A COMPARATIVE STUDY OF THE NICTITATING MEMBRANE OF BIRDS AND MAMMALS

By E. PHILIP STIBBE
University of Liverpool

The necessity for a special mechanism to remove foreign bodies from the eye exists in all land animals, for the preservation of vision. This is not only on account of the immediate interference with vision that all foreign bodies must cause (either directly if situated on the cornea, or indirectly if not on the cornea), but the temporary interference with vision is likely to be followed by a permanent defect if the foreign body be lodged on the cornea. The cornea, like other parts of the body, has its own protective reaction, but this may go on to organisation; and unfortunately it is just in the case of a mechanical irritant that organisation is specially likely to occur. So that, failing the immediate and adequate removal of the foreign body by mechanical means, the result will be a permanent localised interference with vision. That is the reason for the extreme sensitiveness of the cornea; the intense pain caused by a foreign body is to be regarded as the measure of the urgency of the "S.O.S."

The nature of the protective apparatus may be expected to vary in different animals, according to their habitat; it will depend on the liability of the eyes to injury, and upon the needs of the animal in the matter of acuity of vision.

Crawling and burrowing animals—Amphibia, lizards, snakes—are specially liable to injury from dust and mud; but one may suppose that in most instances moderate clearness of vision would meet the necessities of the case.

Mammals, being mostly less near the ground, are correspondingly less exposed to dust and dirt; but one must remember grazing and browsing Mammals, forest life and winds.

Birds, one would say, are the least liable to eye-injury—that is flying birds; but even these are to some extent and at times exposed to dust. And if they are less likely than other animals to suffer injury to the eyes, the consequences of that injury when it does occur are much graver. For birds cannot afford to lose a fraction of their acuity of vision; they have to "spot" prey or enemies at long distances, and must be on the alert for obstacles when travelling at high speeds; so that the lesser frequency of the danger is counterbalanced by the greater acuteness of the danger.

It is to be noticed, also, that a bird cannot afford to have the eye covered, say by an opaque lid, even for a fraction of a second while in flight; that would be fatal while travelling at fifty or sixty miles an hour amongst tree-tops and branches.

The structure provided to meet this necessity for special protection of the eye is the well-known so-called "nictitating membrane"; and this is of interest to human anatomists by reason of the association with it of the plica semilunaris of man. The customary definition of the human plica semilunaris is—"a vestige of the membrana nictitans or third eyelid, which occurs in Birds, Reptiles and Mammals, and is of use in cleaning the cornea" (1, 2).

Now, the implications of such a statement are twofold in nature—physiological and morphological.

Physiologically we state that there is in Birds, Reptiles and Mammals a membrane which nictitates—that is, moves rapidly to and fro over the front of the eye; and that the purpose of this nictitation is to cleanse the front of the cornea.

Morphologically we imply that this structure is the same thing in Birds, Reptiles and Mammals, and that ontogenetically or phylogenetically, or both, it is a third eyelid.

Finally we believe that this structure has lost its function in man, but persists as a vestigial structure, the plica semilunaris.

That is—it is hoped—a not unjust interpretation of the present view of the plica semilunaris and the nictitating membrane.

The purpose of this study is to confirm or modify our view of the nictitating membrane, by investigating the following points:

(1) What are the essential features—structural and functional—of a true nictitating membrane? For this purpose we study in detail the Bird, it being well established that the Bird has a true nictitating membrane.

(Exigencies of time have made it necessary to study only those types which might throw light on the Mammals; the Reptiles are regarded as highly specialised, and as no more likely to help than the Birds; on the other hand Amphibia have been introduced as being less specialised and therefore likely to throw light on the phylogeny of the membrane. The nictitating membrane of Reptiles has been investigated, and in general resembles that of Birds (3).)

(2) Have Mammals a nictitating membrane in the same sense—structurally and functionally—as Birds?

(3) What do we know of the comparative morphology of the membrane in Birds and Mammals?

(4) Is the plica semilunaris of man a vestigial structure, representing this membrane of Birds and Mammals?

(1) THE NICTITATING MEMBRANE OF BIRDS, AND ITS NEURO-MUSCULAR MECHANISM

The nictitating membrane of Birds has been frequently and well described (4). It is found for example as far back as Owen (5). There can be no doubt that Birds possess a true physiological nictitating membrane, with a definite and highly-specialised neuro-muscular mechanism.

The membrane (fig. 1) is a triangular reduplication of the conjunctiva in the region of the inner or anterior canthus; it is almost invisible when not in action, but covers a large part of the front of the eye when it is pulled outwards by its muscles. The apex of the triangle is at the inner canthus; the base—deeply concave—extends in a vertical direction across the front of the eye, from the junction of the inner with the middle thirds of the upper lid, to a corresponding point on the lower lid.

This edge of the membrane is usually everted and deeply pigmented, and its palpebral surface is raised into rough irregular ridges; the ridges are composed of heaped-up keratinised epithelium, and would appear to act as a sort of comb for the deep surface of the lids. The upper and lower edges of the triangular membrane merge into the conjunctiva at the fornices; the membrane has thus fornices deep and superficial to it.

