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THE PALPEBRAL AND OCULOMOTOR APPARATUS IN FISHES: OBSERVATIONS ON MORPHOLOGY AND DEVELOPMENT.

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THIS research was originally undertaken with the object of examining the motor apparatus of fishes' eyes, with especial

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[1] Read at the Meeting of the Anatomical Society of Great Britain and Ireland, July 1899, and at the British Association, Dover, 1899.

reference to any arrangements which might serve to perform the movements of projection and retraction of the bulb. During the course of these observations the conditions of the accessory structures of the eye were noted, and subsequent investigations on their development made.

Examination and dissection of the eye region have been performed in all in seventy species of fishes, which include examples of most British, and some few foreign families.

The following is the list of species examined, the classification is that of Günther (10):—

PALÆICHTHYES.

- CHONDROPTERYGII.
  - *Plagiostomata.*
    - *Selachoidei.*
      - Carchariidæ.
        - Carcharias glaucus (Blue Shark).
        - Zygæna malleus (Hammerhead).
        - Galeus vulgaris (Stinker Dog-fish, Sweet William).
        - Mustelus lævis (Smooth Hound).
      - Scylliidæ.
        - Scyllium canicula (Larger spotted Dog-fish).
        - S. catulus (Lesser spotted Dog-fish).
      - Spinacidæ.
        - Acanthias vulgaris (Spiny Dog-fish).
      - Rhinidæ.
        - Rhina squatina (Angel- or Monk-fish).
    - *Batoidei.*
      - Torpedinidæ.
        - Torpedo narce (Torpedo Ray).
      - Rajidæ.
        - Raja batis (Common Skate).
        - Raja blanda (Blond Ray).
    - *Holocephala.*
      - Chimæridæ.
        - Chimæra monstrosa.
        - Callorhynchus antarcticus.[1]
- GANOIDEI.
  - *Chondrostei.*
    - Acipenseridæ.
      - A. sturio (Common Sturgeon).
  - *Polypteroidei.*
    - Polypteridæ.
      - Polypterus bichir.[1]

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[1] Not dissected.

TELEOSTEI.

- ACANTHOPTERYGII.
  - *A. perciformes.*
    - Percidæ.
      - Perca fluviatilis (Freshwater Perch).
      - Labrax lupus (Bass).
      - Lucioperca sandra (Pike-perch, Zander of Rhine).
    - Mullidæ.
      - Mullus barbatus (Red Mullet).
    - Sparidæ.
      - Cantharus lineatus (Old Wife, Black Sea-bream).
      - Pagellus centrodontus (Common Sea-bream).
  - *A. cotto-scombriformes.*
    - Carangidæ.
      - Caranx trachurus (British Horse Mackerel).
    - Cyttidæ.
      - Zeus faber (John Dory).
    - Scombridæ.
      - Scomber scomber (Mackerel).
      - Thynnus thunnina (Tunny-fish).
    - Pediculati.
      - Lophius piscatorius (Angler, Sea-devil).
    - Cottidæ.
      - Trigla pini (Red Gurnard).
  - *A. gobiiformes.*
    - Gobiidæ.
      - Periopthalmus Koelreuteri.
      - Callionymus lyra (Dragonet).
  - *A. mugiliformes.*
    - Mugilidæ.
      - Mugil chelo (Grey Mullet).
  - *A. gastrosteiformes.*
    - Gastrosteidæ.
      - Gastrosteus aculeatus (Stickleback).
- ANACANTHINI.
  - *A. gadoidei.*
      - Gadus morrhua (Cod).
      - G. æglefinus (Haddock).
      - G. merlangus (Whiting).
      - G. luscus (Pouter Whiting).
      - Merluccius vulgaris (Hake).
      - Molva vulgaris (Ling).
    - Ophidiidæ.
      - Ammodytina tobianus (Sand Eel).
    - Macruridæ.
      - Macrurus cœlorhynchus.
  - *A. pleuronectoidei.*
    - Pleuronectidæ.
      - Hippoglossus vulgaris (Halibut).

ANACANTHINI—*contd.*
- *A. pleuronectoidei.*
  - Pleuronectidæ.
    - Hippoglossoides platessoides (Rough Dab).
    - Rhombus maximus (Turbot).
    - R. lævis (Brill).
    - Arnoglossus laterna (Scaldfish)
    - Pleuronectes platessa (Plaice).
    - P. flesus (Flounder).
    - Solea vulgaris (Sole).
    - S. aurantiaca (Lemon-sole).
    - Platessa cynoglossa (Pole or Witch).

PHYSOSTOMI.
- Cyprinidæ.
  - C. carpio (Carp).
  - Leuciscus rutilus (Roach).
  - L. erythrophthalmus (Rudd).
  - Tinca tinca (Tench).
  - Abramis brama (Common Bream).
  - A. blica (White Bream).
- Scombresocidæ.
  - Belone (Gar-pike).
- Esocidæ.
  - Esox lucius (Pike).
- Salmonidæ.
  - Salmo salar (Common Salmon).
  - S. ferox (Lake-trout).
  - Osmerus eperlanus (Smelt).
  - Argentina silus.
- Clupeidæ.
  - Clupea harengus (Common Herring).
  - C. sprattus (Sprat).
  - C. alosa (Shad, Mai-fisch of Rhine).
- Murænidæ.
  - Anguilla anguilla (Freshwater Eel).
  - Conger conger (Sea Conger).

LOPHOBRANCHII.
- Syngnathidæ.
  - Nerophis lumbriciformis (Little Pipe-fish).

PLECTOGNATHI.
- Gymnodontes.
  - Tetrodon lagocephalus (Globe-fish).
  - Orthagoriscus mola (Sun-fish).

CYCLOSTOMATA.

- Petromyzontidæ.
  - P. fluviatilis (Lamprey).

I. PALPEBRAL APPARATUS.

Within the range of fishes included in the above list there can be found every form of provision for the setting and protection of the outer surface of the bulb, from the most simple and least developed to a complex and highly developed mechanism. Such a series might naturally be expected to be concurrent with an evolution from the simpler to the more complex type of fish, but such a parallelism in development cannot be held to be a real one, since in most cases the complex forms of palpebræ are found in fishes classed within orders nearest the main line of phylogeny, whilst the simpler forms may be found in the more specialised types. This would appear to indicate that the variation of these accessory organs depends peculiarly upon the conditions of life of any particular family, which suggestion is confirmed by the variations of form found in closely allied species.

1. *Palpebral Provision—None.*

There are some, but not many, species in which these negative conditions are found. The actual arrangement of the transition from the skin surrounding the orbit to the outer corneal layer is of two kinds. One in which the passage is by an uninterrupted and even layer of skin which is directly continuous with the transparent outer corneal layer. This arrangement necessarily restricts the movements of the eyeball within the narrowest limits. It is found well exemplified in the common and Conger Eels, also the Lamprey and Globe-fish; in the Conger its influence upon the bulbar muscles is marked. It is also found in a less degree in the commoner Rays.

A second form is that in which the skin passes from the orbital margin to the outer corneal layer by a loose and flexible collar of skin, which allows of free bulbar motion in all the combinations of rotation and rectilinear motions, and also in some cases of projection and retraction. This arrangement can best be seen in the Pleuronectes, where the projection of the bulb allowed by this arrangement gives the eyes of these fishes an appearance not unlike a miniature conning-tower. A similar condition less well marked is found in the Angler.

2. *Palpebral Margins and Conjunctival Fornices defined.*

This form is the one found in the majority of the teleostean fishes. The skin passes from the circular orbital margin towards the centre of the cornea, and after extending thereto in a greater or lesser degree, recurves deeply, forming a palpebral margin. The depression formed by the continuance of the thin inner or conjunctival layer on to the bulb to blend with the outer corneal layer, constitutes the conjunctival fornix. This arrangement, other things being equal, allows of great freedom of rotation and rectilinear movements, according to the depth of the conjunctival fornices. The depth to which the folds extend may differ in the lower and upper parts, but since the angles of the eye are rarely defined, the passage from superior to inferior fornices is uninterrupted.

The circular palpebral margin is in life upon a level with, or makes a gentle slope towards, the flat corneal surface, so providing for the least resistance to water friction during progression.

Such palpebral margins, however, afford but little protection to the eye since the greater part of the cornea remains exposed, but in some species, *e.g.* Sturgeon, the margin is sufficiently wide and of dense tissue, with calcified epidermis, that it makes an efficient protection to the sclero-corneal junction.

Of the condition in which the margin and fornices are small and shallow, the Torpedo (inferior fornix only), Chimæra, Perch and Perch-pike, Gurnard, Grey Mullet, Stickleback, Cod, Haddock, Hake, Carp, Roach and Rudd, and the little Pipe-fish, may be taken as examples; and for the broader margins and deeper form of fornices the Sharks, Sturgeon, Bass, Red Mullet, Bream (sea and fresh), Mackerels, Tunny-fish, Whiting, Ling, Tench, Pike, Salmon, and the Herring. These examples do not allow of any classification into families or according to the habitat of the fish as do other structural variations, for differences are found between closely allied members of the same family, *e.g.* amongst the Cods. Thus in Cod, Haddock, and Hake the margins are narrow and the fornices shallow, whilst in Whiting and Ling the margins are fairly broad and the fornices deep.

3. *Extra Palpebral Folds*—"*Pseudo-Membranæ Nictitantes.*"
(Figs. 1 and 2.)

In the salmon the palpebral margin is of irregular shape. In a condition of repose the larger and posterior part of the margin coincides with the corresponding two-thirds of the corneal margin. From here the upper and lower margins continue anteriorly in gradually converging lines to meet in a curve representing a segment of a smaller circle than that of the corneal margin. The space between this anterior margin and the anterior corneal margin, representing a breadth of about one-third the corneal diameter, is filled by a triangular block of muco-areolar tissue[1] of semi-cartilaginous consistency (fig. 1). Its thin posterior edge is transparent and coincident with the corneal margin, except at its upper horn, where it recedes to its upper attachment. The anterior and thicker part is less transparent, and contains a few scattered pigment spots. The triangular block is attached to the anterior palpebral fold by the edges of its superficial surface by means of a thin conjunctival membrane which produces a conjunctival recess; a like attachment from its deep surface to the bulb produces a second and deeper conjunctival recess.

The angles of the cartilaginous block are affixed to the neighbouring bones by three ligaments, the anterior and strongest ligament to the lacrymal bone, the superior to the supraethmoid, and the inferior to one of the suborbital ossicles; the anterior edges of the block overhang a pair of diverticula of the nasal pouch. Dissection of this extra fold in *Argentina silus* and the Trout shows a similar construction.

