VIII. *On the Asymmetry of the* Pleuronectidæ, *as elucidated by an Examination of the Skeleton in the* Turbot, Halibut, *and* Plaice.

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(Plates XXIX.–XXXII.)

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Introduction.

THAT both eyes of a Turbot, or of the Pleuronectidæ generally, are situated on one side of the head is a fact long interesting to naturalists in connexion with the peculiar habits of these animals. It also affords an interesting field for the anatomist and embryologist to ascertain what relation this asymmetry bears to the morphological plan of the fish-head in general.

And indeed, if we merely look at the exterior of such a fish as the Turbot, the manner in which the transposition of the eyes has been effected is not very apparent. It is, it is true, easy enough to imagine that the mesial line of the top of the head has been simply twisted over to one side, carrying with it the eye of the opposite. But the dorsal fin, which stretches all along the back in what is assuredly the mesial line of the fish, extends also uninterruptedly in the same straight line on to the head, beyond the eyes, and between the nostrils to nearly the end of the snout. If the mesial line of the top of the head has been twisted, why has such a distinctly median structure as the dorsal fin not undergone the same process at its cephalic extremity?

Or we may imagine that, in early development, one of the eyes has passed bodily through the head till it has reached that side where both are now found, and where it has formed for itself a new and anomalous orbit—a view which, it must be confessed, grates a little against most of our preconceived morphological ideas.

But from what we see on the outside of the fish we can only rashly speculate. It is only by means of anatomical and embryological research that we can gain an insight into the true state of the case.

Autenrieth is the oldest writer I have found who alludes to the subject anatomically, in a paper on the anatomy of the Plaice, published in the year 1800 *. His remarks on the osteology of the Plaice, however, are meagre; and his theoretical conclusions must appear to us now-a-days absurd, for he accounts in the following manner for the position of both eyes on the right side of the head. He says, "The examination of the skeleton shows us that the entire left side of the fore part of the cranium is, in reality, wanting, and

* Bemerkungen über den Bau der Scholle (*Pleuronectes platessa*) insbesondere, und den Bau der Fische, hauptsächlich ihres Skelets im Allgemeinen. Von Dr. J. H. F. Autenrieth. In Wiedemann's 'Archiv für Zoologie und Zootomie,' Theil i. 1800, S. 47 *et seq.*

that nature, in order not to lose an eye, was necessitated to put it into the hollow of the right cheek under the single remaining orbit."

Rosenthal (Ichthyotomische Tafeln, Berlin, 1812–1822), a little more rational in his ideas than Autenrieth, held the upper eye of the Flounder to be that of the left or now eyeless side, but accounted for its getting to the right side by supposing its being thrust through the head, and getting "placed between the long processes of the frontal bones after the manner of Cyclopean malformations." The view which occurred to him is then in accordance with the second theory suggested in the beginning of this paper, but which a careful examination of the osteology of a series of different species of flat-fish will easily show to be untenable.

It is, however, to Meckel * that we owe most of our previous knowledge of the subject. He recognized correctly the homologies of the various cranial bones with those of the symmetrical fish, and was undoubtedly the first who saw clearly that, according to the first theory already mentioned, the two eyes of the flatfish are brought round to one side by a twisting process; but his notions as to the prolongation of the dorsal fin along the head are unsatisfactory, as we shall see afterwards†.

Van Beneden, in 1853, published a paper ‡, the first in which, so far as I know, notice has been taken of the development of the Pleuronectidæ. In this paper he has described a young Turbot taken probably soon after its extrusion from the egg, and in which that stage of development does not seem yet to have been reached when the eyes become both placed on one side. "In this young fish the mouth is perfectly symmetrical; the eyes are still on the two sides of the head, but the left is about to pass over to the right side; the nostrils are still symmetrical. The rays of the dorsal fin only yet descend to the middle of the cranium; *afterwards they stretch on in front of the eyes*; but it is necessary first that the twisting of the head should have taken place on the vertebral column." To these observations he adds the result of some made "on a Turbot of nearly adult size, in which the process of torsion is arrested when the eye has arrived at the middle line. The rays of the dorsal fin have not yet descended to more than in the embryo described; the two sides are equally coloured." In remarking upon this paper, I may say that here, for the first time, do we find distinctly announced the fact and doctrine that the dorsal fin is not primarily advanced so far forwards on the head as we find it in the fully developed flatfish, but that it advances after the eye has turned round, and then it proceeds straight forwards, regardless of the deviation of the original mesial line of the head. Thus we are afforded a ready and rational explanation of the difficulty which met us at first, namely as to how, if the middle line of the top of the head has been twisted over to one side, the dorsal fin, a mesial structure, has not followed that twisting. Van Beneden, however, is not the first to notice an occasional condition of the adult flatfish resembling that which he has described in his

* Syst. der vergl. Anatomie, Theil ii.: Halle, 1824. Meckel's first observations on the subject appeared in a paper, "Ueber die seitliche Asymmetrie im thierischen Körper," in his 'Anatomisch-physiologische Untersuchungen,' Halle, 1822, a work which I have not had an opportunity of seeing. † See p. 287, note.

‡ "Note sur la Symétrie des Poissons Pleuronectes dans le jeune âge," Ann. des Sciences Naturelles, 3e série, xx. pp. 340–342.

embryo *; but he seems to me to be the first to appreciate the morphological value of such phenomena.

But very recently Steenstrup has revived the theory of Rosenthal, that the upper eye has passed through the head to the place it now occupies, and that this "migration" of one of the eyes has had a much more important share in bringing about the ocular transposition than any slight twisting that may have taken place †. According to his views, "The eye, at an early stage, must have quitted its primitive position, and, directing itself upwards and towards the interior, pierced the vault of the cranium constituted above the eye by the frontal bone, and formed for itself a new orbit, whether on the internal region of the frontal bone of the same side or between the two frontals." In support of this theory, he refers to the appearances presented by several very interesting young Pleuronectidæ, each about an inch long, brought from various localities in the Atlantic, and deposited in the Museum at Copenhagen, and directs especial attention to one in which one eye seems to be arrested in the process of piercing the head. In addition, M. Steenstrup remarks that the osteology of the head of the adult flatfish confirms his view of the process of ocular transposition in the embryo. Like Rosenthal, he compares the head of a flatfish to that of a Cyclopean malformation, and affirms that the position in which we find the upper eye is not homologous with that occupied by the lower, nor with the orbit of any other fish or vertebrate animal in general.

I can only say that the results of my own investigations do not agree with those statements of the above-quoted distinguished naturalist. What the views are which I have adopted will appear in the following paper; meanwhile I will only remark that the appearances presented by the cranium of the adult flatfish seem to me to be at complete variance with any theory that the two eyes of these animals occupy morphologically different positions from each other. In this communication I have named the bones according to the nomenclature given in Professor Owen's 'Lectures on Comparative Anatomy;' but, in doing so, I do not wish to be considered as committing myself to any of the general morphological ideas which may be associated with that nomenclature. Bones must, however, have names; and so long as our investigation does not trench on the general question of the homologies of the vertebrate skeleton, one system of names, provided it be widely known, may be used as advantageously as any other.

I. *On the Cranium of the Pleuronectidæ.*

In studying the cranium of the flatfishes, we must take into account the cartilage and membrane, which form morphologically as integral a part of the skeleton as the bones

* Cases of similar monstrosities or arrestments of development had been previously recorded, by Donovan as "Pleuronectes Cyclops," by Schleep as "Rhombus maximus duplex," and by Yarrell.

† J. Japetus Sm. Steenstrup "Om Skjaevheden hos Flynderne, og navnlig om Vandringen af det övre Öie fra Blindsiden til Öiesiden tvers igjennend Hovedet." Kjöbenhavn, 1864. Saerskilt Aftryk af Oversigt over d. K. D. Vid. Selsk. Forhandl. i. Nov. 1863.

"Observations sur le Développement des Pleuronectes," par M. Steenstrup (Annales des Sciences Naturelles, Paris, Nov. 1864).

The former of these two papers, being written in the Danish language, I have not yet read.

themselves. It will also be necessary to compare the cranium and its parts with that of a symmetrical fish; and, for this purpose, we may select the cranium of the common Cod (*Gadus morrhua*), a fish belonging to the same suborder (Anacanthina) of the Telostei as the Pleuronectidæ. As a standard for such comparison this cranium will do very well, the differences between its plan of structure and that of the flatfish-skull being really immaterial.

In such a cranium (Plate XXIX. fig. 16) we find three principal parts, each connected with one great organ of special sense.

1. A posterior cavity (Z) containing the brain and organ of hearing, this cavity being, in the macerated skull, widely open in front, and showing a "foramen magnum" behind for the exit of the spinal cord. Into its composition enter the basilar, exoccipital, paroccipital, supraoccipital, petrous, mastoid, orbitosphenoid, alisphenoid, part of the basipresphenoid, and part of the mid or great frontal bones, also a considerable quantity of unossified cartilage.

2. A middle or interorbital part (Y), consisting of part of the frontal bone above, part of the basipresphenoid below, with a fibrous membrane (the "septum interorbitale") extending vertically between them. This septum is formed by the coalescence of two fibrous laminæ, which close to a considerable extent the anterior opening of the brain-case, and also complete a groove on the under surface of the frontal bone into a canal which continues the brain-cavity as far forwards as the nose, and lodges the crura of the olfactory bulbs. Note, that while the basipresphenoid below remains a narrow bar, the frontal bone above forms a large broad arched plate, which both contributes to the general stability of the cranium and forms very efficient roofs for the orbits.

3. An anterior or nasal part (X), which contains no cavity, but presents two openings for the olfactory nerves—one on each side of a central mass of cartilage. This part of the cranium consists of four bones—the vomer below, the nasal bone above, and the two prefrontals on each side, each of which is notched internally for an olfactory nerve. All these bones are supported by the central mass of cartilage already referred to.

Another well-known circumstance in the structure of the skull of the Cod, as of other fishes, must be noticed, viz. that, when the individual bones are disarticulated, certain of them can be removed without in the least interfering with the primordial cartilage, of which a considerable quantity still remains. In the Cod these superficial bones, or "Deckknochen," are invariably the vomer, the basipresphenoid, the frontal, the parietals, and the petrosals. The other bones are so intimately connected to the cartilage, that they cannot be separated without tearing it and carrying away pieces of it in their substance. They are the basioccipital, paroccipitals, exoccipitals, supraoccipital, mastoids, postfrontals, alisphenoids, orbitosphenoids, prefrontals, and nasal.

The only differences worthy of note between the general plan of the Cod's skull as given above and that in the flatfishes are, that the two halves of the single frontal bone in the Cod are represented in the latter by two distinct bones, and that in the flatfishes the membranous interorbital septum contains no tubular prolongation of the brain-cavity. In the Pleuronectidæ and in the Gadidæ the relations of the bones to the cartilage are identical.

One of the simplest crania to be met with among the Pleuronectidæ is that of the Turbot (*Rhombus maximus*), of which illustrations are given in Plate XXIX. figs. 1–7). This cranium, truncated behind and somewhat pointed in front, presents superiorly a longitudinal ridge (fig. 1, β) which, though commencing posteriorly in the middle line, does not divide the head into two equal parts as it advances. On the contrary, the anterior part of the cranium is broader to the left than to the right of this ridge, or of its supposed continuation forwards in a straight line; and this happens both because the skull anteriorly is actually considerably broader on the left than on the right side, and because the ridge itself deviates a little, though very slightly, towards the right side. This ridge supports the cephalic continuation of the dorsal fin. Posteriorly we at once recognize the brain-cavity, with its foramen magnum for the exit of the spinal cord, and various other foramina for cranial nerves. In front of the brain-cavity, and to the left side, is an oval orbit (B), which lodges the upper eye, the lower eye lying free beneath the lower bony margin of that orbit. In front of the orbit we recognize the nasal part of the cranium, with its two olfactory foramina, one on each side of the central cartilage (A).

On comparing this cranium with that of the Cod, we observe that while in the latter the anterior and posterior parts of the skull are connected by two bars of bone—an inferior narrow one (basipresphenoid) and a superior flattened arch-shaped one (frontal)—we have here three bars, the two upper bounding between them the orbit for the upper eye. To the left of these two bars, which forms the lower boundary of the orbit and lies between the two eyes, I shall give the name *interocular*; and to the other one, which bounds the orbit on the right side, and proceeds forward in the apparent middle line, I give the name *pseudo-mesial*.

In the Turbot and its congeners the eyes lie both on the left side usually—the upper one in the orbit, the lower free beneath the lower margin of that orbit, formed by the interocular bar. As, however, in some other groups of flatfishes the eyes are usually on the right side, to prevent confusion I shall, in the description of the bones of the flatfish-head, abandon the terms "right" and "left" altogether, and use instead the terms "eyed" and "eyeless."

Proceeding now to disarticulate the Turbot's cranium, we find that posteriorly the bones are very little altered in their symmetry.

Basioccipital (1). The long axis of this bone is somewhat obliquely placed as regards the transverse plane of the disk on its posterior surface for articulating with the first vertebra, pointing a little towards the eyed side.

Exoccipitals (2). Very symmetrical.

Paroccipitals (4). The posterior projecting process is often longer on the eyeless side.

Alisphenoids (6). Very symmetrical.

Mastoids (8). Very nearly equal in size and conformation. That of the eyeless side, however, is generally a little longer than that of the eyed.

Petrosals (16). These bones are much smaller than in the Cod, and lie quite superficially. That of the eyeless side is in the Turbot always larger than the opposite one, and accordingly on the outside of the skull covers up more of the mastoid and exoccipital bones from view.

The *Postfrontal* (12) is longer on the eyeless side, and its long axis curves a little round to the eyed side. (See fig. 3, Plate XXIX.)

Parietals (7). As in the case of the postfrontals, the parietal of the eyeless side is considerably longer than its fellow. The difference is best seen when the bones are disarticulated.

The bones enumerated in the last paragraph show but little in regard to the symmetry of the head. In those next to be noticed, the indications are more decided.