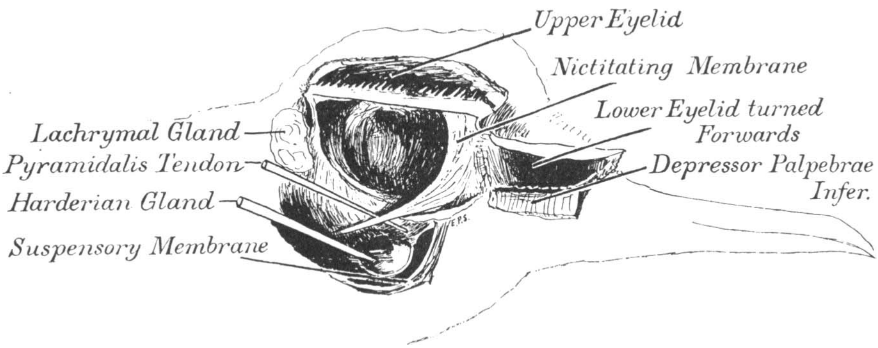

Fig. 1. Nictitating membrane of the Bird (ostrich) as dissected from the front. The lower eyelid has been turned forwards, and the pyramidalis tendon is seen extending round towards the back of the eyeball. Note also conjunctival fornices superficial and deep to the membrane.

The Bird sweeps the membrane across the eye with great rapidity and at frequent intervals without closing the eyelids; the membrane is semi-transparent so that vision is not greatly interfered with. One would suppose from cursory observation of Birds that the movement of the membrane was so rapid as not to permit of analysis in the living animal; but it appears to have been analysed by naturalists (4), who describe it as a pendulum-like movement, the membrane swinging across the eye from an upper fixed point; its rapidity under varying conditions has also been estimated.

By dissection the following points can be seen:

The upper angle of the membrane is firmly fixed into the upper conjunctival fornix; this fornix is shallow, and the upper lid is a short thick rigid structure, and appears not to be movable apart from the eyeball. This agrees with the observation that the upper angle of the membrane does not move. The lower angle blends also with the fornix of the conjunctiva, but this latter is loosely attached to the lid and globe; and the fornix is deep, and the lower lid freely and independently movable.

The pyramidalis muscle. Attached to the lower angle of the membrane is a strong flattened tendon, the tendon of the pyramidalis muscle (fig. 1). This is seen to be coming forwards round the outer side of the eyeball to its insertion into the membrane. The pyramidalis (fig. 2) arises from the outer surface of the sclerotic at the inner side of the eyeball; it is a thin conical slip of muscle, with its free end directed backwards and outwards towards the optic nerve. Before reaching the optic nerve, it ends in a tendon, which has already been seen at the front of the eye; so that this tendon has to wind round the back and outer side of the globe, forming nearly three-fourths of a circle, to its insertion. The pyramidalis thus encircles three sides of the eyeball, lying in close contact with the sclerotic, and pulling, as it were, right round the eye; an arrangement which evidently assures that the membrane will remain in contact with the cornea as it is pulled round.

The manner of insertion of the pyramidalis tendon reminds one of the insertions of the chordae tendineae of the valves of the heart; the tendon spreads out in the substance of the membrane, so that tendon and membrane are a continuous sheet; the effect of this is to prevent any tendency to puckering of the membrane as it slides across the eye.

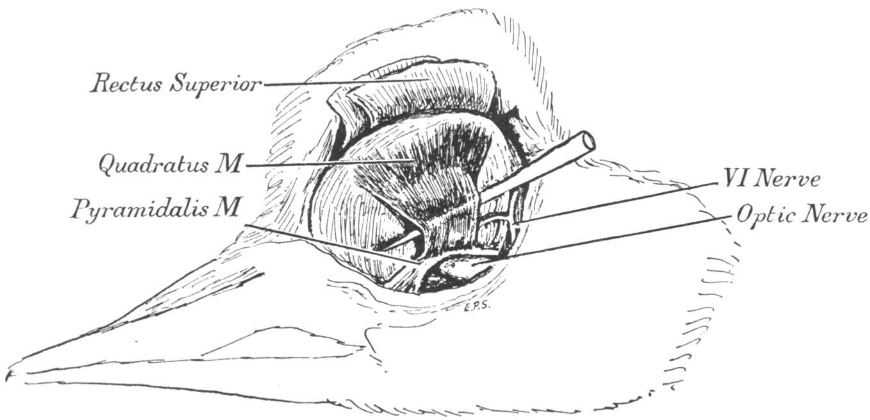

Fig. 2. Orbit of ostrich dissected from behind, to show pyramidalis and quadratus muscles, and their nerve supply from the sixth cranial nerve.

The quadratus muscle. The action of the pyramidalis is modified and reinforced by that of a second muscle, the quadratus (fig. 2). This arises from the sclerotic immediately behind the insertion of the superior rectus; its fibres are directed backwards as a broad flat sheet under cover of the superior rectus, and in contact with the sclerotic. It is inserted into a narrow fibrous pulley-like tunnel placed transversely above the optic nerve; this fibrous sheath invests the tendon of the pyramidalis, which it holds up off the optic nerve; in the specimen shown the pulley-form is not perfect, the quadratus appearing to gain partial insertion actually into the tendon of the pyramidalis. According to Owen (5) and other observers, the action of the quadratus is to prevent the tendon of the pyramidalis from pressing on and injuring the optic nerve.

The quadratus would appear however to have another function; the writer suggests that it is a tractor of the membrane of no less importance than the pyramidalis; the two muscles act together, to fix the direction of pull of the pyramidalis tendon in one direction, no matter what be the position of the eye. This is represented in fig. 3.

Looking at the back of the eye, let Q represent the pull and the line of action of the quadratus; Q can be resolved into two parts at right angles—Q' along the tendon, and Q'' at right angles to it. If α be the angle between Q and Q'', then $Q''=Q \cos \alpha$. Similarly P can be resolved into P' along the tendon, and P'' at right angles to it; and $P''=P \cos \beta$. In a position of equilibrium, the downward pull of the pyramidalis is equal to the upward pull of the quadratus; that is, $Q \cos \alpha=P \cos \beta$.

