Chapter I

Gross Anatomy of the Pineal Complex in Animals

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Abstract

The pineal organ (epiphysis cerebri) has undergone profound morphological and functional changes during phylogeny. In poikilothermic vertebrates it is a complex structure consisting of the pineal organ proper and the parapineal organ in fish, the frontal organ in amphibians and the parietal eye in reptiles. In birds and mammals epiphysis cerebri is represented exclusively by the pineal organ proper, although in some species it is a multipart structure containing two or more fragments (a primary and accessory pineal tissue in birds, a superficial and deep pineal in mammals). The pineal organ proper of all vertebrates originates from the diencephalic roof of the third ventricle located between the habenular and posterior commissures, and more or

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Preview

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less extends to the skull. In the majority of cases the distal part of the pineal organ is better developed than the proximal part. Large interspecies variability in the pineal organ morphology is observed within each class of vertebrates. The complexity of gross anatomical organization as well as the spatial relationship to the third ventricle and to the skull became the basis for some morphological classifications of the pineal organs in mammals and birds. This chapter reviews the data on the gross anatomy of pineal glands in all vertebrate classes, however it focuses on three groups of mammals: farm animals (cow, sheep, goat, pig, horse), farm and domestic carnivores (dog, cat, fox) and small laboratory animals (rat, hamster, gerbil, mouse, guinea pig, degu, rabbit) as well as on domestic birds (chicken, duck, goose, turkey). The anatomical characterization of the pineal glands of the above mentioned species is reported based on literature data and our own studies.

Introduction

The morphology and function of the pineal organ have undergone a deep reorganization during evolution. In lower vertebrates – fish and amphibians - the *epiphysis cerebri* is a photosensory organ showing no signs of morphological adaptation to endocrine activity, although producing large amounts of melatonin in a diurnal rhythm. The pineals of reptiles and birds take an intermediate evolutionary position, between the organs of anamniotes and mammals, and demonstrate large interspecies differences in their organization. The pineals with well-developed photosensory structures as well as the organs with morphology closely resembling typical endocrine glands are present within each of these vertebrate classes. The pineal gland of mammals lacks sensory functions and structures, being a pure secretory organ. From an anatomical point of view, the most important evolutionary modifications of the pineal organ include: reduction of the sensory components, alternation of long axis orientation from the anterior-dorsal to the posterior-dorsal and transformation of the internal structure from a vesicular one into a compact one.

Despite the large variability in the anatomy, histology and cytology of vertebrate pineal organs, the process of their ontogeny shows many common features in all vertebrates. The pineal develops from a vesicular or compact evagination of the dorsal wall of the diencephalon (Oksche, 1965; Garcia-Maurino, 2001; Regodón and Roncero, 2005; Regodon et al., 2006; Snelson et al., 2008). Poikilothermic vertebrates develop a pineal organ proper and a
pineal accessory organ, which is represented by the parpineal organ in fish, by the frontal organ in amphibians, and by the parietal eye in reptiles. Birds and mammals develop only the pineal organ proper.

**Pineal Complex of Fish**

The pineal complex of fish (Fig. 1) consists of two subunits, prominently differing in size, called the pineal organ and the parapineal organ (Völlrath, 1981; Borg et al., 1983; Ekström and Meissl, 1997). Due to very close anatomical location, the dorsal sac is also listed by many authors (Confente et al., 2008; Herrera-Pérez et al. 2011) as a part of the fish pineal complex, however it should be underlined that it does not share any structural or functional features with the pineal organ and the parapineal organ.

![Schematic representation of the fish pineal organ (sagittal section, scale not maintained) consisting of the pineal organ and the parapineal organ (arrow). CR – cerebellum, DS – dorsal sac, HC – habenular commissure, OT – optic tectum, PC – posterior commissure, PO - pineal organ, TI – telencephalon. Scheme is made on the basis of Ekström and Meissl (1997).](image)

At the early stages of embryonic development, the fish pineal complex is visible as a single compact thickening of the prosencephalic roof, located close to the posterior commissure (Ekström et al., 1983; Ekström and Meissl, 1997). The primordium of the pineal organ is situated caudally to that of the parapineal organ. Thereafter, both primordia formed protrusions, elongating in the rostromedial direction. The pineal organ grows much more intensively than
the parapineal organ, which remains rudimentary. The pineal organ takes the median position (although the pineal stalk emanates from the diencephalon with a slight left bias - Liang et al., 2000), whereas the parapineal organ is shifted to the left side (Halpern et al. 2003, Snelson et al., 2008).