Basi-presphenoid (5). This bone is slightly bent towards the eyeless side, a little behind its middle. For description it may be divided into three parts. The posterior flattened part, which overlaps the basioccipital, is symmetrical. The middle part presents above on each side an ascending laminar process or wing, which bounds laterally a channel lodging the origin of the eye-muscles, this channel, however, passing obliquely across the long axis of the bone from the eyeless towards the eyed side. The anterior part, which receives the pointed end of the vomer, is apparently twisted on its long axis up towards the eyeless side, this appearance being principally caused by a greater development in a more vertical direction of that side of the bone.

Orbitosphenoid (10). On the eyeless side this bone is longer than on the eyed side; the direction of its axis also agrees with that of the eye-muscle canal of the basi-presphenoid in pointing obliquely across to the eyed side (see Plate XXIX. fig. 3), the part shaded with horizontal lines indicating the cartilaginous tips of the bones.

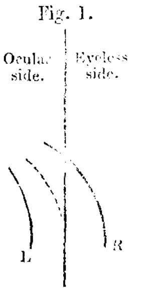
The Supraoccipital (3) presents a scale-shaped "body," forming part of the roof of the cranial cavity, surmounted by a very prominent ridge or spine. The flattened part is tolerably symmetrical; its long axis, often slightly curved, points, however, to the eyed side; but the spine (β), though commencing posteriorly in the middle line, passes forwards, with a slight deviation towards the eyeless side, impinges on the frontal bone of that side, and, if continued further forwards, would pass quite by the eyeless side of the orbit. Its direction, though thus slightly deviating, is, however, nearly in the midde line of the top of the head.

The supraoccipital bone is thus very unequally divided, the larger moiety being on the ocular side.

If now, before we proceed further, we turn to Plate XXIX. figs. 2 and 3, we shall see that, although the basal keel of the cranium is continued forwards in nearly a straight line, the long axis of the cranial cavity, which that keel underlies, points round to the eyed side, anteriorly crossing that keel at an angle. This is well illustrated by the structure of the basi-presphenoid bone itself (5) where the eye-muscle channel, which is simply the lower part of the cranial cavity, crosses the long axis of the bone. This also explains the reason why several of the cranial bones, as the parietal, mastoid, postfrontal, and orbitosphenoid, are longer on the eyeless side, simply because they have a longer extent to traverse, as is illustrated in the accompanying diagram (fig. 1.)

Notice also that, although the long axis of the supraoccipital bone follows the general twist of the cranial cavity in pointing towards the eyed side (indicated by the dotted

Fig. 1.

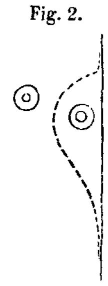


line in the diagram), the spine of the bone continues forwards nearly in the same straight line as the middle line of the entire fish (indicated by the straight line in the diagram). To the first of these lines, continuing forwards the axis of the body of the supraoccipital bone, I give the name "morphological middle line;" and to the line of the spine of the supra-occipital, which also supports the cephalic prolongation of the dorsal fin, the name "pseudomesial."

In advance of the orbitosphenoid, postfrontal, parietal, and supraoccipital bones are two bones (11' & 11), which, from their position, must be the frontals. Each consists of a posterior somewhat square-shaped part, forming part of the roof of the brain-cavity, and of an anterior more slender curved part, which, with its fellow of the opposite side, forms the interocular bony ridge or bar. The anterior part of the bone of the ocular side (*m'*, Plate XXIX. figs. 1 & 7) is strongly curved, the concavity looking upwards and to the eyeless side; at its extremity it articulates with the prefrontal of its own side, touches the nasal bone, and rests likewise on a portion of primordial cartilage, to be presently described (A, fig. 1). The bone of the eyeless side (Plate XXIX., fig. 7, 11) is distinguished by having its posterior part larger, the external anterior angle (*n*) projecting forwards so as to take a slight part in the formation of the pseudomesial bar of the cranium, which bounds the orbit on the eyeless side. The anterior part (*m*) ("inter-ocular process") is much more slender than the corresponding part of the bone of the ocular side, and to which it is closely applied; at its extremity it likewise rests on a portion of primordial cartilage, but does not touch its corresponding prefrontal. It forms the entire lower boundary of the orbit, and, with its fellow of the opposite side, forms the interocular bar of the cranium.

We now see that the morphological mesial line continued from the supraoccipital bone in the line separating the two frontal bones from each other, at first deviating but slightly towards the eyed side, afterwards curves round the orbit along the interocular bar till anteriorly it tends again to coincide with the apparent middle line, as in the adjoining diagram. In the figures of crania (Plate XXIX.) I have also represented the course of the morphological middle line by a dotted line. That this is the true morphological middle line, and that the interocular bar is the only and complete homologue of the frontal arch in the Cod, is proved simply by the fact that between the interocular bar and the basi-presphenoid bone there extends a fibrous membrane, having imbedded in it the olfactory nerves as they proceed to the nasal fossæ in front. This membrane represents the fibrous interorbital septum in the Cod; but, by the twisting over of the mesial plane of the ocular region to one side, this septum in the Turbot, instead of remaining vertical, has become nearly horizontal, and instead of coinciding with the mesial plane of the rest of the fish, has become set nearly at right angles to it. In the Turbot, as in all the other Pleuronectidæ, the olfactory nerves are not contained in a tubular prolongation of the brain-cavity at the top of the interorbital septum as in the Cod, but are simply imbedded in its substance. The ophthalmic branches of the fifth nerve on each side, which in the Cod lie beneath the frontal arch, here curve round between the eyes, along

Fig. 2.



the interocular processes of the frontal bones, till they end in the nostrils and front of the snout.

The main slime-canals, one for either side, which in the Cod pass between the eyes over the frontal arch, here pass between the eyes along the interocular bar, being channelled out in the interocular process of its corresponding frontal bone. (See Part III. of this essay.)

But what, then, is the pseudomesial bar or bridge in the Turbot's cranium, if the interocular bar be the complete representative of the frontal arch in the Cod? This we shall see presently.

We now come to the anterior or nasal part of the cranium, characterized by two olfactory foramina, of which that of the ocular side is more anterior than the other. As in the Cod, this portion of the cranium consists of a central piece of cartilage, supporting four bones, the vomer below, the nasal above, and the two prefrontals, one on each side.

The Cartilage.—This portion of cartilage (A, figs. 1–5), more extensive than the corresponding remnant in the Cod, appears as a very rudely quadrangular plate with a large hole through its middle, connected to bones all round its edges, save the concave posterior one, which is continuous with the fibrous septum between the eyes, already referred to. On each side of it an olfactory nerve passes to its corresponding olfactory foramen in the direction indicated by the bristles in Plate XXIX. figs. 3–5. It therefore indicates the morphological mesial plane of the anterior part of the cranium, and would be vertical were it not for the twisting over to one side which has occurred. It rests beneath on the basi-presphenoid and vomer; in front it supports the nasal bone (15), and laterally, round its anterior inferior angle, it is intimately connected to the prefrontals (14' & 14), one on each side. Above, the anterior extremities of the interocular processes of the frontal bones rest on it, as follows:—A longitudinal notch divides the upper edge of the cartilage into two unequal pointed processes (*g* & *h*, Plate XXIX. figs. 3–5). Of these, that of the eyed side (*g*), by far the largest, is lodged in a hollow on the under surface of the stout interocular process of the frontal of the same side, and supports also the posteriorly directed process (*a*) of the corresponding prefrontal (14); the other one (*h*) is similarly related to the end of the slender interocular process of the frontal of the eyeless side, but is not touched by its prefrontal, save at its very base. Now this notch, separating those two processes, as it indicates the line of separation between the interocular processes of the two frontal bones, must likewise indicate the morphological middle line of the cartilage; so that here we have a mesial cartilage, not only unsymmetrical in its position, but also in the development of its two sides, the greater development being on the ocular side of the fish.

Vomer (13). The posterior part of the vomer, which fits into a groove on the lower aspect of the basi-presphenoid, is more developed on the eyeless than on the eyed side; on the eyeless side also the ala for articulating with the prefrontal is larger, and projects more vertically upwards than on the opposite side; so that, like the anterior part of the basi-presphenoid (p. 268), the vomer has slightly the appearance of being twisted up on its long axis towards the eyeless side. In outward form, however, the head of the bone which bears the vomerine teeth (Plate XXIX. fig. 2) does not participate much in this apparent twisting.

Nasal (15). This bone is tolerably symmetrical as regards the development of its two sides. In front it presents a deep transverse notch, at which point the bone is slightly bent, the concavity being towards the ocular side. We have then the nasal prominence divided into two parts by the aforesaid notch, the upper (*i*, figs. 5 & 6, Plate XXIX.) giving attachment to ligaments connected with the maxillary bones, and continuing forwards the direction of the still oblique morphological middle line; the lower and anterior (*k*) forming an articular ridge, on which the intermaxillary nodule of cartilage glides downwards and upwards, and forwards and backwards, as the jaws open and shut, coincides in its direction with the pseudomesial line also; so that the notch between these two prominences of the nasal bone is the point where the morphological middle line again returns to the apparent middle line of the top of the head (see Plate XXIX. fig. 1).

The two *prefrontals* are at once known by the notch borne by each, and which is completed into an olfactory foramen (c) by the contiguous nasal bone.

The *prefrontal of the eyed side* (14′) is somewhat triangular in shape; anteriorly and to the inner side it presents the notch already spoken of, articulates with the nasal bone, and touches the primordial cartilage. Below the olfactory notch it is extensively continuous with the primordial cartilage, and also sends down a process (*c*) which articulates with the corresponding ala of the vomer. Opposite the olfactory notch, and on the outer side of the bone, is a prominence (*e*) to which the anterior suborbital bone of that side is attached; and posteriorly a pointed process (*a*) is sent back, which articulates with the interocular process of the corresponding frontal bone, and rests internally on the primordial cartilage which forms the anterior part of the " septum interorbitale " (see p. 266).

The *prefrontal of the eyeless side* (14) is much larger, and of a rudely quadrangular shape. Anteriorly it is similarly related to the nasal bone, and presents the same olfactory notch that we saw in the other bone. The same process (*c*) is sent downwards and forwards to articulate with the vomer; and an additional one (*b*) is sent downwards and backwards to articulate with the basi-presphenoid. But the great mass of the bone projects backwards in a great flat quadrangular process (*f*), which, instead of articulating with the interocular process of the frontal of the eyeless side, as the posteriorly directed process (*a*) of the other prefrontal does with its corresponding frontal, passes round the other side of the orbit, and, joining the external angular process of the frontal of the eyeless side, forms, with it, the pseudomesial bar of the cranium, which bounds the orbit on the eyeless side.

The orbit which contains the upper eye, then, is bounded posteriorly and on the outer side by the interocular process of the frontal of the eyeless side, at the anterior angle by a small portion of primordial cartilage (*s*), on the inner side by the external angular process of the frontal of the eyeless side and by the posteriorly directed process (*f*) of the corresponding prefrontal.

If we now examine the prefrontal bones in the Cod, the lateral aspect of one of which is figured in Plate XXIX. fig. 16 (14), and disarticulated in fig. 17, we shall find that the connexions of each bone are as follows:—

1. It shows two processes (*d d*) going towards the nasal bone, with an olfactory notch between them (c).
2. An anteriorly directed process (*c*) for the ala of the vomer.
3. A posterior-inferior process (*b*) for articulation with the basi-presphenoid.
4. A posterior-superior process (*a*) going upwards and backwards to join the frontal bone.
5. A lateral process (*e*), tipped with cartilage, opposite the olfactory notch, to which the anterior suborbital bone is attached.

Now, on comparing the prefrontal of the ocular side in the Turbot with this, we find that everything corresponds exactly, save that the process (*b*) for articulation with the basi-presphenoid is wanting, the interval being filled up by mere cartilage. (Plate XXIX. figs. 2, 4, 5.)

The prefrontal of the eyeless side, though it presents a large process (*b*) for articulation with the basi-presphenoid, shows no trace of the process (*a*) for articulating with the interocular part of the frontal; it does not touch it at all. But what, then, is the large process *f*? That it is not homologous with the process (*a*) projecting upwards and backwards in the Cod and in the other prefrontal of the Turbot, is evident from its bearing no relation to the olfactory nerve of its side, nor to the interocular septum. On the other side, the olfactory nerve runs close beneath the process *a*, as indicated by the bristle in Plate XXIX. fig. 4. It follows, then, that this process (*f*) in the prefrontal bone of the eyeless side is an additional process having no homologue either in the Cod or in the prefrontal of the opposite side in the Turbot. We may call it "external angular," corresponding with that process already described in the frontal of the same side, and which has also no homologue in the Cod or in the eyed side of the Turbot.

And now we see what the nature of that bar of bone is, which I have called pseudomesial (p. 267), and which one is apt at first to think homologous with the whole or part of the frontal arch in the Cod and other symmetrical osseous fishes. Seeing that the true homologue of the frontal arch in the Cod's head has been reduced to a narrow bar, and twisted over to one side (p. 269), we have, in the pseudomesial bar, a secondary formation destined to supply the place of the weak and displaced frontal arch in forming a strong and efficient bridge of connexion between the anterior and posterior parts of the cranium, and also to support the cephalic continuation of the dorsal fin.

The cranium we have just considered is the least asymmetrical and most easily understood which I have met with in the Pleuronectidæ. We shall now proceed to examine and compare with it the crania of some of the other Pleuronectidæ, and note to what further steps the process of distortion proceeds, before finally generalizing on the changes which have taken place.

The cranium of the Brill (*Rhombus vulgaris*) is nearly identical with that of the Turbot. But we must remark that the interocular process of the frontal of the eyeless side is proportionally more slender than in the Turbot, while the external angular process of the same bone is more pronounced, and forms more of the inner wall of the orbit, than in the last-named fish.