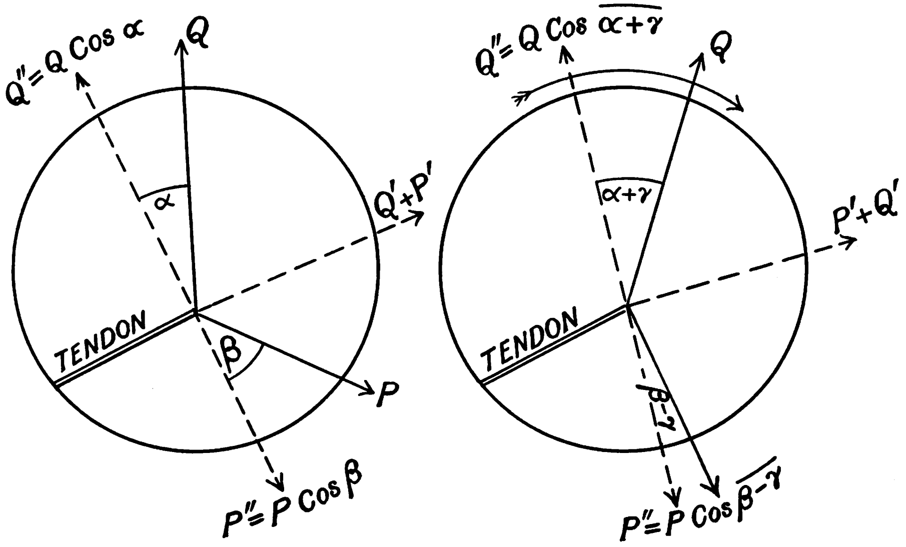

Fig. 3. Diagram to represent action of pyramidalis and quadratus, as explained in text.

Now let the eye be rotated inwards through an angle γ. The angle α now becomes $\alpha+\gamma$, and the angle β becomes $\beta-\gamma$, that is to say that as the eye rotates inwards $\cos \alpha$ diminishes, and therefore $Q \cos \alpha$, the upward pull of the quadratus, diminishes by an amount proportionate to the angle of rotation of the eye; and $P \cos \beta$, the downward pull of the pyramidalis, is similarly increased. The tendon will therefore move downwards till the angle of rotation γ is abolished—that is, the tendon will return to the position of equilibrium.

Similarly if the eye be rotated outwards, the tendon will move relatively upwards till the angle of rotation is abolished.

This means that, whatever position the eye assumes, the tendon of the pyramidalis will move relatively to the globe, so that it always occupies the same position in space; that is, the tendon will not move with the eye, but will always pull the membrane in exactly the same direction.

Such a constant direction of pull, whatever the position of the eye, could not be obtained by the action of one muscle; it can only be produced by two muscles like these, whose actions can be resolved into components in opposite directions.

The nerve supply of the pyramidalis and of the quadratus is from the sixth cranial nerve, which supplies the external rectus, and then turns inwards and backwards under the quadratus to end in the pyramidalis (fig. 2).

The depressor palpebrae inferioris. This muscle is also of interest in connection with the nictitating membrane. It is shown on fig. 1, where it has been detached from the broad suspensory ligament in turning the eyelid forwards. It is a part of the same sheet as this hammock-like suspensory ligament; and it passes forwards as a broad thin sheet to be inserted into the substance of the lower lid, and into the areolar tissue between the lower lid and the palpebral conjunctiva. When the nictitating membrane slides outwards, this muscle will fix the lid and prevent it from being also pulled outwards; in addition, by its conjunctival insertion, it will prevent the membrane from falling into horizontal folds, that is it will help to keep the membrane uniformly applied to the front of the eye.

The nerve supply of this muscle is from the third nerve.

Such is a sketchy account of the nictitating membrane of Birds. How does this compare with that of Mammals?

(2) THE SO-CALLED NICTITATING MEMBRANE OF MAMMALS

Superficially this resembles the nictitating membrane of Birds. It is a crescentic reduplication of the conjunctiva in the inner angle of the orbit, projecting towards the cornea, of the same shape as in the Bird, with the concave free border, and a similar thick pigmented line adjacent to this border. Is this a nictitating membrane functionally?

It is usually described as sweeping over the front of the eye as the eyelids are closed, and possibly it does slide outwards to a certain extent; but it would seem not to be capable of sweeping out very far or easily; for it is a thick rigid structure with a stout cartilaginous basis, and the cartilage is attached into the subconjunctival tissues at the inner aspect of the eyeball, and also to the internal tarsal ligament.

Observation of living animals suggests that what is described as a movement outwards of the membrane might well be a rolling inwards of the eye under the membrane. But without insisting that this is the case, there is another reason for saying that the membrane of the Mammal does not truly nictitate—that is, does not move rapidly across the eyeball independently of the lids—namely that it has not got the necessary muscular apparatus for independent movement. The writer has made numbers of dissections of the orbits of calves, sheep, rabbits and cats, all of which have a well-marked "nictitating membrane," and has failed to find any specialised apparatus for moving the membrane. The examination of serial sections across the fold has revealed at the most a few scattered bundles of unstriped muscle fibres. The nearest approach to a muscle of the nictitating membrane is the levator palpebrae superioris (fig. 4). This muscle (say in the calf) has a wide expansion to its conjunctival insertion—closely resembling the expansion of the human muscle. The inner part of this insertion may be traced as a fairly definite band into the substance of the membrane; it may slightly protrude the membrane, and probably tenses it and helps to fix it while the eyeball rolls inwards under it.