The pineal organ of the fish is an elongated structure extending (dorsally and more or less rostrally) from the diencephalic roof to the skull (Ekström and Meissl, 1997; Confente et al., 2008; Herrera-Pérez et al., 2011). Usually, it consists of a bulb-shaped end-vesicle located distally and a slender, elongated stalk situated proximally. The end-vesicle is attached by connective tissue to the skull roof, which in many species shows prominent modifications of its structure at this place, leading to the formation of the “pineal window” (Srivastava, 2003; Herrera-Pérez et al., 2011). In this zone, melanophores are usually sparsely distributed, bone tissue is thinner than in surroundings or not continuous and a cartilage (considered as lens-like structure) may be present just above the pineal end-vesicle (Srivastava, 2003). The “pineal window” is visible as a light spot on the outer surface of the head (Herrera-Pérez et al., 2011). The pineal stalk attaches the organ to the brain at the area situated between the habenular and posterior commissures. Ventrally and rostrally, the pineal organ joins with the dorsal sac (a large hollow, folded structure), which can completely surround the pineal stalk (Ekström and Meissl, 1997).

The differences in gross morphology of the fish pineal organ mainly concern the size of organ, location in relation to the skull roof, and the proportion between the size of the end-vesicle and the length of the stalk (Vollrath, 1981). Moreover, in some species the presence of short organs located close to the diencephalon (not connected to the skull) and organs consisting of a distal thickening, a slender stalk and a proximal thickening was reported (Vollrath, 1981).

The internal structure of the pineal organ shows large interspecies variability ranging from thin-walled organs with a more or less folded wall and a prominent lumen, to organs with compact structure without a lumen (Vollrath, 1981).

The parapineal organ was found to be present in the majority of fish species studied (Borg et al., 1983). It is formed by a very small group of closely packed cells, located on the left side of the pineal stalk, close to the left habenulae. The presence of the parapineal organ results in a clear asymmetry of the habenular region in fish (Halpern et al., 2003). A nerve tract connects the parapineal organ with the left habenular nucleus.

It is worth noticing that in contrast to fish, the parapineal organ of cyclostome Lampetra planeri is an elongated structure containing an end-
vesicle and a prominent lumen. In this species the parapineal organ underlies the pineal organ (Meiniel and Collin, 1971; Vollrath, 1981).

**Pineal Complex of Amphibians**

The organization of the pineal complex (Fig. 2) differs between three orders of currently living amphibians: anurans, urodeles and caecilians (Vollrath, 1981). The pineal complex of anurans is usually composed of the pineal organ proper (or *sensu stricto*) and the frontal organ (both with similar cellular composition). Urodeles and caecilians exclusively possess the pineal organ proper.

![Figure 2](image-url)

Figure 2. Schematic representation of the pineal complex of amphibians (sagittal section, scale not maintained) consisting of the frontal organ and the pineal organ proper. III – 3rd ventricle, FO - frontal organ, HC – habenular commissure, OS – bones of skull, PC – posterior commissure, POP - pineal organ proper. Scheme is made on the basis of the data presented by Kelly and Van de Kamer, 1960.

At the initial stages of the embryonic development the amphibian pineal complex is visible as a single protrusion of the diencephalic roof, which increases stepwise in size and takes the form of an elongated vesicle, possessing a wide connection with the brain ventricle (Von Haffner, 1951, 1952; Kelly, 1963). In anurans, a distal part of the pineal anlage separates from a proximal part and moves to a new location inside the head skin. This process, leading to formation of the frontal organ, did not occur in urodeles and caecilians (Kelly, 1963). Proliferation of cells in the anlage results in reduction and eventually, in subdivision into parts of the pineal lumen, which in many species loses the connection with the brain ventricular system.
The pineal organ proper (Fig. 2) is usually an elongated structure extending in rostral or rostrodorsal direction from the region of the diencephalon roof located between the habenular and posterior commissures (Oksche, 1955; Kelly and Van de Kamer, 1960; Kelly and Smith, 1964). According to a few published studies regarding the size of this organ, its length ranges from 400 to 1500 \( \mu \text{m} \) and the width from 20 to 400 \( \mu \text{m} \) (Vollrath, 1981). The internal organization of the pineal organ proper varies between species and therefore three forms of the organ could be distinguished: (1) the sac-like organ with short projections arising from the wall into the wide lumen occurring in \textit{Rana esculenta} (Oksche, 1955; Kelly and Van de Kamer, 1960); (2) the organ with prominent septa extending from the wall and dividing the lumen into parts occurring in \textit{Rana pipiens} (Kelly and Smith, 1964); and (3) the almost solid organ with a rudimentary lumen occurring in \textit{Taricha torsa} (Kelly, 1963).

The frontal organ (Fig. 2) is situated in the skin (just under the epidermis) in the median plane between the eyes (Guglielmotti et al., 1997). The place containing this extracranial part of the pineal complex may be visible in living animals as a pale area or a small protrusion. The frontal organ is an oval structure, varying in size between species (usually 100 - 300 \( \mu \text{m} \)) and consisting of a thick wall and a small irregularly-shaped lumen.

