II.—*The Asymmetry, Metamorphosis and Origin of Flat-Fishes.*

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[Plates 4–10.]

Contents.

Introduction.

It is now a well-known fact that every Flat-fish begins life with the eyes in the normal position; the asymmetry of its skull is not born with it, but acquired during the early development. The conversion of a normal fish is thus a constant occurrence, year by year, and we should be able to determine the causes of the phenomenon. The normal condition may be taken for granted; the abnormal requires explanation.

The adult asymmetry of a few forms is also known, but the descriptions are imperfect or incomplete. Each part has an asymmetry of its own, it is said; the frontals display torsion, the eyes have somehow come to one side of the head and the other parts have somehow altered and fitted themselves into the new conditions. No attempt has been made to correlate the changes in the different parts.

The prevailing view is, that Flat-fishes have arisen through adaptation to life on and in the bottom of the sea, meaning that normal fishes seeking the bottom for protection or food have converted their form, or had their form converted, into something more appropriate to their surroundings. This view meets with many difficulties when an attempt is made to work it out in detail, and the supposition that the change of form has taken place after the fish lay on the bottom, is not supported by the present-day conditions. Even if it were physically possible for a bone to rotate on itself or an eye to manœuvre or be manœuvred by its muscles, there is this difficulty, namely, that the asymmetry in all cases begins and develops to an advanced stage whilst the young fishes are pelagic, swimming freely in the water.

From evidence to be given later it appears, that Flat-fishes swim and lie on the side, not from choice or selection, but because they must—from their structure. At least one normal form has the same habit and many fishes live on the sea-bottom without becoming "flat." The weevers, the angler and the sea-rat seem more legitimate adaptations to the demersal life.

But if the metamorphosis of Flat-fishes has nothing whatsoever to do with the demersal habitat, natural selection need not be ruled out of court. At a certain crucial stage in its early career the structures of the Flat-fish become so disorganised and out of balance, that only a drastic change in the head can save its life. This is the point where natural selection may be introduced, since necessity is present and elimination clearly conceivable. The wonder is that any survive. Many normal fishes also approach the danger zone and we can discern how they are saved.

The materials on which the present work is based have been accumulating for a considerable number of years. The collections were begun and the problems first realised at the Gatty Marine Laboratory of St. Andrews, where Prof. McIntosh enabled me to examine the early stages and adult structure of the common British forms. The Mediterranean forms were added later at Banyuls and Naples. But it was the wonderful collection of Dr. Johs. Schmidt of Copenhagen which gave the real clue to the solution of the problems. In addition, the late Prof. Jungersen, whose great knowledge and interest increased the pleasure of the work, allowed me to study the Copenhagen Museum collection and Prof. Adolf Jensen gave me some rare specimens of the Greenland halibut. Some samples were also obtained from Dr. H. C. Williamson of Aberdeen and Mr. C. Tate Regan of the Natural History Museum, South Kensington, gave me a free hand in examining the rich collections there. In this manner it has been possible to study not only the adult structure of nearly all the known species of Flat-fishes but also the young pelagic stages of representative genera.

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The Asymmetry of Flat-Fishes.

The only genera in which the asymmetry of Flat-fishes has hitherto been studied are *Rhombus*, *Hippoglossus*, *Pleuronectes* and *Solea*. In his classic work Traquair examined only the first three, the sole was merely mentioned. The latter has been dealt with by Cunningham. In all other works on the asymmetry (Cuvier, Meckel, Klein, W. Marshall, Cole and Johnstone, etc.) it is always *Rhombus* or *Pleuronectes* which is taken as the type, except in one instance. Steenstrup figures the skull of *Bothus* along with those of *Pleuronectes* and *Rhombus*, but he was more occupied in explaining his particular theory of the metamorphosis of Flat-fishes than in examining the structure, and his description is very defective.

The work of Traquair has always been taken as the standard description of the asymmetry of Flat-fishes, but it is in no sense an interpretation. The bones are correctly named and their immediate relations are so minutely described that any general correlation between one part and another might not exist. Yet it is unreasonable to conclude that each part should have an asymmetry of its own.

For this comparative study of the Flat-fishes it is possible to condense somewhat the usual classifications and arrange the forms in three main groups according to their asymmetry and general structure.

1. Large forms of good height and thickness with solid bones: *Platysomatichthys*, *Hippoglossus*, *Pleuronectes*, *Rhombus*.
2. Slender forms with thin bones but firmly ossified: *Bothus*, *Arnoglossus*, *Citharus*.
3. Elongated forms with comparatively slight ossification: *Solea*, *Cynoglossus*, *Symphurus*.