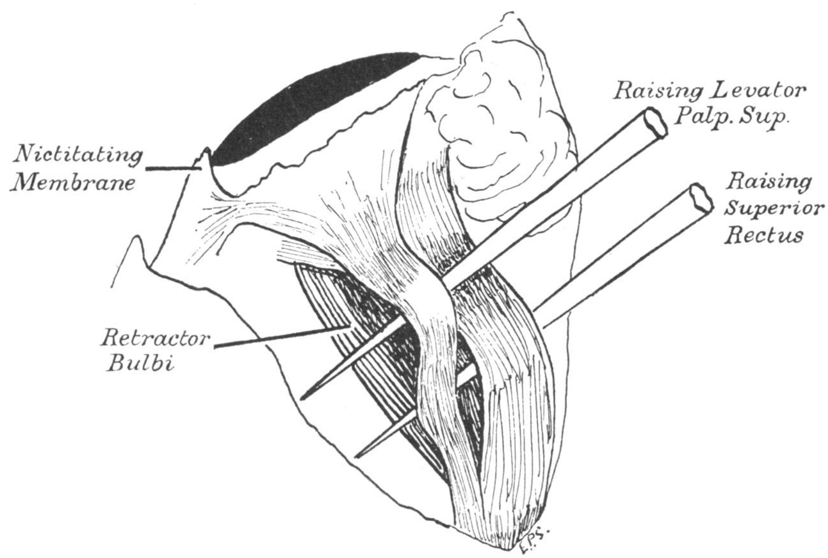

Fig. 4. Superficial dissection of orbit of calf from above, to show connection of levator palpebrae superioris with membrane. Note that the deep muscle—the retractor bulbi—has no connection with the membrane.

In addition, the smaller Mammals, notably the cat, have a poorly developed sheet of retractor fibres, with an indefinite origin in the subconjunctival tissue superficial to the internal rectus. Note that these fibres, like the levator palpebrae, are in the superficial or subperiosteal plane.

There appears to be no muscle directly moving the membrane—nothing to suggest functionally a pyramidalis or quadratus.

Structurally the nictitating membrane of Birds is a simple membranous structure containing a goodly proportion of elastic tissue (fig. 6), but that of Mammals is a complex structure. In fact the essential element in the mammalian plica is not membrane, but a cartilage which has evaginated the conjunctiva. This cartilage is no mere nodule, but a large plate of elaborate design, and most exactly fitting its special purpose of picking up particles from the front of the eye. For reasons that will be given, it is proposed to call this the INTERCEPTING CARTILAGE, and the membrane the INTERCEPTING MEMBRANE—CARTILAGO ET MEMBRANA INTERCIPIENS LACHRYMARUM, terms which more correctly indicate the nature of their function.

It is also formally proposed to drop the term "nictitating membrane" when speaking of Mammals.

The intercepting cartilage. This is shaped something like a pickaxe, with a stout, rather flattened handle and a long thin blade. It is quite a large structure, being in the calf more than half an inch long, and in a small Mammal like the rabbit more than a quarter of an inch long; while the thin blade stretches vertically across the cornea, and is of the same length as the maximum vertical diameter of the cornea.

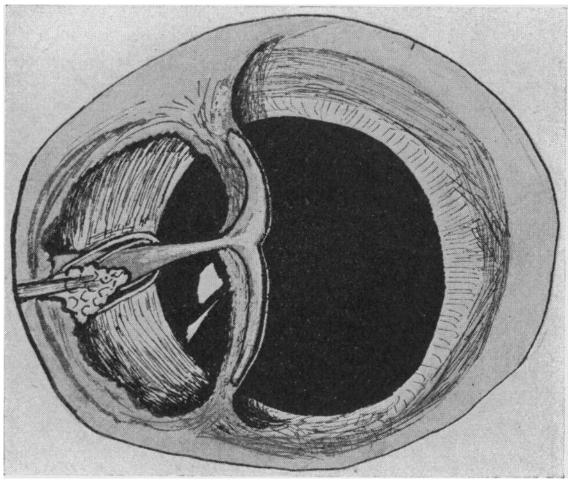

Fig. 5. Dissection to show the structure of the nictitating or intercepting membrane of a calf.

The handle or horizontal limb of the cartilage is stout and somewhat club-shaped, its thicker end being buried in the subconjunctival tissue at the inner side of the eyeball, under cover of the structures at the inner canthus. To its superficial aspect is attached a deep membranous prolongation of the internal tarsal ligament. The cartilage extends outwards, curving round the inner side of the globe, and becomes slender as it approaches the cornea. Near the inner margin of the cornea it joins the blade or vertical limb which occupies the margin of the evaginated conjunctiva—that is to say, the main limb splits into two limbs at right angles to its long axis.

The cartilage thus forms a sort of "squeegee" at the inner side of the orbit, under which the eyeball can roll. The cartilage is of course covered on both sides by conjunctiva, so that there is a deep internal fornix between it and the globe, and a shallower superficial internal fornix between it and the lids. The part of the internal fornix bounded by the lower lid is the lacus lachrymalis, and is open internally, where it becomes flush with the skin at the side of the root of the nose; at the junction of skin and conjunctiva is the caruncula lachrymalis.

The blade or vertical limb of the cartilage extends exactly across the greatest width of the cornea, and is curved to lie accurately on the convexity of the globe. The corneal aspect is smooth; the palpebral aspect of the conjunctival covering is raised into a series of thick irregular ridges, pectinate in appearance and palpable to the finger.

The Harderian gland (fig. 5). In Birds this gland is situated at the back of the orbit, and drains into the deep internal fornix; there is also a lachrymal gland draining into the outer part of the upper fornix.