In the group of flatfishes to which the Flounders belong, we find the rays of the dorsal fin advancing only so far as the middle of the orbit; and the eyes are normally placed on the right side of the head. There is also a very marked tendency for the mouth to become twisted towards the opposite side of the body to that on which the eyes are placed.

As characteristic of this group, we first consider the cranium of the Halibut (*Hippoglossus vulgaris*) (Plate XXIX. figs. 8–11).

On looking at the under surface of the Halibut's cranium (Plate XXIX. fig. 9), we find the basal keel pretty straight in itself; but when the head is *in situ* on the end of the vertebral column, this keel points strongly to the eyeless side. In the occipital region the skull is apparently broader on the eyed than on the eyeless side; this is due to a greater prominence on that side of the mastoid (8) and exoccipital (2) bones; the petrous (16) is also larger. The middle line of the posterior aspect of the skull is also strongly curved, the convexity being towards the ocular side, and corresponds with a similar curve, to be afterwards alluded to, in the spinous processes of the anterior vertebræ (p. 285).

The *basioccipital* (1) is unsymmetrical, the middle line of the inferior surface pointing to the eyeless side, while that of the upper surface of the bone, indicating the twist of the cranial cavity, diverges towards the eyed side. The mesial vertical plane of the bone is therefore pushed over to the eyed side anteriorly.

The *basi-presphenoid* (5) presents in a much more exaggerated form than in the Turbot the apparent twisting-up of its anterior part on its long axis towards the eyeless side; here, indeed, the groove in which the end of the vomer is inserted looks quite to that side. The axis of the entire bone points to the eyeless side, as I have already noticed.

The *postfrontal* of the eyed side (12) has the semilunar excavation, which, by a similar one in the alisphenoid bone, is completed into an articular cavity (D) for the head of the epitympanic, placed further forwards on its surface than on the eyeless side, so that the attachment of the suspensory apparatus to the cranium reaches further forwards on the former than on the latter side. This is important in connexion with the conformation of the bones of the face (p. 278).

The *orbitosphenoid* (10) is larger on the eyeless than on the eyed side, and its long axis points considerably over towards the eyed side. In the view of the under surface of the skull given (Plate XXIX. fig. 9) the real size of this bone is not apparent, owing to its concealment by the basi-presphenoid.

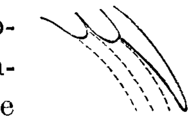
The *supraoccipital* (3) shows in a more marked manner than in the Turbot the divergence of the morphological from the apparent middle line at the back of the head. Its direction is indicated by the red line in the figure.

The *parietal* of the eyeless side (7) is broader than the opposite one, which latter, however, is often a little longer.

The *frontal* of the eyed side (11′) corresponds very much in shape with the same bone in the Turbot. But that of the eyeless side (11) has its external angular process much more developed, forming more than one-half of the inner wall of the orbit, while the interocular process is reduced to a mere curved spiculum (*m*, fig. 11), passing all round the outer margin of the orbit, closely applied to the stouter interocular process of the other frontal bone. A ridge continued from the supraoccipital bone passes over the frontal of the eyeless side, and on to its external angular process; it supports the cephalic continuation of the dorsal fin.

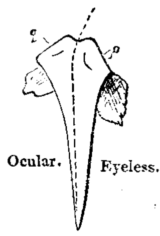
Anterior Part of the Head.—The Cartilage (Plate XXIX. figs. 8–10, A).—This is thinner and smaller than in the Turbot, but its shape and relations are analogous. Its upper border is divided by two notches into three very unequal processes, of which that on the ocular side, by far the largest, extends posteriorly, and supports the process (*a*) of the prefontal of the ocular side. Into the larger notch (*g*) on the ocular side is inserted the extremity of the interocular process of the frontal of the same side; and into the smaller notch (*h*) on the other side is inserted the extremity of the corresponding part of the frontal of the eyeless side, in the manner represented in Plate XXIX. fig. 8. This cartilage, then, as in the Turbot, is very unequally developed on its two sides, the side corresponding to the eyeless side of the fish appearing as if quite atrophied—corresponding with the small size of the interocular process of the frontal and the complete non-development of the process (*a*) of the prefrontal of the eyeless side (see p. 272).

Fig. 3.



Vomer (13).—This bone appears twisted on its long axis up towards the eyeless side, as in the Turbot, but in a more exaggerated degree (see Plate XXX. fig. 3, where the vomer is seen from the front). Anteriorly it presents two articular facets (*p* & *q*, figs. 8, 9, Plate XXIX.), of which that on the eyeless side (*p*) is larger, and looks more laterally than the opposite one (*q*); a line bisecting the angle formed by these two facets would pass obliquely towards the eyeless side, as in the adjoining diagram. The lateral ala on the eyeless side, besides being larger, and directed more vertically upwards, is also directed more posteriorly than the opposite one; so that the bone, in addition to being twisted on its long axis upwards and to the eyeless side, has that axis turned to the eyeless side at its extremity, as indicated by the dotted line in the diagram. The full import of this will be seen when we consider the bones of the face.

Fig. 4.



Nasal.—The prominence (*k*) on which the intermaxillary cartilage glides is obliquely directed towards the eyeless side. The nasal bone in the Halibut is more expanded transversely than in the Turbot, and thus comes to enter into the boundary of the orbit (Plate XXIX. figs. 8 & 10, 15). It is also apparent that this increase of size transversely is chiefly due to development on its eyeless side.

Prefrontals (14' & 14).—These are more nearly of the same size as in the Turbot, though that of the eyeless side is still a good deal larger than its fellow. I have already alluded to the fact that in the Turbot the process (*a*) of the prefrontal of the ocular side, which articulates with the interocular process of the corresponding frontal, is not at all developed in the prefrontal of the eyeless side, an interval filled by cartilage (*s*, Plate XXIX. fig. 1) being left between the frontal and prefrontal anteriorly on that side. In the Halibut the prefrontal of the eyeless side, at the place where the process (*a*) should be given off, is still less developed, and, the primordial cartilage in this region being less extensive than in the Turbot, a space is left in the anterior wall of the orbit, which is filled up by a development from the corresponding side of the nasal bone. (Compare the boundaries of the orbit in Plate XXIX. fig. 1 and in fig. 8.)

In the cranium of *Platessa pola* the interocular process of the frontal of the eyeless side presents a form intermediate between its condition in the Halibut and that in the Plaice, next to be described. It is continued between the eyes as a very slender spiculum, much more delicate than the corresponding part in the Halibut, and very apt to be broken off in disarticulating the skull. The external angular process of the same bone is very largely developed, and, with the corresponding part of the prefrontal of the eyeless side, forms the pseudomesial bar of the cranium into an expanded and flattened vertical plate, apparently designed to support the curious series of ampullated mucous canals on the eyeless side of the head of this fish (see Plate XXXI. figs. 6, 7). The two frontal bones are represented in Plate XXIX. fig. 15.

In the Plaice (*Platessa vulgaris*) the general form of the cranium is much the same as in the Halibut; but some of the asymmetries indicated in the latter have run to a much greater excess.

The keel, on the under surface of the cranium (Plate XXIX. fig. 13), is strongly bent towards the eyeless side, and its anterior extremity is also twisted strongly upwards on its long axis towards the same side.

The external angular process of the frontal of the eyeless side (Plate XXIX. fig. 14 *n*) is similar to that in the Halibut; but the interocular process (*m*) is almost completely non-developed, so that the greater part of the lower or external boundary of the orbit is formed by the frontal of the ocular side; and this circumstance might easily lead a superficial observer to imagine that the interocular process of the bone of the ocular side is homologous with the external angular of the opposite one. This seems to have been Rosenthal's idea when he speaks of the upper eye being "placed between the two long processes of the frontal bones, after the manner of Cyclopian monstrosities" *. But the untenableness of this idea will be at once apparent if we refer to the series of frontal bones figured in Plate XXIX. figs. 7, 11, 14, 15, and to the relations of the interocular fibrous septum and olfactory nerves, which here occupy an exactly similar position to what they do in the Turbot (p. 269).

The prefrontals (14′ & 14) are fashioned much as in the Halibut; that of the ocular side is pushed forwards somewhat in advance of the other (Plate XXIX. fig. 12).

The *nasal* bone forms a large part of the orbital wall; anteriorly it is much more developed on the side corresponding to the eyeless side of the head. The ridge (*k*) on its anterior surface, on which the intermaxillary cartilage glides, is very obliquely directed towards the eyeless side (Plate XXIX. fig. 12, Plate XXX. fig. 7). Compare this with the direction of the analogous part in the Turbot (p. 271).

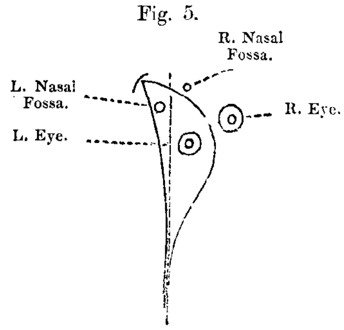
Vomer.—The two facets (*p q*, Plate XXIX. fig. 12) on the end of this bone, and on which the heads of the superior maxillary bones glide, are so placed that the line bisecting the angle which they form with each other passes very obliquely to the eyeless side,

* *Loc. cit.*

in the same direction as the articular ridge above on the nasal bone. In consequence of this conformation of the nasal bone and vomer the long axis of the oral apparatus points obliquely to the eyeless side, and when the mouth opens it is protruded in the same direction. (See description of facial bones.)

The cranium of the Plaice, then, is more unsymmetrical than that of the Halibut in the almost complete non-development of the interocular process of the frontal bone of the eyeless side; and, in consequence, the corresponding process of the other frontal forms almost the whole of the external or lower boundary of the orbit. The nasal bone enters more largely into the boundary of the orbit in front, and the process of twisting of the anterior part of the skull upwards towards the eyeless and downwards towards the eyed side, as well as the bending of the axis of the keel of the cranium towards the eyeless side, has proceeded to a greater extent. In the adjoining diagram the dotted line represents the apparent middle line of the head of a Plaice, the thick black line the axis of the keel of the cranium, and the thin black line the morphological middle line.

Fig. 5.



The changes from the symmetrical type which have taken place in the cranium of the Pleuronectidæ may be summed up in the following propositions :—

1. The mesial vertical plane of the cranium has become inclined over to the now binocular side of the head, very slightly in the posterior part of the cranium, very much in the region of the eyes (so that the original vertical interorbital septum becomes now nearly horizontal), returning in the nasal region nearly to its original vertical position in the Turbot, but never doing so in the Halibut or Plaice.

2. In consequence of this, the middle line of the base of the skull remains still comparatively straight; while the middle line of the upper surface, diverging from the apparent or pseudomesial line, curves round between the eyes (which the turning-over of the mesial plane has of course brought to one side), and returns to the middle in front. Having got in front of the eyes and nasal fossæ in the Turbot, it again coincides, or nearly so, with the apparent middle line; but in the Halibut, and still more so in the Plaice, the apparent and morphological middle lines, if produced, would cross each other.

3. In the anterior part of the cranium, the parts on the eyeless side of the middle line of the *base* are, in all the Pleuronectidæ, more developed than on the ocular side. This is exemplified in the more strong development of the eyeless side of the anterior part of the basi-presphenoid, in the greater breadth of the ala of the vomer on that side, in the greater breadth of the orbitosphenoid, and in the great development of the processes (*c* and *b* in the figures) sent down by the prefrontal to articulate with the vomer and basi-presphenoid. While, on the ocular side, the orbitosphenoid is narrower, the ala of the vomer is smaller, and the prefrontal does not articulate at all with the basi-presphenoid. Not only are those parts, on the eyeless side of the middle line below, more developed than on the ocular side, but their development is in a more vertical direction upwards; so that the whole anterior part of the cranium assumes an appearance as if it

were twisted, up to the eyeless side, down towards the ocular side. In connexion with this, we must notice the greater elevation on the eyeless side of the olfactory foramen, and of the articulation to the cranium of the palatine apparatus and of the anterior suborbital bone.

4. On the top of the head the interocular parts of the frontal and prefrontal bones are more developed on the ocular side. The interocular process of the frontal of the ocular side is always much stouter than that of the other bone, and always articulates with a corresponding process sent back from the prefrontal. But the prefrontal of the eyeless side sends back no process to articulate with the frontal of the same side, whose interocular part, if examined in a series of flatfishes, gets smaller and smaller, till in the Plaice it seems almost gone. The same condition affects the morphologically mesial plate of cartilage forming the anterior part of the interocular septum, which cartilage we have already seen to be chiefly developed on the ocular side.

5. To accommodate the two eyes, now both on one side of the head, the anterior parts of the frontal bones remain as a narrow bar, never widening out into a broad arch as in the Cod and other fishes. Accordingly, to maintain the requisite stability of the cranium, a new bar or bridge of bone is formed (pseudomesial) by the union of a process sent forwards from the anterior external angle of the frontal of the eyeless side with one sent back from the corresponding prefrontal. By means of this bar the upper eye becomes closed round by a bony orbit, whose boundaries in the Turbot consist of the interocular process of the frontal of the eyeless side, the external angular process of the same bone, the external angular process of the corresponding prefrontal, and a small portion of cartilage in front. In the Halibut and Plaice, however, the nasal bone comes to take part in the boundary of the orbit principally by a development from its eyeless side; and in the latter fish, owing to the atrophy of the interocular portion of the frontal of the eyeless side, the corresponding part of the other frontal forms almost the entire external boundary of the orbit.

6. The olfactory foramen and the place of suspension of the anterior suborbital bone are further forward on the ocular side, slightly in the Turbot, to a marked degree in the Halibut and Plaice, in which latter fish the entire prefrontal bone is on this side pushed further forwards. The articulation of the epitympanic bone to the cranium, in the Halibut and Plaice, likewise extends further forward on the ocular side.

7. The axis of the keel of the cranium, pretty straight in the Turbot, points, however, in the Halibut, and still more so in the Plaice, to the eyeless side. In the Sole, on the other hand, it is bent with the convexity downwards—a condition apparently connected with the peculiar mechanism of the jaws in that fish.