In the common Herring there exists an extra fold similar to that of the Salmon tribe, but more complete in its formation (fig. 2). In this fish the corneal surface is exposed only in a narrow vertical palpebral fissure formed by the help of three folds, two anterior and one posterior. Of the anterior and posterior each forms a broad thin transparent fold, which is directly and smoothly continuous from the surrounding skin to its thin free edge, where, recurving sharply, it makes a deep conjunctival fornix, and within the anterior fold the extra fold

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[1] This constitution was shown by microscopic examination.

is found. At the dorsal extremity of the palpebral fissure is a union of all three folds, anterior, 'extra,' and posterior; the ventral extremity, however, is not so formed, for the posterior fold makes a sharp curve convex anteriorly, which is overlapped by a similar convexity existing on the lower horn of the 'extra' fold. The separation of anterior and 'extra' folds extends for fully two-thirds of the extent of the latter, and results in the formation of a well defined extra conjunctival recess. The two folds blend for their lower third.

The measurements of the depths of the fornices in a medium sized fish were:—

Posterior fornix,	10 mm.
Superficial anterior fornix,	5 mm.
Deep anterior fornix,	4 mm.

The same blind diverticula from the nasal pouch exist beneath the anterior edges of the extra fold of the Herring, as in the Salmon.

The Maifisch presents a modification of this structure owing to the greater fusion of the two anterior folds, so that the sulcus separating them is small, and occupies a position in the anterior-superior region of the eye. There is also a rather narrower palpebral fissure than in the common Herring.

In the common Mackerel there is a narrow vertical palpebral fissure, but the anterior folds are here completely united, a shallow groove only indicating a double arrangement, as in the Herring, whilst in the Horse Mackerel the whole anterior margin is so reduced as to be almost unrecognisable.

This extra fold or false nictitating membrane has been noted in the Salmon by Rosenthal (26, p. 398), who says "there is heaped up at the anterior angle of the eye an immobile gelatinous mass, which forms so as to say a rudimentary 'Nickhaut,' and which fills a part where the bony wall of the orbit is incomplete"; and in a later paper (27, p. 419) he makes a similar suggestion as to the use of the fold. John Hunter (16, p. 413) appears to have noted its presence, but his description is not so certain.

The structure is shown in almost all the species of Salmonidæ delineated in the beautiful plates of Agassiz and Vogt (2), and its position is indicated by Günther (11) in several outline drawings of Salmons' heads. No mention of it is found in Haller's work on these fish (12).

The structure may probably be considered as filling the gap in the orbital wall as suggested by Rosenthal. It will also serve to protect the eye from injury by its acting as a 'fender.' The large extensions of the margins of both 'extra' and posterior folds in Herrings tends to support this view. Whilst in the absence of any means of regulating the relations of the folds to the pupil, the tissue forming them retains a considerable delicacy and transparency of substance at the edges. It is noteworthy that this structure is developed in fishes frequenting shallow waters and rivers, where such a protection would be especially advantageous.

4. *The Nictitating Membranes of Selachians.*

My dissections of British fish possessing this membrane were completed at Plymouth in Easter 1898, after which date I commenced to work at its development. In June of that year Dr Ridewood (25) read before the Anatomical Society a paper dealing with the same subject from his observations on dissections of adult fish. As this paper has covered the ground for the adult morphology, and the descriptions of the myology are excellent in their accuracy and lucidity, I can add nothing to the anatomy of the musculature.

Regarding Ridewood's suggestion of the possibility of the existence of a nictitating apparatus in the horizontal duplicature of skin below the eye of Scyllium, Wiedersheim shares this view, for he has included *S. canicula* with other fish already recognised as possessing the membrane (35, p. 431). Regarding the movements of the eyelids of this fish, it may be pertinent to record my observations. I had had doubts as to the free mobility of the lids by the muscles attached thereto, by reason of the toughness of its skin, but these doubts were dissipated by some observations made on the fish within one of the tanks of the Brighton Aquarium. I saw a specimen of the Larger Spotted Dog-fish slowly gliding towards me, and when within a few inches of the glass front of the tank, and of my eyes, the creature gave a most unmistakable wink, by which the whole eye seemed to be covered by the lids. The succeeding day I was able to make a longer observation on a specimen of the Smaller Spotted Dog-fish; the fish was lying motionless on the gravelled floor of the tank and in contact with the glass front; a crab approached and walked over the dog-fish's head; the only sign of a sensitiveness on the part of the fish to this act of aggression was the complete closure of its eye.

In this action the greatest part was played by the nictitating membrane, *i.e.*, the upper of the two folds constituting the whole lower eyelid (fig. 6). Assistance came from the straightening, depression, and slight eversion of the upper lid so as to completely fit over the nictitating membrane. The elevation of the membrane was so complete that the deep sulcus normally existing between the membrane and the lower lid was almost obliterated, and the lower lid was itself slightly elevated with the extension of the nictitating membrane.

Regarding the relative values of the eyelids of Carcharias, Zygæna, Galeus, Mustelus, and Scyllium, it appears, from an examination of the palpebral apparatus of all vertebrates, that the trend of progression in the evolution of these structures is towards a greater completeness in the organisation of the upper and lower lids, and that the condition of the nictitating membrane is one of secondary importance. With this proposition in view, a comparison of the apparatus in Carcharias, Zygæna, and Galeus, with that found in Mustelus and Scyllium (figs. 3, 4, 5, and 6), will show that although the former group presents a marked specialisation of the nictitating membrane, yet its true upper and lower lids are feebly developed, since they inclose a large round palpebral fissure which would leave the eye exposed and unprotected were it not for the development of this highly specialised secondary membrane. On the other hand, in Mustelus and Scyllium the palpebral fissure is oval and the bulb receives a considerable screen from upper and lower lids as well as from the membrane, and both the true lids can be moved in the defence of the eye, so that the excursion required of the membrane not being so great, its specialisation is arrested. It will therefore follow that in these latter fish, Mustelus and Scyllium, we have a nearer coincidence with the line of progressive evolution than in Galeus, Carcharias, and Zygæna. To substantiate this proposition it is necessary to show that the development of the membrana nictitans (*i.e.*, the inner fold of the lower lid) is later in date and secondary in site of origin to the true lower lid.

5A. *The Development of the Membrane—Previous History.*

The earliest suggestion regarding its origin appears to be that given by Müller (23, p. 121): he states that it is a duplicature of the skin growing from the inner surface of the eyelid. On what ground this statement is made I cannot discover, for he does not add any reasons for the opinion given. I can only believe that it is made from an analogy of the position of the membrane in the shark and that in the bird, for in his description of the naked-eye appearance of the fish's membrane, he contrasts it with the delicate conjunctival structure of the bird. Subsequently Müller's statement has been repeated in the text-books of Balfour (3, p. 416), Wiedersheim (35, p. 434), Hertwig (13, p. 431), and others; whilst Minot (22, p. 727) states that "nothing accurate is known concerning its development."

I am unable to find any further hypothesis as to its origin, or attempted elucidation of its development, until we come to that contained in the paper by Ridewood. This zoologist follows an exceedingly interesting and suggestive line of argument based upon the variations in the form of the membrane in the adult fishes possessing it. He notes the fact that the membranes of Galeus and Mustelus differ in their 'finish': the opposing surfaces of the lower lid and membrane in Galeus and Carcharias are free from shagreen, whilst in Mustelus the inner surface of the lower lid possesses shagreen. From this he argues that the nictitating membrane is the old lower lid, whilst the present lower lid is a new duplicature of skin, which by the specialisation of the lids in Galeus has lost its shagreen, but the structures in Mustelus being incompletely evolved have not yet thrown off this internal armature of denticles.

This line of argument, apart from my observations on embryos, I believe to be open to criticism, for it is equally permissible to apply the facts adduced in support of a conclusion the direct reverse of the one just quoted, namely, that since in the Galeus, etc., the proper lids are deficient in growth, the deficiency is made good by an extra mobility of the membrane, and consequently the contiguous epiblast of the lower lid remains free from shagreen; whereas, on the other hand, the reason why in Mustelus shagreen is developed to a slight extent upon the contiguous surfaces of lid and membrane is that the membrane of these fishes has ceased its evolution or is on the downgrade, the more extended growth of the true lower lid being followed by a limitation of growth of the membrane, and an extension of calcification of surface epiblast. It is the development of the lids, I would repeat, and not of the nictitating membrane, which is a mark of progressive evolution. This argument I believe to be the true one. It will accord with the variations in the musculature,—the differentiation of form and scope of function is wider in Galeus than Mustelus or Scyllium,—and finally it is supported by actual observations of the origin of the membrane in embryos.

With regard to Acanthias, I am still in doubt as to the mobility of its palpebral folds; muscles are found in connection with them; they are figured by Vetter (34, pl. xiv. fig. 3) and Ruge (28, fig. 14); but although I watched the movements of captive specimens of this fish for long times, I did not succeed in observing any movement of the lids.

5B. *The Development of the Membrane—Observations on Embryos.*

The development of these structures I have followed in Mustelus embryos obtained from the Naples Marine Station. Four specimens have been used of the lengths of 18, 30, 38, and 48 mm. Of these, the first, second, and third correspond fairly well to the stages 'N,' 'P,' and 'Q' of Balfour (4, p. 79); the fourth has advanced beyond the last of this series, but might correspond to a stage 'R' were this series continued. I shall accordingly refer to them under these letters.

Length of Embryo.	Stage and Letter.
18 mm.	'N,' Balfour's series.
30 mm.	'P,' do.
38 mm.	'Q,' do.
48 mm.	'R,' do. continued.

In the first of these, 'N,' the bulb has arrived at that degree of development where the cavity of the lens is almost filled with the exuberant growth of its posterior cells, but is still apparent as a narrow sharply-curved slit in the transverse section. Also, the cavity of the optic cup exists at its extremities, whilst at the posterior pole the two layers are nearly in contact. The channel of the optic stalk is pervious, so that the cerebral vesicles are in connection with the cavity of the optic cup. No cartilage has appeared in the mesoblastic cranial covering, but occasional patches of denser tissue indicate the sites of growth of the walls. The ocular muscles are already developed, but there is no indication of the formation of a definite optic capsule.

In embryo 'P' the development has advanced considerably. The lens cavity is wellnigh closed, that of the optic cup is only distinguishable at its extreme edge and in the immediate neighbourhood of the entrance of the optic nerve. This structure is now recognisable as a nerve, and the cavity of the original stalk has disappeared. The cranium presents a growth of cartilage in its floor, which is extending up the side walls to the lateral edges of the roof. An investment of closely-packed cells around the retina shows the formation of an optic capsule.

Embryo 'Q' is an advance upon the former in size, and in the increase of the complexity of its parts and the greater completeness of its cartilaginous skeleton. The optic capsules are well defined, but are not yet cartilaginous.

In embryo 'R,' a delicate layer of cartilage has appeared within the optic capsule, the retina shows stratification, and the cranial skeleton is well grown.

In the earliest of these embryos, 'N,' there is no sign of palpebral growth, the bulb is invested on its external aspect by a uniformly smooth covering of surface epiblast which takes a bold curve, convex outward, due to the supporting optic cup and lens. A considerable interval exists between this epiblastic covering and the sunken epiblast of the lens, for as yet no mesoblast has penetrated the space. The angle made by the passage of the ocular investing epiblast to the general investing epiblast is acute, and in the dorsal region it amounts to a fairly deep recess, but the overhanging bulge does not represent the commencing palpebral folds, which are seen in the succeeding embryo to grow from the bulbar investment.