The skull of the adult Flat-fish is so misshapen that it is difficult to find any starting-point for the comparison of the different structures. The least asymmetrical is the posterior or otic region as far forward as a plane through the hyomandibular fossæ and prootics. From this plane forwards to the prefrontals the asymmetry follows the same general rules in the majority of forms, whether the eyes are on the right (dextral) or left side (sinistral). As anterior boundary of this middle or orbital region may be taken a plane through the olfactory foramina, which is seldom if ever symmetrical. The most symmetrical bones in all forms are the prootics, the least symmetrical the prefrontals.

The posterior region varies in shape and symmetry. In the first group the configuration ranges from almost normal—deep fossæ and prominent ridges, with posterior face sloping downwards to basioccipital condyle which lies most posteriorly (*Platysomatichthys*, *Psettodes*)—to quadrilateral with lateral ridges and fossæ almost effaced, vertical posterior wall and condyle level with or even in front of wall (*Rhombus*, *Pleuronectes*). In the second group this region is more box-shaped or rounded, without lateral fossæ or ridges and the basioccipital condyle is distinctly under the overhanging posterior wall. In the third group it is deep and almost spherical, smooth and bulging out backwards over the receding condyle; in these also the cranium proper is much shorter but deeper than in the other groups.

Lateral asymmetry is also present. In the first group a line drawn from the centre of the basioccipital condyle up through the middle of the foramen magnum and supraoccipital is not vertical but curved, with convexity to the eyed side (figs. 6, 7). Thus, the condyle and supraoccipital ridge are both to the eyeless side of the vertical median plane, but whilst the supraoccipital continues towards the eyeless side above, the long axis of the basioccipital below returns to the median line (figs. 1, 5). Laterally, the hyomandibular fossa and trigeminal foramen of the eyed side are slightly anterior to those of the eyeless side.

In the second and third groups a lateral asymmetry is difficult to detect, but in *Bothus* (figs. 12, 16) we have a very remarkable development. In old male specimens of this form the posterior wall of the skull appears to be high and narrow, also symmetrical except where a single median bone, which at first sight might be taken for the supraoccipital, inclines to the eyeless side above. On dissection with potash, however, the wall is resolved into three median bones, basioccipital, supraoccipital, frontal of eyeless side, and three paired bones, exoccipitals, epiotics, parietals. Thus, the roof of the skull has been raised backwards and upwards on to the posterior wall; sometimes it goes further and rests on the neural spines above the pectoral girdle. This change can be followed directly on comparing young and old specimens.

Along the ventral aspect the junction of the basioccipital and parasphenoid shows some interesting variations. In forms of least asymmetry (fig. 5) the parasphenoid does not reach quite to the condyle and is forked, but in most other forms it ends bluntly on the condyle and in older specimens of *Pleuronectes* it has been found projecting beyond the condyle on to the centrum of the first vertebra. In the third group the basioccipital is not covered by the parasphenoid, the two bones meet at an angle owing to the bulging downwards of the cranium (figs. 10, 11, 19). This is most marked in *Solea*, where the two bones project downwards and the parasphenoid cuts deeply into the basioccipital; this process also seems to increase with age.

In the middle region the asymmetries may be described as deflections, mainly lateral but also vertical. Thus, along the ventral axis the parasphenoid bends to the eyeless side, as a rule soon after it leaves the basioccipital, but the amount and nature of the deflection varies in the different groups.

In the first group the deflection is very gradual from the otic region forwards, so that the greatest departure from the middle line lies at the anterior end of the parasphenoid. The deflection may be slight, one branch of the parasphenoid fork being near the middle line, the other (eyeless side) more to the side and above (fig. 5). In other forms the deflection is very distinct, but varies from 5° to 15° even in different specimens of the same species (*Pleuronectes*).

In the second group there is the same bending to the eyeless side, but the maximum deflection is found near the posterior end and consists of an abrupt kink or break to the eyeless side (figs. 2, 15). The axis then continues forwards on this new line.

In the third group there is a wide range of variation between the almost symmetrical parasphenoid (*Symphurus*) and the most deformed (*Solea*, figs. 3, 4). The latter is the most expressive; the parasphenoid bends into a deep bow with convexity to the eyeless side; further, it also bends upwards and backwards. Both of these bows consist of two parts, the posterior bending to the eyeless side and upwards (viewed from the posterior region), the anterior bending to the eyed side and downwards or forwards. It will be seen that the latter corresponds to the deflection in other groups.

