MEDIAN EYES

We have already seen [1] that it is not unusual for the region of the mid-brain (diencephalon) of certain Vertebrates—and particularly the ependymal cells lining the posterior portion of the first embryonic vesicle which persists as the third ventricle of the brain—to show evidences of an optical as well as a glandular function. From this region the optic vesicles which form the lateral eyes emerge as out-pouchings ; from the floor is derived the neural portion of the pituitary gland ; in the ventral area are nuclei of internal secretion [2] ; and from the thin roof is given off the pineal
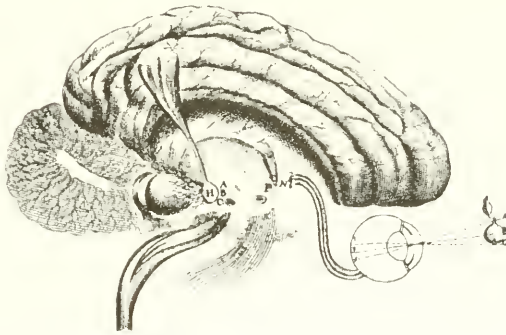

Fig. 852.—Descartes's Original Diagram Illustrating the Effect of Light upon the Rational Soul Lying in the Pineal Gland (from a photograph by Prof. J. F. Fulton).

apparatus (or epiphysis), which, although usually glandular in function, becomes differentiated into a median eye in some species. This dorsal up-growth of the roof of the diencephalon is represented in varying degrees in all Vertebrates with the exception that the pineal process is absent in the dugong (*Halicore*), a decadent and sluggish sea-cow, and in whales (Cetaceans), while the pineal body is absent in the armadillo (*Dasypus*) and in the dolphin (*Delphinus*).

The significance of the pineal body has always been an enigma. The ancient Romans described it as the *glandula pinealis* and by such anatomists as William Cooper (1666–1709) and Jacob Henle (1809–1885) it was considered as a lymphatic " gland." In the more speculative philosophy of René Descartes the body was a machine directed by a " rational soul " which dwelt in the pineal gland. This conception, sarcastically derided by Voltaire, is illustrated in Fig. 852, taken from Descartes's work *De homine figuris et latinitate donatus a Florentio Schuyl* (Leyden,

[1] p. 537.   [2] p. 557.

René des Carles *Philosophe et Gentilhomme François né en Tourai ne et decede en Suede l'an 1650. agé de 54 ans.*

Gravé par E Desrochiers et se vend chez ... ... a Paris rue St Jacques au Mecenas

Definir la Nature et de l'ame et du Corps,
De la Terre et du Ciel decouvrir les ressorts,
D'vn être Souverain demontrer l'existence,
Voila quel fut l'employ de René du Perron,
Et luy seul eut plus de Science
Que n'en eurent ensemble Aristote et Platon.

FIG. 851.—RENÉ DESCARTES (1596–1650).

1662), which demonstrates figuratively the effect of light upon the soul lying within the gland.

It is impossible to overestimate the influence of RENÉ DESCARTES (1596–1650), the great French philosopher, on the development of European thought. In contradistinction to Francis Bacon, the great empiricist who based his philosophy on observed facts, he disregarded the role of experimentation and sought to build a mechanical conception of the universe on mathematical principles. In pure mathematics, he invented coordinate geometry, making it algebraic, and developed the conception that mass and time were dimensions as fundamental as those of space. Finding the intellectual atmosphere of France unsympathetic, he went to Holland
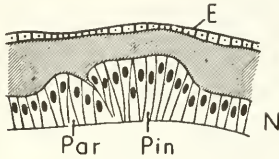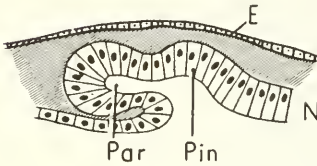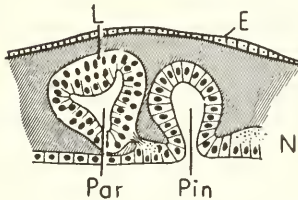

FIG. 853.

FIG. 854.

FIG. 855.

FIGS. 853 TO 855.—THE DEVELOPMENT OF THE MEDIAN EYE IN THE EMBRYO OF A LIZARD, *LACERTA*.

Medial sections through the roof of the diencephalon showing the development of the pineal and parietal organs. Fig. 853 in an embryo of 3 mm.; Fig. 854, 5 mm.; and Fig. 855, 7 mm.

