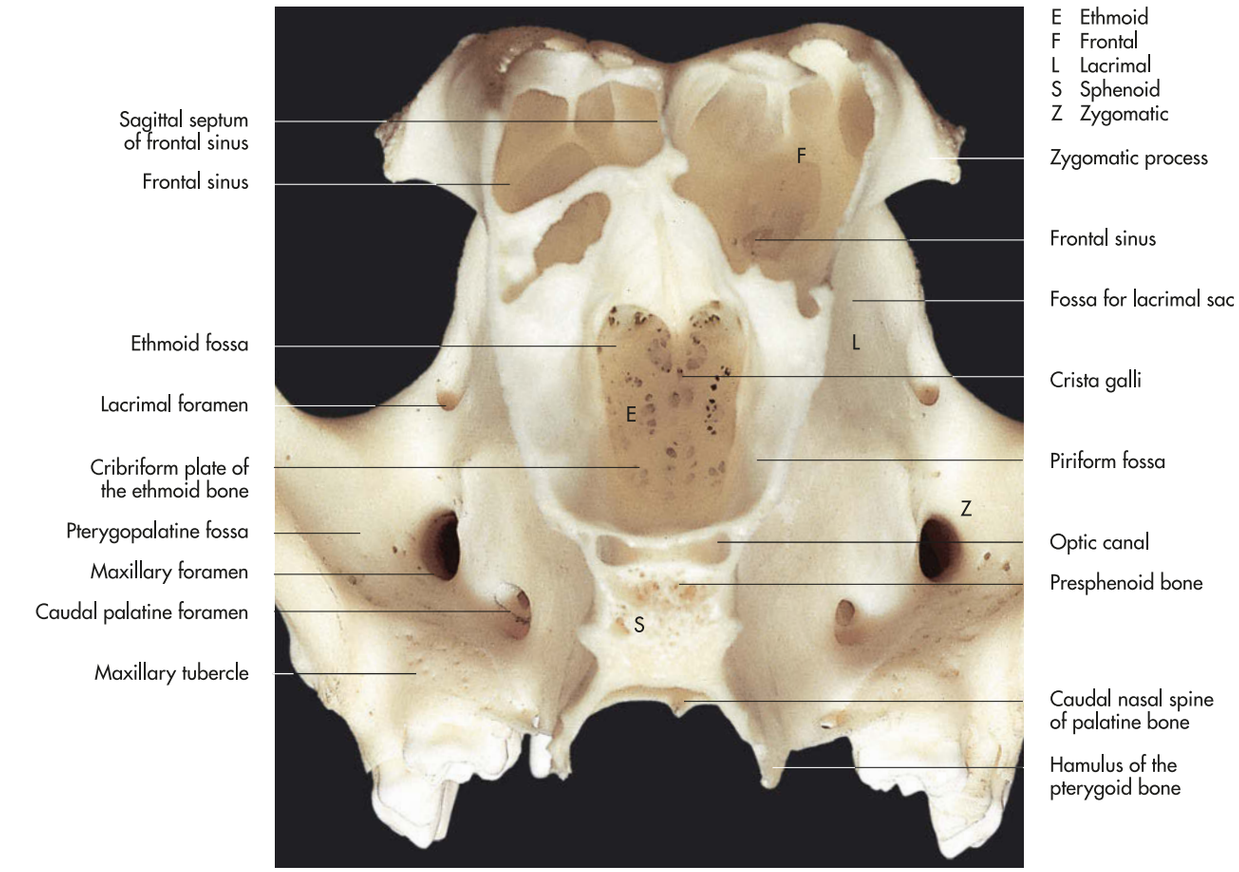

Fig. 2.8 Transverse section of a canine cranial cavity caudal to the zygomatic process of the frontal bone.

its functions are replaced by the **oval foramen**, the **spinous foramen** and the **carotid canal** in carnivores and by a **oval foramen** only in ruminants (▶ Fig. 2.6).

The **pterygoid processes** (processus pterygoidei) arise from the rostral border of the basisphenoid (▶ Fig. 2.5). They project ventro-rostrally and form the boundaries of the choanae, together with the palatine and pterygoid bones. The base is perforated by the **alar canal** (canalis alaris), through which the maxillary artery passes. It originates with the **caudal alar foramen** (foramen alare caudale) and terminates with the **rostral alar foramen** (foramen alare rostrale).

Temporal bone (os temporale)

The temporal bone of the newborn animal consists of three distinct parts (▶ Fig. 2.1 and ▶ Fig. 2.2), which unite later in life:

- squamous part (pars squamosa, squama temporalis),
- petrosal part (pars petrosa, petrosum) with its mastoid process (processus mastoideus) and
- tympanic part (pars tympanica).

The petrosal and tympanic parts are sometimes also called the pyramid and are firmly fused to the squamous part in carnivores and in the ox, but remain separated in the other domestic mammals.

The **cerebral surface** (facies cerebralis) of the **squamous part** (pars squamosa, squama temporalis, squamosum) contributes to the formation of the lateral wall of the cranial cavity. It unites with the frontal, parietal and sphenoid bones in firm osseous sutures.

The long **zygomatic process** (processus zygomaticus) arises from the temporal surface (facies temporalis) of the squamous part. It extends rostrolaterally to unite with the **temporal process of the zygomatic bone**, forming the **zygomatic arch** (arcus zygomaticus) (▶ Fig. 2.4 and ▶ Fig. 2.6). The base of the zygomatic process expands to form the articulating surface of the **temporomandibular joint** (articulatio temporomandibularis). This articulating surface consists of a transversely elongated **articular tubercle** (tuberculum articulare) rostrally and the **mandibular fossa** (fossa mandibularis) caudal to it (▶ Fig. 2.12).

The **mandibular fossa** is deliniated caudally by the **retroarticular process** (processus retroarticularis) (▶ Fig. 2.6). While the articular tubercle is missing in carnivores, these species have an especially well-developed **retroarticular process** (▶ Fig. 2.6).