The vomer in front of the parasphenoid may simply be turned on its axis towards the eyeless side (fig. 5), or may still further increase the asymmetry of the parasphenoid (fig. 1), or return somewhat to the middle line (fig. 2). In *Solea* we again have an extraordinary complication; the shaft of the vomer lying in the fork of the parasphenoid is directed, like the latter, to the eyed side, but the head is directed downwards and slewed round to the eyeless side (figs. 3, 4). Viewed obliquely from the side, the parasphenoid-vomer axis in *Solea* is like an elongated S.

Considering the parasphenoid-vomer axis as a whole we have three types of asymmetry: single, double, and triple lateral deflection. Common to all three types is the deflection at the junction of the parasphenoid and vomer. The double and triple deflections have this in common: that the head of the vomer is flexed in the opposite sense to the former deflection. The condition in *Solea* is anomalous.

Anteriorly the two branches of the parasphenoid end in the ethmoid cartilage on each side of the vomer. In the normal Teleost the lateral ossifications of the ethmoid (prefrontals) grow downwards and touch the upper margin of the parasphenoid on each side. This is just the place, however, where the parasphenoid-vomer axis in Flat-fishes is deflected and we find that the connection between prefrontals and parasphenoid has been disturbed on both sides. On the eyed side in all forms the lateral ossification of the ethmoid does not reach down to the parasphenoid, a small piece of cartilage persisting between them. On the eyeless side the connection is solid and prolonged further back than in the normal fish.

Such is the condition also in *Solea*, but on examining this form more closely it is seen that the bones of the eyeless side are not disposed as in other forms. The anterior, upper end of the parasphenoid is not connected with the prefrontal; a space or foramen intervenes, and the junction of the two bones extends backwards a considerable distance from the foramen; further, the anterior border of this foramen is formed by the vomer-prefrontal connection (fig. 11). But the normal position of the olfactory foramen is further forward, near the junction of the prefrontal and mesethmoid, the parasphenoid and vomer taking no part in it. It appears, therefore, that both the olfactory foramen and the parasphenoid-prefrontal connection are situated in a posterior, abnormal position, indicating that greater changes have occurred here in *Solea* than in the other Flat-fishes. See later also the anterior eye-muscles.

The asymmetry of the ethmoid mass corresponds mainly with the asymmetry of the anterior part of the parasphenoid-vomer axis. In the second group, for example, the whole ethmoid region is with the axis to the eyeless side of the longitudinal median plane (figs. 2, 15). In the first group the more solid structures show only a partial displacement; the lower part of the cartilage shows the same lateral deflection as the dermal bones below, the dorsal or mesethmoid part remains more or less in the median longitudinal line (fig. 9), giving an appearance of "torsion" to the ethmoid region. Thus, the nasal ridge in front slopes downwards to the eyeless side, and the lateral wings appear to be "rotated" in such a way that the prefrontal of the eyeless side lies above and behind that of the eyed side. In *Bothus* this relative change of position of the prefrontals continues throughout life (especially in male specimens), so that the posterior end of the prefrontal of the eyeless side comes to lie above the occiput, whilst the anterior end of the other prefrontal approaches the head of the vomer (figs. 12–14).

In the third group (*Solea* and *Symphurus*) the condition of the ethmoid mass is entirely different from the above, in that there is no appearance of "rotation." In *Solea* the mesethmoid is not connected with the vomer anteriorly, but projects freely in a long snout, and there is no nasal ridge on it for the maxillary cartilages, which operate below on the head of the vomer. The prefrontals are both situated far back at the posterior end of the ethmoid cartilage, instead of being on a level with the main part of that cartilage. On the eyed side the prefrontal is reduced to a small thin crescent (fig. 10); on the eyeless side the prefrontal is a large bone, with strong posterior processes to the parasphenoid and its own frontal.

The frontals above are, as a rule, flexed in the opposite sense to the deflection of the parasphenoid-vomer axis, thus giving rise to the appearance of "rotation" in the middle region of the skull. In the first group the frontal of the eyeless side is separated anteriorly from its prefrontal, the central ethmoid coming between the two. Posteriorly and along the eyed side this frontal forms the boundary of the upper orbit and a stump (containing remnants of the lateral line canal) projects forward on the blind side (fig. 9) to form the so-called pseudomesial bar with the posterior process of its prefrontal. In this group the deflection of the frontals is mainly at their anterior ends, corresponding to the anterior deviation of the parasphenoid.