In embryo 'P' (figs. 7 *a*, *b* *c*) the sections in the anterior region of the eye show the growth of the upper and lower lids as rounded protuberances arising from the bulbar investment, the upper some distance from, and the lower much nearer the side of the head; of the two, the lower fold is the stouter. In sections more posterior, the earliest growth of the membrana nictitans can be distinguished as a small tongue of dermal tissue appearing upon the ocular side of the lower lid. In the anterior sections it is sessile, but it becomes more tongue-shaped towards the posterior region. In this embryo the epidermis is unfortunately loosened from portions of the environing dermis of both eyes, but this does not at all invalidate the evidence of the specimen, as the dermis is the determining factor of the growth of these structures, and in all the sections the definition of the cells of both layers is quite clear—they are at the site of the membrane, of extra large size, both in dermal and epidermal layers.

In embryo 'Q' (figs. 8 *a*, *b*, *c*) the further growth of the membrane is shown. In the more anterior sections the membrane has not appeared, and the lower lid is thick and rounded; further back the sections show the membrane as a thin tongue of epiblast-clad dermis springing from the ocular edge of the lower lid. More posteriorly the method of deepening of the sulcus between membrane and lid appears, the epidermis penetrates the cleaving dermis as a double row of cells whose contiguous surfaces are as yet unseparated by any formation of cuticle.

In embryo 'R' (figs. 9 *a*, *b*) the membrane now projects from the ocular surface of the lower lid to a considerable extent, and the covered part is separated from the lower lid by a fissure, penetrated by epiblast, of a depth equal to two-thirds the length of the projecting portion of the membrane.

In later embryos up to 'full-time' the position and form of the membrane has been observed, and it is to be noted that at no date is there any tendency to that union of the upper and lower eyelids which forms permanently in reptiles and temporarily in mammals (Donders, 8, p. 291).

The conclusion I would draw from these observations is, that the growth of epiblast-clad dermis which constitutes the membrana nictitans arises from the ocular surface of a previously formed lower lid.

Of the sections reproduced, those numbered 7 *c*, 8 *c*, and 9 *b*, are taken through that part of the bulb in which the posterior part of the optic nerve appears, so that the sections represent as nearly as possible the same level, and by comparison the rate of growth can be observed.

6. *The Development of the Musculature of the Membrane.*

Although the musculature of these structures would seem somewhat complicated from the many names attached thereto, yet examination of their connections shows that there is no one muscle which is independent of another; all are more or less closely connected or continuous with the other muscles of the membrane or of the spiracle.

The latest description, by Ridewood, recognises the following muscles in this region :—

1. *Levator palpebræ nictitantis.*
2. *Depressor palpebræ superioris.*
3. *Retractor palpebræ superioris.*
4. *Constrictor spiraculi.*
5. *Dilator spiraculi.*

With this differentiation my own dissections agree, and in referring to the muscles I shall adhere to this nomenclature.

These five muscles appear from the gross anatomy to constitute two sets only, a superficial and a deep.

The first or superficial set appears to comprise the *retractor palpebræ superioris* and the *constrictor spiraculi.* Ridewood suggests their origin may be from "a purely dermal system of muscles." The unity of the *levator palpebræ nictitantis* and *dilator spiraculi* is a most obvious one, and with these is closely associated in its origin the *depressor palpebræ superioris.* These constitute the deep muscle sheet, a view shared by Hubrecht (15, p. 100), Tiesing (32, p. 92), Allis (1, p. 571), and Ridewood; and, to quote the last named, they "would together represent that undifferentiated pre-spiracular muscle of Heptanchus which

Vetter has described as the *constrictor superficialis dorsalis*" (25, p. 242).

In the earliest of the Mustelus embryos, 'N,' sections through the middle of the branchial plate immediately in front of the anterior limb-bud show the state of the development of the musculature of the region (fig. 10). The muscle plates are represented by two crescentic masses lying on each side lateral to the neural canal and notochord, and extending ventrally by two partially separated blocks of tissue into line with the dorsal aorta. Dorsally, the plates of each side are separated by a considerable interval, and within the cells forming the extremities there yet remains the cavity of the myotome. The protoplasm of the cells of the main masses is increasing in quantity, and the cells show a radial arrangement from the centre to the periphery. Two small masses of muscle-cells appear in the mesoblast, on each side ventro-lateral to the heart bulge; these in the lower sections can be traced into connection with the muscle plate. Besides these masses there is seen the muscle of the branchial bar, which appears as a mass of spindle-shaped cells lying lateral to the cardinal vein, and much nearer to the dermis than the muscle plate. Passing ventrally, this mass divides into two parts, a larger extending superficially to the dorsal invagination of the gill pouch and into the branchial bar, and a smaller, deeper part which penetrates between the dorsal invagination of the gill pouch and the cardinal vein. A comparison of these and more posterior sections shows that the relation of the anlage of these branchial muscles to the dermis and muscle plate differs from that borne by the anlage of the limb muscles to these structures. The latter can be traced into direct connection with the ventro-lateral extension of the muscle plate, whilst the branchial muscle has a much closer connection with the mesoblast of the dermis than with that of the muscle plate. This is especially the case in sections through higher regions.

Tracing these muscle masses upwards, it is found that in the sections immediately posterior to the auditory epiblast the muscle plate is not seen, but the branchial muscle anlage can be traced until the region posterior to the eye is reached.

In the second embryo, 'P,' the muscle plate has given place to a dorsal musculature arranged in a characteristically laminated and symmetrical fashion. The branchial muscles have increased in size, the deeper part to the greater extent; the connection of the deep part with the branchial cartilages is distinct, whilst the superficial can in parts be traced into a ventro-lateral extension. The connection of the conjoined dorsal extremity of both superficial and deep portions with the superficial dermis is more pronounced. The dorsal musculature has now extended over the auditory invagination for some distance; but, occupying a position still anterior to this, the branchial muscle can be traced; it forms two parts, a small superficial mass of cells lying beneath the surface epiblast in close connection with the roof of the spiracle, beyond which it cannot be traced, and a deeper portion which is more differentiated as muscle tissue, and can be traced, anteriorly to the spiracle, into connection with the maxillary cartilage. In the hinder sections both these portions unite in the dorsal region.

In the fourth embryo, 'R,' the state of the general muscular development shows a considerable advance on the former. As regards the spiracle region, the same masses of muscle described in the previous paragraph are to be seen. From a common mass situated dorso-lateral to the spur of the auditory capsule (fig. 11) they separate out as a maxillary mass and a spiracular mass (fig. 12); the former passes to the maxillary cartilage and the latter to the skin in the region of the spiracle. Besides these masses there is a new and third mass which appears first in the region of the branchial bar, which is the second after the spiracle, as a thin streak of cells lying in the superficial mesoblast of the dorso-lateral region (fig. 11); tracing this forwards, it is found to become shorter and thicker and more definite, until nearing the spiracle it forms a sharply defined mass of cells of small size, closely applied to the angle formed between the roof of the spiracle and the skin. A few sections further forwards the other spiracular mass separates from the maxillary mass and blends with this third mass, and the two make a single mass of considerable size upon the roof of the spiracle (fig. 12). A part of this mass remains closely applied to the skin after the spiracle has been passed (fig. 13), when it becomes elongated and extends somewhat ventrally; later it separates into two portions, a large ventral and a smaller dorsal portion, which are lost in the skin-fold covering the posterior angle of the ocular cavity at two spots, from which a few sections further forward there arise the upper and lower lid-folds (fig. 14).

To summarise the description of the musculature of these embryos, it may be said that the branchial muscles arise in the dermal tissue at some distance from the muscle plate, these pass as two divisions, superficial and deep in their relations to the dorsal pouch of the gill slit, and that there can be traced in the region of the higher arches the origin of a yet more superficial musculature within the most superficial layer of the dermis. Further, that a like origin can be found for the muscles of the spiracle region; of these the deepest portion is seen to be connected peripherally with the maxillary cartilage, and the two superficial sets with the spiracle walls and the contiguous skin.[1] And lastly, that in the latest embryo parts of these two superficial muscle masses can be traced anteriorly beyond the spiracle into the eyelid folds.

The proportion existing between the state of the spiracle and its muscles in the adult Plagiostomata, and the degree of development of the nictitating membrane and its musculature is striking. It is in an inverse ratio. What may be the determining factor of this relation I am unable to suggest.

Species.	Spiracle.	Spiracle Muscles.	Nictitating Membrane.	Muscle to Lids.
Rays, . .	very large	distinct	none	none
Rhina, . . .	do.	do.	do.	do.
Acanthias, .			do.	simple retractors
Scyllium, . .			simple fold	
Mustelus, . .				
Galeus, . .	very small			
Carcharias Zygæna,	absent	traces only	perfect	large and complex

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[1] This derivation of branchial and spiracular musculature from homologous sources confirms the homologies given for these systems by Vetter (34, p. 407, *et seq.*).

The close relation which spiracle and eyelids have in the embryo and young fish is not apparent from examination of adult species; in the latter, growth has separated the two considerably. A comparison of the measurements of the shortest distance between the palpebral fissure and the spiracle to the length of the palpebral fissure will illustrate this. The proportion is shown in an index giving the ratio of palpebral-spiracle distance to the palpebral fissure length taken as 100 :—

Fish.	Length of Fish.	Palp. Fissure.	Palp. Fiss. to Spiracle.	Index of Approximation.
Galeus (adult) .	about 1000 mm.	35 mm.	25 mm.	71
Mustelus (do.) .	,, 700 ,,	25 ,,	10 ,,	40
,, (embryo)	,, 260 ,,	12 ,,	1·5 ,,	13
,, (do.)	,, 200 ,,	8 ,,	1 ,,	12
,, (do.)	,, 70 ,,	5 ,,	0·5 ,,	10

Regarding the ultimate source of origin of the muscle masses above described, the relation which the ordinary branchial muscle anlages are found to bear to the dermis is the same as that generally accepted. This dermal tissue has been shown to be the derivative of the outer layer of the myotome, so their source is that common to all muscle tissue, but the indirectness of their connection indicates an evolution antecedent to such muscle tissue as that of the limb-buds where the derivation is a direct one. Of the presence of the most superficial mass of muscle tissue arising within the superficial dermis in the higher branchial segments (figs. 11 and 12, *m.s.s.*), I can find no record of previous observations. In time of origin it is later than the other branchial musculature, but its dermal source, since it is the more superficial, indicates an origin from an earlier dermal outgrowth from the myotome, but whether this will show the morphological value of the muscle as of primitive or later evolution I am unable to determine.