The caudal part of the squamous part forms the **occipital process** (processus occipitalis); the ventral surface forms the **retrotympanic process** (processus retrotympanicus), which surrounds the **external acoustic meatus** (meatus acusticus externus) caudally. The **retroarticular foramen** (foramen retroarticulare) exits caudal to the latter process and forms the end of the **temporal canal** (meatus temporalis) (▶ Fig. 2.11). The temporal canal is rudimentary in the cat and pig.

The **petrosal part** (pars petrosa, petrosum) is the caudoventral portion of the temporal bone and is bordered by the squamous and the **tympanic parts**. It encloses the **inner ear** with the **co-**

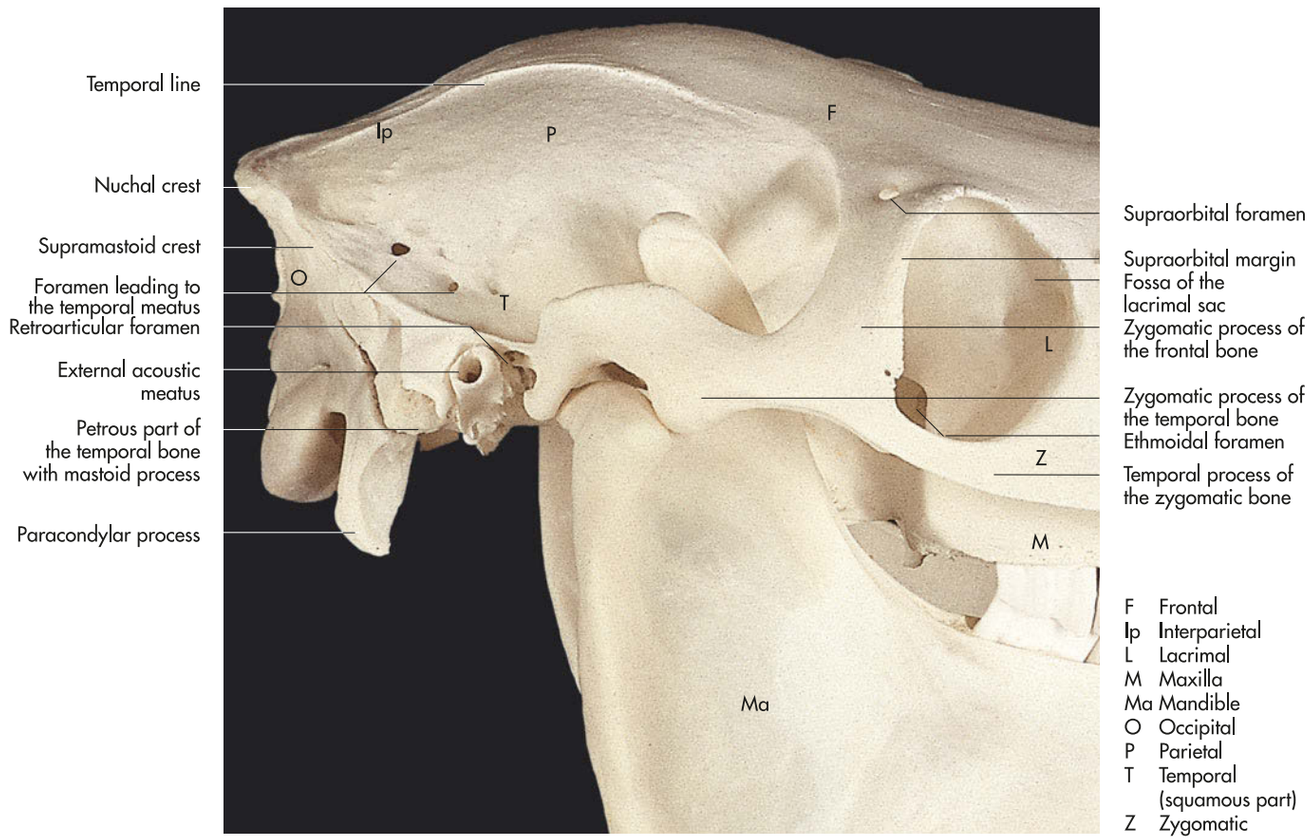

Fig. 2.9 Bones of the cranial part of an equine skull (lateral aspect).

chlea, the **vestibule** (vestibulum) and the **semicircular canals** (canales semicirculares). Its medial surface (facies medialis) is perforated by the entrance (porus acusticus internus) of the **internal acoustic meatus** (meatus acusticus internus) (▶ Fig. 2.5 and ▶ Fig. 2.10), through which the cranial nerves of the face, the **facial nerve** (n. facialis) and of hearing and balance, the **vestibulocochlear nerve** (n. vestibulocochlearis) pass. The rostral and medial surfaces of the petrosal part are separated by the sharp-edged **petrosal crest** (crista partis petrosae) in carnivores and the horse.

Caudally, the petrosal part extends beyond the skull, forming the **mastoid process** (processus mastoideus) ventrally. The mastoid process is a strong, bulb-shaped projection in the horse, whereas it is smaller in the other domestic mammals. Attachment for the **hyoid apparatus** (apparatus hyoideus) is provided by the cylindrical **styloid process** (processus styloideus) in horses and ruminants, which is positioned rostroventral to the external acoustic meatus of the petrosal part (▶ Fig. 2.12 and ▶ Fig. 2.14). The styloid process is absent in carnivores and the pig and therefore the hyoid apparatus articulates with the mastoid process of the petrosal part in carnivores (▶ Fig. 2.6) and the nuchal process (processus nuchalis) of the squamous part, which is located close to the base of the paracondylar process in the pig. The external opening of the facial canal, where the facial nerve emerges, the **stylomastoid foramen** (foramen stylomastoideum) is situated between the styloid and mastoid process in ruminants, the pig and the horse and between the mastoid process and the tympanic part in carnivores (▶ Fig. 2.38 and ▶ Fig. 2.40).