E, epidermis; *N*, neural ectoderm of the roof of the diencephalon. The hatched area represents mesoderm. *Pin*, the anlage of the pineal organ; *Par*, the anlage of the parietal organ; *L*, the anlage of the lens (after Novikoff).

(1628) and there published his two great works, the *Discourse on Method* (1637) and the *Principles of Philosophy* (1644), both of which were placed on the list of prohibited books in Rome and Paris (1663). Rejecting the classical view of his time derived from Aristotle that nature was a single system hierarchically ordered with a Deity at the apex, he reasoned that the material universe was a homogeneous mechanical system composed of qualitatively similar activities following quantitative mechanical laws susceptible to mathematical analysis. Alongside this machine-world which included the human body, animals, plants and inorganic nature, there was a spiritual world in which the body of man alone of all material things participated by virtue of his soul. Ever since his time this dualism of the Cartesian philosophy has permeated European thought; and although to us today the designation of the pineal body as the meeting place of the two worlds may seem speculative and fanciful, it must be admitted that regarding the function of this organ our ideas are still as nebulous.

In its most elaborate form the pineal apparatus consists of two parts which arise from the middle of the epiphyseal arch, the most posterior of

the three arches of the roof of the diencephalon—a PINEAL ORGAN or EPIPHYSIS [1] lying more posteriorly and a PARIETAL or PARAPINEAL ORGAN lying more anteriorly, sometimes arising in association with the pineal body, but sometimes independently of it. The former is connected with the posterior commissure ; the latter with the superior (habenular) commissure ; their development in the embryo of the lizard (*Lacerta*) is seen in Figs. 853–5). The pineal body is connected nervously with the right habenular ganglion, the parietal with the left, suggesting that originally they may have been right and left members of a pair.

The highest development of a median eye is seen in the most primitive Vertebrates, the CYCLOSTOMES (Fig. 856). The lamprey (*Petromyzon*) is provided with both a pineal and a parietal organ having the structure of an eye with a considerable degree of retinal differentiation (Fig. 864) ; but in Myxinoids no trace of either is seen. The presence of an impression in the mid-line of the roof of the cranial cavity in fossil remains of the closely-related Agnatha (*Pteraspis, Cephalaspis*)—the oldest known Vertebrates—is an indication of the occurrence of a pineal organ in these very primitive types, and since the impression is often duplicated the presumption is that the median eye at this stage in evolution was paired (Gaskell, 1908 ; Wood-ward, 1922 ; Heintz, 1932 ; Hills, 1933).

Among FISHES certain old-fashioned ganoid types retain a relatively well-developed median eye somewhat resembling the parietal eye of Cyclostomes. In the sturgeon, *Acipenser*, in addition to supporting cells of ependymal character, the vesicle contains many cells of a sensory type with ganglion cells and efferent nerve fibres ; the structure thus resembles the parietal sense-organ rather than a secretory gland. A somewhat similar organ is seen in the primitive fish, *Polypterus*, found in African rivers, and the Holostean, *Amia* (Hill, 1894 ; and others). In Selachians (skate, shark, dogfish, etc.) the pineal body is set on a long stalk and often per-forates the skull through a pineal foramen to appear beneath the skin as a closed vesicle (Fig. 857) ; alternatively it may lie within the skull in a recess in its cartilaginous roof (Holocephali). In these fishes the eye-structure has disappeared, the vesicle is small and consists of ependymal cells, and the tendency is probably towards glandular formation (Cattie, 1882 ; Locy, 1894). In Teleosteans (trout, salmon, pike, herring, etc.) the pineal apparatus is not so well developed, and is somewhat variable ; in contrast to "ganoid" and cartilaginous fishes, the vesicle tends to be large and the stalk short. In these bony fishes it rarely reaches the under-surface of the skull, and although it contains cells of neural and glial character among the ependymal cells, it never shows a developed ocular structure. It is interesting, however, that in this class of fishes the superficial

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[1] Galen (*c.* A.D. 130–200) used the non-committal, topographical Greek term—ἐπί, upon, φύσις, growth ; the Latin term is descriptive of the shape—*pinus*, a fir-cone. The term " epiphysis " is usually applied to the deeply situated glandular organ seen in Mammals in contrast to the sensory " pineal eye " of the lamprey or *Sphenodon*.

structures, including the skull, are sometimes transparent while occasionally the degree of opacity of the integument is regulated by chromatophores (Breder and Rasquin, 1950). In some cases (the trout, *Salmo trutta*) a smaller off-shoot from the roof of the diencephalon may perhaps represent a vestigial parietal organ. In the lung-fishes (Dipnoi) the pineal apparatus is degenerate and makes no attempt to reach the surface or assume a sensory structure.