The conclusion of these observations is that the musculature of the eyelids of Mustelus is derived from a musculature primarily belonging to the spiracle; also that there is evidence to show that *this arises from two original sources,—the one a superficial dermal layer, the other a portion of a deeper dermal muscle layer.*

7. *The Nerve Supply of the Musculature.*

Previous to my dissections of the adult fishes in Easter 1898 at the Plymouth Laboratory, I had read the statement that the muscles of the membrana nictitans were supplied by the N. abducens—Huxley (17, p. 67), Stannius (30, p. 163). In dissecting out the connections in Mustelus, and later in Galeus, I was able to trace the whole of this nerve into the M. rectus externus, and to note the origin of the 'nervus nictitans' from the maxillo-mandibular division of the N. trigeminus. This observation I communicated then to Mr Holt (hon. naturalist to the M. B. Assn.), and a few days later to Professor Macalister. Ridewood gives this origin for the nerve in his paper. Since then I have repeated the dissection with the same result.

The N. abducens escapes from the skull by the same foramen as the N. trigeminus, and is bound up in the same tough fibrous sheath; it enters the substance of the M. rectus externus immediately on leaving the foramen, so that it does not appear exposed in the orbital cavity, and the muscle must be opened out before the nerve can be seen. The N. abducens was separated from the N. trigeminus in its entire course, and found to be entirely free from connection with the N. nictitans. The origin of this nerve was traced into the trigeminal, and in its substance through the cranial foramen. Beyond this I could not follow it.

In embryo 'R' I have traced the nerve from the periphery along the posterior orbital wall to its connection with a portion of the N. trigeminus trunk close to the Gasserian ganglion. This part of the trunk, on being traced peripherally, gave origin to the nerve of supply to the M. levator maxillæ superioris.

In embryo 'N' the same tracing could be followed to the inner side of the ganglion, and the connection appeared to be continued from here to the medulla through the ventral part of the root. I give these observations with due reserve, for it is very difficult to feel sure that one is following the same small group of neurons through many transverse sections, when the group is contiguous with or surrounded by neurons of an exactly similar character. The difficulty was recognised by Balfour (4, p. 197).

That the N. nictitans has no connection with the N. abducens I am well assured, but I could not eliminate the possibility of a connection with the N. facialis, which in the embryo is situated in close connection with the ventral root of the N. trigeminus, and it seems likely that the ultimate source of the nerve may be from the N. facialis. The close connection which these two cranial nerves make in their origin is well shown in the schematic figures of longitudinal sections of Scyllium embryos in stages 'L' and 'N,' by Marshall and Spencer (21, pl. xxvii. figs. 10 and 11). Also, on this point the observations of Stannius on the cranial nerves of Plagiostomes may be quoted (31, p. 30). In Plagiostomes, N. trigeminus and facialis arise conjointly from three roots, the most anterior of which arises from the ventral surface of the medulla by two short roots, which unite shortly after leaving the brain. This root is in Raja mainly the motor-supply of the muscles by which the respiratory movements of the anterior wall of the spiracle are effected, and also of certain other muscles in connection with the jaws. Ewart (9, p. 529), on the nerves of Læmargus, describes the origin of the nerves supplying the muscles in front of the spiracle, from the mandibular division of the trigeminal, and later notes the close connection of part of the facial complex with this nerve. These observations on the nerve supply of the spiracle muscles are significant, in view of the origin of the musculature of the eyelids from these muscles, as I have shown above.

8. *The Outer Corneal Layer.*

In the descriptions of the simpler forms of palpebral apparatus, I have frequently referred to the above-named structure in connection with the bulbar attachment of the conjunctiva. In a very large number of species, by incising the skin immediately around the bulb, there can be stripped off a thin layer of transparent 'skin' from the front surface of the bulb. It is always attached to the remaining or bulbar part of the cornea, to a greater or lesser degree, by delicate connective tissue which can be seen tearing up as the flap is pulled off. In some fishes the connection is so slender that the separation can be made and the 'space' injected by forcing fluid through a hole made in the outer layer, when it will be demonstrated that the 'space' has no connection with other subcutaneous tissue. In diseased conditions of captive fish this potential 'space' frequently becomes actual and distended with gas; a like condition may affect loose tissues elsewhere. I have seen a similar condition in freshly caught Pouter-whitings, and I am informed that this is always the condition of this fish immediately on removal from the water, but there is no appearance of it in the healthy free-swimming fish.

In Eels the layer is removable with some difficulty, and then the bulbar part of the cornea can be stripped off layer by layer of transparent connective tissue.

The outer corneal layer is separable in almost every species of sea-fish, excepting those of voracious habits. It is not separable in those whose habitat is fresh or fresh and salt water, thus:—

It is inseparable in Selachoidei, Batoidei, Holocephala, Chondrostei, Perciformes, Cotto-scombriformes (ex. Lophius), Mugiliformes, Cyprinina, Esocidæ, Salmonidæ (ex. Smelt), and Clupeidæ.

It is separable in Gastrosteiformes, Gadoidei, Pleuronectoidei, Muræenidæ, Syngnathidæ, and Gymnodontes.

The only exceptions to the generalisation from habitat are Smelt and Stickleback. Both these fish were very small and soft, being winter specimens, so that the exception may be accounted for by ill-condition. The Eels appear exceptions, but the remark on the mode of separation for these fish shows them to be on the border line. The histology of the cornea in Cod, Eel, and Trout has been treated by Lightbody (20, p. 40), who shows there is in Cod a layer of muco-areolar tissue dividing the cornea into two parts. I have made similar observations on the Plaice, which show that the proper substance of the cornea is not completely organised.

II. RELATION OF BULB TO ORBITAL WALLS.

1. *The Orbital Sac* (fig. 16).

On opening the orbital cavity of a fish by an incision through the skin of the lower eyelid or palpebral margin, the cavity will be seen in most species to present the appearance of a large lymph sac containing a small quantity of pale straw-coloured fluid. Into the cavity projects the bulb, and across it stretch the bulbar muscles and nerves. The cavity is lined by a membrane which is reflected over the walls of the orbit, the bulb and the structures connected therewith, thus forming visceral and parietal reflections of the sac. It may extend from the region of the optic foramen to the cul-de-sac produced by the union of the conjunctiva and the outer corneal layer, and arising from below the bulb it tends to enfold bulb and muscles, and to meet above these structures. It can be found in a small but sharply defined state in the Angler, where an incision below the eye will give entrance to a smooth and thick walled bursal-sac which turns up slightly before and behind the bulb; the special features of the sac found in this fish show an excellent adaptation for the service of the eye, which needs to be protected from the action of the huge subjacent pharyngeal muscles during the spasmodic working of the trap-like jaws. In the Salmons and Ling the sac is larger, the visceral layer forming a funnel-like investment to the bulb and its muscles. In other fish this layer has become more discrete, affording separate investments to each of the muscles. Such a condition is found in the Pleuronectids.

2. *The Recessus orbitalis.*

In these fishes the sac is unusually large, and has in connection with it a reticulated muscular diverticulum, which lies without the orbital wall posteriorly, and between the mandible muscles and the dorso-lateral skin. It has been described by Holt (14, p. 422) as the recessus orbitalis. I have found the recessus according with the description given in all the species of the fishes I have examined, which include a few beyond those named by Holt. I have further attempted to determine the nerve supply of the recessus. By ordinary dissection no more can be ascertained than that the structure is crossed by two slender branches of the N. trigeminus, as stated by Holt; so the examination was continued in two ways, experimental and histological.

By the courtesy of the officials of the Brighton Aquarium, I was able to stimulate the nerves of the region in a freshly killed plaice. A Dubois Reymond coil and platinum electrodes were used, and the effects of the current in single, slowly repeated and rapid induced shocks observed, after testing the current on the ordinary skeletal muscles with satisfactory effects. These methods were used on the branches of the N. trigeminus in relation to the recessus, on the blood-vessels supplying the saccus, in the hopes of stimulating sympathetic fibres, and lastly on the recessus itself, but in each case the result was negative.

Further, portions of the fresh recessus were treated by Dogiel's methylene blue and Löwit's gold chloride methods for tracing nerve endings. By both these means of preparation several fine nerve fibres could be followed in their course within the elastic outer coat of the recessus; these nerves arose from the N. trigeminus, and in one case there was an appearance of short thin twigs given off at right angles to one of these fine nerve branches to end in the underlying muscle tissue, but this was seen in only one gold preparation, and in only a small part of that, so that without repetition it cannot be accepted as evidence of the manner of the nerve ending. The blood-vessels make a very complete network in the elastic coat. The muscles can be seen arising from the proximal portion of the recessus as fasciculi, which give off many branches to connect with neighbouring fasciculi; at the periphery of the recessus many slender branches arch over to connect with similar branches from the other side.

I have not yet succeeded in tracing the origin of the recessus from the orbital sac. The origin of the latter can be clearly followed in the Mustelus embryos (fig. 7*c*). It arises by a simple cleavage of the mesoblast packing which fills the interval between the developing optic capsule and cranial walls; it is therefore analogous in its formation to the other greater connective-tissue spaces of the body.

3. *The Capsule of Tenon* (fig. 16).

Within the visceral layer of the orbital sac, and separating it from the sclerotic, is a fibrous capsular investment to the bulb. I have applied the above name to it since the capsule corresponds very well to the ocular investment known by this name in the higher mammalian anatomy. It is separated from the osseous, cartilaginous, or fibrous sclerotic by loose connective tissue, which may contain more or less mucous tissue. It is united with the fibrous sheath of the optic nerve near the entrance of the latter into the bulb, and it blends with the tissue of the palpebral margin or lids and that of the subconjunctival region. Each bulbar muscle receives an investment which extends in the direction of the origin of the muscle. Langhans (18) and Owen (24, p. 334) include this in the tissue of the sclerotic, but I think the relation which it bears to the bulbar muscles is sufficient to separate it from the true sclerotic. The capsule, however, can hardly be considered to perform the pulley-like action for the muscles, ascribed to the like investment in man, except in the case of pleuronectids (*infra*, Section III. 3), since the sclerotic is so stiff as to need no protection from muscle pressure. In one species the capsular investments are peculiarly strong, to the detriment of the muscles; in the Conger the muscles are small and obscured by the dense white membrane covering them. This fact, together with the absence of conjunctival fornices, and the density of the skin connecting the cornea with its surroundings, accounts for the immobility of the eye. A captive specimen of this creature spends most of its time reposing in the shade of some drain-pipe provided for its delectation, or with its nose deep in some corner; any motion required for the extension of its vision appears to be supplied by the movements of its flexuous body.

In certain fishes the capsule comes into special prominence in connection with a structure, the—

4. '*Cartilago sustentaculum oculi*' (figs. 15 and 16).

The rod of cartilage to which I apply this name has been noticed by many observers. Sömmerring (29) names the earlier of these observers, and himself briefly describes the cartilages found in Raja and Acanthias, and figures the excised eyes of these fish with the cartilages attached. Its presence in most Plagiostomata has been noted by Owen (24, p. 337), Günther (10, p. 112), and incidentally by Leuckart (19, p. 167), and Ruge (28, p. 243). Each has applied some loosely descriptive name such as 'Cartilaginous peduncle,' 'Augenstiel,' and 'Knorpelstab.'