In Mammals the Harderian gland is situated in the substance of the nictitating membrane. It covers the superficial aspect of the inner two-thirds of the handle of the cartilage, and is to some extent wrapped round on to its deep surface. The gland has from one to four ducts; these are most easily demonstrated in the calf, in which there are four; they open at the bottom of a small pouch on the ocular surface of the membrane, at a point a short distance within the free edge of the membrane. The ducts wind across the borders of the cartilage to pierce the conjunctiva; they are sufficiently large in the calf to take bristles, and can then be dissected out; their length outside the gland is about half an inch.

The secretion of the gland is thick and sticky. These Mammals have the usual lachrymal gland at the upper and outer part of the orbit, with a serous secretion.

MICROSCOPIC APPEARANCES IN BIRD AND MAMMAL

(Figs. 6, 7 and 8.)

In the Bird the nictitating membrane has a basis of fibrous tissue, most of the bundles tending to be longitudinal, but some crossing these at right angles (fig. 6).

The membrane is said to retract by its own elasticity, and one confidently looked to find much elastic tissue in it. In picro-carmine sections, however, while the elastic tissue is very evident, it cannot be said to be excessive.

The conjunctival covering consists of stratified epithelium which, on the palpebral surface, is strongly heaped up, especially near the free edge of the membrane where it forms the pectinate ridge already alluded to. There is no glandular tissue in the membrane; the duct of the Harderian gland opens into the deep internal fornix.

In the Mammal the following are the microscopic appearances (fig. 7):

The cartilage is hyaline with very plentiful cells which appear to be rather small, and which exhibit no very definite grouping.

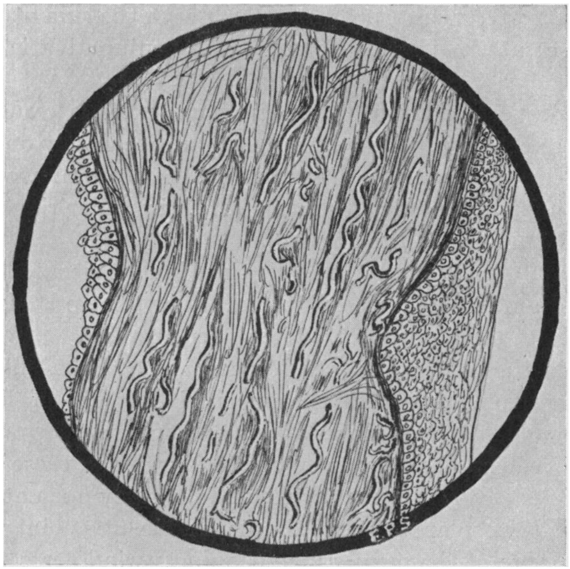

Fig. 6. Section across the nictitating membrane of a cock stained with picro-carmine to show yellow elastic tissue.

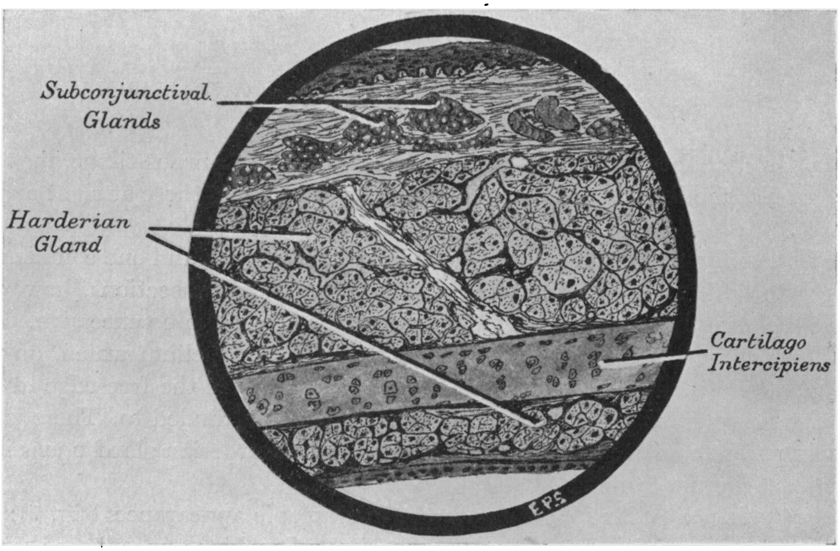

Fig. 7. Cross section of the nictitating membrane of a calf.

The Harderian gland is in its greater part a typical alveolar serous gland, and would pass for a serous salivary gland. There is however a peculiar part of the gland near its inner or anterior end (fig. 8). It consists of round or oval alveoli lined by cubical epithelium, and containing a homogeneous colloidal-looking substance; some alveoli contain cell debris which has been desquamated from the alveolar wall, and give the impression that the cells are undergoing a colloidal change. Moreover, the interalveolar spaces are largely filled with cuboidal epithelial cells with large round nuclei, and interstitial substance proper is scanty. The writer is not certain of the interpretation of this appearance; it would almost pass for an adenomatous goitre. The substance of the membrane, other than gland and cartilage, is made up of compact areolar tissue.

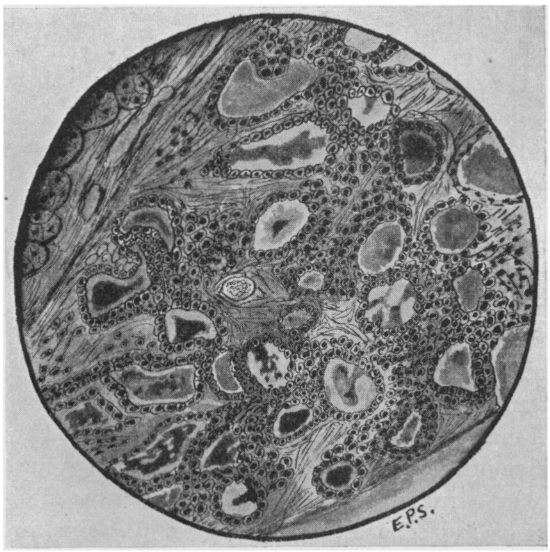

Fig. 8. Section of the colloidal portion of the Harderian gland of a calf.