FIGS. 856 TO 859.—THE PINEAL AND PARIETAL ORGANS IN VERTEBRATES.
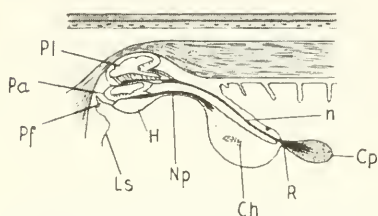

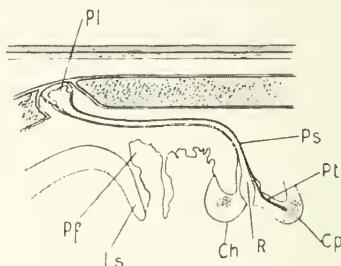FIG. 856.—In Cyclostomes (the lamprey).
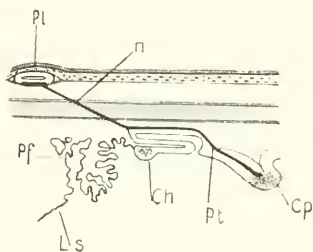

FIG. 857.—In Selachians.
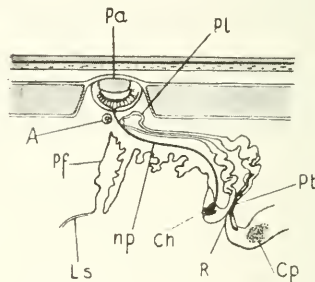

FIG. 858.—In Amphibians.

FIG. 859.—In Reptiles (*Sphenodon*).

A, accessory parietal body ; *Ch*, habenular commissure ; *Cp*, posterior commissure ; *H*, habenular ganglion ; *Ls*, lamina terminalis ; *n*, pineal nerve ; *np*, parietal nerve ; *Pa*, parietal organ ; *Pf*, paraphysis ; *Pl*, pineal organ ; *Ps*, pineal stalk ; *Pt*, pineal tract ; *R*, pineal recess (after Tilney).

Among AMPHIBIANS, the primitive tailed class, Urodela (salamanders, newts, *Ambystoma*, *Proteus*, etc.), possesses a very rudimentary pineal organ, but the occasional possession of pigment granules (the olm, *Proteus*) and even of some nerve fibres suggests some affinity with a photosensitive structure. In the degenerate blind and limbless Cæcilians (Apoda) the pineal organ is similarly degenerate. In the tailless Amphibians (Anura), however, it is more fully represented in the early stages of development. Thus in the young frog (*Rana*) the pineal body comes to the surface above the skull as an eye-structure, its position being indicated by a pale area where the cutaneous pigment and glands are scanty or absent, but it
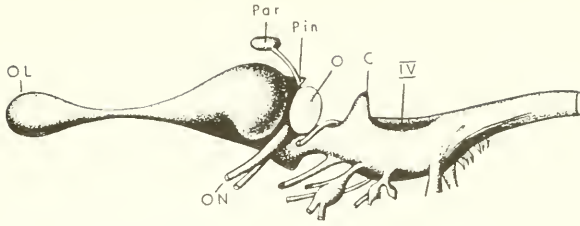
FIG. 860.—THE PARIETAL AND PINEAL BODIES OF *SPHENODON PUNCTATUS*.

A lateral view of the brain. *C*, cerebellum ; *O*, optic lobe ; *OL*, olfactory lobe ; *ON*, optic nerves : *Par*, parietal eye ; *Pin*, pineal body (epiphysis) ; IV, fourth ventricle. The structures issuing below are the cranial nerves, III to XII.

degenerates and disappears in adolescence leaving a rudiment of an eye connected by a nerve with the posterior commissure (Fig. 858) (Leydig, 1891 ; Braem, 1898 ; and others).