II. *Bones of the Face.*

Jaws. Palato-suspensory Apparatus. Opercular Apparatus.—The bones of the face in the Pleuronectidæ are also unsymmetrical, but in a much less degree than those of the cranium. Before proceeding to study their asymmetries, however, we must take into account the following circumstances, which seem to act as the conditions on which these asymmetries depend :—

1. The form of the jaws and the direction in which the mouth opens. These conditions vary somewhat in the different Pleuronectidean types. In the Turbot and Brill the jaws are pretty symmetrically conformed, and the mouth opens nearly straight forwards, as in an ordinary fish; whereas, in the Halibut and in the Flounders, the jaws on the eyeless side are considerably stronger and more arched than on the eyed side, and the axis of the mouth, in opening, always tends to point towards the eyeless side. In the Sole, on the other hand, it is by means of the strange conformation of the jaw-bones of the eyeless side that the mouth is rendered chiefly effective on that side, the jaws on the eyed side being even (as is well known) perfectly toothless; and we find, dependent on the peculiar shape of the jaws, variations in the form of the palato-suspensory apparatus of each side, wherein the Sole differs remarkably from the other Pleuronectidæ I have examined.

2. The flattened form of the eyeless side of the fish, and the more arched form of the ocular one.

3. The fact that the cheek of the eyed side must accommodate an eye, while the other side has been relieved of its corresponding one.

4. The greater and more vertical development on the eyeless side of the ala of the vomer, and of the corresponding part of the prefrontal; so that the articulation of the palate-bone to the cranium is higher on the eyeless than on the eyed side.

5. The more anterior position of the parts about the olfactory region which belong to the ocular side, so that the articulation of the palate-bone to the cranium is further forwards on that side. In the Halibut and Plaice this condition affects parts further back (see p. 273), so that the articulation of the suspensory apparatus is also further forwards on the eyed side.

The symmetries of the bones of the face are not much altered in the Turbot and Brill. A greater degree of asymmetry is found in the Halibut and in the Flounders; while the facial bones of the Soles are the most unsymmetrical of all.

Turbot and Brill.—In the Turbot and Brill the mouth looks nearly straight forwards, and, in the movements of opening and shutting, the upper jaw-bones move *en masse* nearly straight forwards and backwards—a circumstance brought about by the nearly straight back-and-forward direction of the ridge on the nasal bone for the intermaxillary cartilage, and by the symmetrical position of the facets on the vomer for the heads of the superior maxillary bones. The intermaxillary and maxillary bones are very nearly alike in size on the two sides; the intermaxillary of the ocular side is a little longer, more arched, and furnished with more teeth than its fellow. The head of the superior maxillary bone of the ocular side has a smaller articular facet for gliding on the vomer. The lower jaw is longer, and somewhat stouter on the eyeless side; the dentition is much the same on both suspensory and opercular apparatus. In the Brill we generally find that the epitympanic and preopercular bones are slightly longer on the ocular side; in the Turbot they are very nearly equal. But in both the Turbot and Brill the operculum and suboperculum are larger on the eyeless side; the interoperculum is also broader, but invariably also much shorter than on the ocular side, because, on the latter side, the articulation of the lower jaw is further forwards. The slightly greater breadth of the opercular bones on the eyeless side, in the Turbot and the Brill, is the only circumstance I know of in the osteology of the face in the flatfishes which shows the least discrepancy with the principles laid down.

Pterygo-palatine Apparatus.—Corresponding with the general flattened form of the whole fish on the eyeless side, and because the cheek of that side has no eye to accommodate, the palate, entopterygoid, and ectoptergoid bones are considerably flatter on the eyeless side; while on the opposite side, to form the floor of a sort of orbit for the lower eye, the entopterygoid bone must arch considerably inwards. In the Turbot and Brill the articulation of the lower jaw to the suspensory apparatus is on much the same level on both sides; but we have seen that in all the Pleuronectidæ the attachment of the palate-bone to the cranium is higher on the eyeless side; therefore the palate and ectopterygoid bones, having more space to traverse on that side, are considerably larger. They are also much stouter than on the ocular side. The entopterygoid bones of both sides are about the same length; but that of the ocular side is rather the broader of the two.

In Plate XXX. figs. 1, 2, the palato-suspensory and opercular apparatus of each side of *Rhombus maximus* are figured, the bones being numbered according to the list given at the end of this essay.

In the Halibut (*Hippoglossus vulgaris*) the facial bones are asymmetrical on the same principles as those which operate in the case of the Turbot above described; but two additional circumstances connected with the jaws exaggerate that asymmetry very considerably.

1. The mouth seems to be twisted on its own axis, so that not only is the articulation of the palate-bone to the cranium higher on the eyeless side, but so is also the articulation of the lower jaw to the hypotympanic. (See Plate XXX. fig. 3, where the end of the cranium, with the attached palato-suspensory apparatus of each side, is seen directly from the front.)

2. The mouth does not open straight forwards, but when the fish gapes it points obliquely towards the eyeless side, the upper jaw-bones, when the mouth opens and shuts, gliding downwards and forwards, upwards and backwards, on the oblique ridge on the nasal bone and the oblique facets on the vomer already described (see p. 274).

Accordingly we find the intermaxillary and maxillary bones a little stouter on the eyeless side; the maxillary of the eyeless side is flatter, and has the tubercle for attachment of the tendon of the retractor maxillæ muscle much larger, and situated lower down, than in the bone on the other side; the convex facet on the head of the bone for gliding on the vomer is likewise larger. The lower jaw is a little longer, and considerably more arched on the eyeless side; its dentary bone is likewise armed on this side with a greater number of teeth.

Suspensory and Opercular Apparatus.—As in the Turbot and Brill, the epitympanic bone is larger on the eyed side; and the disproportion between the bones of the two sides is still greater, because the articulation of the lower jaw is lower down on the ocular side. And because that articulation is also further forwards on the ocular side, we have the mesotympanic, pretympanic, and hypotympanic longer on this side,—the disproportion being, however, least marked in the case of the mesotympanic. But in all the three bones there would have been still more disproportion, were it not that the articulation of the epitympanic to the cranium extends further forwards on the eyed side (see p. 275). And because the articulation of the palate-bone to the cranium is further forwards on the ocular side, we have the entopterygoid slightly longer on that side. But that articulation of the palate-bone being much higher on the eyeless side, we have an increase in length and stoutness of the palate and ectopterygoid bones of the eyeless side, which would have been still more marked, were it not that the articulation of the lower jaw to the hypotympanic is higher on the side in consideration.

Opercular Apparatus.—Both on account of the more arched form of the eyed side of the head, and because the articulation of the epitympanic advances on this side further forwards, so that the opercular bones have more space to cover, we find on the eyed side the operculum and suboperculum larger in every way than their fellows of the eyeless side. And because of the more anterior position of the articulation of the lower jaw on the ocular side, we find the interoperculum longer on the same side. A combination of these two circumstances, together with the fact that the articulation of the lower jaw is lower on the eyed side, renders also the preopercular bone of the eyed side larger in every way, the increase in length being, however, most marked in its horizontal ramus.

In Plate XXX. fig. 3, I have figured the cranium and palato-suspensory apparatus of the Halibut, seen directly from the front. Observe, on the eyeless side, the more elevated position of the olfactory foramen, of the attachment of the palate-bone to the cranium, and of the trochlear articular surface for the lower jaw, and the general flatness of the palato-suspensory apparatus.

In the Plaice (*Platessa vulgaris*) the facial bones are constructed and arranged on exactly the same principles as those in the Halibut last described, but with some exaggeration of the asymmetries. Indeed when a Plaice gapes, its mouth turns round towards the eyeless side in a most remarkable manner; and that side being undermost when the fish is swimming in its natural position, I suppose it is thereby better enabled to pick up from the sea-bottom the small shell-fish, crustacea, and sandstars which are always abundantly found in its stomach when opened. The principles on which this is effected are the same as those on which the minor degree of the same sort of obliquity depends in the Halibut, and may be thus enunciated.

1. The very oblique direction of the articular ridge on the front of the nasal bone, on which the cartilage supporting the intermaxillary bones glides. Its direction necessitates these bones, when the mouth opens, to move downwards, forwards, and to the eyeless side.

2. The great obliquity of the axis of the two facets on the front of the vomer, on which the heads of the superior maxillary bones, along with the interposed fibro-cartilaginous disks, glide. That of the ocular side looks forwards rather than laterally; and a line bisecting the angle formed by the two facets would pass obliquely to the eyeless side. Accordingly, in their movements, the superior maxillary bones follow the intermaxillaries in passing towards the eyeless side when the mouth opens.

3. The articulation of the lower jaw to the suspensory apparatus is further forwards

on the ocular side, so that the direction in which the lower jaw works is towards the eyeless side. (See Plate XXX. fig. 6.)

4. The conformation of the jaws themselves is also very important in connexion with the obliquity of the mouth. The superior maxillary bone of the eyed side is to some extent smaller than that of the eyeless side. But the intermaxillary of the eyed side is very much smaller than its fellow; its ascending process is at a more obtuse angle to the body of the bone, which bears only 4–7 teeth, while the bone of the eyeless side, stout and strong, with its ascending process, set at nearly a right angle to its body, is set with 25–30 teeth or more. The *lower jaw* of the ocular side, rather flat, is shorter than that of the eyeless side; its dentary bone bears, like the corresponding intermaxillary, only 4–7 teeth. The longer lower jaw of the eyeless side has, on the other hand, its dentary part much curved and set with 25–35 teeth; so that not only does the mouth, when opened, point to the eyeless side, but that side of the mouth is more arched and prominent, even when shut, and contains almost all the teeth.

In Plate XXX. fig. 4, is figured the palato-suspensory and opercular apparatus of the ocular side of the Plaice, seen laterally; and in fig. 5 that of the eyeless side. Fig. 7 represents the cranium and palato-suspensory apparatus of both sides, seen exactly from the front; while fig. 6 gives a view of the lower jaw and opercular apparatus of both sides, seen from below.

III. *On the Superficial Face-bones and on the Distribution of the Slime-canals.*

We have still to consider whether there be in the Pleuronectidæ any representatives of the supratemporal and suborbital ranges of bones, and of those bones called by Cuvier "nasal," by Owen "turbinal."

In osseous fishes generally these bones are intimately connected with a system of dermal tubular organs, the "mucus-" or "slime"-canals; and hence it will be necessary for us also to study the relations and arrangement of these canals in the Pleuronectidæ.

The arrangement of these canals on the heads of osseous fishes follows, on the whole, a very definite plan*; and if we adhere to the Cod as our standard of comparison, we shall find how completely the plan of the arrangement of the mucus-canals in the Pleuronectidæ corresponds with that of the same organs in the Cod, and how that plan has been modified entirely in accordance with the theory of the Pleuronect cranium already given.

The Symmetrical Arrangement in the Cod.—The plan of this arrangement I have represented in a diagram (Plate XXXII. fig. 1). The mucus-canal of the lateral line (*a a*), supported all the way along by peculiarly modified scales, extends on to the head, runs along grooves in the mastoid, postfrontal, and frontal bones, and then, lodged in the grooved turbinal (19), terminates near the end of the snout, and to the inner side of the nostril. On the surface of the frontal bone it forms a commissure (*e*) with its fellow of the opposite side. On its way, it gives off the following branches:—

* The arrangement of these canals in the symmetrical fish has been described by Monro in his work, 'The Structure and Physiology of Fishes explained and compared with those of Man and other Animals,' Edinburgh, 1785; and also by Stannius in a paper, "Ueber die Knochen des Seitenkanals der Fische," Froriep's Neue Notizen, Bd. xxiii. S. 97–100 (April 1842).

1. The supra-temporal branch (*b*) at the back of the head, supported by the supra-temporal bones (72), indicated in the diagram in outline.

2. The operculo-mandibular (*c c*), running in a groove, first in the præoperculum and then along the lower jaw, where it ends near the symphysis.

3. The suborbital (*d*), supported by the suborbital bones (73'), running along beneath the eye, and terminating near the end of the snout, close to the end of the main canal, but to the outer side of the nostril.

The Arrangement in the Pleuronectidæ.—In the genus *Rhombus* (Diagram, Plate XXXII. fig. 2), the lateral canal of the eyed side (*a' a'*) pierces the suprascapular bone (50), then enters the first supratemporal bone, which bifurcates. The canal coming from the lower branch of the latter bone then enters the mastoid, passes from it to the frontal, and, arriving at the posterior margin of the orbit, gives off a branch (*e*) to communicate with the main canal of the opposite side. It then pursues its way in the stout inter-ocular process of the frontal, emerges from it at the anterior margin at the orbit, and ends, to the inner aspect of the nasal fossa of the ocular side, in a curved tubular ossicle (19'), which we at once recognize as the "turbinal."

This canal gives off, on its way, the following branches, as in the Cod:—

1. The supratemporal (*b'*), issuing from the upper limb of the tubular bifurcated first supratemporal bone, proceeds, supported in a series of about sixteen little tubular ossicles constituting the rest of the supratemporal range, towards and along the base of the cephalic end of the dorsal fin, to beyond the middle of the upper eye, where it ends. These little bones have been indicated in the diagram by simple outline (72).

2. The operculo-mandibular (*c'*), given off while the main canal is still in the mastoid bone, runs in a tube hollowed out in the præoperculum and lower jaw-bones, and ends near the symphysis of the jaw.

3. The suborbital branch (*d'*), given off opposite the origin of the commissural branch (*e*) already referred to, runs in a series of about nine minute tubular ossicles (73') under the lower eye, and ends, to the outer side of the nasal fossa of the ocular side, in an ossicle much larger than the rest, which is suspended to the prefrontal bone of the same side. The series of little ossicles is the suborbital range of bones; the larger anterior one is of a triangular shape, elongated, and with the apex directed posteriorly; on its surface is a tube which lodges the terminal portion of the mucus-canal. This terminal portion, however, seems to be isolated and distinct from the rest of the suborbital canal.