In the second group the prefrontal of the eyeless side may retain the connection with its frontal anteriorly (*Arnoglossus*) and the frontals have their principal deflection posteriorly, corresponding to the posterior deflection of the parasphenoid. In *Bothus* the frontal of the eyeless side is removed entirely from the middle to the posterior region of the skull (figs. 12, 14); its prefrontal comes between the two frontals and grows freely upwards and backwards to form the front margin of the upper orbit (figs. 13, 17), Comparison of young and old specimens shows that this process continues long after metamorphosis, the prefrontal pushing the eye and therewith the whole orbit back on to the posterior wall, as already mentioned. The frontal and prefrontal of the eyed side retain their original positions; hence one side of the skull is for the most part normal, the other half has been destroyed and loosely rebuilt (figs. 13, 15). In the compulsory migration of the eye in the adult *Bothus* we see written large what also happens in all other Flat-fishes, but in the early stages.

In *Solea* the separation of the prefrontal and frontal of the eyeless side is complete, and even the frontal of the eyed side is free anteriorly from its prefrontal (at least in old specimens), so that the loose anterior ends of the two frontals glide forward on the ethmoid cartilage well in front of the prefrontals. Thus, both the prefrontals have lost their original connections with both the parasphenoid beneath and the frontals above, and it is only the secondary growths of the prefrontal of the eyeless side, pseudomesial bar and connection with parasphenoid, that afford any rigidity to the skull (fig. 11).

In *Symphurus* (figs. 19, 20) the frontals appear to be absent, the roof of the skull being bare except for a thin membrane. Laterally, however, a thin rod continues forward on each side from the parietal and sphenotic. These rods converge anteriorly and that of the eyeless side bends over, to form a bridge in front of the space, and fuses with its fellow of the other side, the united portions continuing forward on the eyed side to the ethmoid. These rods represent at least the marginal parts of the frontals. Anterior to the transverse bridge there is a second space or fontanelle, bounded on the eyeless side by the posterior process of the prefrontal of that side. The eyes do not have any definite orbits. The median portions of the frontals—which should close in the roof of the cranium—are represented by two other slender, ossified rods or processes, situated above and separated from the skull, except anteriorly where the process of the eyeless side is attached to the anterior corner of the prefrontal of that side. The process of the eyed side ends freely. Above the eyes the processes meet and fuse, running backwards (possibly as part of the parietal ossification) to the base of a third long process, which is evidently the supraoccipital spine. It appears, therefore, that the median part of the frontals has been flexed upwards, not laterally as in other forms (except *Bothus*). This phenomenon will be more fully described under the metamorphosis.

One important structure in the skull remains to be mentioned, the interorbital membrane. This is a fibrous septum, partly ossified occasionally, which extends forwards between the orbits from the opening of the cranium to the ethmoid and contains in the normal Teleost a dorsal groove or canal for the olfactory nerves. In most Flat-fishes this canal is obliterated, the nerves being simply embedded in the septum, nearer the parasphenoid than the frontals. Anteriorly the membrane ends in a cartilaginous lamina (*cl*), which crosses obliquely downwards from the ethmoid to the parasphenoid, and in front of the lamina is a space or fenestra (homologized with the single olfactory pit of *Myxine* by W. K. PARKER).

In the young stages of the Flat-fishes, as in the normal Teleost, there is no fenestra here, the membrane continuing forward between the primordial cartilage above and below, and on each side bearing the insertions of the oblique eye muscles (figs. 49, 64, 86). This membrane has consequently been ruptured during development, the lamina of cartilage probably preventing the rupture from extending backwards. The insertions of the eye muscles in the first two groups are now found on the inner face of the prefrontal of the eyeless side, following the deflection of the trabecular cartilage to that side (*x*, fig. 9 ; *cf.* fig. 49).

In *Bothus* the interorbital membrane is vertical and entire right to the end of the ethmoid (fig. 14), but when the bones are separated by means of potash, a vertical piece of the membrane, just in front of the cartilaginous lamina, comes away with the prefrontal of the eyeless side (fig. 18). Thus, instead of the membrane here being carried over to the prefrontal, as in the common forms, the membrane remains vertical and the prefrontal has been carried up to it. Further back, the prefrontal is folded on itself, forming a canal with the frontal of the eyed side (fig. 18, *a*), and at the lower end of this are the insertions of the oblique eye muscles (*x*). Thus, even here these insertions have been moved from their original positions, and we can associate this with the pushing back of the eye by the prefrontal. In the middle region of the skull the interorbital membrane is almost vertical, attached above to the frontal of the eyed side, and along this we find the groove or channel for the olfactory nerve (fig. 18), just as in the normal Teleost. On the eyeless side of the membrane the olfactory nerve and organ have atrophied, though a remnant of the original canal appears to persist in a blind groove on the frontal of the eyed side above the groove for the nerve of its own side (fig. 18, *c*).