The **tympanic part** (pars tympanica, tympanicum) is the ventral portion of the temporal bone. Its bulbous enlargement, the **tympanic bulla** (bulla tympanica) encloses the **tympanic cavity of the middle ear** (cavum tympani) (▶ Fig. 2.6, ▶ Fig. 2.13 and ▶ Fig. 2.14). In the cat, the tympanic cavity is divided into two parts and the medial wall is formed by the cartilagenous precursor of a separate endotympanic part (pars endotympanica).

The **external acoustic meatus** (meatus acusticus externus) opens dorsolaterally (porus acusticus externus) (▶ Fig. 2.9 and ▶ Fig. 2.14) and is separated from the tympanic cavity by a membranous diaphragm, the **tympanic membrane** or **eardrum** (membrana tympani), which is attached to the **tympanic ring** (anulus tympanicus). The dorsal part of the tympanic cavity encloses the auditory ossicles (ossicula auditus), the stapes, malleus and incus. The **muscular process** (processus muscularis) extends from the mediorostral walls of the tympanic bulla. This is especially prominent in horses and ruminants. The groove-like auditory tube (semicanalis tubae auditivae) is medial to the muscular process and adjacent to the groove of the tensor veli palatini muscles (semicanalis musculi tensoris veli palatini) in the musculotubal canal (canalis musculotubarius), which connects the tympanic cavity to the pharynx.

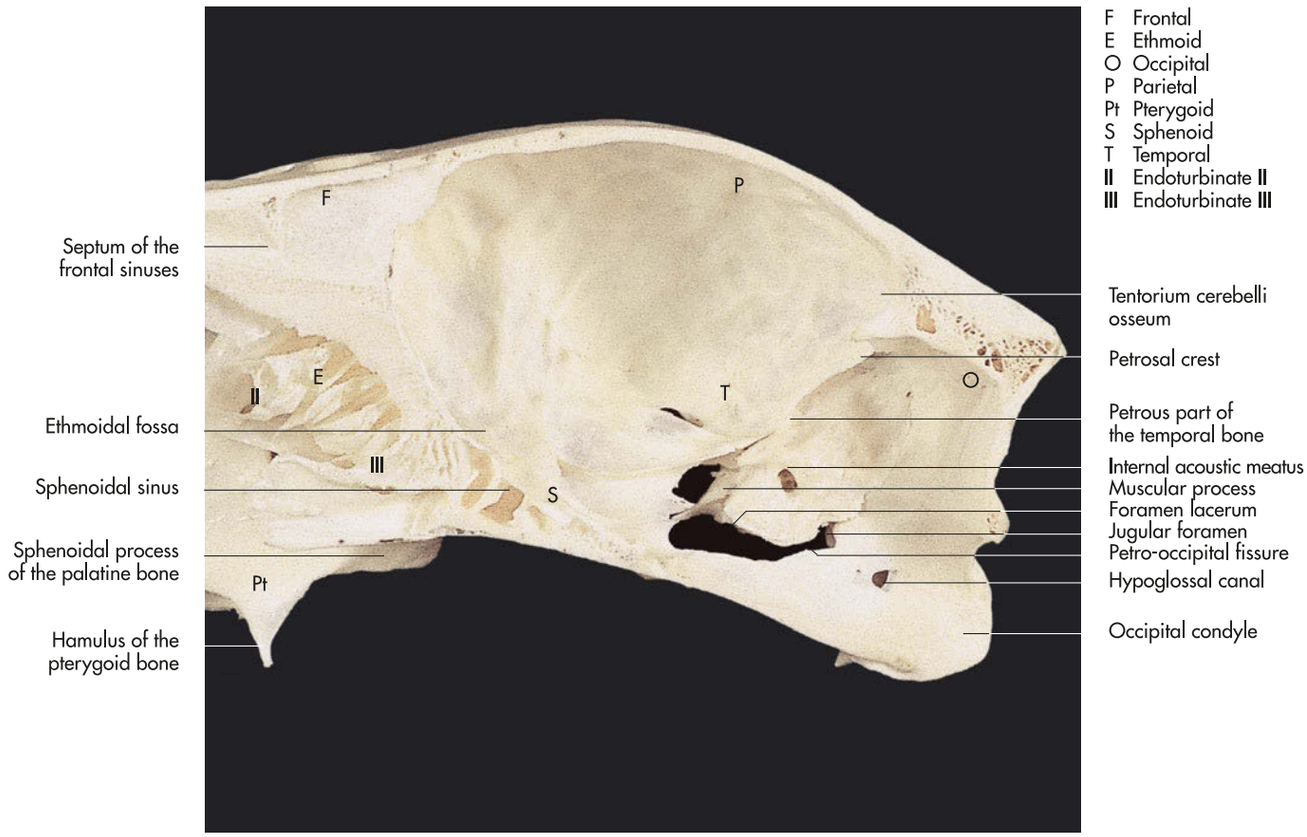

Fig. 2.10 Bones of the cranial part of an equine skull (medial aspect of sagittal section).

Frontal bone (os frontale)

The paired frontal bones are situated between the cranium and the face (▶ Fig. 2.1 and ▶ Fig. 2.2) and are united in the **interfrontal suture** (sutura interfrontalis). Each frontal bone encloses, depending on the species, one or more air-filled cavities, the frontal sinuses (sinus frontales) (▶ Fig. 2.10). Based on their location the frontal bone can be divided in four segments:

- frontal squama (squama frontalis),
- orbital part (pars orbitalis),
- temporal surface (facies temporalis) and
- nasal part (pars nasalis).