On this side, the arrangement is very plain, the main canal curving round between the eyes, following the morphological mesial line, while the supratemporal branch proceeds forwards according to the apparent or pseudomesial line, along with the dorsal fin.

On the eyeless side the lateral canal is similarly related to the suprascapular and first supratemporal bones, and to the mastoid. The supratemporal branch proceeds forwards, with the dorsal fin, in the pseudomesial line; and the operculo-mandibular branch is given off and pursues its course exactly as on the ocular side. But the main canal having entered the frontal bone, and arrived at the posterior margin of the orbit, it gives off a commissural branch to join that of the other side (*e*) already mentioned. It then passes between the eyes, lodged in the slender interocular process of the corresponding frontal bone (eyeless side), till it ends in front of the orbit, and to the inner side of the nasal fossa of the eyeless side, in a "turbinal" ossicle (19), which is longer than its fellow of the opposite side.

We have thus the main stem of the mucus-canal of the eyeless side also following the morphological middle line of the top of the cranium, crossing the pseudomesial line beneath the cephalic part of the dorsal fin, and beneath the supratemporal canals of *both* sides, and passing between the eyes side by side with its fellow of the opposite side, and with which, as in the Cod, it is connected by a transverse commissure. This arrangement we may also regard as additional evidence that the "interocular" bar in the Pleuronect cranium is the only and entire homologue of the arch of the frontal bone in the Cod and other fishes.

But where are the suborbital canal and chain of bones of the side under consideration? We have seen that a mucus-canal, contained in a range of minute bones ($b' b'$), lies alongside the upper eye; but we have also seen that this is the supratemporal branch of the eyed side. We must accordingly look for some other. From the point behind the orbit where the main stem of the eyeless side gives off its commissural branch, is given off in the opposite direction a branch ($d\,d$) running at first a little backwards, till it emerges from the frontal bone, when it turns forwards and proceeds, in the skin of the eyeless cheek, pretty closely alongside the pseudomesial bar of the cranium, till it ends in the outer side of the nostril of the eyeless side. This canal, enclosed in seven tubular ossicles (73'), of which the anterior one is largest, is undoubtedly the suborbital of the side on which it is found, and that which should appertain to the upper eye of the flatfish, but situated on the other side of the head from that on which its eye is now found; and not only so, but between it and its eye we find the pseudomesial bar of the cranium, the cephalic extremity of the dorsal fin, and the supratemporal canals and ranges of bones of both sides. In fact, the one eye has passed over to the now binocular side of the fish, leaving its suborbital range behind it, while the other structures before mentioned have got interpolated between the dorsal fin and the supratemporal canals proceeding forwards from behind, the pseudomesial bar being formed partly by a process sent back from the prefrontal, and by one sent forward from the frontal bone of the now eyeless side. It must be observed, however, that this suborbital canal of the eyeless side, though it has not followed its eye completely round, is yet situated much higher on the side of the head than its fellow opposite; indeed, as far as it is concerned, the turning-process has proceeded so far, and then become arrested.

In the Halibut, in which I have examined these canals with some care, the arrangement is much the same. We find the main canal of each side curving round between the eyes, one contained in the interocular process of each frontal bone, in the same manner as is represented in the diagram of the Turbot (Plate XXXII. fig. 2). The main canal of the eyeless side, however, here pierces also the nasal bone, as shown by the two little openings in the bone 15 (Plate XXIX. fig. 10), thus confirming what I have already stated (page 274), that that part of the nasal bone entering into the boundary of the orbit in the Halibut and Plaice is a development from the part of the bone appertaining to the eyeless side.

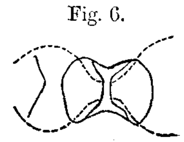
In Plate XXXI. fig. 1, are represented the superficial face-bones on the eyed side of a Halibut; in fig. 2, those of the eyeless. On the ocular side observe the suborbital range (73′), extending along in direct relation to its eye (the lower one); but with this peculiarity, that the anterior suborbital bone(73′ a), stout, oblong, and pointed at both ends, is separated from the rest by an interval, and that the mucus-canal does not extend on to it, but stops short at the preceding little tubular ossicle. Observe also the supratemporal range (72) following the direction of the dorsal fin, and extending along the upper side of the upper eye like a pseudo-suborbital range for it. The "turbinal," or *os terminale* (19′), is also seen, and above it, lying on the top of the head, is seen the corresponding ossicle of the eyeless side (19). On the eyeless side (fig. 2) observe the supratemporal range (72), following the direction of the dorsal fin; and the suborbital range, lying on the cheek higher up than the corresponding range on the other side, but with no eye visible in relation to it. On the top and front of the snout is again seen the turbinal (19) of this side. The anterior suborbital of the ocular side is a stout oblong bone, pointed at both ends, and articulated to a process (+) of the prefrontal, opposite the olfactory foramen, and is also closely related to the anteriorly projecting process of the palate-bone. As already stated, it is not perforated by any mucus-canal. That of the eyeless side (73′, fig. 2) is similarly related to the corresponding prefrontal and palate-bones, but is smaller, flatter, and perforated by the mucus-canal, which traverses the rest of the range. The turbinal of the ocular side is larger than the opposite one, is curved, flattened, and contains a branching canal. All the rest of the superficial face-bones of the Halibut are very delicate tubules, often showing lateral branchlets, through which little ducts pass to ramify in the skin and open on its external surface. As they get smaller towards the ends of the several ranges, they often cease to be complete tubes, and appear like little scales with the edges folded up. As to number, these little bones are apt to be irregular. The supratemporal ranges generally consist of from twenty-two to twenty-five ossicles each, and the suborbital of the ocular side of from seventeen to nineteen; but two often supply the place of one. The suborbital range of the eyeless side, however, consists pretty constantly of nine bones—about one-half the number found on the opposite side.

In the Plaice the arrangement has undergone a little modification (see diagram, Plate XXXII. fig. 3). The canal of the ocular side, as usual, extends between the eyes, and ends in its turbinal ossicle. The operculo-mandibular, the suborbital, and the supratemporal branches are on both sides, similar to those in the Halibut; and so is also the cross commissure. But as the interocular process of the frontal bone of the eyeless side is non-developed (p. 275), the main mucus-canal of that side no longer extends between the eyes, but stops short at the commissure. Anteriorly we find, to the inner side of the nasal fossa of the eyeless side, a minute turbinal ossicle, containing as it were a little follicle, with two openings on the skin, this little mucus-cavity being in fact the remnant of the main canal of the eyeless side, but detached altogether from the rest by the atrophy or non-development of the intermediate portion. (For more details I refer the reader to Plate XXXI. figs. 3 and 4, and to the diagram, Plate XXXII. fig. 3.)

This arrangement prevails in the genus *Platessa*, the interocular portion of the mucus-canal of the eyeless side having completely disappeared in all the species I have examined. In *Platessa limanda* the turbinal ossicle of the eyeless side is about as small as in the Plaice; in *P. flesus* it is a little larger.

But the most remarkable condition of the mucus-canals in the genus *Platessa*, and indeed in the whole group of flatfishes as far as I know, is that seen in *Platessa pola**. In this fish we have on the ocular side (Plate XXXI. fig. 5) nothing very peculiar to notice: the arrangement seems to be just as in the Plaice, excepting that there is no cross commissure. The suborbital and supratemporal bones are very small and delicate, and generally have not closed over so as to form complete tubules. But on the eyeless side the mucus-canals are dilated into large, circular, flattened ampullæ, the outline of which I have given in Plate XXXI. fig. 6. These ampullæ are twenty-six in number; six of these are situated on the main trunk, two on the detached nasal portion, four on the supratemporal branch, eight on the operculo-mandibular, and six on the suborbital. The supporting bones of this system are also peculiarly modified: the suprascapular, mastoid, frontal, and preopercular bones, also the lower jaw, are furnished with excavations for the support of the ampullæ belonging to the main canal and the opercular mandibular branch. The supratemporal bones (72) five in number, are very delicate laminæ of bone pierced with many minute holes (when macerated), their lateral edges folded in, and connected by a bridge across the middle, where the whole bone is constricted. The hollow of each bone is therefore hourglass-shaped, and takes part in the support of two ampullæ, which communicate by the narrow part passing beneath the bridge aforesaid, as in the adjoining diagram. The *os terminale*, or turbinal, has the same structure, as likewise have the five suborbitals, except the anterior one, which is somewhat trigonal, and takes part in the formation of three ampullæ. I have said that there is no cross commissure; the branch (*e*), on the ocular side, analogous to the commissural branch in the Plaice, ends almost immediately in a blind point on the eyeless side; the anterior ampulla on the main canal, indicated in dotted outline in fig. 6, is situated more deeply than the rest, being partly overlapped by the ampulla behind, and by the anterior two supratemporal ones in front. This arrangement may be regarded as an indication of a commissure, but none is really effected.

Fig. 6.



IV. *Vertebral Column.*

The vertebral column in the Pleuronectidæ is usually supposed to be quite *symmetrical.* In some it is not so, however, as I will presently point out.

The vertebral column of the Plaice displays the following peculiarities:—

1. The mesial vertical plane of the vertebræ is curved, the convexity being toward the eyed side, the concavity towards the eyeless. This is most strikingly seen in the anterior vertebræ, such as the first, which I have represented (Plate XXXII. fig. 6) as seen from

* The ampullated condition of the mucus-canals on the eyeless side of the head in *P. pola* has been already noticed by Dr. M'Donnel in the 'Trans. Royal Irish Academy,' vol. xxiv. Science, 1862. On the morphological arrangement of these ampullæ, he has, however, made no observations.

the front. The spinous process is seen to be strongly bent over towards the eyeless side; a similar curve is seen affecting the middle line of the posterior aspect of the cranium (fig. 5).

This condition gradually diminishes posteriorly; but throughout the entire series of caudal vertebræ the superior and inferior spinous processes are set at a slight angle to each other, consequently the entire skeleton of a Plaice is convex on the ocular surface, concave on the eyeless.

2. The transverse processes of most of the abdominal vertebræ are unsymmetrical, slightly in their place of origin on each side from the bodies of their vertebræ, considerably so as regards the direction in which they proceed. Seen from below, these processes on the eyeless side arise a little further forwards on the bodies of their vertebræ, and project nearly directly outwards, sometimes even a little anteriorly; while those of the ocular side are directed considerably backwards. The four anterior vertebræ and the thirteenth (last abdominal) are pretty exempt from this condition; but it affects the intermediate ones pretty strongly. Plate XXXII. fig. 8, shows the under aspect of the series of abdominal vertebræ in the Plaice, and how a line joining the tips of the transverse processes of one of the middle vertebræ of that series passes very obliquely across the long axis of the column. Again, when seen from before backwards, the transverse processes of the abdominal vertebræ project more vertically downwards on the eyeless than on the eyed side—a circumstance in accordance with the more flattened shape of the fish on the former side. The transverse processes of the caudal region, in accordance with the well-known greater development of the lateral muscle on the ocular side, are also more prominent on the same side.

The vertebræ of the Halibut present the same sort of asymmetries which we have observed in the Plaice: some differences are to be observed in the Turbot and Brill. Here asymmetry is chiefly to be seen in the transverse processes, which agree with those of the vertebræ of the Halibut and Place in this, that those of the abdominal region are more directed vertically downwards on the eyeless side, and those of the caudal region are on the same side less prominent. But, when looked at from above or below, the transverse processes in the abdominal region are seen to project more posteriorly on the eyeless side—a condition exactly opposite to that found in the Plaice.

V. *The Dorsal Fin.—Conclusion.*

The dorsal fin, it is well known, extends in all the Pleuronectidæ all along the back, and advances forwards on the top of the head. Its advance on the head depends on two circumstances.

1. A more and more oblique direction forwards of the anterior interspinous bones, till the first one, becoming horizontal or nearly so, carries the anterior rays of the fin to opposite the middle of the upper eye (*Hippoglossus Platessa*) or to beyond both (*Rhombus Solea*, &c.).

2. A bodily advance forwards of these interspinous bones themselves on the top of the cranium.

In the Sole only about five interspinous bones arise on the top of the cranium, and their places of attachment proceed no further forward than the supraoccipital bone. But the anterior one is of considerable length, and, directed forwards, curving also a little downwards, carries the anterior rays of the dorsal fin in front of the eyes and even of the mouth.

In the Halibut and Plaice there are six to eight of these bones on the top of the skull. In their origins they have advanced from the supraoccipital bone on to the frontal of the eyeless side; but the anterior one is not so long proportionally as in the Sole, and only carries the first rays of the fin to opposite the middle of the upper eye.

In a specimen of the Brill, I found ten interspinous bones on the upper aspect of the head, their cranial attachments advancing over the supraoccipital and over the frontal of the eyeless side, till the anterior one takes its origin even from the prefrontal of the same side. This anterior interspinous bone carries the first rays of the dorsal fin to beyond the eyes, but not so far as in the Sole.

We thus find that in the Brill and in the Sole the dorsal fin has advanced along the head further than in the Halibut and Plaice: in the Sole this has been effected by an excess of the first method of advance, in the Brill by an excess of the second. The direction in which the fin advances is nearly straight forwards, in the same straight line as the middle line of the back, inclining only very slightly towards the eyeless side. It thus completely disregards the morphological middle line of the top of the head, being supported anteriorly on the pseudomesial bar of the cranium, and on the ridge extending on to this bar from the centre of the supraoccipital bone. A part of the lateral muscle passes on each side on to the top of the head, along with the dorsal fin, and is arranged alongside that structure in equal disregard of the morphological middle line, as likewise are the supratemporal canals.

Now, of this remarkable circumstance, there are only two explanations possible. Either the dorsal fin is in its original morphological position*, and the upper eye has passed under it, or the fin has advanced forwards from behind after that eye has turned over from the side to which it originally belonged. To the latter view, which is indicated in the paper by Van Beneden already quoted, I must, for the following reasons, give in my adherence.