The variations in its form in adult rays and sharks can be best illustrated by reference to the following fishes:—

The Blond Ray (fig. 15) shows it in its highest development as a broad flat cartilaginous rod which springs from the depth of a small depression of the cranial wall, and passes outwards and upwards in a gentle curve to end in a cup-shaped enlargement which is within the capsule of Tenon. This cup articulates with a semicircular enlargement of the bulbar cartilage, the whole forming a well developed cup-and-ball joint. In this fish the cup end of the cartilage is stayed by three fibrous strands which are affixed to the anterior and posterior orbital walls, and to the mesial wall at the posterior edge of the optic foramen. In Acanthias the cartilage is long, slender, and cylindrical, and the cup small; the relations to the bulb and Tenon's capsule are the same, but there is no special bulge on the bulbar surface for the articulation, also there are no ligamentous stays to the stem stretching across the orbital cavity; there is, however, a radial arrangement of strengthening fibres in the capsule, passing from the stem to the periphery of the capsule. In Galeus (fig. 16) the stem bears the same relation to the cranial wall and the capsule; the bulbar end is, however, not cup-shaped, but presents a plain smooth-surfaced knob, which is separated from the sclerotic by a pad of soft muco-areolar tissue. In Mustelus the cartilage is yet more reduced, and its connections with both cranium and capsule so fragile that it is displaced on the slightest manipulation.

In Zygæna the central end does not reach the cranium, but abuts on the common tendon of origin of the recti muscles (see Section III. 1). It is not found in Scyllium.

In all these cases the relation borne by the cartilage to the optic nerve is the same; the cartilage is posterior and slightly dorsal to the nerve, and separated from it at its central end by a considerable interval.

The uses which such an ocular support subserve are fairly obvious in the Skate, in which fish the eye is held at a level considerably above that of the surrounding skin. Apparently the fish has no power of altering the elevation of the eye, but the liability to risk of injury from slight violence, consequent on the projection, is minimised by the flattening of the upper surface of the bulb, and the cartilage, though hyaline, is sufficiently elastic to allow of depression with greater force.

In Sharks the cartilage compensates for the lack of support afforded the bulb by the unusually large size of the orbital cavity, and also appears to facilitate rapid and long continued bulbar movements. In watching a captive Acanthias, it was observed that with each stroke of the tail in swimming the head was deflected, whilst the eyes made a reverse and compensatory swing to maintain the constancy of vision.

The obliquity of the position of the cartilage obviates the defects to which inelastic support is liable.

Development.—The mesoblast is known to condense around the optic evagination, and one would suppose this cartilage to be developed in a portion of the mesoblast which surrounded the optic nerve and the distance between nerve and cartilage in the adult to be a result of separation by intercallary growth of the orbital wall; reference to the embryo, however, shows this is not the case.

In the earliest embryo there is no orbital sac; the small interval between the relatively large bulb and the condensing mesoblast of the skull is filled up by the growing orbital muscles and nerves, together with a quantity of loose mesoblastic tissue. In embryo 'P' (fig. 7*c*) the mesoblast becomes vacuolated in portions of the orbital cavity, whilst at a spot removed from the site of the optic nerve, by a considerable distance in a dorso-posterior direction, the mesoblast forms a denser band which connects the forming skull wall. with the condensing optic capsule; within this mass cartilage is found in embryo 'Q.' Even at this early date the site of the connection of the anlage of the cartilage with the cranial wall is depressed, and it is from the bottom of this depression the column of mesoblast springs. Thus the cartilage has an origin independent of the immediate mesoblastic investment of the optic nerve, and seems to arise at a situation where the bulb and orbit are in longest and least obstructed contiguity.

5. *The 'ligamentum tenaculum oculi.'*

A fibrous band attaching the bulb to the mesial wall has been noted by Sömmerring (29, p. 70), Owen (24, p. 337), Günther (10, p. 112), and Leuckart (19, p. 169). In the majority of cases in which I have found the ligament present, it has formed a cord of variable strength lying anterior and parallel to the optic nerve, so that it differs in position from the sustentacular cartilage. It is present in this form in all freshwater fishes, *e.g.*, Pike, Tench, Carp, Trout, Bream, Perch; also in fishes frequenting salt and fresh water, as Salmons, Sturgeon, Herrings, Bass. It is present in a few only of the sea fishes, and these are Red Mullet, Mackerel, Tunny-fish, Grey Mullet.

The ligament in the Sea-bream (fig. 17) is noticeable in that it is separated from the optic nerve in its central attachment. The strong short fibrous cord of each eye springs from the same spot on the membranous interorbital septum, which is strengthened by a patch of dense white-fibrous tissue; the attachment to the bulb is, as usual, anterior and superior to the entrance of the optic nerve. In the Pike the ligament is very strong, Leuckart (19, p. 169) describes it as a slender elastic cartilaginous bar; I find it consists of a strong fibrous tube, within which is some soft glassy-looking material. Microscopical sections of the hardened ligament prove this to be merely muco-areolar tissue, and no trace of cartilage cells are to be found within it or the surrounding fibrous sheath; the strength of the structure lies in the fibrous outer part, so that it is essentially the same as the ligament of other fish. In the Rudd and Roach the ligament is double, for a narrower band lies posterior to the nerve in addition to the usual anterior ligament; the two meet in a web, and are attached to the bulb immediately above the optic nerve.

Regarding the origin of this ligament, I have made no observations on embryos, but I think that it will differ from that of the sustentacular cartilage in being merely a thickening of the mesoblast around the optic stalk, and not a separate growth, as is the cartilage; this suggestion is supported by the presence of the ligament parallel to the optic nerve, in addition to the cartilage, in the case of the Ray (fig. 15).

III. The Oculo-Motor Muscles.

1. *General Scheme.*

Within the large range of fishes examined the arrangements of the ocular muscles are singularly simple and regular; they consist of the usual musculi recti and musculi obliqui, and it is in but few species that variations in the shape and mode of attachment can be found.

As regards the origin of these muscles, the M. recti arise in most cases in immediate relation to the optic foramen at the posterior part of the orbit, and the M. obliqui from the anterior portion close to each other. The relations and variations of the origins in Plagiostomata are shown in the figures of Tiesing (32, taf. v.), and the connections for bony fishes are described by Stannius (30, pp. 59 and 174).

The variations from these plans are few. In *Chimæra monstrosa* there is, as noted by Gegenbaur (9*a*, p. 942), a displacement of the origin of the M. rectus internus, the muscle is much shorter than usual, and arises from the posterior edge of the frontal cartilage immediately in front of the membranous interorbital septum; it is supplied from the third nerve (Cole, 6, p. 642, and plate i.) by a long branch which passes over the optic nerve and across the interorbital septum to the muscle origin.

The origin of the M. recti of *Zygæna malleus* is described by Owen (24, p. 336) in the following terms: they "are remarkable for their length, since they arise from the basis cranii and extend along the lateral processes of peduncles, at the free extremities of which the eyeballs are situated"; a similar statement is made by Günther (10, p. 112). In the specimen of the fish which I dissected (spirit specimen, length 52 cm.), this was certainly not the arrangement found (fig. 18). On removing the skin from the inferior aspect of the lateral processes, the long strap-like optic nerve was seen; pulling this aside, there was exposed on its deep surface a fibrous band extending, in company with the oculo-motor nerves, from the basis cranii to within a short distance of the bulb; from this band there arose by a common tendon the four recti, which were no longer than those found in other sharks of the same size;[1] between the common tendon and the bulb there was the usual sustentacular cartilage. The measurements of the muscles were:—

Length of Fish.	Length of Lateral Process.	Length of Cranio-Muscular Ligament.	Length of Muscles, average.	Length of N. Opticus.
520 mm.	50 mm.	32 mm.	14 mm.	40 mm.

The insertions of the muscles vary within certain narrow limits. The usual method is by a thin flat tendon to the peripheral edge of the sclerotic. The M. rectus internus falls short of this attachment in Herrings and in the Salmon *Argentina silus* (the irregularity is not found in the common salmon or trout). In these fish the muscle is short and attached to the posterior pole of the bulb immediately anterior to the optic nerve; in all these cases the bulb is large, and fills the orbit very completely, so that the shortening may be the effect of pressure.

The relation which the insertions of the M. recti et obliqui superiores make with each other varies in form. In the Plagiostomata the muscles approach from the opposite angles of the orbit, and are inserted \/-fashion into the sclerotic, their tendons being separated by a small interval; in other fish, Chimæra, Sturgeon, Caranx, Cantharus, Tunny, Perch, Hake, Roach, and Brama, the meeting is complete as a V-shaped insertion; in yet others the M. obliquus superior overlaps the M. rectus superior, as in the John Dory (figs. 17 and 19), and Sea-bream, Red Mullet, Cod, Ling, Tench, Rudd, Salmon, and Sun-fish; this progression increases until a complete crossing results, a condition found in Mackerel, Grey Mullet, Whiting, Haddock, and Little

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[1] In re-examining Müller's figure of the dissection of the nictitating membrane of this fish (23), I find that this arrangement is indicated therein. No description is attached.

Pipe-fish. A similar relationship is found for the inferior muscles.

In some fish there is an intimate connection of the muscle-sheath, and even part of its tendon, with the subconjunctival tissue, as in the case of the M. rectus externus of Ling and all Pleuronectids. This tendency to form palpebral-retractor muscles is seen at its maximum in Orthagoriscus, an excised eye of which fish I have examined; the eye is of enormous size, the bulb being about the size of a closed fist, and each muscle a thick fleshy strap, having dimensions about 15 × 4 × 2 cm.; the mass of the M. rectus superior passes under the oblique muscle to its bulbar insertion, but a small part, superficial and anterior in position, passes on to blend with a detached superficial set of fibres of the oblique muscle; these conjoined fibres are then inserted into the tissue beneath the conjunctival. I am unable to give their relation to palpebral folds, if such exist, as the eye was too closely excised. A like relation exists in the M. recti et obliqui inferiores; the M. rectus internus also divides and is inserted in a similar double fashion, but no division appears for the M. rectus externus, though the connection of its tendon with the conjunctiva is close.

The description of the variation in the muscles of Pleuronectes is reserved for Section III. 3, of this paper, and remarks on the musculature of the Lamprey are reserved for a later paper.

2. *Variations for Projection and Retraction.*

In certain fish whose bodies have become much flattened laterally, whilst they still retain the dorso-ventral position normal to fish, there are effects arising out of the relation of the muscles to the bulb which can produce projection of the bulb. In watching the movements of a captive *Zeus faber*, it appeared that the fish had the power of projecting outwards the bulb, especially in the posterior quadrant, so increasing its range of vision nasal-wards. Dissection of a specimen showed that there was no special apparatus whereby this could be performed, but that the M. rectus internus was unusually long, and that the position of the muscle in its passage from the sub-cranial canal along the mesial aspect of the discoid bulb to its insertion was such that a contraction of the muscle must result in the movement of the bulb in an outward direction (fig. 19), any substantial internal rectification such as could be effected in a more spheroidal eye, being prevented by the coincident pressure of the bulb against the long strap-like muscle and the posterior ocular wall. In this case the short M. rectus externus would act as a retractor.