The frontal organ is connected with the pineal organ proper by the frontal nerve (Guglielmotti et al., 1995). After leaving the frontal organ this nerve runs caudally in the dermis or just below it, penetrates the cranium at the level of the telencephalon and joins the pineal tract located inside the pineal organ proper.

**Pineal Complex of Reptiles**

The pineal complex of reptiles (Fig. 3) is largely variable in its organization. In more than half of the lizard species the pineal complex consists of two separate components: the parietal eye (also called the third eye) and the pineal organ proper (Gundy and Wurst, 1976; Vollrath, 1981). The remaining lizard species, turtles and snakes, only possess the pineal organ proper. The pineal complex is absent in all investigated representatives of the order Crocodilia. According to the frequently cited study of Gundy et al. (1975) lizards without parietal eyes occur at low geographical latitudes, whereas species living at higher latitudes comprise these photoreceptive
structures. The differences in the presence of the parietal eye have also been reported between burrowing and arboreal lizards (Gundy and Wurst, 1976).

The pineal complex of reptiles develops as an evagination of the diencephalic roof, which divides early into two parts lying in an anteroposterior direction. The anterior part is the anlage of the parietal eye, whereas the parietal organ proper develops from the posterior part (Petit, 1967 after Vollrath, 1981).

![Figure 3. Schematic representation of the pineal complex of reptiles (sagittal section, scale not maintained) consisting of the parietal eye and the pineal organ proper. HC – habenular commissure, OS – bones of skull, PC – posterior commissure, PE - parietal eye, POP - pineal organ proper. Scheme is made on the basis of the data presented by Kummer-Trost (1956) and Ung & Moltendo (2004).](image)

The parietal eye (Fig. 3) is a small structure located inside the dorsal skull roof, in the median plane, slightly caudally to the eyes (Eakin, 1973). Like the amphibian frontal organ, it is visible in living lizards as a differentially pigmented spot on the skin. The parietal eye has a form of an oval vesicle, usually with more or less prominent differentiation of its wall into two parts called the lens and the retina, showing a distinct histological organization. In addition, the cornea - a specific transparent part of the integument – is distinguished in some species. The parietal eye is connected with the central nervous system by the parietal nerve.

The pineal organ proper (Fig. 3) is an elongated structure extending in the rostodoral direction from the diencephalon roof (Gundy and Wurst, 1976; Owens and Ralph, 1978). Due to prominent interspecies differences of the internal structure, three morphological forms of the organ can be distinguished: (1) tubular with a more or less convoluted wall, (2) follicular
and (3) solid (Vollrath, 1981; Kalasow et al., 1991). The first two forms are typical for lizards and turtles, the third one – for snakes. It is generally accepted that there is no communication between the pineal lumen of the fully developed organs of the tubular form and the brain ventricular system (Owens and Ralph, 1978). The neuronal connection between the pineal organ proper and other structures of the brain occurs via the pineal tract.

**Pineal Organ of Birds**

The avian *epiphysis cerebri* is represented exclusively by the pineal organ proper. It develops as a single evagination of the diencephalic roof located between the habenular and the posterior commissures (Menaker and Oksche, 1974; Vollrath, 1981). The structure of the pineal organ undergoes a deep transformation during both the embryonic and post-embryonic development.

The avian pineal organ shows large interspecies morphological variability, being a probable consequence of its intermediate evolutionary position between the photosensory pineal of lower vertebrates and the secretory pineal of mammals (Quay, 1965; Menaker and Oksche, 1974; Vollrath, 1981; Binkley, 1988). From an anatomical point of view, Quay and Renzoni (1967) distinguished six types of pineals in birds, differing from one another in the proportion between the distal and proximal parts of the organ as well as in the attachment to the intercommissural region. The most frequently observed are the pineals of types I, II and III, which are composed of a prominent, superficially located distal part and a tapering, strongly reduced proximal part. The differences between types I, II and III concern the attachment of the organ via the parenchymal stalk to the intercommissural region, which is difficult to follow in type I, apparently lacking in type II and unquestionable in type III. The pineal organs of type IV are rod-like in shape and extend from the intercommissural region to the roof of the skull. Type V includes the pineals consisting of two separate parts – proximal and distal. The pineal organs of type VI have atrophic distal parts. The weakness of this widely cited and used classification proposed by Quay and Renzoni (1967) is the distinguishing of the types I, II and III based on the connection of the pineal with the intercommissural region, where the details are difficult to follow even in serial histological sections and may undergo significant changes during postnatal development. It is worth noting that the most commonly occurring form of the avian pineal organ consists of a prominent superficially localized distal part.
and a tapering or slender proximal part, connected with the intercommissural region via the choroid plexus and eventually a parenchymal stalk. The shape of the superficial parts differs markedly between species.