In the primitive REPTILES the eye-structure reaches its highest development in the parietal organ (Figs. 859–860) ; in the New Zealand tuatara (*Sphenodon*), for example, it passes through the skull by a " parietal foramen " and lies beneath the skin, the scales of which become specialized and transparent in this region. In this animal as well as in some other types, an ACCESSORY PARIETAL ORGAN lies contiguously : it is variable in structure, vesicular or solid, and tends to disappear with maturity. In lizards such as *Lacerta*, the arboreal lizard, *Iguana*, and the slow-worm, *Anguis* (a limbless lizard), the parietal eye loses connection entirely with the pineal body and
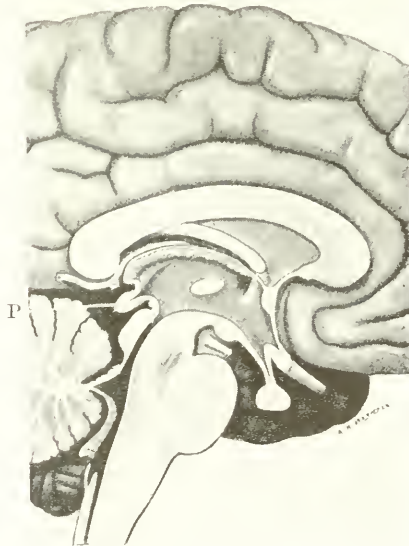

FIG. 861.—THE PINEAL GLAND IN MAN (from Gladstone and Wakeley, *The Pineal Organ*).

has an independent parietal nerve associated with a near by parietal centre, a connection which in many cases is transitory and degenerates before maturity so that the organ would appear to lose its function. In these species the pineal body is always rudimentary and the vesicle is usually absent. It is also interesting that the presence of a parietal opening in the roof of the skull of fossil labyrinthodont amphibians and extinct reptiles of the Palæozoic and Mesozoic eras suggests that a functional eye existed in these species also. In the more recent reptiles, such as geckos, snakes, tortoises, turtles, crocodiles, and alligators, the eye-structure disappears and the epiphyseal arch gives rise to a glandular organ, an arrangement retained in the higher animals. In some birds and mammals analogous rudiments appear in embryonic life which disappear with development,[1] but in these types the pineal organ has a glandular structure and lies snugly hidden on the roof of the diencephalon between the cerebrum and the cerebellum (Fig. 861). It is thus evident that the pineal organ constitutes a definitive eye only in the lamprey and to a less extent in certain primitive "ganoid" fishes, while the parietal organ forms an eye-like structure in the lamprey and also in primitive reptiles ; otherwise the latter organ is vestigial.
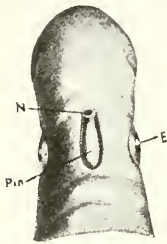

Fig. 862.—The Lamprey, *Petromyzon*.

Dorsal view of the head end of the animal showing the eye, *E*, the nasal aperture, *N*, and the pineal area, *Pin*.

the median eye of the lamprey lies under a localized area of transparent skin on the midline of the dorsal surface of the head immediately behind the single median nostril (Fig. 862). It consists of two diverticula lying vertically one upon the other (Ahlborn, 1883 ; Beard, 1889 ; Stúdnicka, 1905 ; Dendy, 1907 ; Mygind, 1949). The more superficial and dorsal vesicle is the pineal, the lower the parietal eye (Fig. 856). Together they form an organ incapable of optical imagery but doubtless able to appreciate differences in light intensity. Of the two the pineal eye is the more elaborately developed (Figs. 863 and 864). It forms a vesicle lying directly underneath the skin ; the cells of the superficial wall are elongated to form a flat and imperfect lens ; those of the deeper wall form a pigmented retina comprised of sensory and supporting cells, ganglion cells and nerve fibres which pass as the pineal nerve in the posterior commissure to the right habenular ganglion. The retinal pigment is of two types—a dark melanin-like pigment and whitish-yellow granules corresponding closely to the guanine-like pigment of the skin ; the first has an absorbent, the second probably a reflective function analogous to the similar pigment in the compound eyes of some Arthropods. The free ends of the sensory cells face the lumen of the vesicle which is filled with a nucleated syncytial "vitreous." The parietal organ forms a somewhat similar vesicle of simpler construction, varying considerably in size ; the rudimentary parietal nerve leads through the habenular commissure to the left habenular ganglion.

the median eye of lizards and *Sphenodon* [2] is derived from the parietal body and forms a remarkably eye-like organ (Spencer, 1886 ; Leydig, 1887 ; Strahl and Martin, 1888 ; Klinckowström, 1893 ; Virchow, 1901 ; Stúdnicka, 1905 ; Dendy,