The eye of Periophthalmos is credited with the movements of projection and retraction. Günther (10, p. 488) writes:—"The peculiar construction of their eyes, which are very movable, and can be thrust out of their sockets, enable them to see in the air as well as in the water; when the eyes are retracted they are protected by a membranous eyelid." I have had no opportunity of observing the movements of the living fish, but have examined and dissected a small spirit specimen. The large round eyes were raised freely from the lateral surface and above the level of the dorsal osseous crest; their appearance of isolation from their surroundings was heightened by the presence of a deep sulcus existing between the bulb and the subjacent bulge of the maxillary muscles; no eyelid formation was visible, the surrounding skin formed a collar of soft tissue which was probably loose in the fresh state. A wide circular incision allowed the whole of the skin of the side of the head with the bulbar skin collar and the outer corneal layer to be removed with ease, and no part of the removed skin showed any special thickening, as would be necessary for the formation of a 'membranous eyelid.' The exposed orbital cavity was roomy and completely lined by the orbital sac, which extended between the skin of the infraorbital sulcus, above described, and the upper surface of the maxillary muscles. No contractile or elastic part of the sac, such as the recessus orbitalis, could be found; but I must here repeat, the specimen was small. The muscles were normal, except for the relation of the M. rectus et obliquus inferiores: these crossed each other in their mid-lengths, the obliquus being the superficial.

My impression from the examination of this specimen is that the special motion of the eyes of this fish must be a *vertical elevation and depression* rather than projection and retraction. In the deep and wide infraorbital sulcus, the extent of which is not indicated in the figure attached to Günther's description, there exists a provision which would allow of considerable depression of the bulb in the flaccid state of its muscles, whilst the position of their orbital attachments and the 'cradle' formed by the crossing of the inferior muscles are such that general contraction of the muscles, to even a moderate degree, would elevate the bulb from its resting-place.

The above examples, and that of the Pleuronectid fishes (*vide* 'orbital sac' and *infra*), are the only cases in which projection and allied motions could be found. Occasionally, in handling fish preparatory to killing them, I have noticed a decided retraction of the eye: this has been mostly in freshwater fish, *e.g.* Pike and Tench, but I have seen no such effects in swimming captive specimens.

3. *Modifications in Pleuronectid Fishes.*

Observations of the eye movements of captive specimens of these fishes will show that, beyond the power of projection described by Holt, there is a distinct power of *rotation* of the eyes,—a power which I think is peculiar to them, and one which probably depends upon a secondary adaptation of the eye muscles to their habits of life. The eyes can be moved around a central axis, passing through the cornea to the posterior pole of the bulb, and the rotatory excursion may extend to as much as one-eighth of a circle. This peculiarity of motion is amply accounted for by a specialisation of the M. obliquus superior, a muscle which in these fishes is of unusually large size relatively to the others.

I shall describe the arrangements of the muscles in the Halibut, a convenient fish on account of the great size of its eye muscles (fig. 20). The M. obliquus superior takes origin from the anterior angle of the orbit, and passing outwards to the bulb in the direction of the usual site of insertion, it now enters an investment of Tenon's capsule and divides into two parts. The larger is inserted by a thin flat tendon into the sclerotic just behind the sclero-corneal junction, and in close connection with the tendon of the M. rectus superior; the smaller portion, after leaving the main mass, crosses the M. rectus superior, and lying within a sheath derived from Tenon's capsule, it follows the posterior quadrant of the bulb until reaching the level of the M. rectus externus, where it is inserted by a thin tendon into the bulb on the line of its greatest circumference immediately deep to that muscle. The slip is supplied from the N. trochlearis by a branch which separates from the main trunk before it reaches the muscle. This special slip is present in both eyes of all the species which I have been able to obtain, in both dextral and sinistral fish, and in both large and small specimens.

The degree of separation of the slip from the main oblique mass differs: it is more complete in the common Plaice than in the Halibut, still more so in the Rough Dab, and most in the Flounder, where the division extends for the greater part of the muscle length. In this fish the M. obliquus superior is more extended in its insertion, part of its fibres crossing the upper surface of the M. rectus superior. No such special arrangement is found in the inferior muscles, but the M. obliquus crosses the M. rectus superficially in a manner described for other fish; and in Turbot and Brill these muscles are so diminished in size that their insertion is by two small superimposed tendons immediately ventral to the optic nerve.

Cunningham (7, p. 50), in his monograph on the Sole, devotes considerable space to the eye muscles. He notes a disturbance of the origin of the oblique muscles of the displaced eye, and also the crossing of the inferior muscles near their insertion; but in his description of the M. obliquus superior, no mention is made of this special development.

It is evident that this specialisation of the M. obliquus superior is calculated to extend the field of vision in a manner peculiarly advantageous to a fish which, from its adoption of a sedentary life, will lose the range obtained by the rapid body movements of more active and free-swimming fish.

It is worthy remark in this connection that in those creatures whose eyes are situated laterally in the head, and have their visual axes lateral, the M. obliqui are simple in their character; but in creatures whose visual axes are capable of convergence, there is a specialisation of the M. obliquus superior. The direction of the visual axes of Pleuronectid fishes, in the projected state of the eye during life, is frequently one of convergence: the eyes of many mammals are capable of rotating about convergent axes, *e.g.* the horse, and the condition is complete in man. In all these there is a specialisation of the M. obliquus superior, and broadly speaking along the same lines—one of extension of the muscle.

Regarding the M. rectus externus and internus, both of these are subject to some variation. In most of these fish there is a diminution in the size of the external muscle. In the Halibut it is a small rounded muscle, deficient in contractile substance for the distal third of its length, a great contrast to the broad strap-like appearance of the other muscles; the insertion is by a slender tendon which runs for some distance in a fibrous sheath, closely adherent to the subconjunctival tissue, to its insertion at the extreme edge of the sclerotic; some of its fibres pass into the subconjunctival tissue. This diminution was found to a greater or less degree in all the species examined. The causation is not clear; it may be due to a decrease coincident with increase of the anterior muscles to allow more freely of convergence; in some cases it seemed as though the hump caused by the mandible muscles obscured the range of vision posteriorly, and with this the smallness may be connected. In the case of the Rough Dab, this is undoubtedly connected with a partial displacement of other M. recti; the M. rectus superior is more posterior in insertion than usual, so as to be almost parallel with the M. rectus externus, thus sharing its action, whilst the M. rectus internus has become more superior than in others of the genus.

The following are the measurements of the muscles of a large Halibut and Turbot; the heads of the fish were of nearly full size, as is shown by the measurements taken from the symphysis of the mandible around the gill cover to its dorsal extremity. The smallness of the muscles of the Turbot and Brill, with the shortened insertion of the inferior muscles, and the feeble power of projection possessed by the latter fish, Holt (14, p. 429) appear to be correlated with the inelasticity and lack of volume in the circumcorneal skin collar.

Measurements of Muscles (millimetres).

Fish.	Jaw-gill length.	Superior Oblique.		R. Supr.	R. Ints.	R. Exts.	R. Infr.	Inf. Obliq.
		Main mass.	Special Slip.					
Halibut	370	43×20×4	40× 4×2	84×11×4	85×8×5	81×5×3	80×13×3	39×12×4
Turbot	228	28× 4×1	16×1·5×0·5	43× 4×2	44×3×2	46×1×1	36× 4×2	20× 4×2

In concluding, I wish to state my indebtedness to Dr Harmer, Curator of the Zoological Museum, Cambridge, for access to fish which could not be obtained by purchase; and to the Worshipful the Company of Fishmongers for their nomination to a table at the Plymouth Laboratory of the Marine Biological Association.

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DESCRIPTION OF PLATES I.–VI.

Fig. 1. The "pseudo-membrana nictitans" of *Salmo salar*, dissected out. The broad ligament is the anterior. The curved groove on the surface is the impression of the anterior palpebral fold. $\times \frac{1}{1}$.

Fig. 2. The head of *Clupea harengus*, showing the three palpebral folds and narrow vertical palpebral fissure. $\times \frac{1}{1}$.

Figs. 3, 4, 5, and 6. The right eyes of (3) *Carcharias glaucus*, (4) *Galeus vulgaris*, (5) *Mustelus lævis*, and (6) *Scyllium canicula*. Figs. 3 and 6 are life size, 4 and $5 \times \frac{1}{2}$.

Figs. 7 *a*, *b*, *c*. Series of transverse sections through the lower palpebral apparatus of *Mustelus lævis* embryo 'P.'

Fig. 7*c* also shows the formation of the cartilago sustentaculum oculi (*c.s.a.*) and of the orbital sac (*o.sc.*).

Figs. 8 *a*, *b*, and *c*. Series of sections through the lower palpebral apparatus of Mustelus embryo 'Q.'

Figs. 9 *a* and *b*. Series through same structure of embryo 'R.'

Fig. 10. Transverse section through mid-pharyngeal region of Mustelus embryo 'N,' to show state of musculature. Shows position of branchial muscle (*m.b.*), with its portions superficial and deep to the dorsal gill pouch.

Fig. 11. Transverse section post-spiracular region, Mustelus embryo 'R,' showing musculature. Dorsal muscle (*m.d.*), the maxillo-spiracular muscle mass (*m.m.s.*), and the origin of the most superficial spiracular muscle tissue (*m.s.s.*).

Fig. 12. Transverse section through spiracle, same embryo, shows separation of maxillo-spiracular muscle mass into M. levator maxillæ (*m.mx.*), and M. spiraculi (*m.sp.*); also the union of the latter with the M. spiraculi superficialis (*m.s.s.*).

Fig. 13. Transverse section through præ-spiracular region, same embryo, shows continuation anteriorly of part of spiracle muscle mass, as musculature of eyelids (*m.pp.*). It can be seen to be composed of two strata of cells.

Fig. 14. Transverse section through posterior extremity of the orbit, same embryo. The palpebral muscle mass of the preceding section is seen to be divided into a small dorsal and a larger ventral masses situated within the palpebral margin; these can be further traced to the lids.

Fig. 15. View of the orbit of *Raja blanda*. The bulb is raised to show the cartilago sustentaculum oculi (*c.s.*) and its three ligaments, anterior l', internal l'', posterior l'''. $\times \frac{2}{3}$.

Fig. 16. Coronal section through orbit of *Galeus vulgaris*, at the posterior edge of the optic foramen (*f.o.*), shows orbital sac and its reflections (*o.sc.r.*). Tenon's capsule (*T.c.*), its sheathing evagination to M. rectus superior (*T.c.s.*). The M. rectus inferior is seen within the capsule (*r.if.*). The connection of the cartilago sustentaculum oculi (*c.s.*) with the capsule, and the muco-areolar pad (*m.*) which separates its bulbous end from the sclerotic. The section shows well the relations of the palpebræ and membrana nictitans to the conjunctival fornices. $\times \frac{2}{3}$.

Fig. 17. Dorsal view of dissection of left orbit of *Pagellus centrodontus*, to show ligamentum tenaculum oculi. $\times \frac{1}{1}$.

Fig. 18. Ventral view of head of *Zygæna malleus*, showing dissection of eye muscles. The N. opticus has been pulled aside to show the tendinous band (*t.b.*) from which arise the M. recti. $\times \frac{1}{2}$.