Some avian species have a minute structure consisting of a few follicles or solid nodules, named the accessory or secondary pineal tissue. Quay and Renzoni (1967) reported its presence in about 20% of the examined birds, however it is suspected that this structure occurs more frequently but is overlooked due to its small size. The accessory pineal tissue is located rostrally to the habenular commissure and the pineal stalk. In more than 50% of the species possessing this structure, it is shifted to the left side from the midsagittal plane (Quay and Renzoni, 1967). The presence of the accessory pineal tissue enables to consider that the avian pineal organ may be a bipartite structure consisting of the primary pineal organ and the secondary pineal tissue (Vollrath, 1981).

Interspecies and intraspecies variability of the pineal size are also prominent. The largest pineals were observed in *Dromaeus novaehollandiae* (17 mm in length and 0.1 g of weight), *Struthio camelus* and *Rhea Americana* (Starck, 1955; Vollrath, 1981). Functional activity of the pineal gland has an important effect on the pineal volume. It is known that both the photoperiod and the wavelength of light influence the pineal gland volume (Johnson et al., 1982). The diurnally active birds usually have the pineals of moderate to large size and the species with nocturnal or crepuscular activity - small or atrophic organs (Quay, 1972). In contrast to these data, more recent studies have revealed the presence of well-developed, functionally active pineals in some nocturnal birds (Haldar and Bishnupari, 2001). The studies performed on house sparrows showed that young, immature birds have larger pineals than adult ones (Ralph and Lane, 1969). However, our research concerning the domestic turkey demonstrated the increase of the pineal size during the post-hatching development (Przybylska-Gornowicz et al., 2005).

The internal structure of the avian pineal organ also shows significant interspecies variability of the pineal size are also prominent. The largest pineals were observed in *Dromaeus novaehollandiae* (17 mm in length and 0.1 g of weight), *Struthio camelus* and *Rhea Americana* (Starck, 1955; Vollrath, 1981). Functional activity of the pineal gland has an important effect on the pineal volume. It is known that both the photoperiod and the wavelength of light influence the pineal gland volume (Johnson et al., 1982). The diurnally active birds usually have the pineals of moderate to large size and the species with nocturnal or crepuscular activity - small or atrophic organs (Quay, 1972). In contrast to these data, more recent studies have revealed the presence of well-developed, functionally active pineals in some nocturnal birds (Haldar and Bishnupari, 2001). The studies performed on house sparrows showed that young, immature birds have larger pineals than adult ones (Ralph and Lane, 1969). However, our research concerning the domestic turkey demonstrated the increase of the pineal size during the post-hatching development (Przybylska-Gornowicz et al., 2005).

The internal structure of the avian pineal organ also shows significant interspecies differences and therefore three main forms of the organ are distinguished: saccular, tubulofollicular and solid lobular (Vollrath, 1981). In many species the histological organization of the pineal shows regional variations (Przybylska-Gornowicz et al., 2012) and in view of this, an additional form called a solid-follicular has been separated (Ohshima and Hiramatsu, 1993; Haldar and Bishnupari, 2001). It should be emphasized that the internal organization of the avian pineal undergoes prominent changes during the period of post-hatching development, which differs significantly
between species (chicken – (Boya and Calvo, 1978); turkey – (Przybylska-Gornowicz et al., 2005)).

Pineal Organ of the Chicken (*Gallus domesticus*)

The pineal organ of the domestic chicken (Fig. 4) is situated in a triangular space between the cerebellum and two hemispheres of the telencephalon. In adult birds, the organ is clavate in shape, approximately 2.8 mm long and 1.8 mm wide (Sato and Wake, 1983).

Figure 4. The pineal organ of the chicken (*Gallus gallus domesticus*) in situ. (a). Sagittal section through the head – notice the pineal (arrows) in relation to the cerebellum and cerebral hemispheres. (b) Dorsal view of the brain. CH - cerebral hemispheres (L- left, R – right), CR – cerebellum, OS – bones of skull, PG – pineal gland.
It ventrally tapers and passes into a solid stalk, which attaches the pineal to the intercommissural region. The pineal organ of the adult chicken belongs to type III according to the classification of Quay and Renzoni (1967).

The internal structure of the chicken pineal organ undergoes a prominent transformation during the postembryonic life (Boya and Calvo, 1978). The organ has the tubulofollicular form in young birds and the solid lobular form in adult animals.

Pineal Organ of the Domestic Turkey (*Meleagris gallopavo*)

The turkey pineal organ (Fig. 5) consists of a narrow proximal part and a club-shaped top. The narrow part is located between the cerebrum and the cerebellum. The club-shaped top closely attaches to the dura mater. The narrow part of the pineal organ extends into the pineal stalk, which in young birds is attached to the intercommissural region of the diencephalon, closer to the habenular commissure than to the posterior commissure.