1. The structure of the cranium shows clearly that the transference of the upper eye is connected with the deviation, in the ocular region, of the original middle line of the top of the head over to the now binocular side, and that the eye in question preserves its morphological relations to the frontal bones and the neighbouring structures quite intact, the view that it has migrated beneath any of the parts of the skull in the manner held by Rosenthal and Steenstrup being quite untenable. Now, the structures accompanying the cephalic end of the dorsal fin showing the same disregard of the morphological

* This was Meckel's opinion, as may be gathered from the following extract from his 'Comparative Anatomy.' Speaking of the interspinous bones on the top of the cranium in the Pleuronectidæ, he says, "This disposition is extremely interesting; it helps to establish the analogy of the cranial bones with the vertebræ; these accessory rays are placed in fact on the occipital and parietal crests in the same way as those of the trunk are situated over the superior spinous processes." (*Op. cit.* French edition, p. 312.)

This passage would indicate that Meckel had quite overlooked the fact that those cephalic fin-rays are not placed over the morphological middle line.

middle line as the fin itself, it is hardly possible to imagine that middle line and one eye migrating beneath the superimposed parts without the symmetry of the latter being affected, had they been in their present position at the time that the supposed migration took place.

2. All those parts accompanying the dorsal fin in the head show traces of having come from behind. That part of the lateral or body-muscle, which lies on the top of the head consists of the anteriorly reflected portions of muscle-segments posterior to the cranium. The nerves supplying the fin-rays and muscles in this region are derived from the dorsal branches of the first three or four spinal nerves, which turn forwards over the head from behind. The supratemporal mucus-canals and bones, which, commencing posteriorly, also proceed forwards in defiance of the morphological middle line, are supplied by branches of the vagus nerve, which of course also turn round from the back of the skull and run forwards. Lastly, the blood-vessels supplying the fin-rays, &c., on the top of the head accompany the branches of spinal nerves already mentioned, and proceed to their destination from behind forwards.

3. The embryological observations of Van Beneden seem to favour the same view; and I have already referred (p. 264) to the paper wherein he describes a young Pleuronect in which the two eyes were still one on each side, and the dorsal fin only yet descended to the middle of the cranium. To this observation I may add one of my own. In the summer of 1863 I obtained, in dredging over a sandy bottom in the Frith of Forth, three young Pleuronectidæ, each about half an inch long, and apparently belonging to the genus *Platessa*. In two of them the eyes and dorsal fin were conformed as in an adult Flounder, but in the third (the anterior part of which is figured, Plate XXXII. fig. 9, magnified five diameters) one eye was nearly on the middle line, with, as in M. van Beneden's specimen *, the dorsal fin stopping short behind it.

4. The structure of certain malformations occasionally found amongst flatfishes also confirms the view I have adopted. These monstrosities are specimens of Pleuronectidæ where the upper eye is found more towards the top of the head than usual, the dorsal fin not being fixed down by the side of it, but projecting above it, supported on a free pointed process. Many of these specimens have been already recorded†. The most remarkable case I am acquainted with is one described and figured by Schleep ‡, occurring in a Turbot, which he calls *Pleuronectes maximus duplex*, thinking that possibly it might be a distinct species. Here the two eyes are still one on each side of the head; the right one, however, is higher than the left, and seems just about to make the turn, while the anterior part of the dorsal fin projects over the eyes supported on a free pointed process.

I have seen cases of this condition both in the Turbot and Flounder (*Platessa flesus*), though not in so exaggerated a degree as in Schleep's specimen. In Plate XXXII. figs. 8–9, are represented both sides of the head of such a specimen of *P. flesus*, the mucus-canals being indicated by the shading in horizontal lines. The upper or left eye is seen to be situated on the top of the head, having, we may say, just turned the corner and no more; while the dorsal fin presents the appearance already referred to. Here also, on the

* *Loc. cit.*

† See Yarrell's 'British Fishes,' vol. ii.

‡ Oken's 'Isis,' 1829, S. 1049.

eyeless side, the relation of the suborbital canal to the upper eye is very obvious, the fin not having become interpolated between them as in the perfectly developed flatfish.

These monstrous Pleuronectidæ may be accordingly defined as flatfishes in which the turning-round of the upper eye to the other side of the fish has been arrested when it has got about the middle of the top of the head, and in consequence the passage forwards and tying down of the anterior part of the dorsal fin has also been stopped, or obviously it would cross over the eye instead of passing by the inner side of it, as in the normal flatfish. It accordingly projects upwards and forwards on a pointed process overhanging the eye, as in the specimen figured. It is worthy of remark that all those abnormal specimens are equally coloured on both sides, as if the animal, not having perfectly acquired the characteristics of a flatfish, swam with either of its sides upwards and exposed to the light at pleasure. In the case of Turbots affected with this condition, the bony tubercles also, usually characteristic only of the ocular side, are found equally distributed on the eyeless one.

As we must consider those monstrosities to be dependent on arrested development, the only developmental circumstances which we can safely infer from the appearances presented are, that the upper eye turns round on the top of the head, and that then the dorsal fin advances past it.

But the young *Plagusiæ* figured by Steenstrup would seem to contradict directly the above-advocated theory, and prove that the upper eye gets to its present position by passing beneath the dorsal fin. In some of his specimens the transposition seems never to have taken place at all; but the one which seems most fully to justify his views is one where the animal seems to have three eyes, the eye of one side projecting also through a little fissure above that of the other side, which side becomes thus binocular. This appearance is so striking that one might readily be excused in thinking with M. Steenstrup, "Can we imagine a more striking demonstration of the passage of the eye across the head than an eye arrested in this position?" Another specimen described by him has an eye on each side of the head, but above the left eye is a little slit where the other should appear.

Although it must at once be acknowledged that these observations are very remarkable, and not to be cast aside merely because they do not tally with our preconceived theories, yet it seems to me that considerable research is still required before we can accept these specimens as representing the normal process of development in all the Pleuronectidæ; for the structure of the head of the adult flatfish seems to me most conclusively to prove that the upper eye does not pass beneath or through any part of the bony cranium, and that the dorsal fin and its associated structures advance from behind, while the structure of the well-known "monsters," and the observations of Van Beneden and also of myself on young Pleuronectidæ, certainly indicate that in the genera *Rhombus* and *Platessa*, at least, the dorsal fin advances after the upper eye has turned round on the top of the head.

But M. Steenstrup's strange specimens certainly open up the question whether there be any group of flatfishes in which, in the normal course of development, the dorsal fin extends forwards, and bridges over the upper eye before it has completed or even commenced its turn. But, before a conclusive answer can be given to that question, much more extensive observations on Pleuronectidean embryology are necessary.

Concluding Note.

Since writing the foregoing Memoir, my attention has been drawn to a paper, on Steenstrup's views on the obliquity of Flounders, by Prof. Wyville Thomson, in the 'Annals and Magazine of Natural History' for the present month (May 1865). As far as can be gathered from the abstract of Prof. Steenstrup's original paper, which Prof. Thomson has in the present communication afforded us, the learned Danish naturalist attempts no explanation on developmental principles of the singular "double" monstrosities occurring in flatfishes, and also questions the accuracy of Van Beneden's observations already quoted. In his critical remarks on this paper, Prof. Thomson has expressed the same views as to the morphological relations of the eyes to the two frontal bones, and as to the constitution of the pseudomesial beam or bar of the cranium, as those advocated in the preceding pages, though so far agreeing with M. Steenstrup as to consider that the "eye of the blind side actually passes from its own side of the head to the other side—at all events under the integuments and under the subcutaneous tissues, which contain the rudiments of the dermal bones forming the support of the anterior border of the dorsal fin, if not actually through the head itself."

In justice, however, to myself I may be permitted to state that the Memoir just concluded is hardly altered from that which formed my Graduation Thesis at Edinburgh in 1862, and which may be consulted in the library of the University there, where it is deposited *. The same views were also expressed by me in a criticism of Prof. Steenstrup's paper in the 'Annales,' read by me before the Royal Physical Society of Edinburgh, on the 25th of January of the present year, and about to be published in the forthcoming part of its 'Proceedings.'

* The Medical Faculty of the University of Edinburgh awarded a gold medal to this Thesis, 1st August, 1862.

EXPLANATION OF THE PLATES.

In all the following illustrations, the same numbers apply to the same bones. They are also the same as those by which Prof. Owen has distinguished the various bones of the fish's head in his 'Lectures on Comparative Anatomy.'

1. Basioccipital.	15. Nasal.	29. Articular.
2. Exoccipital.	16. Petrosal.	30. Angular.
3. Supraoccipital.	17. Sclerotal.	32. Dentary.
4. Paroccipital.	19. Turbinal.	34. Preopercular.
5. Basi-presphenoid.	20. Palatine.	35. Opercular.
6. Alisphenoid.	21. Maxillary.	36. Subopercular.
7. Parietal.	22. Inter- or pre-maxillary.	37. Interopercular.
8. Mastoid.	23. Entopterygoid.	44. Branchiostegal.
10. Orbitosphenoid.	24. Pterygoid.	50. Suprascapular.
11. Frontal.	28 *a*. Epitympanic.	51. Scapula.
12. Postfrontal.	28 *b*. Mesotympanic.	52. Coracoid.
13. Vomer.	28 *c*. Pretympanic.	72. Supratemporal.
14. Prefrontal.	28 *d*. Hypotympanic.	73′. Suborbital.

Plate XXIX.

In all these figures the primordial cartilage is shaded in with horizontal lines. The numbers refer to the list already given.

Figs. 1–7. Illustrations of cranium of Turbot (*Rhombus maximus*).

Fig. 1. The cranium seen from above.

A. The piece of cartilage supporting the four bones of the nasal end of the cranium, and forming the anterior part of the septum between the eyes.

B points to the orbit, bounded on one side by the interocular process (*m*) of the frontal of the eyeless side (11), and on the other by the process (*f*) of the prefrontal of the same side (14).

C′ C. The two olfactory foramina.

11′. Frontal bone of the ocular side.

11. Ditto of the eyeless side.

14′. Prefrontal of the ocular side.

14. Ditto of the eyeless side.

e. A process on each prefrontal, to which the anterior suborbital is attached.

f. A process of the prefrontal of the eyeless side, sent back to join the process (*n*) of the corresponding frontal. Thus is the pseudomesial bar formed, and the orbit bounded on the inner side.

m′. Interocular process of frontal of ocular side.

m. Ditto of eyeless side.

i. Process on the nasal bone above the apparatus of the jaw.

k. Process on the nasal bone on which the intermaxillary cartilage glides.

β. The ridge or spine of the supraoccipital bone, proceeding forwards in the pseudomesial line and a little towards the eyeless side.

The dotted line M L represents the direction of the morphological mesial line.

Fig. 2. Under surface of the same cranium.

D. Cotyloid cavity for the rounded head of the epitympanic bone.

a. A process of the prefrontal of the eyed side, sent between the eyes to articulate with the interocular process (m') of the corresponding frontal.

b. A process sent downwards and backwards by the prefrontal of the eyeless side to articulate with the basi-presphenoid.

Fig. 3. Upper aspect of the same cranium, the two frontals, the two parietals, and the anterior part of the supraoccipital being removed. The interior of the brain-cavity is thus partially exposed; a bristle is passed through each olfactory foramen in the direction pursued by the olfactory nerve.

g. A process of the cartilage (A) supporting the interocular process of the frontal of the ocular side, and the corresponding process (*a*) of the prefrontal of the same side.

h. A smaller process of the same cartilage, supporting the interocular process of the frontal of the eyeless side.

10, 10. The two orbitosphenoids, their cartilaginous tips pointing over towards the ocular side.

Fig. 4. Anterior part of another cranium seen from above, but slightly tilted round towards the eyeless side. The frontal bones are removed, and two black bristles are passed, one through each olfactory foramen, as in fig. 3.

Fig. 5. Same part of the cranium, but drawn from another specimen, seen from the ocular side, though slightly tilted round towards the eyeless one. A bristle is passed through the olfactory foramen of the eyeless side.

Fig. 6. The same, seen from the eyeless side. The lettering in this and the two preceding figures is explained under figures 1, 2, 3, and 17.

Fig. 7. The two frontal bones of the Turbot.

11′. That of the ocular side: m', its interocular process.

11. That of the eyeless side: *m*, its interocular process; *n*, its external angular one. The position of the eyes is diagrammatically indicated in dotted outline.

Fig. 8. Upper surface of the cranium of the Halibut (*Hippoglossus vulgaris*). The orbit is here on the right side, instead of on the left as in the Turbot.

A. Cartilage of the nasal part of the cranium, as in the Turbot.

g. A notch in the cartilage, into which a laminar projection from the interocular process (m') of the frontal bone of the ocular side is received.

h. A smaller notch in advance of the other, which receives a similar lamina developed on the end of the more slender interocular process (*m*) of the other frontal.

p q. Two facets on the end of the vomer; that of the eyeless side (*p*) is larger and looks more laterally than the other (*q*). On these two facets move the heads of the corresponding superior maxillary bones, with the interposed fibro-cartilaginous disks.

k. The prominence on the nasal bone on which the intermaxillary cartilage glides, and directed obliquely towards the eyeless side. Compare this with the corresponding part in the Turbot (fig. 1).

Fig. 9. Under surface of the same cranium. Lettering as in the corresponding view of the Turbot's cranium.

Fig. 10. Anterior part of another cranium, seen from above, though slightly tilted towards the eyeless (left) side; the two frontals removed. A bristle passed through each olfactory foramen.

g h. The two notches in the primordial cartilage, already referred to under fig. 8. The remaining lettering is the same as in the figures of the Turbot's cranium.

Fig. 11. The two frontal bones of the Halibut. Lettering as in figure 7.

Fig. 12. Cranium of the Plaice (*Platessa vulgaris*), seen from above. Lettering as in the figure of the Halibut's cranium (fig. 8). The prefrontal bone and olfactory foramen of the eyed side (right) are much in advance of the corresponding parts on the eyeless (left side); and the ridge (*k*) on which the intermaxillary cartilage glides is directed to the eyeless side at an angle of 45°.