In *Solea* the interorbital membrane also appears to be entire, but the condition is quite different. The cartilaginous lamina is present between the olfactory foramina, but the space in front is occupied by the ascending process of the vomer. The oblique eye muscles, instead of being inserted on the prefrontal of the eyeless side, as in the previous forms, are here separated and are attached, each pair to its respective prefrontal, on their own side of the median line. This change of position, outwards and backwards, takes place during the early development, like the corresponding change in the other forms.

From this comparative survey of the asymmetry of the skull in Flat-fishes certain conclusions may be drawn. In the first place, if the changes in shape and position can be referred to any discoverable cause, these causes are not present in the skull itself. This may be concluded from the rupture of the tissues (*e.g.*, of the frontal and prefrontal and interorbital membrane) as well as from the independent variation of the asymmetries of the different regions. In the second place, the asymmetry of the skull has begun along the ventral axis. For example, the changes in the frontal region can be referred to the prefrontals (witness *Bothus*), and the changes in the latter to the changes in the trabecular cartilage and parasphenoid-vomer (*cf.* interorbital membrane and oblique eye muscles in *Solea* and other forms). Thirdly, the independent asymmetry of the posterior region suggests some correlation with the trunk, just as the anterior asymmetries indicate some connection with the jaws and arches.

In the head region outside the skull the asymmetries or departures from the normal are found in both osseous and muscular tissues. For descriptive purposes the principal parts may be grouped in two systems concerned respectively with the closing and opening of the mouth.

The closing of the mouth is controlled by the so-called cheek-muscles, which arise from the hyomandibular arch, pterygoids and alæ of the parasphenoid. The muscles from these different structures are not everywhere of the same relative strength; in *Pleuronectes* and *Solea*, for example, the parasphenoid portions are more developed than in other forms and, since they act more vertically than the muscles from the arch, they may be co-ordinated with the greater deflection of the jaws and parasphenoid-vomer axis in these forms; but these minor differences need not be dwelt upon here. The cheek-muscles converge downwards and forwards to a strong tendon directed towards the process of the articular bone of the lower jaw, just above the articulation with the quadrate, but ending mainly in the oral membrane. Before this, however, a muscular slip is released from the upper margin and runs upwards alongside then across the pterygopalatine to be inserted as a tendon into the posterior head of the maxillary (fig. 45). Thus both the upper and lower jaws are closed by one and the same process, the oral membrane acting as the intermediary. The pre-maxillaries and the pterygopalatines have no muscles attached to them. All the structures and the muscles show asymmetry.

On examining the muscular attachments anteriorly, we find that in all forms except *Psettodes* the maxillary slip is always absent or undeveloped on one side or the other. In most forms of the first and second groups the maxillary connection is distinct only on the blind side; in *Glyptocephalus* and the members of the third group the connection is present on the eyed side and not on the blind side.

These muscular disturbances are accompanied by changes in the disposition and shape of the bones forming the jaws. In most forms of the first and second groups (fig. 21) the mandibular and maxillary rami of the blind side are the longer, with a different slope (*e.g.*, *Pleuronectes*). But in *Psettodes* and *Glyptocephalus* the rami are practically equal; in *Lepidorhombus* and its allies the rami of the eyed side are the longer. In the third group *Achirus* also has equal rami, but in *Solea* and the Cynoglossids the upper rami (eyed side) are the longer (fig. 24).

With but a few exceptions there is therefore a close correlation between the jaws and the cheek-muscles; the rami are longer on the side where the maxillary slip persists. *Solea* and Cynoglossids conform to the rule, but they show the reverse condition to what is found in the other groups; further, it is only in this group that the premaxillary ramus (of the blind side) articulates with the dentary of the mandibular (fig. 24).

The asymmetries of the mandibular and hyomandibular arches are complementary. On the side which has the longer rami, the bones of the hyomandibular arch are shorter though stouter than those on the other side. This can be seen most clearly in *Pleuronectes* (shorter bones on blind side) and *Solea* (eyed side). In this connection the lateral asymmetry of the posterior region of the skull in the first group may be recalled; the hyomandibular fossa is more posterior on the blind side (*cf.* fig. 1).

The opening of the mouth is performed by a force which acts normally along the median longitudinal line, namely, by the paired geniohyoid muscle connecting the symphysis of the mandibular rami with the hyoid arch (ceratohyal mainly); but the hyoid arch is itself retracted by a strong muscular connection with the pectoral arch. Thus, the mouth is opened directly or indirectly by a force acting from the body (fig. 27).