![Figure 5. The pineal organ of the turkey (*Meleagris gallopavo*).](image)

(a) Sagittal section through the pineal organ of a two-week-old turkey, HE staining. (b) Schematic representation of changes occurring in the pineal gland of a domestic turkey during the post-hatching development. CP – choroid plexus, CR – cerebellum, HC – habenular commissure, PC – posterior commissure, PG – pineal gland.
This connection is reduced in older birds. Rostrally, the pineal organ joins with well-developed choroids. The caudal part of the organ contains the pineal lumen, which extends into the stalk lumen. The accessory pineal tissue is located close to the proximal part of the pineal stalk. The pineal organ has a tubulofollicular form.

The turkey pineal gland undergoes prominent transformation during the post-embryonic development (Przybylska-Gornowicz et al., 2005). The pineal gland increases in size from 7 mm (1-day-old birds) to 15 mm (56-week-old bird) in length (Fig. 5). The proximal part of the stalk shows age-dependent reduction. In turkeys aged two weeks and younger the pineal stalk has a lumen, which connects with the third ventricle. In older birds this connection obliterates. As a consequence of these changes, the pineal organ in adult turkeys can be categorized as type II in the above-mentioned classification of Quay and Renzoni (1967). The thickness of the wall of follicles increases stepwise with age and simultaneously their lumen is reduced (Przybylska-Gornowicz et al., 2005). Specific, calcified concrements are formed in some follicles (Przybylska-Gornowicz et al., 2009). Despite these changes, the organ retains the tubulofollicular form during its entire postnatal life.

The Pineal Organ of the Domestic Goose (*Anser domesticus*)

Figure 6. The pineal gland of the goose (*Anser anser*) in situ. (a) Dorsal view of the brain. (b) Caudal view of the brain after removing the cerebellum. The pineal organ - arrows, remnant of the dura matter – asterisk. CH - cerebral hemispheres (L- left, R – right), CR – cerebellum, PG – pineal gland.
The pineal organ of adult geese belongs to type II, according to the classification of Quay and Renzoni (1967), and possesses a tubulofollicular form (Fig. 6). It is an elongated organ measuring lengthwise from 6 to 8 mm, situated between the cerebrum and cerebellum. It consists of a wide distal part (covering a quarter of the pineal) with a diameter up to 2.5 mm and a narrow, middle-proximal part (comprising the remaining three quarters) with a diameter of about 1.5 mm. The superficially localized distal part is connected to the dura mater. At its proximal pole the pineal is attached via the choroid plexus to the diencephalon, but the pineal stalk cannot be traced entirely to its origin. The most proximal part of the stalk, which can be observed, appears to be atrophic and does not contain a lumen. The pineal lumen has not been observed (Quay and Renzoni, 1967; Prusik et al., 2006). The accessory pineal tissue is lacking.

The Pineal Organ of the Domestic Duck
(*Anas Platyrhynchos F. Domestica*)

The adult duck pineal organ has a form of type II according to the classification of Quay and Renzoni (1967). It is an elongated organ of a length of 4 – 5 mm. The pineal consists of a club shaped top located distally with a diameter of 2 - 2.5 mm and a narrow proximal part with a diameter of about 1 mm. The distal part is closely attached to the dura mater. At its proximal pole, the pineal is connected via the choroid plexus to the diencephalon. As in the goose, the most proximal part of the pineal stalk is reduced. The pineal lumen is lacking. In the duck, there is no occurrence of the accessory tissue.

Pineal Gland of Mammals

The mammalian pineal gland develops from the diencephalic roof as a single protrusion (Garcia-Maurino, 2001; Regodon and Roncero, 2005; Regodon et al, 2006). During the postnatal life it is a solid organ, extending from the region located between the habenular and posterior commissures in the caudo-dorsal direction (Vollrath, 1979, 1981). The mammalian pineal gland shows large variability of its shape ranging from round or oval organs located close to the third ventricle to elongated organs reaching the skull roof. In some species possessing the elongated pineals the distal part is well
developed, whereas the proximal one and especially an intermediate part are rudimentary. In this case the pineal may consist of two parts: a prominent superficial part located below the skull and a small deep part located in the intercommissural region. Both parts are connected via a thin pineal stalk, which could be partially lacking. Independent from the shape of organ, at its proximal pool, the pineal gland joins with the pineal recess of the third ventricle. The rostral surface of the gland is associated with the choroid plexus, which forms the suprapineal recess.

Figure 7. Schematic representation of the forms of the pineal glands in mammals according to Vollrath’s classification.