The **frontal squama** is bordered by the nasal and lacrimal bone in large animals and is limited to the wall of the orbital cavity in carnivores. It extends to form the **zygomatic process** (processus zygomaticus) laterally (▶ Fig. 2.8, ▶ Fig. 2.9 and ▶ Fig. 2.11), which forms part of the **dorsal margin of the orbit** (margo supraorbitalis). The zygomatic process articulates in a species-specific way. In ruminants it forms an osseous union with the frontal process of the zygomatic bone (processus frontalis ossis zygomatici), in horses with the zygomatic process of the temporal bone (processus zygomaticus ossis temporalis) (▶ Fig. 2.11 and ▶ Fig. 2.18). In carnivores the dorsal margin of the orbit is formed by the **orbital ligament** (ligamentum orbitale). This ligament is often ossified in the cat. The osseous orbit is indented by the lacrimal gland (fossa glandulae lacrimalis), which lies under the zygomatic process or the orbital ligament, respectively.

The frontal squama is separated from the temporal surface by the **temporal line** (linea temporalis), which extends caudally as the **external sagittal crest** (crista sagittalis externa) (▶ Fig. 2.11 and ▶ Fig. 2.18). While it is a prominent structure in the dog, horse and ox, it is insignificant in the other domestic mammals. In horned ruminants the caudal end of the frontal squama carries the paired **cornual processes** (processus cornuales), which support the horn.

The **nasal part** (pars nasalis) is the rostral extension of the frontal bone and is neighboured by the nasal bone rostrally and the lacrimal bone laterally. The **orbital part** (pars orbitalis) forms the major part of the medial wall of the orbital cavity, and is perforated ventrally by the **ethmoidal foramen** (foramen ethmoidale) (▶ Fig. 2.6 and ▶ Fig. 2.14). In the horse the ethmoidal foramen opens on the border between the frontal and sphenoid bone (▶ Fig. 2.38). Medial to the base of the zygomatic process, the orbital part is indented by a shallow groove for the attachment of the dorsal oblique muscle of the eyeball.

Caudal to the orbital part is the small, concave temporal surface (facies temporalis). It forms the rostral part of the temporal fossa (fossa temporalis), which provides attachment for the temporal muscle (▶ Fig. 2.11).

Parietal bone (os parietale)

The **parietal** is paired and forms most of the dorsolateral part of the cranial wall. It is bordered by the occipital bone caudally and the frontal bone rostrally (▶ Fig. 2.1 and ▶ Fig. 2.2). The external

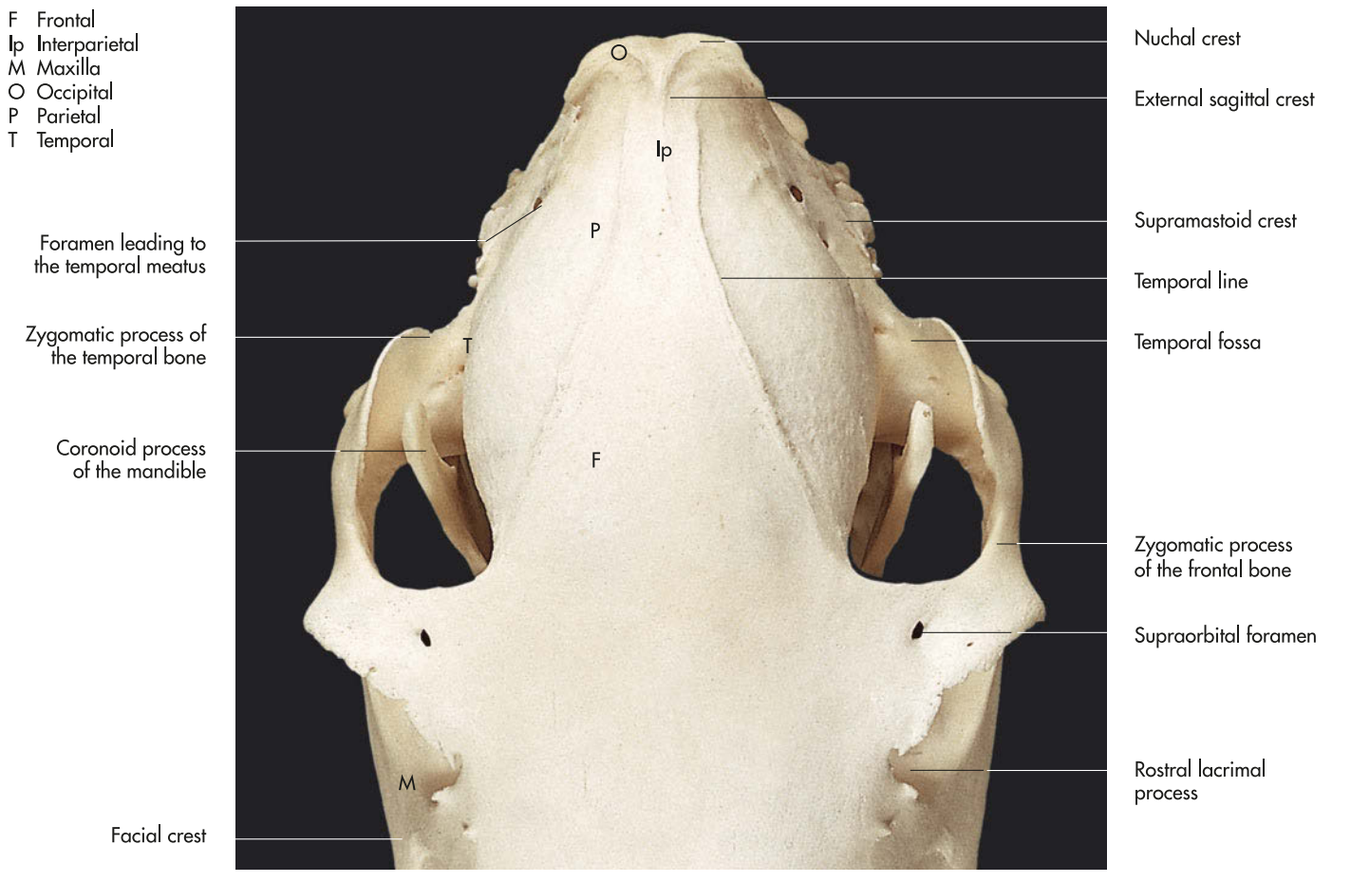

Fig. 2.11 Bones of the cranial part of an equine skull (dorsal aspect).

surface (facies externa) can be divided into a **parietal plane** (planum parietale) forming the dorsal wall of the neurocranium and a **temporal plane** (planum temporale) forming the lateral wall. The ox has an additional **nuchal plane** (planum nuchale), which contributes to the formation of the nuchal aspect of the skull.