Fig. 19. Dorsal view of left orbit of *Zeus faber*, to show relation of M. rectus internum to discoid bulb to produce projection in direction of arrow. $\times \frac{1}{1}$.

Fig. 20. Dorsal view of right eye of *Rhombus maximus* with muscles attached; the extension of the recti into the subcranial canal is not indicated. To show form and position of the special rotatory slip of M. superior obliquus (*o.s.x.*). $\times \frac{2}{3}$.

Scale of figures of microscopic sections.

Scale 1, figure 7*a*, for figs. 7 *a*, *b*, 8 *a*, *b*, *c*, 9 *a*, *b*.
Scale 2, figure 10, for figs. 7*c* and 10.
Scale 3, figure 11, for figs. 11, 12, 13, and 14.

INDEX TO FIGURES.

a.c.o.	anlage of optic capsule.
ao.	aorta.
b.b.	branchial bar.
c.c.	cranial cavity.
c.s.	cartilago sustentaculum oculi.
c.s.a.	anlage of sustentaculum oculi.
c.w.	cranial wall.
f.o.	foramen opticum.
g.s.	gill slit.
ht.	heart.
l.	lens.
l′, *l″*, *l‴*.	ligamentous strands to cartilago sustentaculum oculi,—anterior′, internal″, and posterior‴.
l.t.	ligamentum tenaculum oculi.
m.	muco-areolar pad.
m.b.	branchial muscle.
m.d.	dorsal muscle.
m.md.	m. levator mandibularis.
m.m.n.	m. lev. palpebræ nictitantis.
m.m.s.	maxillo-spiracular muscle mass.
m.mx.	m. lev. maxillaris.

m.p.	muscle plate.
m.p′.	muscle plate ventral extension.
m.pp.	palpebral muscle mass.
m.ps.	muscle mass to upper lid.
m.sp.	do spiracle.
m.s.s.	superficial dermal muscle to spiracle.
m.t.	mucous tube.
md.	mandible.
md.c.	mandibular cartilage.
mx.c.	maxillary cartilage.
N. II.	N. opticus.
N. III.	N. oculo-motorius.
N. IV.	N. patheticus.
N. V.	N. trigeminus.
N.*n.*	nasal branch of N. V.
N. X.	N. pneumogastricus.
o.c.	orbital cavity.
o.i.	m. obliquus inferior.
o.s.	m. obliquus superior.
o.s.x.	m. obliquus *special rotatory slip.*
o.sc.	orbital sac.
o.s.c.r.	reflection of orbital sac.
o.w.	membranous orbital wall.
ot.c.	otic capsule.
p.a.	anterior palpebral margin.
p.e.	extra palpebral fold—'pseudo-membrana nictitans.'
p.f.	palpebral fornix.
p.i.	inferior palpebral fold.
p.m.n.	membrana nictitans.
p.p.	posterior palpebral margin.
p.r.g.	posterior root ganglion.
p.s.	superior palpebral fold.
ph.	pharynx.
r.	retina.
r.e.	m. rectus externus.
r.if.	m. rectus inferior.
r.it.	m. rectus internus.
r.s.	m. rectus superior.
sp.	spiracle.
t.b.	tendinous band giving origin to m. recti of *Zygæna.*
T.c.	capsule of Tenon.
T.c.s.	muscular sheath derived from capsule of Tenon.
v.	vitreous

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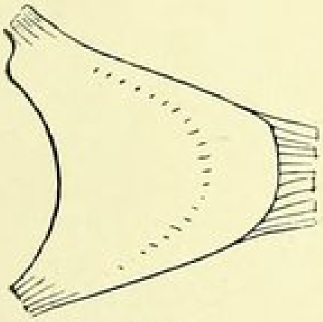

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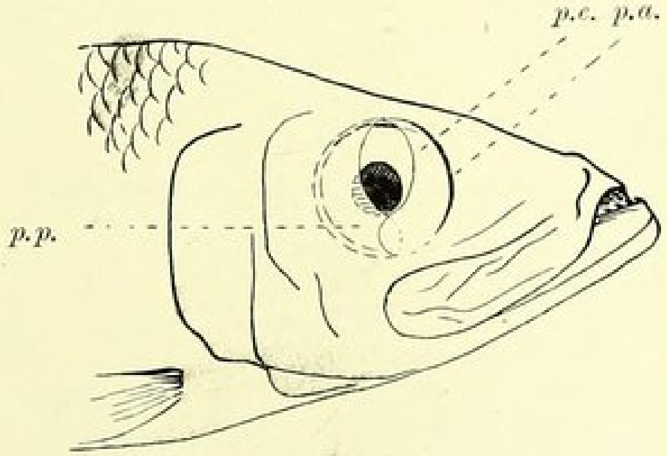

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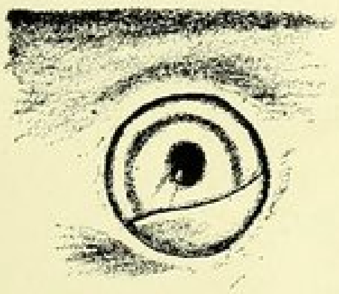

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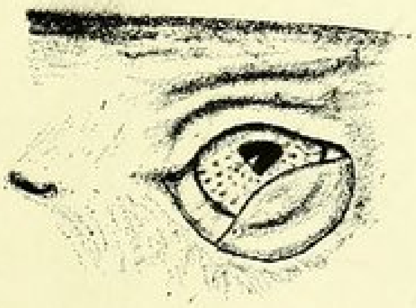

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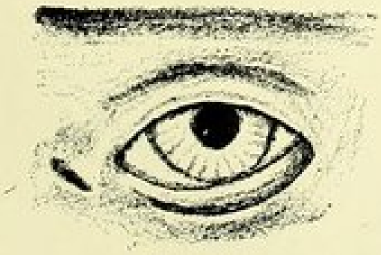

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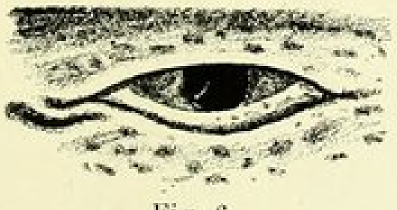

Fig. 6.

N. B. H., *del.*

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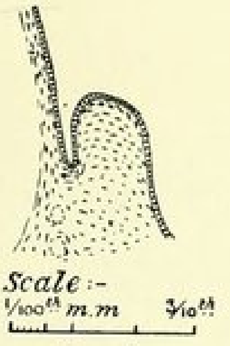
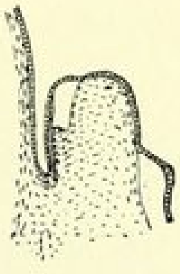


Fig. 7*a*.



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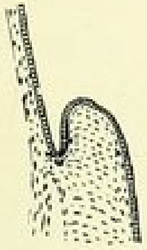
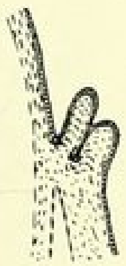


Fig. 8*a*.

Fig. 8*b*.



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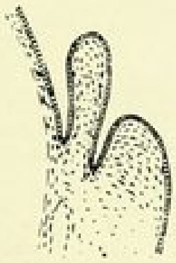

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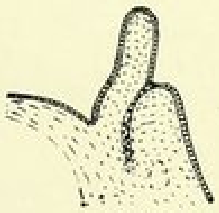

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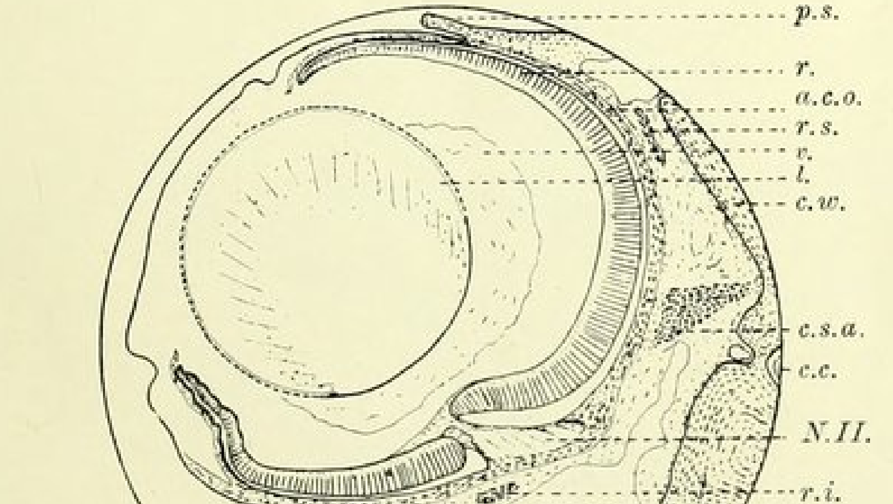

Fig. 7*c*.

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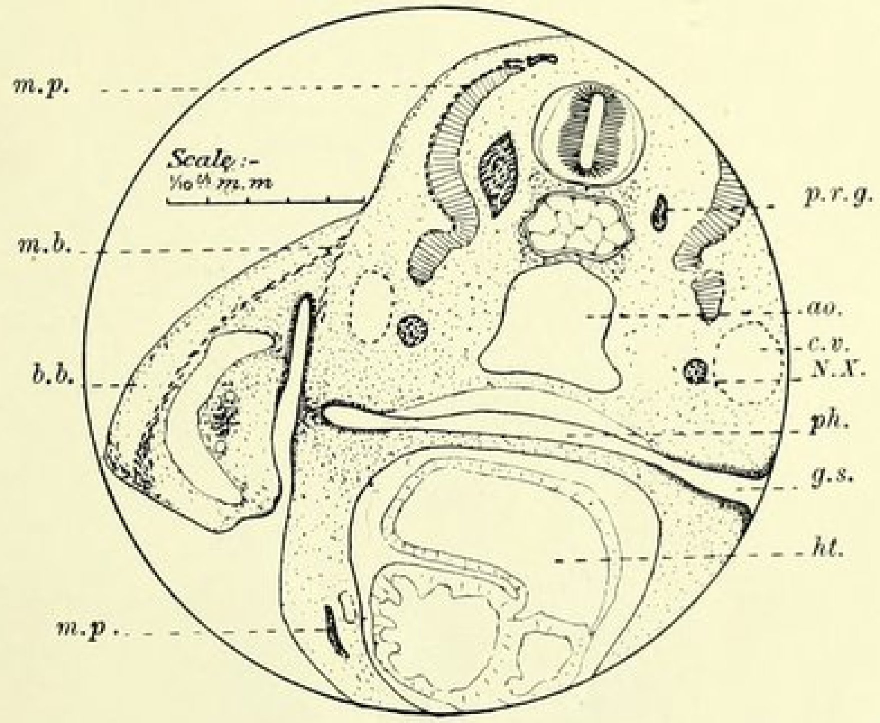