Considerable variations in morphology of the mammalian pineal glands became the basis for the classification developed by Vollrath (1979, 1981), taking into account the shape of the pineal gland, the spatial relationship to the third ventricle and the continuity of the pineal parenchyma. This classification highlighted six types of mammalian pineals (Fig. 7). Type A (proximal) includes the pineal glands situated in the immediate vicinity of the third ventricle, which are usually round or oval in shape. In this type, the pineal
tissue may be in close contact with the cerebrospinal fluid. Type AB (proximo-intermediate) is similar to type A, but the length of the gland exceeds at least twice the width of the organ. Type ABC (proximo-intermediate-distal) includes an elongated, rod-shaped pineal gland extending from the intercommissural region to the dura mater. Type AβC is similar to type ABC, but possesses a reduced intermediate part (located between the proximal and distal parts). Type αβC is represented by elongated glands, in which the proximal and intermediate parts are reduced and the distal part is well developed and closely related to the dura mater. Type αC is similar to type αβC, but the intermediate part is missing. The presence of atypical pineals was reported in a few mammalian species. The pineals composed of the diffused pineal tissue bordering the pineal recess and lying on the dorsal surface of the habenular commissure occur in the elephant (*Loxodonta africana* – (Haug, 1971)) and the rock hyrax (*Procavia capensis* – (Quay and Millar, 1971)). In the opossum (*Didelphys virginiana*) the pineal is a hollow structure surrounding the pineal recess (Hofer et al., 1976). Similarly, the pineal of the European beaver (*Castor fiber*) also possesses a very deep pineal recess (Bulc, 2009).

The size of the pineal gland differs markedly between species (from 0.2 mg in the house mouse to more than 3000 mg in the Weddel seal and the walrus) and it is not proportional to the weight of the animal. The detailed survey of the data concerning the pineal weight and volume is presented by Vollrath (1981).

### Farm Animals

The pineal glands of the sheep and the goat are classified as type A, while these organs in the pig, the bovine and the horse belong to type AB according to the classification created by Vollrath (1979). They are located directly on the dorsal part of the diencephalon and covered by the telencephalon hemispheres and the cerebellum (Vollrath, 1979; Møller and Baeres, 2002).

**The Pineal Gland of the Bovine (*Bos taurus*)**

The bovine pineal gland (Fig. 8) is located among the rostral colliculi, in the median fissure of the brain. The gland demonstrates an ovoid shape, with a
length ranging from 8 to 12 mm and a width ranging from 4 to 8 mm. It is connected to the habenular and posterior commissures by a stout stalk. The proximal part of the gland joins directly with the pineal recess of the third ventricle (Basile et al., 1986, our own observations). The shape, location and connection with the third ventricle are similar in newborn and adult individuals. During the period of postnatal development, the pineal gland exhibits a notable increase in size before puberty. Similar anatomical features are characteristic to the pineal gland of the buffalo *Bubalus bubalis* (Carvalho et al., 2008).


The Pineal Gland of the Sheep (*ovis aries*)

The ovine pineal gland (Fig. 9) is a pea-like structure with a diameter of 4.0 – 8.0 mm (inter-individual differences), located close to the epithalamus. On the sagittal section through the brain it is visible as a round or oval structure, situated between the habenular and posterior commissures. The ventral surface of the gland joins the pineal recess of the third ventricle. Rostrally, the pineal is connected to the choroid plexus. According to Redondo et al. (2003), the size of the ovine pineal gland does not increase significantly during the period of postnatal life.
Figure 9. The pineal gland of the sheep (*Ovis aries*) *in situ*. (a) Dorsal view of the brain. (b) Sagittal section of the brain. (c) Part of the sagittal brain section showing the connection of the pineal gland with the commissures in magnification. (d), (e) Dorsal view of the pineal gland and the corpora quadrigemina after tilting of the cerebellum and (d) after cutting of the corpus callosum and removal of the choroid plexus (e). III – 3rd ventricle, CC – corpus callosum, CH - cerebral hemispheres (L- left, R – right), CQ – corpora quadrigemina, CR – cerebellum, HC – habenular commissure, PC – posterior commissure, IC – inferior calliculi, PG – pineal gland, SC - superior colliculi, T – thalamus.
The Pineal Gland of the Goat (*Capra hircus*)

Generally, the goat pineal organ is very similar to that of sheep. In one-day-old goats, it has a shape of a truncated cone with a length of 3 – 4 mm, and a width of 2.5 – 3.0 mm. Its shape and location do not undergo significant changes up to 3 years of age, but its size increases about 150% (Nowicki and Przybylska-Gornowicz, 2006).

The Pineal Gland of the Pig (*Sus scrofa*)

The pineal gland of the domestic pig (Fig. 10) is located between the posterior and habenular commissures, close to the third ventricle (Przybylska,
It is shaped like a grain of rye and in mature animals it measures 7.0 ± 0.4 mm in length and 3.5 ± 0.5 mm in width. In newborn piglets the size of the pineal gland is three times lower than in adult pigs (Przybylska, 1990). The gland has a short stalk with a shallow pineal recess of the third ventricle.