The internal surface (facies interna) is characterised by vascular grooves and numerous depressions and ridges, which correspond to the sulci and gyri of the brain. In the horse and pig the internal surface is marked by the median **internal sagittal crest** (crista sagittalis interna), which is accompanied by the groove of the dorsal sagittal sinus (sulcus sinus sagittalis dorsalis). The caudal aspect of the internal surface of the parietal bone has a medial projection (processus tentoricus), which forms part of the **osseous tentorium cerebelli** (tentorium cerebelli osseum) in carnivores and horses (▶ Fig. 2.5, ▶ Fig. 2.10 and ▶ Fig. 2.20).

Interparietal bone (os interparietale)

The **interparietal** is centrally placed between the occipital bone and the parietal bone, with which it fuses during adult life, with the exception of the cat, where the sutures are still visible in the adult (▶ Fig. 2.1 and ▶ Fig. 2.2).

The tentoric proesses on the cerebral surface, fuse with the like-named processes of the parietal and occipital bones, forming the **osseous tentorium cerebelli** (tentorium cerebelli osseum) (▶ Fig. 2.5, ▶ Fig. 2.10 and ▶ Fig. 2.20).

Ethmoid bone (os ethmoidale)

The **ethmoid bone** is situated deep in the walls of the orbit and contributes to the formation of the cranial and facial parts of the skull (▶ Fig. 2.1 and ▶ Fig. 2.2). The **external lamina** (lamina externa) of the tube-like ethmoid bone consists of the **roof plate** (lamina tectoria), the **floor plate** (lamina basalis) ventrally and the extremely thin paired **orbital plates** (laminae orbitales) to each side. The **cribriform plate** (lamina cribrosa) separates the ethmoid bone from the cranial cavity. A median sheet of bone, the **perpendicular plate** (lamina perpendicularis), divides the ethmoid into two tubes. The paired **ethmoidal labyrinth** (labyrinthus ethmoidalis) protrudes from the dorsal and lateral walls of these tubes. The ethmoidal labyrinth is composed of delicate bony scrolls, the **ethmoturbinates** (ethmoturbinalia), with the **air-filled ethmoidal meatus** (meatus ethmoidales) between them (▶ Fig. 2.17).

The **cribriform plate** (lamina cribrosa) is a sieve-like partition between the nasal and cranial cavities (▶ Fig. 2.5, ▶ Fig. 2.7 and ▶ Fig. 2.8). The cribriform plate is perforated by numerous foramina through which the **olfactory nerve bundles** pass. These nerves pass from the olfactory cortices of the brain to the olfactory bulbs. The cerebral surface is divided into two parts by a median ridge, the **crista galli**, which is considered to be the intracranial continuation of the perpendicular plate (▶ Fig. 2.7). Each half is deeply concave, forming the **ethmoidal fossae** (fossae ethmoidales), which enclose the olfactory bulbs (▶ Fig. 2.17).