[1] Pigeon (Livini, 1905), guinea-pig (Chiarugi, 1919), ox (Favaro, 1904).
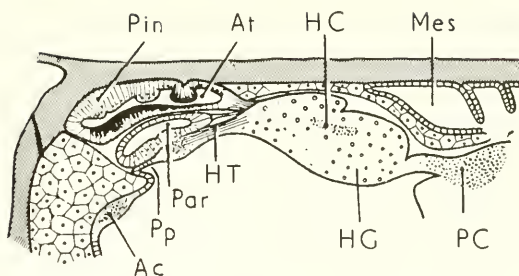[2] p. 379.

Fig. 863.—The Median Eye in the Ammocœte of the Lamprey, *Petromyzon*.

Longitudinal section through the roof of the fore- and mid-brain. *AC*, anterior commissure ; *At*, atrium of the pineal organ ; *HC*, habenular commissure ; *HG*, habenular ganglion ; *HT*, habenular tract ; *Mes*, mesencephalon ; *Par*, parietal organ ; *Pin*, pineal organ ; *PC*, posterior commissure ; *Pp*, paraphysis (after Studnicka).

Fig. 864.—The Median Eye of *Lampetra fluviatilis*.

Section through the head of the animal showing the two vesicular-like structures in the centre of the figure, the pineal and parietal bodies, lying in the ventricle underneath a relatively transparent area of skin and subcutaneous tissue. The two solid masses in the lower portion of the picture represent parts of the brain (Mallory's phospho-tungstic acid hæmatoxylin) (× 24) (Katharine Tansley).

1907–11 ; Nowikoff, 1910 ; Gasson, 1947 ; Trost, 1953). It is situated in the parietal foramen of the cranial roof immediately under the integument and is covered by a specially modified scale where the black pigment is absent and the green is only feebly represented so that it is relatively transparent (Fig. 459). The eye takes the form of a flattened vesicle lying in a connective tissue capsule ; the cells of the distal wall are elongated to form a lens which sometimes contains a central pigmented area ; the cells of the proximal wall are differentiated to form a retina (Fig. 865). In some types such as the American " chameleon ", *Anolis*, the latter is relatively crude but usually there is a reasonably well-differentiated sensory layer composed of visual and

intercalary cells, the latter being pigmented except in *Sphenodon* in which the pigment is extracellular. In the lizards this pigment shows adaptive changes, moving towards the sensory terminations of the cells on exposure to light (Nowikoff, 1910). Peripheral to the visual cells lies a layer of bipolar ganglion cells, the nerve fibres issuing from which form the parietal nerve which runs down the parietal stalk either to the right (*Anguis, Lacerta*) or left (*Sphenodon*) habenular ganglion. The surfaces of the visual cells of the retina as well as those of the lenticular cells facing the cavity of the vesicle are richly provided with cilia ; the cavity itself is filled with a delicate syncytium with a few oval nuclei enclosing spaces filled with fluid constituting a " vitreous."

It is to be noted that in all cases the surface ectoderm takes no part in the formation of the ocular vesicle, there is no secondary invagination, and the retinal cells are verted, resembling the eyes of Invertebrates rather than the paired lateral eyes of Vertebrates.
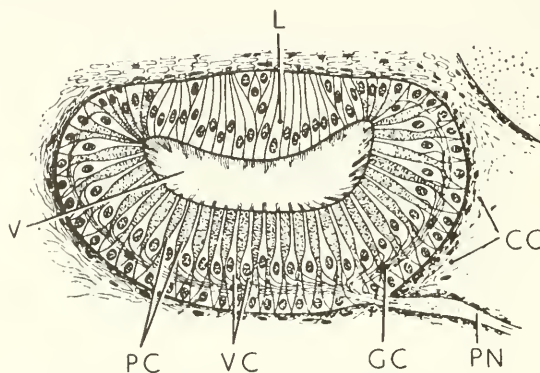

Fig. 865.—The Parietal Eye of the Slow-worm, *Anguis fragilis*.

CC, connective tissue ; *GC*, ganglion cells ; *L*, lens ; *PC*, pigment cells ; *PN*, parietal nerve ; *V*, vitreous ; *VC*, visual cells (after Nowikoff).