Figure 11. The pineal gland of the horse (*Equus caballus*) *in situ*. (a) Dorsal view of the brain. (b) Sagittal section of the brain. (c) Part of the sagittal brain section showing the connection of the pineal gland with the commissures in magnification. (d) Caudal-dorsal view of the corpora quadrigemina and the pineal gland. (e) Caudal-dorsal view of the pineal gland and the choroid plexus (arrows) after half-opening the cerebral hemispheres. (f) Rostral view of the diencephalon and the corpora quadrigemina after removal of the choroid plexus. III – 3rd ventricle, CC – corpus callosum, CH – cerebral hemispheres (L – left, R – right), CR – cerebellum, HC – habenular commissure, PC – posterior commissure, PG – pineal gland, SC – superior colliculi, T – thalamus.
The Pineal Gland of the Horse (*Equus caballus*)

The pineal gland of the horse (Fig. 11) has the shape of a regular oval with a length from 12 to 18 mm and a maximal width from 6 to 9 mm. Its position in relation to the third ventricle is similar to that of the bovine pineal.

**Farm and Domestic Carnivores**

The cat pineal gland (Fig. 12) is located close to the third ventricle, between the habenular and posterior commissures. It is pear-shaped, with a length of 3.0 – 3.2 mm and a width of 2.6 – 3.0 mm in the proximal part (Duvernoy and Risold, 2007; own unpublished data).

![Figure 12. Schematic representation of the pineal gland of the cat (*Felis catus*) – a sagittal section, scale not maintained. III – 3rd ventricle, CC – corpus callosum, CHR – right cerebral hemisphere, CR – cerebellum, HC – habenular commissure, PC – posterior commissure, PG – pineal gland, T – thalamus.](image)

The pineal gland of the dog is reported as belonging to type A or AB of the classification proposed by Vollrath (1979). It is round, oval or conical in shape (Calvo et al., 1990). In our studies, we observed large inter-individual variations regarding the size of the dog pineals, which in many cases could not be explained as differences between breeds (unpublished data). The largest pineal in our studies has a diameter of 5.0 mm and was found to be in a small-
size, mixed-breed male. In many individuals, usually at ages beyond 10 years, the pineal glands were not found during autopsy.

The fox pineal gland (Fig. 13) represents type A according to Vollrath’s classification. It is completely covered by the corpus callosum. The shape of the pineal varies from round (with a diameter of 4.0 – 5.0 mm) to conical (5 - 6 mm long and 3 - 4 mm wide).

Figure 13. The pineal gland of the fox (Vulpes vulpes) in situ. (a) Caudal-dorsal view of the part of the brain after tilting of the cerebellum. (b) The pineal at the frontal edge of the colliculi visible after slicing of brain hemispheres. III – 3rd ventricle, CH - cerebral hemispheres (L- left, R – right), CR – cerebellum, HC – habenular commissure, PG – pineal gland, SC - superior colliculi.

Small Laboratory Animals

Rodents

The Pineal Gland of the Rat (Rattus norvegicus)

The rat pineal gland (Fig. 14) extends from the roof of the third ventricle to just beneath the skull and represents type αβC or αC of Vollrath’s classification (Gregorek et al., 1977; Vollrath, 1979). It is segmented into two parts - a deep pineal (located in the dorsal-posterior diencephalon) and a superficial pineal (located beneath the surface of dura mater). The superficial pineal is club-shaped with a diameter ranging from 600 to 2000 µm. It
constitutes about 95 – 99% of the entire pineal weight. The deep pineal is formed by a small accumulation of the pineal parenchyma located between the habenular and the posterior commissure. It has a variable connection with the third ventricle. Both parts of the gland are connected with a thin stalk, which may be not continuous. According to the study of Boeckmann (1980) on Sprague-Dawley rats, a continuous parenchymal stalk is present in only 18% of individuals, whereas it is interrupted in 76% of individuals and lacking in 6% of rats. The study of Djeridane (2008) showed that in Wistar rats the pineal represents a single organ rather than a complex organ and should be classified as type C. The deep pineal appeared to be lacking and the choroid plexus never abuts the true pineal parenchyma. The habenular commissure is directly fused to the posterior commissure in the diencephalic roof, which means there is no pineal recess. The stalk extending from the superficial pineal is mainly composed of the connective tissue (Djeridane, 2008).

Figure 14. The pineal complex of the rat (*Rattus norvegicus*) *in situ*. (a) Dorsal view of the brain. (b) Caudal-dorsal view of the corpora quadrigemina after slicing of brain hemispheres. (c) the pineal gland - notice shape and presence of the stalk. (d) Schematic representation of the part of the brain (scale not maintained). CH - cerebral hemispheres (L- left, R – right), CR – cerebellum, HC – habenular commissure, IC – inferior calliculi, PC – posterior commissure, PG – pineal gland, S – pineal stalk, SC - superior colliculi.
The Pineal Gland of the Gerbil (*Meriones Unguiculatus*)


The gerbil pineal (Fig. 15) is an elongated, solid structure, which varies in length from 2400 µm to 2800 µm. It consists of a deep pineal, a stalk and a superficial pineal (Nielsen and Møller, 1978). The deep pineal lying superior to the habenular commissure measures 200 - 300 µm in thickness and joins with the III ventricle by the pineal recess. The pineal stalk (50-100 µm thick) lies on the superior surface of the midbrain and joins the deep pineal with the superficial portion of the gland, which is an elongated structure (280-350 µm
in size). The superficial part of the pineal is posterior to the telencephalon, and anterior and dorsal to the midbrain (Gregorek et al., 1977; Japha et al., 1977; Binkley, 1988). The extension of the choroid plexus of the third ventricle forms the prominent pineal sac. This sac makes the roof of the diencephalon rostral to the habenular commissure and the pineal gland (Gregorek et al., 1977; Vollrath, 1981).