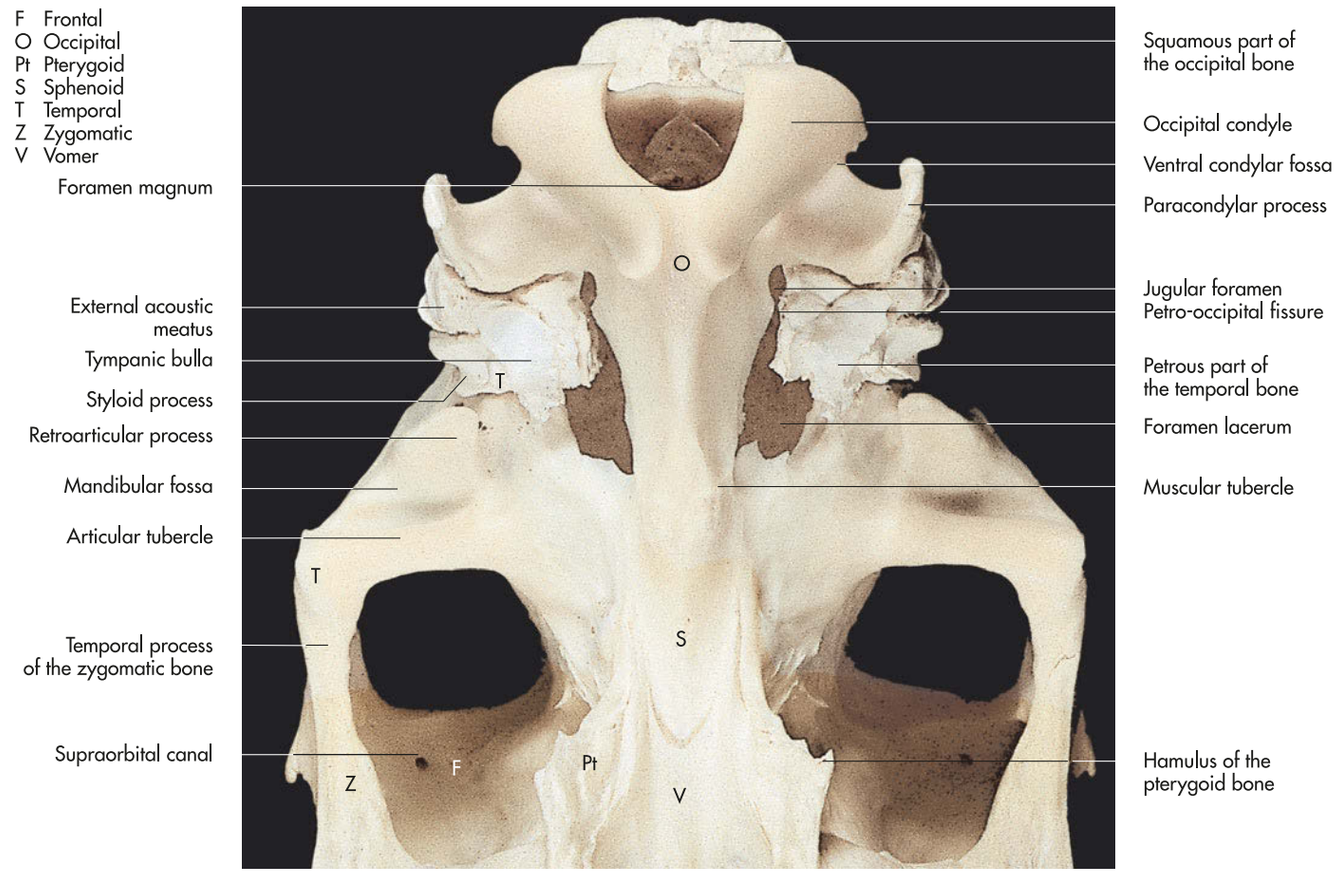

Fig. 2.12 Bones of the cranial part of an equine skull (ventral aspect).

The **ethmoturbinates** (ethmoturbinalia) arise from the dorsal and lateral walls of the ethmoidal bone. They are arranged in two rows, except in the horse, where there are three (▶ Fig. 2.17). Each ethmoturbinate possesses a basal leaf, which attaches to the walls of the ethmoid or the cribriform plate, and a spiral leaf, which projects into the nasal cavity. The majority of the ethmoturbinates have a single scroll and turn ventrally, but some divide into a dorsal and a ventral scroll. Additional secondary turbinates can be found in all the domestic mammals, but are especially common in the dog.

The **ethmoturbinates** can be divided into long, deeply lying **endoturbinates** (endoturbinalia), which extend far into the nasal cavity, and shorter, more superficial **ectoturbinates** (ectoturbinalia). Ectoturbinates are normally arranged in a single row, with the exception of the horse, where they form a double row. The number of the turbinates on each side varies in the different species: Four endoturbinates and six ectoturbinates are found in the dog, seven endoturbinates and 20 ectoturbinates in the pig, four endoturbinates and 18 ectoturbinates in ruminants, six endoturbinates and 25 ectoturbinates in the horse.

The **first endoturbinate** (endoturbinale I) is the longest and most dorsal turbinate and extends far into the nasal cavity. It forms the osseous base of the **dorsal nasal concha** (concha nasalis dorsalis) and attaches to the ethmoidal crest of the nasal bone (▶ Fig. 2.15, ▶ Fig. 2.16 and ▶ Fig. 2.17).

The **second endoturbinate** (endoturbinale II) is second in the row next to the first and forms the bony part of the **middle nasal concha** (concha nasalis media) (▶ Fig. 2.17). The following turbinates diminish in size, with the exception of the dog, in which the second to fourth endoturbinates are especially well-developed. While the dorsal and middle nasal concha are formed by the endoturbinates, the **ventral nasal concha** (concha nasalis ventralis) is part of the **upper jaw** (maxilla) (= maxilloturbinate).

The osseous structure of the **conchal bones** (ossa conchae) are described in the following summary:

- **endoturbinate I** (concha nasalis dorsalis) forms the dorsal nasal concha,
- **endoturbinate II** (concha nasalis media) forms the middle nasal concha and
- **maxilla** forms the ventral nasal concha (concha nasalis ventralis = maxilloturbinate).

The endoturbinates protrude into the nasal cavities and form part of the nasal meatus. There are three nasal meatuses:

- **dorsal nasal meatus** between the roof of the nasal cavity and the dorsal nasal concha,
- **middle nasal meatus** between the two nasal conchae, and
- **ventral nasal meatus** between the ventral nasal conchae and the floor of the nasal cavity.