Fig. 13. Under surface of same cranium. Lettering as before.

Fig. 14. Frontal bones of the Plaice, the position of the eyes in relation to them being indicated in dotted outline. Lettering as in fig. 7.

Fig. 15. Frontal bones of the Pole (*Platessa pola*), showing a condition, of the interocular process of the bone of the eyeless side, intermediate between that in the Halibut (fig. 11) and in the Plaice (fig. 14).

Fig. 16. Cranium of the Cod (*Gadus morrhua*), seen from the left side.

Nasal part of the cranium: c, olfactory foramen.

Orbital portion, the interorbital fibrous septum being indicated in dotted shading.

The brain-cavity and auditory part of the cranium.

Fig. 17. Left prefrontal of the Cod, disarticulated.

a. Process going upwards and backwards to join the frontal.

b. Process going downwards and backwards to join the basi-presphenoid.

c. Process to join the ala of the vomer.

d d. Two processes going towards the nasal bone, with an olfactory notch (c) between them.

e. Process to which is attached the anterior suborbital bone.

The representatives of these processes in the prefrontal bones of the flatfish are marked with the same letters in the preceding figures. Note, that in the Cod there is no representative of the process *f* in the flatfish.

PLATE XXX.

Fig. 1. Suspensory, palatine, and opercular bones of the ocular side in the Turbot. Cartilage shaded with horizontal lines.

Fig. 2. The same bones, but of the eyeless side.

Fig. 3. Front view of the cranium and palato-suspensory apparatus of the Halibut, to show the greater flatness of the latter bones on the eyeless side, the greater elevation on the same side of the olfactory foramen (c), the articulation of the palate-bone to the prefrontal, and of the articulation of the lower jaw to the trochlea (*) on the hypotympanic.

Fig. 4. Suspensory, palatine, opercular apparatus, and jaws of the eyed side of the Plaice, drawn from dried specimens.

Fig. 5. The corresponding bones on the eyeless side.

Fig. 6. Lower jaw and opercular apparatus of Plaice, seen from below.

Fig. 7. Cranium and palato-suspensory apparatus of Plaice, seen directly from the front. Lettering as in fig. 3.

PLATE XXXI.

Fig. 1. Opercular and oral apparatus of the Halibut, together with the "superficial face-bones," as seen on the ocular side.

a a. Tubular scales of the lateral line.

72. Supratemporal chain.

73'. Suborbital chain of the right or lower eye.

73 *a*. Anterior right suborbital, very much larger than the rest, from which it is separated by an interval. It has no connexion with the mucus-canal.

19'. Right "turbinal" ossicle, or *os terminale*.

19. Left turbinal, situated on the top of the snout.

A. Retractor maxillæ muscle.

B. Masseter.

c'. Right olfactory foramen.

e. Point at which the supratemporal mucus-canal sends down a branch to join the cross commissure.

Fig. 2. The same head as seen on the left or eyeless side.

a a. Tubular scales of lateral line.

72. Left supratemporal range of ossicles.

73'. Left suborbital range, thus situated on the other side of the head from its eye, and having the dorsal fin and both supratemporal ranges interpolated between.

19. Left turbinal, or *os terminale*.

Fig. 3. Sketch of the distribution of the mucus-canals on the right or ocular side of *Platessa vulgaris*, the Plaice.

a a a a. The main canal, extending from the tail along the lateral line and along the head, between the eyes, till it ends on the inner or left side of the nostril, giving off on its way many little ducts, which open on the surface of the skin of the supratemporal branch, *b b*, which branch, though usually simple, is here bifurcated.

c c c. Operculo-mandibular branch.

d d. Right suborbital canal.

e indicates the cross commissure given off to join the mucus-canal system of the opposite side. It gives off a little duct to the skin at the posterior margin of the orbit, and then passes to the left side, beneath the cephalic end of the dorsal fin.

Fig. 4. The same head, seen from the eyeless side.

a a a a. The main canal as before, but stopping short at the cross commissure (*e*).

b. Supratemporal canal, not so long as in the right side.

c c c. Operculo-mandibular canal.

d d d. Left suborbital canal, still remaining on this side, while its eye has been transferred to the right side.

a'. A small follicle or detached portion of mucus-canal, the representative of the nasal extremity of the main canal of this side, the portion intervening between it and the cross commissure having disappeared. (See also Plate XXXII. fig. 3, where this arrangement is represented diagrammatically.)

e. Cross commissure.

E. Upper eye, a small portion of which is, in the Plaice, visible from the left side.

Fig. 5. Sketch of the distribution of the mucus-canals on the right or ocular side of the head of *Platessa pola*. The same letters refer to the same canals as in the head of the Plaice, fig. 3. The commissural (*e*), however, ends blindly: thus there is in this fish no connexion between the canal-systems of the two sides.

Fig. 6. The left side of the head of the same fish, the mucus-canals being here seen to be dilated into large ampullæ, which communicate with each other by small openings. Each ampulla generally sends only one little duct to the external surface of the skin.

a a a a a a. The lateral canal and the series of six ampullæ on the main canal of the head.

a'. The part detached from the rest, and lodged in the left turbinal. It is the homologue of the little follicle marked *a'* in the Plaice, fig. 4.

b b b b. The four ampullæ into which the supratemporal canal is dilated.

c c c c. The eight ampullæ of the operculo-mandibular branch.

d d d d. The six ampullæ of the suborbital branch.

Fig. 7. Skeleton of the left side of the head in *Platessa pola*, showing the bones supporting the ampullated mucus-canals.

50. Suprascapular.

72. The five supratemporal bones.

73'. The five suborbitals.

19. Turbinal ossicle, or *os terminale*.

34. Præoperculum; and

29, 30. Lower jaw, hollowed out to contain the eight ampullæ of the operculo-mandibular canal.

8. Mastoid; and 11, left frontal: also hollowed, to support the ampullæ of the main canal.

14. Left prefrontal.

Fig. 8. Sketch of head and fore part of body of a monstrous specimen of ***Platessa flesus***; the mucus-canals indicated in outline.

Fig. 9. Anterior part of the same fish, but seen from the eyeless side; the mucus-canals also indicated in outline. The lettering in both this and the preceding figure corresponds to that in figures 3 and 4.

Plate XXXII.

Fig. 1. Diagrammatic view of the mucus-canals and superficial face-bones on the head of the common Cod (*Gadus morrhua*).

a a a a. Mucus-canal of lateral line, extending along the top of the head, and ending in the turbinal ossicle (19), which is indicated in outline.

b. Supratemporal canal; supratemporal bones (72) also in outline.

c. Operculo-mandibular canal, which has no communication with the main canal in the Cod (Munro).

d. Suborbital canal; 73′, suborbital bones.

e. Cross commissure.

Fig. 2. Diagram of the corresponding parts in the Turbot.

a′. Left lateral canal.

b′. Left supratemporal branch, with the supratemporal ossicles indicated in outline.

c′. Left operculo-mandibular branch.

d′. Left suborbital canal and bones.

e. Commissural branch.

a. Right lateral canal, crossing the head beneath the dorsal fin (which is indicated by the line D F), and beneath both supratemporal canals, as it curves round between the eyes, side by side with its fellow of the left side.

b. Right supratemporal canal and chain of bones.

c. Right operculo-mandibular.

d. Right suborbital canal and bones.

19′. Left turbinal, and 19, right turbinal ossicle.

L N F. Left nasal fossa.

R N F. Right nasal fossa.

D F. Line of dorsal fin.

Fig. 3. Diagram of the corresponding structures in the Plaice. Here the eyes are placed upon the right side.

a′ *a*′. Right lateral canal, extending between the eyes all the way to the nose, where it ends in a well-marked "turbinal ossicle."

b′. Right supratemporal canal and range of ossicles.

c′. Right operculo-mandibular branch.

d′. Right suborbital branch and chain of bones.

d^{+}. Anterior suborbital bone of the right side, separate from the rest, and having no connexion with the mucus-canal.

a a. Left lateral canal, apparently stopping short at the commissure (*e*).

a^{+}. A small detached portion of that canal, being in fact its nasal extremity. Owing to, or at least coincident with, the imperfect development of the interocular process of the left frontal in the Plaice, the part of the left mucus-canal which should extend between the eyes in that process has likewise not been developed.

b. Left supratemporal canal.

c. Left operculo-mandibular canal.

d. Left suborbital branch and range of bones.

e. Commissure.

D F. Line of dorsal fin.

R N F. Right nasal fossa.

L N F. Left nasal fossa.

Fig. 4. Diagram of the top of the head in the Plaice, showing the manner in which the orbit is formed. The dotted line, D F, indicates the morphological middle line; the other dotted line, F H, shows the direction of the dorsal fin. The shaded parts are those parts of the original and symmetrical plan of the head which have become developed; the parts of the same plan which have not become developed are indicated in dotted outline, while the parts in entire outline are additional developments.

11′. Right frontal, with its interocular process (*m′*).

11. Left frontal, its interocular process atrophied, while a new process (*n*) has sprung from its external anterior angle.

14′. Right prefrontal, sending back a process (*a*) to articulate with the interocular part (*m′*) of the right frontal.

14. Left prefrontal—the part *a*, in dotted outline, and corresponding to the process (*a′*) of the bone of the other side, not having been developed, while a new process (*f*), not found on the right prefrontal, is sent back to articulate with the process (*n*) of the left frontal. By the union of the process (*f*) of the left prefrontal and the process (*n*) of the corresponding frontal, the "pseudo-mesial" bar of the cranium is formed, and the orbit bounded on the left side.

15. Nasal bone; the unshaded part indicates a development from its left side, which enters into the anterior boundary of the orbit, apparently pushing aside the left prefrontal.

C C. Olfactory foramina.

R E. Right eye.

L E. Left eye.

Fig. 5. Posterior surface f cranium of the Plaice. The dotted line, M P, shows the curve of the mesial line in this region, the convexity being towards the ocular or right side.

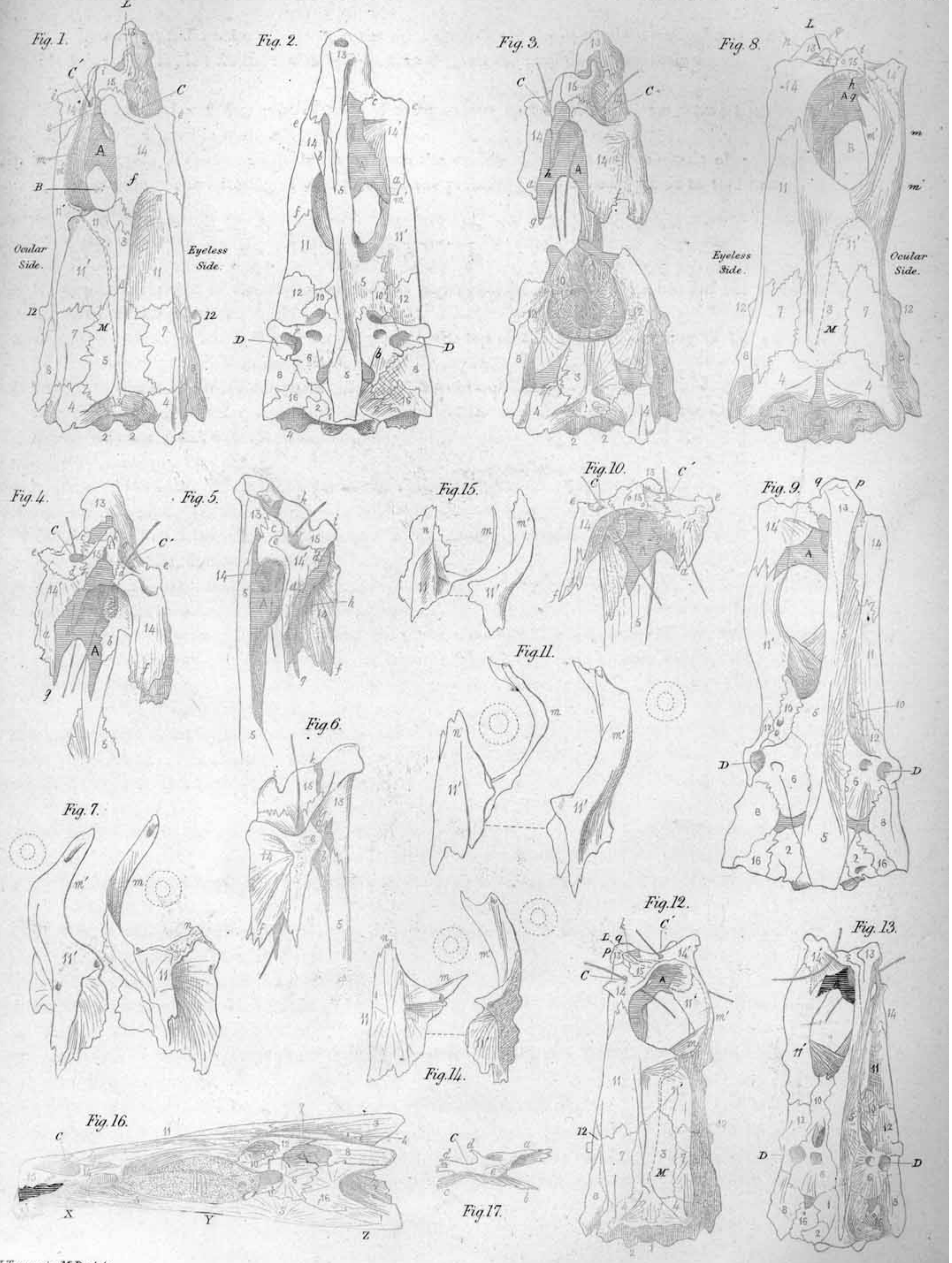
Fig. 6. First vertebra of the Plaice, seen from the front, showing how its mesial vertical plane is convex towards the right or ocular side.