Normally the hyocleithral connection consists of a paired muscle arising from the anterior surfaces of the cleithra and passing forward to end in a strong double tendon, but embedded in the muscle anteriorly and giving rise to the double tendon is a small vertical slip of bone, formed in the membrane separating the two halves of the muscle. The double tendon may divide (like the muscle) into four parts, which pass forwards to be attached to the hypohyals and basibranchials. Among the Flat-fishes this condition is only found in *Psettodes*, *Symphurus*, *Synaptura* and *Cynoglossus* (figs. 30, 31); in *Psettodes* there is a definite articulation of the bone with the first or second basibranchial. In all other forms the abdominal muscles also take part in the connection and the simple membrane bone, the urohyal, becomes a large cartilaginous bone of a peculiar shape (figs. 27, 28, 29). In the former the urohyal lies close to the hyoid and branchial arches (fig. 98); in the latter it is nearer the cleithra (fig. 78), sometimes resting on these and even articulating with them (*Glyptocephalus*, left cleithrum).

In the common forms the urohyal is shaped like a hook or sickle, the handle anteriorly connected with the hyoid arch, the haft running horizontally backwards towards the cleithra and the blade curving downwards and then forwards to end in a point under the handle; thus, the anterior face of the bone shows a more or less deep curve. From its position and connections, posteriorly with the cleithra only, the upper part represents the original line of connection between the cleithra and hyoid arch, the lower part connected with the abdominal muscles being a new structure peculiar to the Flat-fishes in which it occurs.

This hook-shaped urohyal is formed in the early stages during metamorphosis; the lower part of the muscle is ruptured anteriorly and retracted, cartilage forming along the ruptured edge which bends forwards below with the forward growth of the abdominal muscles, and pelvic fin or fins in some cases, as will be described later. The significance of this change can be determined by experiment. If we pull on the upper part of the hyocleithral muscle, thus the original part, when the mouth is nearly closed, the latter does not open but rather closes more firmly than before. If we pull on the pelvic fins or lower prong of the hook, the urohyal rotates, lowering the anterior upper end; the hyoids are thus retracted downwards, then the interopercula open and these, through their connection with the articular, open the lower jaw sufficiently for the geniohyoid muscle to continue the process.

Other changes are found in this ventral region, in the hyoid and branchial arches, as well as in the pharyngeal muscles; the membrane connecting the urohyal with the cleithra may even be separated from one of the cleithra, the interbranchial septum may be ruptured (*Lepidorhombus*, etc., fig. 27); but these need not be dealt with here. The significant fact is, that important changes have occurred in the ventral mechanism which has to do with the opening of the mouth, just as in the dorsal mechanism closing the mouth.

As mentioned, however, the ventral mechanism remains simple and primitive in *Psettodes* and the third group. On comparing these with the common Flat-fishes, we find that the shape of the mouth is different; the mandibular rami have a more horizontal slope, as in the normal Teleost, so that the line of action of the geniohyoid muscle passes below the articulation of the lower jaw with the quadrate (fig. 95); in the common Flat-fishes the mouth is more vertical than horizontal (fig. 75). But the more vertical position of the jaws is clearly due to the foreshortening of the skull, arising from the deflection of its ventral axis. Hence the rupture of the hyocleithral connection and forward growth of the abdominal muscles can be correlated with the changes in the anterior region of the skull.

The connecting link between the ventral mechanism opening the mouth and the dorsal mechanism closing it, is the pterygopalatine arch. This serves as a buttress to the ethmoid region of the skull with its base resting on the quadrate; superiorly the palatine usually has a double head, the first articulating with the skull at the junction of the prefrontal with the parasphenoid, the second head passing forward to articulate with the maxillary. In the normal Teleost the arch slopes backwards from the skull to the quadrate at an acute angle and the only movement possible is a slight rotation laterally and longitudinally of the palatine head on the skull. In the Flat-fishes the attachments of the palatines are loosened, the slope of the arch is more vertical than horizontal and is not the same on the two sides of the head; the shape on the two sides is also different.

In the first and second groups the pterygopalatine of the eyeless side is almost straight with slight or no curvature (fig. 23); the slope is almost as much horizontal as vertical and the anterior maxillary head is free and may retreat backwards on to the parasphenoid (*Bothus*). In *Solea* and the Cynoglossids it is the eyed side which has these characteristics (fig. 22). On the other side of the head (eyed side in first two groups, eyeless in third group) the pterygopalatine is more vertical, shorter owing to a distinct bend inwards and both heads of the palatine are protracted upwards on the skull, the maxillary head sometimes appearing as a promontory on the surface (*Bothus*, old males). On the one side the pterygopalatine retreats from the skull, on the other side it is higher up on the skull, corresponding thus to the apparent "torsion" of the prefrontals.