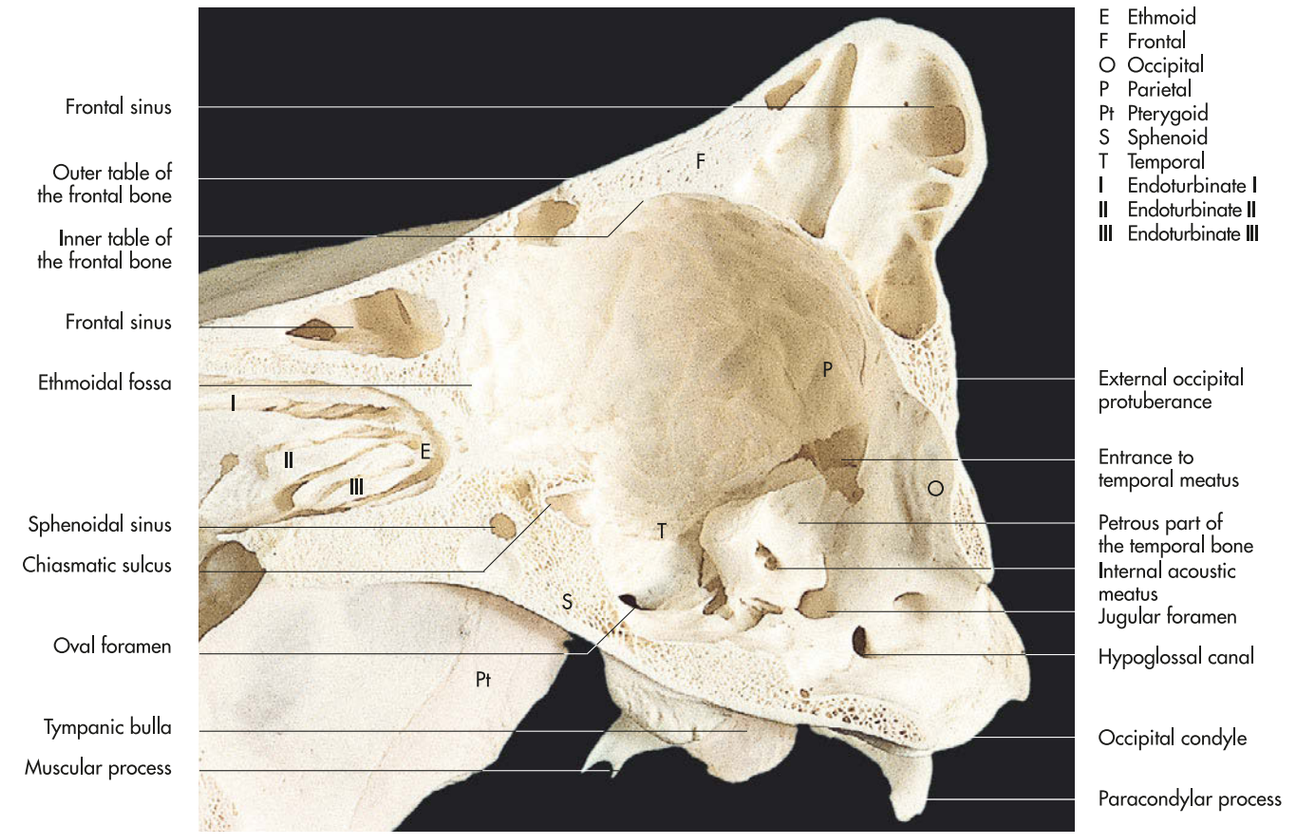

Fig. 2.13 Bones of the cranial part of a bovine skull (medial aspect of sagittal section).

2.4.2 Skull, facial part (facies, viscerocranium)

The **bones of the facial part of the skull** (ossa faciei) form the walls of the nasal cavities, the floors of which form the osseous roof of the oral cavity. The floor and the lateral walls of the oral cavity are completed by the **lower jaw (mandible)** and supported by the **hyoid bone** (os hyoideum) ventrally. The walls of the facial part of the skull are composed of the following segments in all domestic mammals:

- **the lateral walls of the nasal cavity**, formed by:
  - paired lacrimal bones (os lacrimale),
  - paired zygomatic bones (os zygomaticum),
  - paired upper jaw (maxilla) and
  - paired incisive bones (os incisivum);
- **the floor of the nasal cavity/the roof of the oral cavity**, formed by the:
  - paired palatine bones (os palatinum),
  - paired upper jaw (maxilla),
  - paired incisive bones (os incisivum) and
  - unpaired vomer;
- **the roof of the nasal cavity (dorsum nasi)** formed by:
  - paired frontal bones (os frontale) and
  - paired nasal bones (os nasale);
- **the roof or lateral walls of the pharyngeal cavity**, formed by the:
  - paired pterygoid bones (os pterygoideum),
  - parts of the unpaired vomer,
  - paired palatine bones (os palatinum) and
  - paired sphenoid bones (os sphenoidale).

The **ethmoid bone** separates the nasal and cranial cavities. The dorsal and middle nasal conchae, formed by the first and second endoturbinate, and the ventral nasal concha, formed by the maxilla, extend far into the nasal cavity. The nasal cavity is divided vertically into two equal halves by the median **nasal septum** (septum nasi) (▶ Fig. 2.17).

Nasal bone (os nasale)

The **nasal bone** forms the roof of the nasal cavity and has a concave external surface (facies externa), except in some breeds of cat, pig and horse which have a convex nose (▶ Fig. 2.1 and ▶ Fig. 2.2). The **ethmoidal crest** (crista ethmoidalis) is on the internal surface (facies interna) and forms the attachment for the **dorsal nasal concha** (endoturbinale I). The paired nasal bones present a blunt margin towards each other, articulating in a plane suture (sutura plana). The **rostral processes** (processus rostrales) form the apex of the nasal bone (▶ Fig. 2.21 and ▶ Fig. 2.37). This ends centrally in the pig, sheep and horse, laterally in carnivores and has separate apices for each nasal bone in the ox. There is an additional process on the internal surface of the nasal bone of carnivores, which forms part of the nasal septum (processus septalis). The rostral process reaches beyond the bones located ventrally to it, thus forming the **nasoincisive notch** (incisura nasoincisiva) between the nasal and the incisive bone (▶ Fig. 2.37).