The Pineal Gland of the Mouse


The pineal gland of the PET mouse arises between the habenular and posterior commissures and has a prominent pineal recess, which is continuous with the third ventricle of the diencephalon (Fig. 16). This elongated organ is dorsocaudally flexed and located anterior and dorsal to the corpora quadrigemina of the midbrain. Its length varies from 850 to 1200 µm and it is
usually narrower near its proximal end, which connects this structure with the commissures. The distal portion is enlarged and measures 350 µm in diameter (Gregorek et al., 1977). The pineal sac, like in the gerbil, forms the roof of the diencephalon rostral to the habenular commissure and the pineal gland (Gregorek et al., 1977; Vollrath, 1981; Binkley, 1988). The pineal gland of the white-footed mouse (Peromyscus leucopus) consists of three parts: a superficial pineal, a stalk and a deep pineal. Like in the rat, there is a difference between individuals concerning the pineal stalk, which is continuous in 31% of examined mice (Quay, 1956).

The Pineal Gland of Hamsters

The golden hamster pineal complex is generally similar to the other rodent pineals described above. It is composed of a deep pineal, a superficial pineal and a connecting stalk. The deep pineal spans the area between the habenular and posterior commissures. It is oval-round in shape, with a length of 340 - 380 µm, a width of 200-260 µm and possesses a small pineal recess. The superficial pineal is oval in shape, with a length from 600 to 820 µm and a diameter from 400 to 600 µm. These two parts are connected through the stalk without parenchymal cells with a length from 2700 to 3200 µm. The dorsal sac abuts to the deep pineal, the pineal stalk and a dorsal fragment of the superficial pineal (Gregorek et al., 1977; Vollrath, 1981). The pineal complex in the Chinese hamster, as in the golden hamster, is also composed of the same three components. The shape and size of the deep and superficial pineals are similar. However, distinguishable from the golden hamster, the deep pineal prolongs into the stalk, which means that it has a parenchymal nature. The dorsal sac extends over the deep pineal and stalk (Gregorek et al., 1977).

The Pineal Gland of the Guinea Pig (Cavia porcellus)

The pineal gland of the guinea pig (Fig. 17) is an elongated, dumbbell-shaped organ extending from the intercommissural region to the skull roof. It is classified as type ABC or AβC, if an intermediate part is much thinner than proximal and distal parts. The length of the pineal gland is 1000 - 1300 µm and width is 100 - 200 µm at the intermediate part and 200 µm at the proximal and distal parts.

The Pineal Gland of Degu (Octodon degus)

The pineal gland of degu (Fig. 18) is located close to the third ventricle, between the habenular and posterior commissures. It belongs to type A of
Vollrath’s classification (Uria et al., 1992). The gland is round in shape and has a diameter of 2000 – 2300 μm.

Figure 17. The pineal complex of the guinea pig (*Cavia porcellus*) in situ. (a) Caudal-dorsal view of the brain with the pineal situated between the brain hemispheres (arrows). (b) Rostral view of the diencephalon and the superior colliculi – notice the size and shape of the pineal gland. III – 3rd ventricle, CR – cerebellum, HC – habenular commissure.

Figure 18. The pineal gland of the degu (*Octon degus*) in situ. (a) Dorsal view of the brain after tilting of the cerebellum. (b) Dorsal view of the corpora quadrigemina after cutting of the corpus callosum and removing of the cerebellum. III – 3rd ventricle, CQ – corpora quadrigemina, CR – cerebellum, IC – inferior colliculi, PG – pineal gland, SC – superior colliculi.
The Pineal Gland of the Rabbit (*Oryctolagus Cuniculus*)

The rabbit pineal gland (Fig. 19) is an elongated organ, extending from the intercommissural region to the skull roof. Its length changes from 3 mm in neonates (Garcia-Maurino, 2001) to 8 mm in adults (Romijn, 1973). The gland possesses a thickened distal part, therefore it is classified as type αβC of Vollrath’s classification. The characteristic features of the rabbit pineal include the invagination of the distal part of the gland into the confluence of sinuses and the close contact of the organ with the great cerebral vein (Smith, 1971; Romijn, 1973).


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