Combining now the appearances of the jaws and arches with the skull, we have the following principal correlations (*cf. Pleuronectes* and *Solea*):—

1. On the blind side in first and second groups (eyed side in third group): longer rami of mandibular and maxillaries; shorter hyomandibular arch, cheek muscles complete; longer, straighter pterygopalatine; palatine heads retracted; parasphenoid-vomer axis bends to this side anteriorly; lateral ethmoid deflected upwards and backwards.
2. On the eyed side in first and second groups (eyeless side in third group): shorter rami of mandibular and maxillaries, premaxillary and dentary articulated in third group; longer hyomandibular arch, cheek muscles usually incomplete; shorter, more vertical, curved pterygopalatine; heads of palatine protracted; parasphenoid-vomer axis bends away from this side anteriorly; lateral ethmoid deflected downwards and forwards (in *Solea* both lateral ethmoids retracted).

A few forms display exceptions to these correlations in one regard or another, *e.g.*, *Psettodes*, *Glyptocephalus*, *Lepidorhombus*, but the differences are correlated with other differences in the body and head.

In the abdominal region the asymmetries appear as longitudinal curvatures of the vertebral column and vertical, lateral flexures. These are most clearly marked in the first group, especially *Pleuronectes*.

In the first group the vertebral curvature consists of two longitudinal flexures; beginning at the second or third caudal vertebra the column tends to the blind side and the parapophyses are inclined more posteriorly on that side than on the other. On the ventral margin of the abdomen the abdominal rod or first interspinal of the anal fin is also directed to the blind side (figs. 25, 26). Thus, the lower half of the body tends to that side. At the pectoral girdle, however, the curvature of the column changes direction and the first three to four vertebræ tend to the eyed side (fig. 32). These anterior vertebræ are also flexed downwards and this is the only curvature distinctly seen in the second and third groups, though in *Solea* they are also turned towards the eyed side (fig. 8).

In a vertical section of *Pleuronectes* the dorsal and ventral margins of the body are seen to be inclined over to the blind side relative to the spinal column (fig. 33) and the flexure is seen in the neural spines and parapophyses as well as in the abdominal rod. In *Rhombus* and the second and third groups the neural spines are not appreciably flexed, but the ventral structures are asymmetrical, as a rule to the eyeless side (*cf. Solea*, fig. 83). In *Lepidorhombus* the abdominal rod has a distinct double curvature (fig. 26).

The pectoral arch has the same asymmetry as the abdominal region. In *Pleuronectes* the bones on the blind side are almost vertical, on the eyed side they curve outwards then inwards, so that the foot of the cleithra is to the eyeless side relative to the base of the skull. Dorsal to the pectoral arch the flexure to the eyeless side is seen again in the supraoccipital spine, which is bent over to that side in a vertical plane (best seen in *Rhombus* and *Lepidorhombus*, forms with high supraoccipital spine). Between these flexures of the dorsal and ventral margins the anterior abdominal vertebræ and the basioccipital tend to the eyed side, following the reversed curvature of the spinal column. Thus the posterior region of the skull is slewed round relative to the pectoral arch, the dorsal part to the eyeless side, the basioccipital to the eyed side. In connection with the asymmetry of the latter, it may be noted that the strong pharyngeal retractors arise from the ventral surface of the third to sixth abdominal vertebræ; their tendency is to depress the skull and maintain its base in the same line as the anterior vertebræ.

The asymmetry of the body can thus be co-ordinated with the asymmetry of the skull. The pectoral arch is part of the body and the asymmetry of the abdominal muscles reappears in the hyoid arch. The asymmetry of these muscles is also expressed in the ventral or pelvic fins. The growth forward of the dorsal and ventral muscles of the body and the structures connected with them is a well-known phenomenon; their asymmetry is what is remarkable in the Flat-fishes.

The nature of the body flexure in Flat-fishes is opposed to the current view, that these are secondary developments connected with the demersal habitat. In the first place, these flexures are variable according to a rule which has nothing to do with the habitat (*e.g.*, symmetrical neural spines in *Rhombus*, asymmetrical in *Pleuronectes*). Secondly, if the flexures are due to muscular action after the fish have sunk to the bottom, they should be in the direction of the stronger action. But, in the strongly asymmetrical *Pleuronectes* the muscles of the eyed side in the adult are considerably more developed than those of the eyeless side (fig. 33); yet the flexures of the spines dorsally and ventrally are to the eyeless side. These body flexures are therefore primary and impressed on the structures before or during ossification.