The membrane is lined on its palpebral surface by a stratified epithelium, set on small papillae; and on its ocular aspect by a single or double layer of rather flattened cells.

THE FUNCTION OF THE PLICA OF MAMMALS

The physiological explanation of the plica and cartilage of Mammals is to be found in the consideration of the manner in which the eye gets rid of foreign bodies; and the human eye furnishes a satisfactory means of investigating this. If one goes out in a dust storm, one's eyes rapidly fill with dust, and as rapidly get rid of it. Where does the dust go? It will be found collected together into a little sticky mass at the inner canthus; and that mass is situated on skin, in the angle internal to the caruncula lachrymalis, in which situation it causes no irritation and does no damage. There can be no doubt that this is brought about by the intervention of the plica semilunaris, which is not so vestigial a structure as the descriptions of it might imply; it is in fact a very respectable fold, with an underlying conjunctival fornix often a quarter of an inch in depth.

When a foreign body gets on to the eyeball, two mechanisms are set working. First there is an excessive secretion of tears, the object of which is to float the object up off the surface of the globe. The lids are instinctively closed, thus forming a sort of cistern, so that the front of the eye is freely bathed, and a light object will be floated forwards.

It is probably a reasonable conjecture that the photophobia of foreign bodies is a purposeful reflex; the temptation to close the eye persists in the dark.

The hypersecretion of tears is accompanied by the well-known action of the orbicularis palpebrarum, which sweeps tears and foreign matter across to the inner side of the eye, and *past* the openings of the lachrymal canaliculi—not into the canaliculi. It must be remembered

(*a*) that the orifices of the canaliculi are very minute—about one-tenth of a millimetre in diameter;

(*b*) that the flood of tears has raised the orifices from contact with the eyeball;

(*c*) that the orifices tend to face down-stream, especially when the orbicularis is in action.

It is therefore reasonable to suppose that foreign particles cannot escape by the lachrymal canaliculi.

Now the internal conjunctival fornix is bridged across by the plica semilunaris, which in man has a very thin free concave edge, like the lunula of a watch-pocket valve of the heart. So the tears and foreign matter are diverted forwards across the caruncular region. The caruncle is closely packed with large glands resembling sebaceous glands (fig. 9). The foreign body thus reaches a region of fine hairs and much fatty sebaceous material, and the rest of the story is obvious.

If the eye be kept open when there is a foreign body in it, the ball will be seen to be repeatedly turned inwards, in an effort to get the body picked up by the plica and diverted towards the caruncular region. An eyelash, for example, has been observed in a patient's eye; it was carried inwards by the tears and the action of the orbicularis, but slipped *under* the plica semilunaris; it was brought out from this position by an outward sweep of the eye abolishing the deep internal fornix; and after several trials it was finally picked up by the plica, and transferred to the skin at the inner canthus.

It is for these reasons that the terms PLICA INTERCIPIENS and CARTILAGO INTERCIPIENS have been suggested.

Incidentally it would seem that the correct treatment for a foreign body in the eye is to close the lids and wait.

Such would appear to be the mechanism in man and Mammals, and it fits in well with our conception of their requirements; Birds must have the speediest method possible, Mammals can sacrifice speed in this matter to thoroughness.

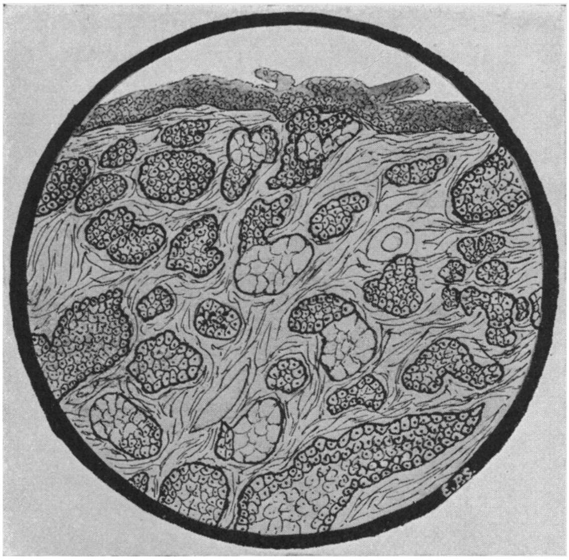

Fig. 9. Section across human caruncula lachrymalis, showing numbers of large glands closely packed together.

WHAT DO WE KNOW OF THE MORPHOLOGY OF THE NICTITATING MEMBRANE, AND OF THE INTERCEPTING MEMBRANE AND CARTILAGE?

The writer has not yet been able to make the attempt to trace the ontogeny of the mammalian membrane and cartilage; it would therefore not be proper to form any definite views as to its morphological value, though it may not be out of place to express a very tentative opinion that the mammalian structures are morphologically different from those of the Bird, an opinion based on the belief that the neuro-muscular mechanism constitutes a morphological entity, as suggested below.

The same uncertainty is not felt, however, in regard to the nictitating membrane of the Bird; it can definitely be homologised with a part of the lower eyelid of certain of the Amphibia, as exemplified by the frog and the newt.