The function of the pineal organ in those species in which it assumes an ocular formation is undoubtedly optic although it would appear that it is confined to the directional appreciation of light and is incapable of optical imagery (Mygind, 1949). In those species wherein a glandular structure is evident, even among Mammals, the function of the pineal body is still obscure despite the considerable amount of research which has been devoted to the subject by morphologists, histologists, pathologists and clinicians. In man it reaches maturity between the ages of 6 and 7 years whereafter involutive phenomena begin to appear in the form of hyalinization, calcification and cystic formation (Rio-Hortega, 1922–29 ; Globus and Silber, 1931 ; and others). This involution after puberty together with the variations in the size of the organ observed during pregnancy, with sexual activity or after castration both in human subjects [1] and in animals,[2] have confirmed the clinical impression that its main association concerned skeletal growth and the sexual functions. It is to be remembered, however, that Pelizzi's (1910)

[1] Brandenburg (1929), Frada and Micale (1941).
[2] Santamarina and Venzke (1953).

classical syndrome of macrogenitosoma præcox has been reported as occurring in about 50% of cases in patients without pineal disturbances, while the majority of cases of pineal tumours do not exhibit sexual syndromes (Haldeman, 1927). It may even be that when these symptoms occur they may be caused by pressure on neighbouring structures such as the pituitary body and hypothalamus. The whole question of the existence of an endocrine secretion and what it may do is thus unsolved.

It is interesting that the association of the integumentary pigment with the visual system is maintained in some amphibians ; thus pigmentary changes always occur in 10-day-old tadpoles if they are fed on pineal tissue (McCord and Allen, 1917), while the injection of pineal extract induces contraction of the melanophores of the African toad, *Xenopus* (Bors and Ralston, 1951).

The function of the parietal organ remained enigmatic until its eye-like structure in lizards was described by Leydig (1872) and confirmed in *Anguis fragilis* by De Graaf (1886) and in *Sphenodon* by Baldwin Spencer (1886). From these observations arose the view that the pineal apparatus is a primitive, unpaired, median, upward-looking eye, which has degenerated except in a few instances. It is more probable, however, that the hypothesis of Todaro (1888) is the more correct, that although often apparently unpaired, the organ is the result of the fusion of a pair (see Sterzi, 1912 ; Gladstone and Wakeley, 1940). The evidence derived from fossil remains of extinct Vertebrates, the duplication of the organ in primitive types, its occasional bifurcation in the higher species, and the frequent bilaterality of its nervous connections, is convincing. There is a strong case to be made that its primary function was sensory. In extinct fossil species it seems clear that a median eye coexisted with lateral eyes, olfactory organs and static organs, and the closure of the foramen in the roof of the cranium even in these early types indicates a regression of the organ and the loss of its visual function even in remote geological times, a tendency possibly due to the gradual predominance of the lateral eyes. Whether, as Patten (1890–1912) suggested, the pineal organ is linearly derived from the median eye of arthropods, particularly primitive arachnids, is a more debatable question.

On the other hand, the view has been put forward that its optical function is not essentially primitive but is rather the result of a secondary transformation, in which case the pineal body of Mammals cannot be looked upon as a vestigial and metamorphosed remnant of an eye. According to Tilney and Warren (1919) the histology of this region provides evidence that in all Vertebrates this portion of the brain possesses a pluripotential activity. Usually the fundamental tendency is in the direction of glandular formation, the secretion being contributed in a few cases to the cerebro-spinal fluid, but in most cases and in the Mammalia, to the blood stream as a hormone. In some species (Cyclostomes, Amphibians, and primitive Reptiles) the arch has become specialized with a visual function, an adaptive modification

answering the needs of the animal which in most cases is of sluggish habit
with slow movements and a limited range of vision. In this view the two
tendencies appear to run parallel rather than to be linearly derived. Which
theory is correct must still remain a matter for discussion.

For the phylogeny of the pineal body, see the elaborate monograph of Gladstone
and Wakeley (1940) ; its morphology and histology are well discussed in those of
Stúdnicka (1905), Tilney and Warren (1919) and Rio-Hortega (1932) ; its physiological
functions (as a gland of internal secretion) are fully noted by Kidd (1913), Schäfer
(1926) and Bors and Ralston (1951) ; the vast clinical literature is found in Bailey
and Jelliffe (1911), Boehm (1920), Laignel-Lavastine (1921), Horrax and Bailey (1925)
and Calvet (1934) ; the veterinary literature in Santamarina and Venzke (1953).

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