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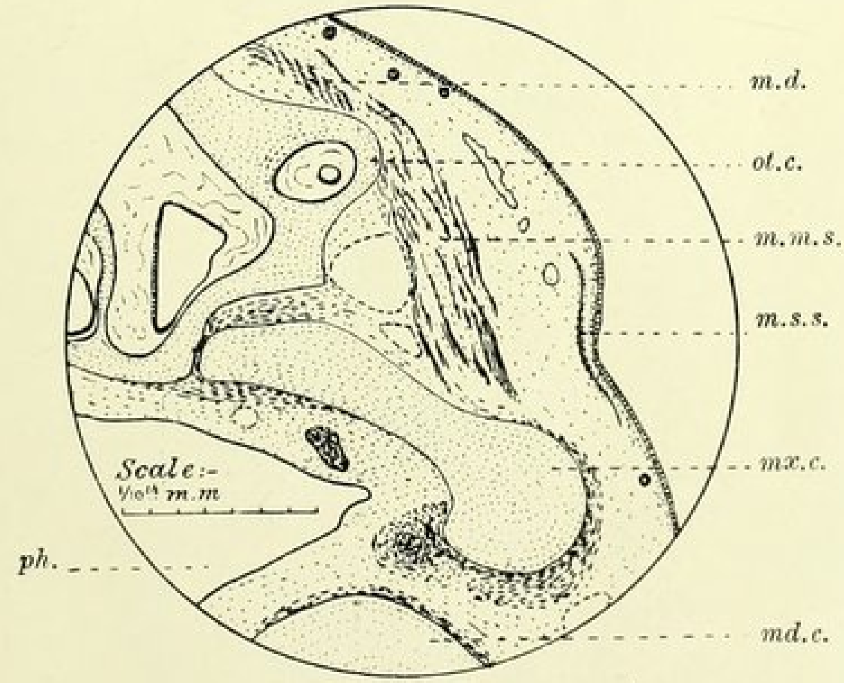

Fig. 11.

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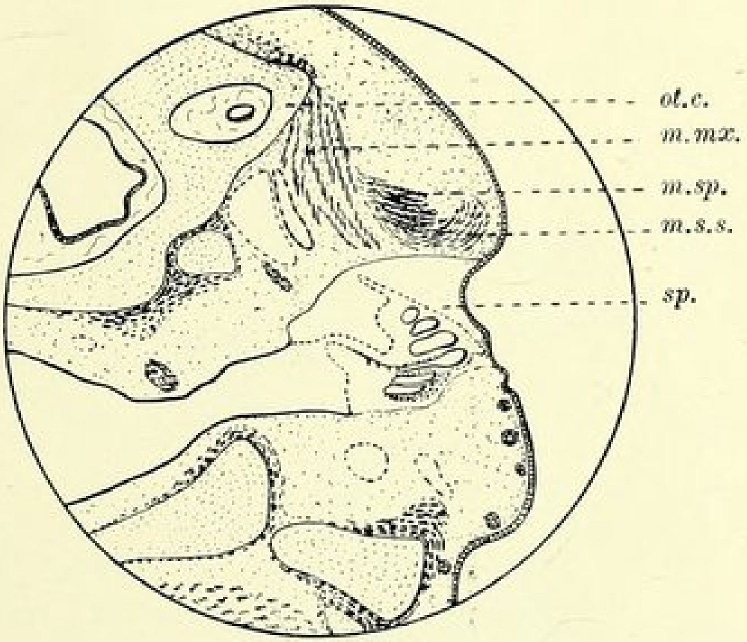

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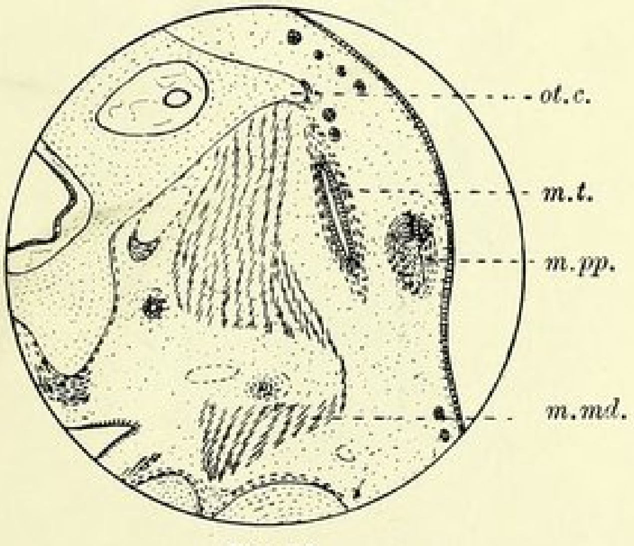

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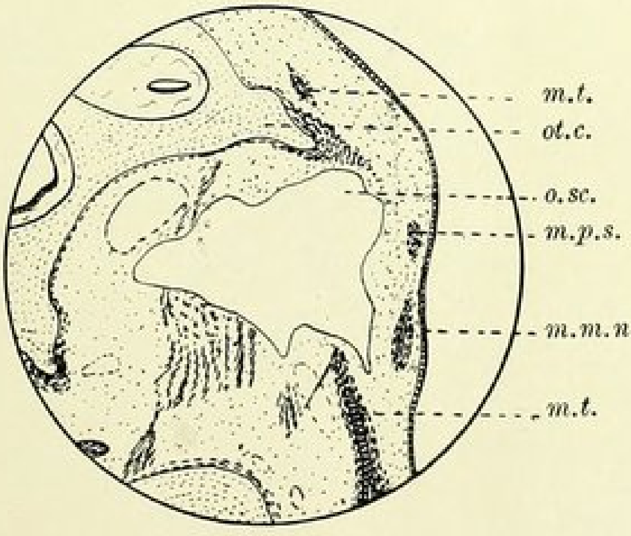

Fig. 14.

N. B. H. *del.*

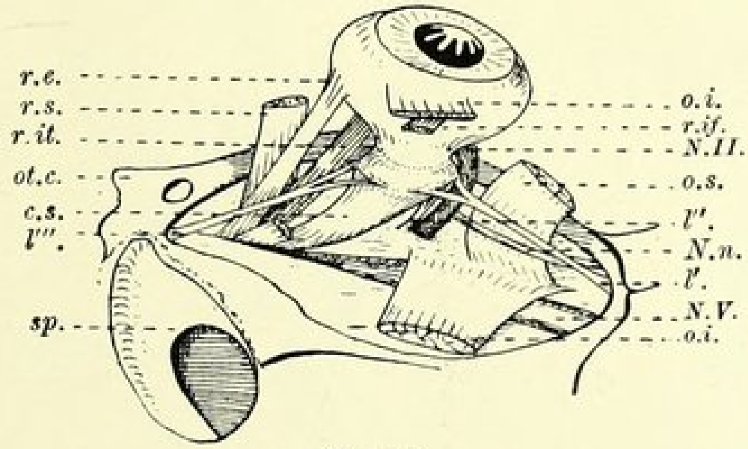

Fig. 15.

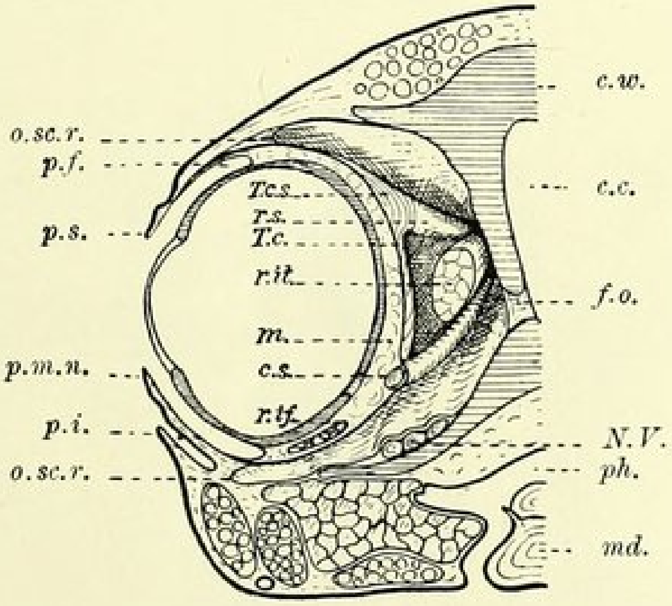

Fig. 16.

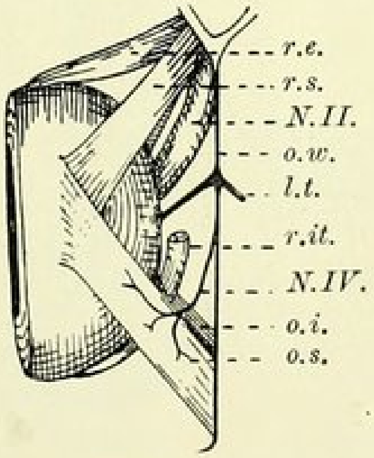

Fig. 17.

N. B. H., *del.*

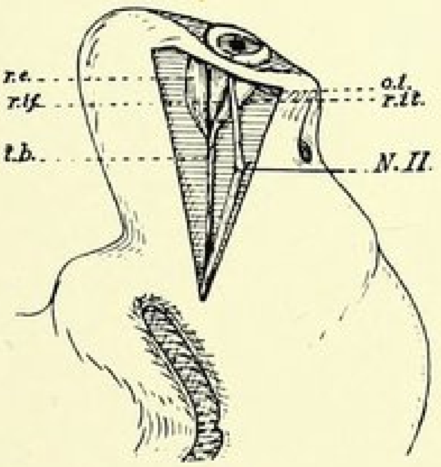

Fig. 18.

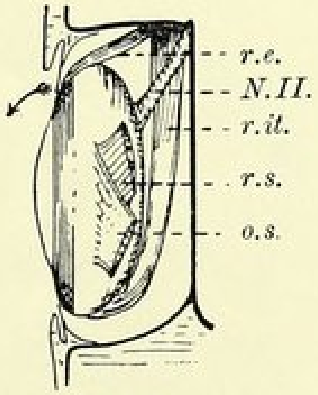

Fig. 19.

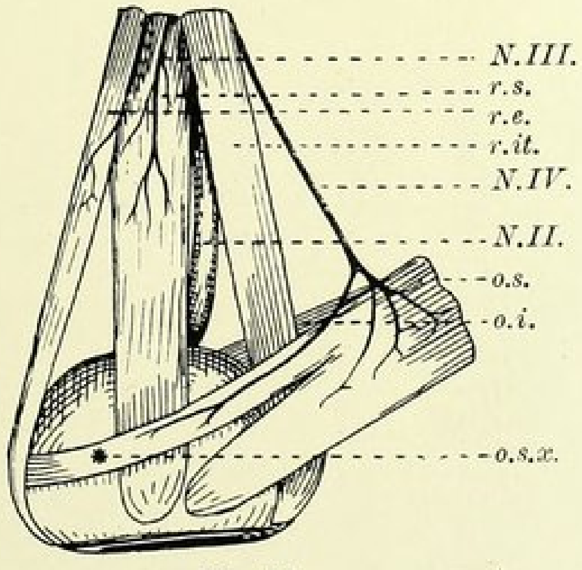

Fig. 20.

N. B. H., *del.*