The following considerations are suggestive:

The eyelids of the frog (fig. 10). The upper lid of the frog resembles that of the bird, being short and somewhat rigid with a shallow conjunctival fornix; and it moves up and down with the eye, and appears unable to move independently of the eye. The lower lid is wide with a deep fornix, and moves freely and independently of the eye; and it is transparent in its upper two-thirds. The eye is closed by drawing the lower lid up over the lower three-fourths of the globe, and at the same time turning down the eye itself which carries with it the upper lid, and so the lids meet. This lower eyelid resembles a nictitating membrane in its transparency, and in addition it bears comparison with the nictitating membrane in respect of (1) its position; (2) its muscular and nervous mechanism.

(1) When the lower lid is not in use, the transparent upper part slides down within the opaque lower part; that is, it comes to occupy the plane between the ocular conjunctiva and the palpebral; this is the position of the nictitating membrane of the Bird. We can thus differentiate the lower lid of

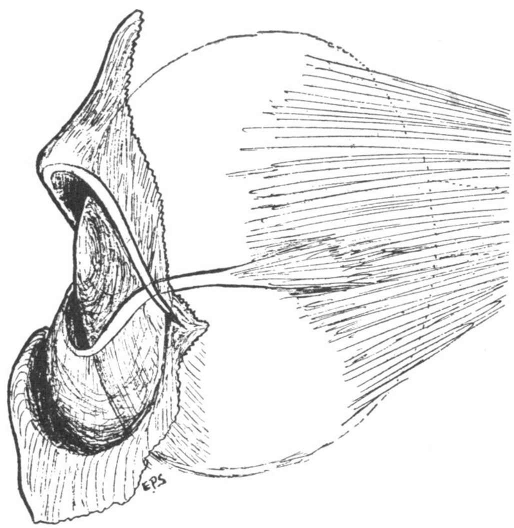

Fig. 10. Diagram of eyelids of frog, with pyramidalis muscle seen from outer side.

the frog into two parts—the inner transparent nictitating part, and the outer opaque skin-covered lid-part. Now a vertical section across this compound lower lid has the same appearance as a section across the developing lids and nictitating membrane of a chick (3) (fig. 11). Ontogenetically the lower lid is a double or bifurcating outgrowth.

In the anurous Amphibia the inner part of this double lid grows more rapidly and to a greater size than the external; this results in the differentiation of the adult lid into its two parts as described. In the Bird the two parts of the developing lid grow more equally, resulting in a separate nictitating membrane under cover of a well-marked and freely movable lower lid (3).

The study of developing chicks earlier than the eleventh day suggests that the nictitating or inner part may be the primary lid, and the part which becomes the lower lid a secondary outgrowth from the nictitating membrane.

The nictitating membrane of the Bird is of course at the internal canthus, but this need not cause great difficulty in comparing it with that of the frog. The upper lid of the frog always overlaps the lower at the external canthus; if we slightly rotate the lower lid of the frog so that the outer angle becomes the lower, and the inner angle slips up under the upper lid, we have the position of the nictitating membrane of the Bird. And, as we shall see, the outer angle of the lid of the frog has the pyramidalis muscle attached to it, thus corresponding with the lower angle of the true nictitating membrane. Such a change in position would be brought about by a change in the direction of the rima palpebrarum, namely a relative descent of the anterior or inner end of that fissure. Tentatively it may not be fantastic to suppose that such a change might be associated with the development of a frontal region of the brain, and of a roof to the orbit.

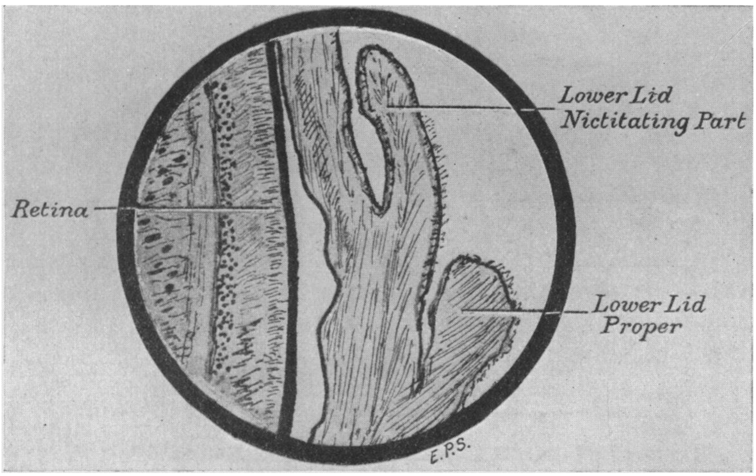

Fig. 11. Vertical section of developing lower eyelid and nictitating membrane of chick—10 days.

(2) *The neuro-muscular apparatus.* The lower eyelid of the frog is elevated by a tendon inserted into its outer angle. This tendon pierces the conjunctiva of the upper lid, just above the external canthus; it then runs back through the fibres of the pterygoid muscle (which, in the frog, occupies the outer part of the orbit), and is continued back to a muscular belly arising from the outer side of the sclerotic. But this muscle is not an isolated entity; it is a partially detached portion of the choanal or retractor bulbi muscle. The choanal muscle wraps round the optic nerve, is intimately related to the external rectus, and is supplied by the sixth nerve.

The elevator of the lower lid of the frog thus can be compared to the muscles of the nictitating membrane of the Bird; these are part of a deep sheet around the optic nerve and posterior part of the eyeball, are closely related to the external rectus, and are supplied by the sixth nerve.

Now, if the eye muscles are the representatives of three pre-otic head segments (6), the immediate pre-otic being supplied by the sixth nerve, and the most anterior segment by the third nerve, then we may reasonably say that the pyramidalis of the Bird is morphologically the same as the elevator of the lower lid of the frog; it is proposed to call this latter muscle the pyramidalis of the frog.