Fig. 7. Seventh abdominal vertebra of the Plaice, seen from before, showing the more vertical direction downwards of the left transverse process.

Fig. 8. Abdominal vertebræ of the Plaice, seen from below, and showing the unsymmetrical obliquity of the transverse processes from the fifth to the twelfth inclusive.

Fig. 9. Anterior part of an embryo Flounder, magnified five times, showing the upper eye not yet fully turned round, and the dorsal fin not so far advanced on the head as we find it in the adult. The dorsal fin-rays are a little injured a little behind the head; but about the ocular region there is not the slightest trace of abrasion to be seen, so that there is no reason at all to suppose that *there* any rays have been removed by violence.

a. Line showing the natural size of the figured portion of the specimen.



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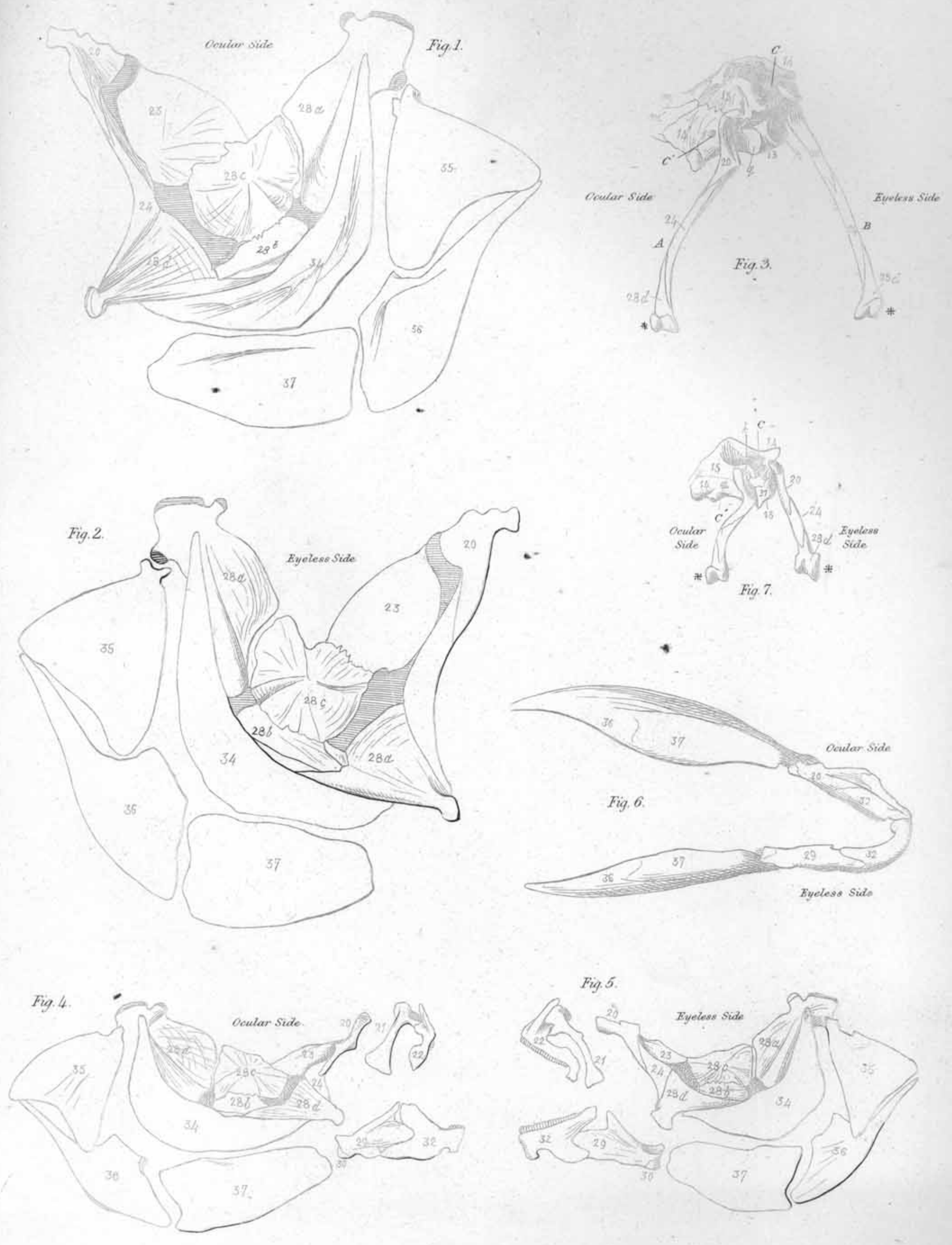

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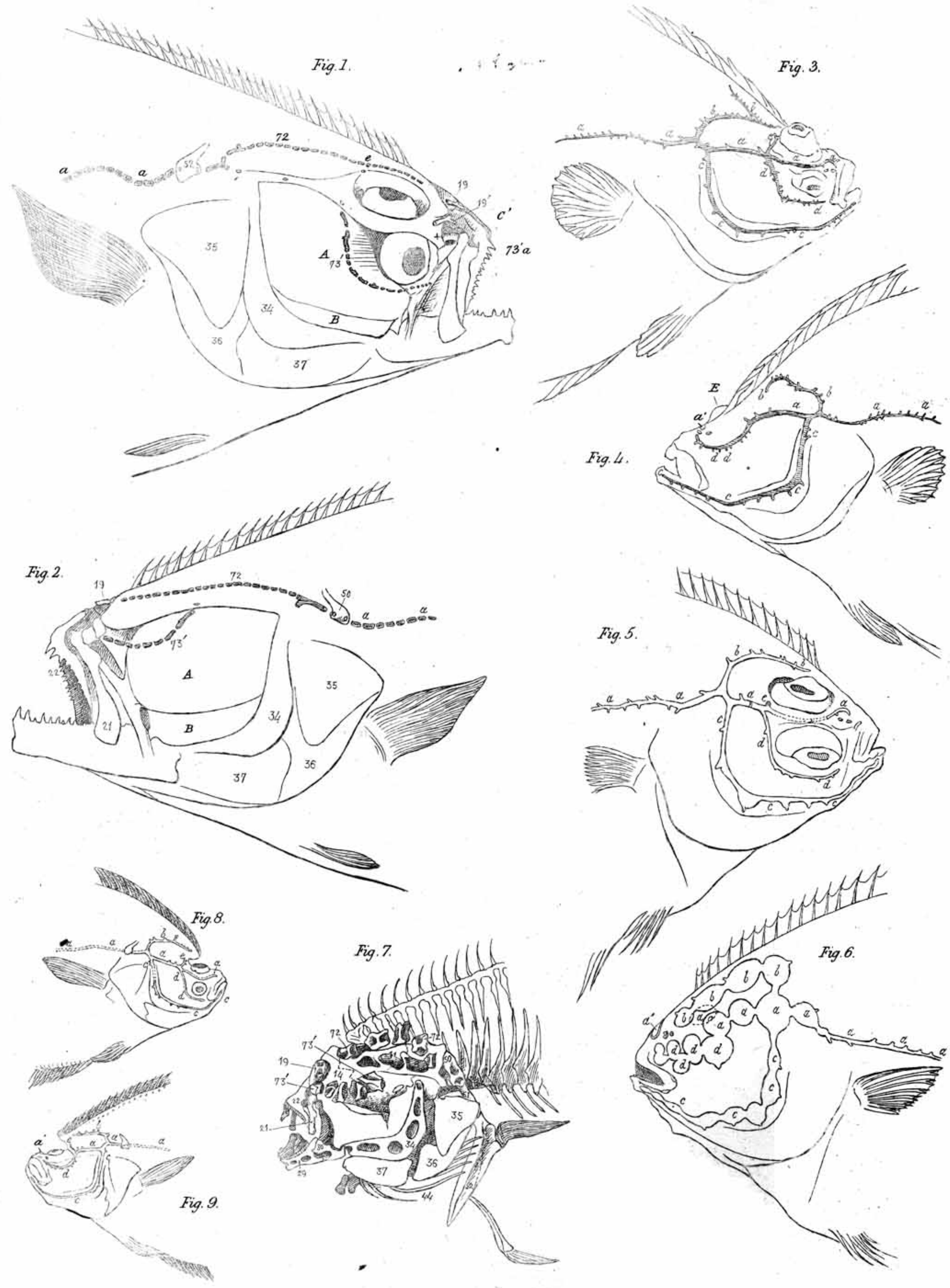

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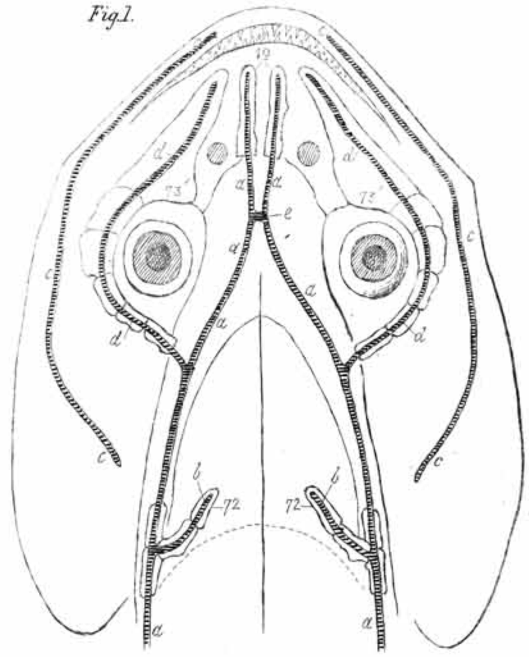
Fig. 1.



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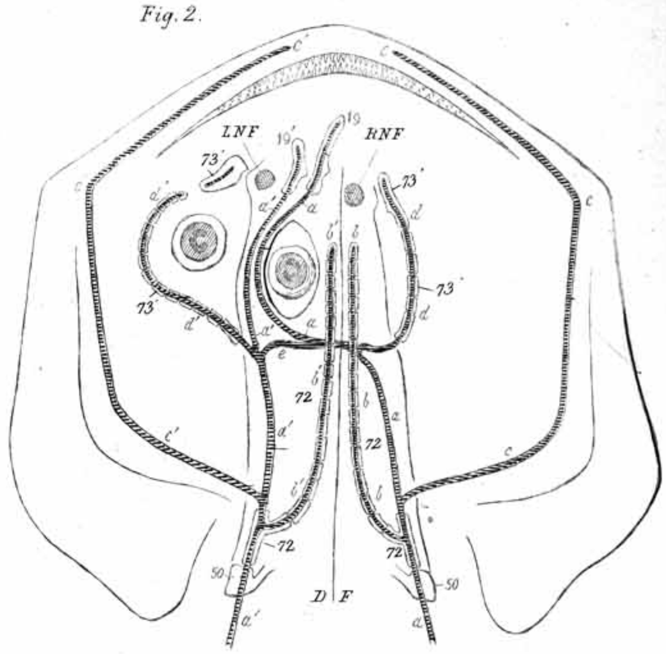

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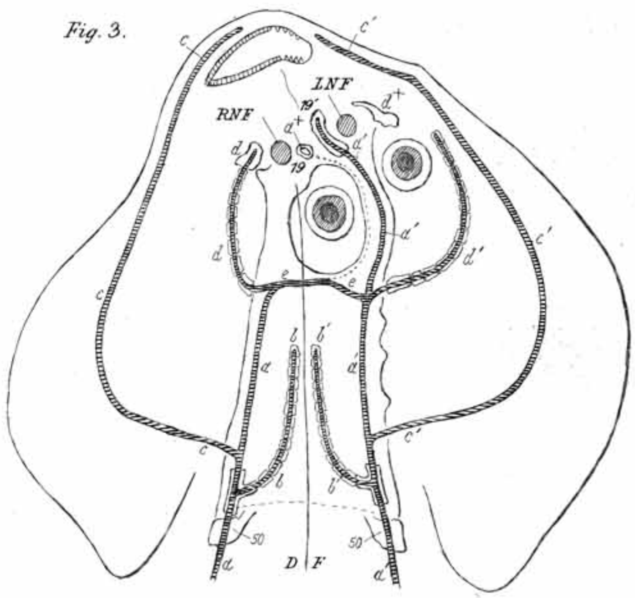

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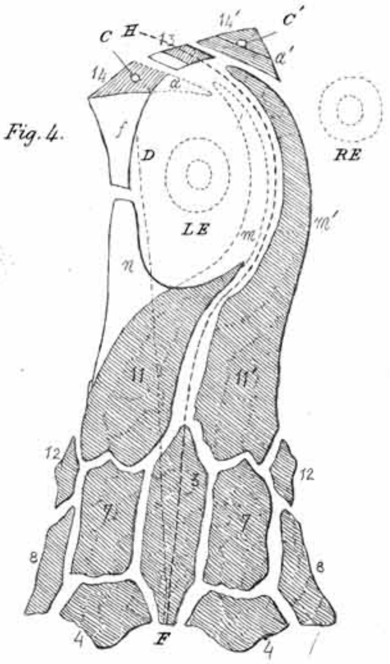


Fig. 8.

Fig. 5.

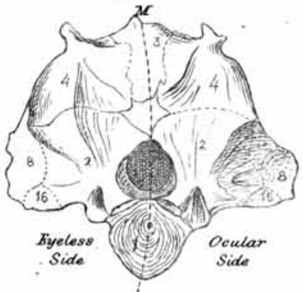


Fig. 6.

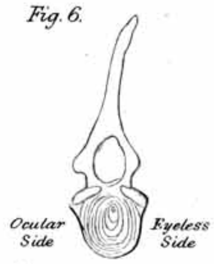


Fig. 7.

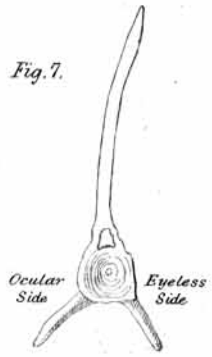
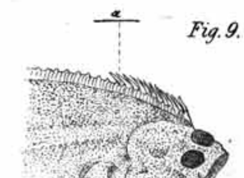


Fig. 9.



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