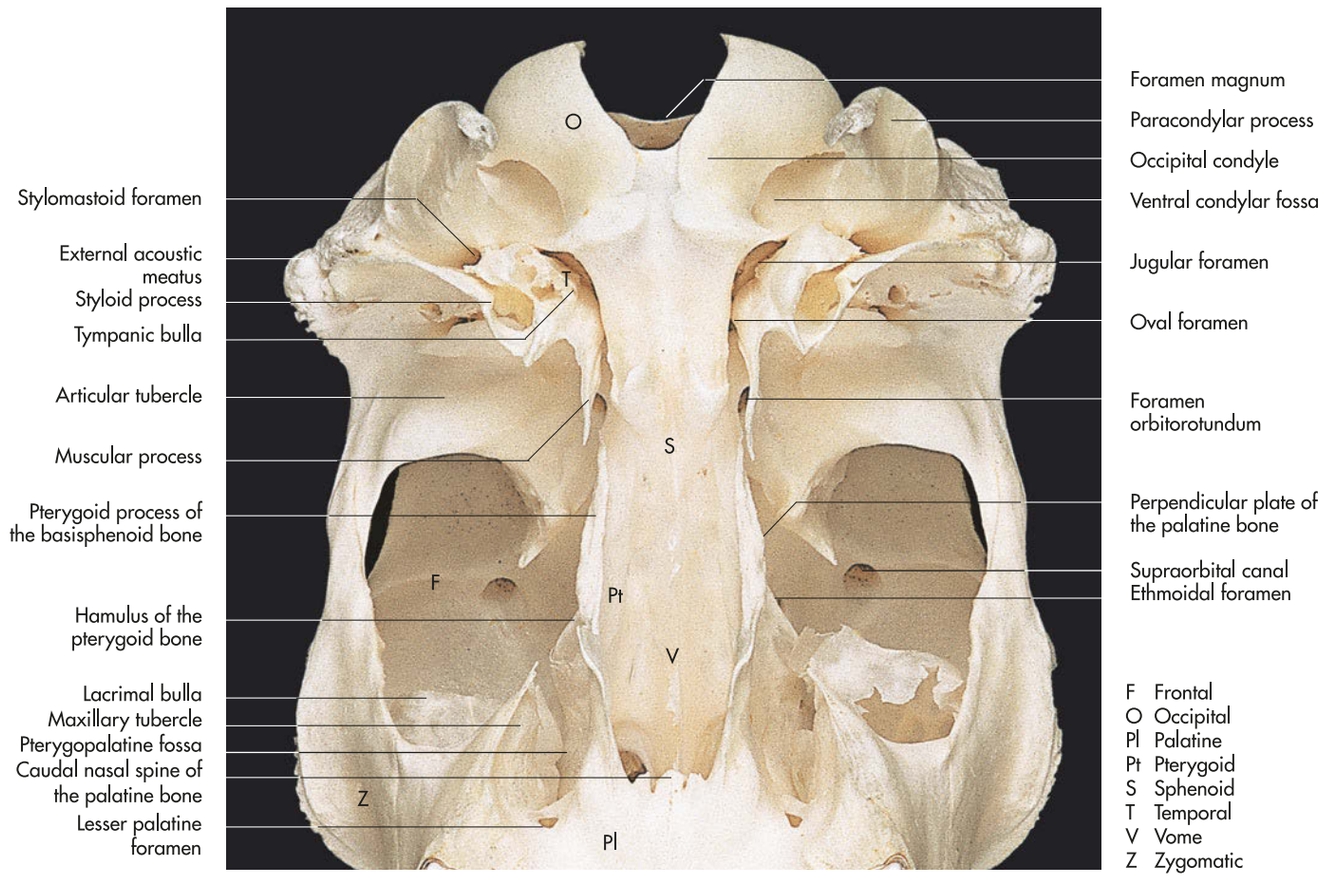

Fig. 2.14 Bones of the cranial part of a bovine skull (ventral aspect).

Lacrimal bone (os lacrimale)

The **lacrimal bone** is a small bone situated near the medial canthus of the eye forming parts of the orbit and the lateral wall of the face (▶ Fig. 2.1 and ▶ Fig. 2.2). It articulates with the frontal bone, the zygomatic bone and the maxilla in all domestic mammals and in ruminants and the horse; it also articulates with the nasal bone and in carnivores with the palatine bone. The **lateral surface** (facies lateralis) of the lacrimal bone can be divided into an **orbital part** (facies orbitalis) and a **facial part** (facies facialis), which are separated by the **supra-** and **infraorbital margins** (margo supraorbitalis, margo infraorbitalis), respectively. Near the margin of the orbital surface there is a funnel-shaped fossa, which is occupied by the dilated origin of the nasolacrimal duct (fossa sacci lacrimalis). Caudal to it is a depression for the origin of the ventral oblique muscle of the eye (fossa muscularis).

In ruminants the orbital part is large and bears the expanded thin-walled **lacrimal bulla** (bulla lacrimalis) ventrally, which contains an extension of the maxillary sinus. The nasal surface (facies nasalis) forms the rostral limits of the frontal and maxillary sinuses and is crossed almost horizontally by the **nasolacrimal canal**.

Zygomatic bone (os zygomaticum)

The **zygomatic bone** lies ventrolateral to the lacrimal bone (▶ Fig. 2.1 and ▶ Fig. 2.2) and forms parts of the bony orbit and the zygomatic arch (▶ Fig. 2.4, ▶ Fig. 2.6 and ▶ Fig. 2.18). The **zygomatic arch** (arcus zygomaticus) is formed by the union of the **temporal process** (processus temporalis) of the **zygomatic bone** and the **zygomatic process** (processus zygomaticus) of the **temporal bone** (▶ Fig. 2.9, ▶ Fig. 2.27 and ▶ Fig. 2.28). It extends towards the frontal bone, as the frontal process (processus frontalis), in all species except the horse. The frontal process articulates with the zygomatic process of the frontal bone in ruminants to form the **supraorbital margin** (margo supraorbitalis) (▶ Fig. 2.9).

The supraorbital margin of the horse is formed by the zygomatic processes of the frontal and temporal bones. In carnivores and the pig the frontal process of the zygomatic bone is joined to the zygomatic process of the frontal bone by the **orbital ligament** (ligamentum orbitale) – thus completing the orbital wall. The orbital ligament often ossifies in the cat.

The orbital surface (facies orbitalis) joins the laterally situated facial surface (facies lateralis) in the infraorbital margin (margo infraorbitalis).

The lateral surface is marked by a longitudinal ridge, the **facial crest** (crista facialis), which is continuous rostrally with the like-named ridge on the maxilla. The facial crest is very prominent in the horse, S-shaped in ruminants and less distinct in carnivores and the pig (▶ Fig. 2.37).