The frog has also a depressor palpebrae inferioris, which is part of a complete muscular sling, and corresponds to the fibrous sling and depressor muscle of the Bird (fig. 1). This muscle is in both cases supplied by the third nerve, and therefore belongs to the first segment of the head.

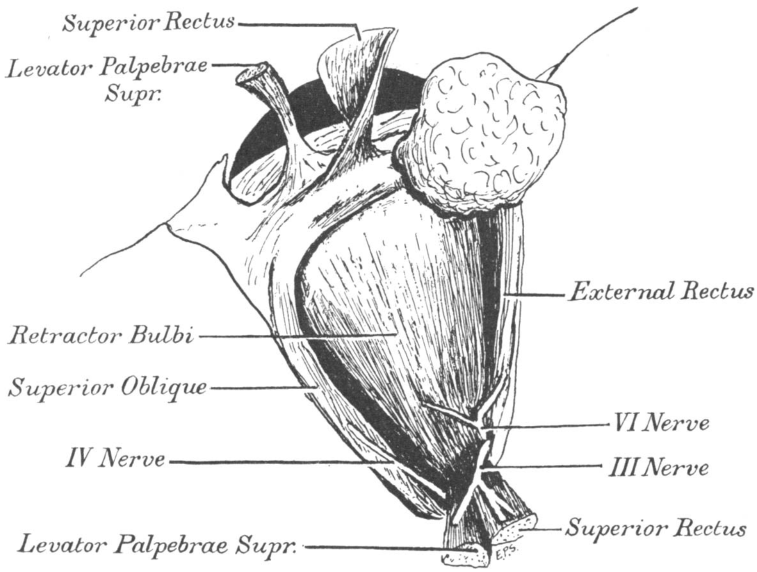

Fig. 12. Retractor bulbi muscle of calf, dissected from above.

Neuro-muscular apparatus in the Mammal. We have seen that structurally and functionally the plica of the Mammal differs from that of the Bird, and that its neuro-muscular mechanism—if any—is also different from that of the Bird. We now have to face the fact that the Mammal has nevertheless a well-marked retractor bulbi muscle, corresponding to the choanal muscle of the frog and to the two muscles of the nictitating membrane of the Bird, yet this muscle shows no anatomical connection with or relation to the plica.

The retractor bulbi is present in all the Mammals dissected for this investigation as a well-marked thick muscular cone, folded round the outer side of the optic nerve and almost completely surrounding it; it is inserted into the sclerotic behind the recti, under cover of which it lies (fig. 12). There are described in Mammals protrusor fibres (represented in man by the sphenoidal-fissure-fibres of Müller), and it is supposed that these push the eye up to the plica, and the retractor bulbi pulls it back again. Without entering into the merits of this view, we may simply say it does not make these muscles anatomically the mechanism of the plica. Further, the retractor bulbi is closely related to the external rectus, and is supplied by the sixth nerve.

One is tempted therefore to think there are two distinct mechanisms—a third-nerve mechanism for eyelid, and a sixth-nerve mechanism for nictitating membrane.

In the frog both mechanisms are present in connection with the lower lid; in the Bird both are present in connection with two separate structures—lower lid and nictitating membrane; in the Mammal both are present, but the sixth-nerve mechanism has no connection with plica or lid.

In conclusion, it has been assumed that the plica semilunaris of man is the same as the plica of Mammals; cartilage has been found in the plica of negroes, and occasionally in Europeans. The writer has as yet not found any cartilage in a number of sections of the plica semilunaris.

SUMMARY

(1) A special protective apparatus for the eye is necessary in all land animals, and will vary according to habitat and needs.

(2) It is generally stated that the plica semilunaris of man and the nictitating membrane of Mammals, Birds and Reptiles are representatives of the same structure; this is our problem.

(3) The following steps towards the investigation of the problem are taken, in order:

(*a*) Full investigation of a typical nictitating membrane and its neuromuscular mechanism, as seen in a Bird—the ostrich.

(*b*) Comparison of this with the so-called nictitating membrane of Mammals, and discussion of the function of the mammalian structure and of the plica semilunaris of man.

(*c*) Estimation of the probable morphological value of the nictitating membrane of the Bird, by comparison with the lower lid of the frog, and by study of its ontogeny.

(4) These studies lead to the following conclusions:

(*a*) That structurally and functionally the plica of man and Mammals differs entirely from the nictitating membrane of Birds. It is proposed to drop the term "nictitating membrane" in speaking of Mammals, and to call the plica the "plica intercipiens" and its cartilage the "cartilago intercipiens."

(*b*) That there is reasonable ground for supposing that the plica of man and Mammals is morphologically different from the nictitating membrane. But the morphology of the mammalian structures has yet to be worked out by a study of their ontogeny before any definite conclusion can properly be stated.

Acknowledgment has to be made to Professor W. H. Wood for permission to do this work in the Anatomy Department of Liverpool University, and for the advantage of many discussions of the subject with him; to Dr J. Beattie, of the Zoological Gardens, for material; and to Professor Sir Arthur Keith for that interest and advice which he is always so ready to give.

REFERENCES

(1) QUAIN'S *Anatomy*, 11th ed. vol. III, part II, p. 174.
(2) WHITNALL. "The Retractor Bulbi in Man." *Journ. Anat. and Phys.* vol. XLVI, p. 38.
(3) JOHNSON, LINDSAY. *Phil. Trans. Royal Society*, B, p. 215.
(4) SLONAKER. *Journ. Morphology*, vol. XXIX, no. 2, pp. 361 *et seq.*
(5) OWEN. *Comparative Anatomy and Physiology of Vertebrates*, vol. II, p. 142.
(6) NEAL, H. V. "History of the Eye-muscles." *Journ. Morphology*, vol. XXX, no. 2, pp. 433 *et seq.*