The occurrence of abnormalities may also be noted here. Thus, cyclopean malformations, in which the transit of the eye has been only partial, have been found in some forms, *e.g.*, *Rhombus* and *Symphurus*, and reversed specimens are common in some species, *e.g.*, *Psettodes* and *Pleuronectes flesus*, and a quite symmetrical flounder has been found. Further, *Lepidorhombus* appears to be persistently reversed; the double nature is seen in the body (*vide* fig. 26), whilst the head shows both sinistral and dextral characters. These variations are readily explained on the theory to be elaborated here, that the asymmetry begins in the body, extends to the jaws and arches, and thereafter leads to varying degrees of deformation of the skull.

Summary regarding the Asymmetry.

1. Comparison of many different types of Flat-fishes shows that the asymmetries of the skull anteriorly have their beginning in the parasphenoid-vomer axis. Rupture of tissue is apparent at a certain spot; below between parasphenoid and prefrontal of one side, mesially in the interorbital membrane, and above between the other prefrontal and its frontal. That the movements of the migrating eye are determined by the growth of the prefrontal of the eyeless side is clearly seen in *Bothus*.

2. Rupture of the tissues of the skull may extend posteriorly to the cranium proper, *e.g.*, in *Bothus*, where the roof of the cranium—frontal, parietals, and epiotics—is forced upwards and backwards on to the posterior wall, and even over the pectoral arch; also in *Symphurus*, where the dermal frontals, parietals, and supra-occipital are separated from the skull except posteriorly and anteriorly (one frontal); it may also extend anteriorly, *e.g.*, in *Solea*, where the vomer is separated from the ethmoid, except for a small part posteriorly. In *Bothus* and probably in *Solea* the asymmetry of the skull increases with age.

3. The jaws, pterygopalatine, hyomandibular and hyoid arches, and the attachments of the cheek muscles are all asymmetrical, with isolated exceptions in one or two particulars. These asymmetries and the asymmetries of the anterior parts of the skull are so closely co-ordinated that they must spring from common causes.

4. The trunk is also asymmetrical, showing in many cases both longitudinal and vertical flexures; the dorsal and ventral margins of the body are not in the same plane as the vertebral column. The condition in *Pleuronectes* shows that these asymmetries are primary, not secondary. The pectoral arch and pelvic fins, and the supraoccipital ridge dorsally have the asymmetry of the body, as also ventrally the hyoids and jaws. Co-ordinated with these conditions, we have in the common forms the rupture of the hyocleithral connection and in all the asymmetry of the skull. The original source of asymmetry has, therefore, to be sought for in the body.

5. There are two quite distinct types of asymmetry, the one represented mainly by temperate forms (*Pleuronectes*, *Hippoglossus*, *Rhombus*, etc.), the other mainly by tropical forms (*Symphurus*, *Solea*, *Cynoglossus*, etc.). The asymmetries of the second type are the reverse of those of the first, that is, the characteristics of the eyed side are found on the eyeless side, and *vice versâ*. In the second type the premaxillary is articulated with the dentary; this is never the case in the first type.

6. Primitive characters have been discovered in several forms. Thus, one side of the skull in *Bothus* retains its primitive shape as regards prefrontal, frontal, complete interorbital septum, and infraorbital canal for the olfactory nerve. These characters are not found in any other form. Again, the urohyal is of the primitive type in *Psettodes*, *Symphurus*, and the Cynoglossids.

The Metamorphosis of Flat-Fishes.

Since the middle of last century the larval and post-larval characteristics of a large number of Flat-fishes have been described by many authors, chiefly for the purpose of distinguishing one species from another. In this way it has been determined that all Flat-fishes begin life like normal fishes, and that the change to asymmetry occurs during a more or less prolonged pelagic existence. Very few authors, however, have dealt with the inner development of the asymmetry (Pfeffer, 1886; Williams, 1902; Mayhoff, 1914), and these have restricted their attention to the skull of only two or three species, assuming at the same time that the asymmetry begins in the orbital region.

For present purposes, the Flat-fishes may be divided into four groups, with the following general characters:—

1. Pleuronectoid type: large elongated dextral forms, without air-bladder in early stages; *Platysomatichthys, Drepanopsetta, Glyptocephalus, Pleuronectes.*
2. Rhomboid type: large rounded sinistral forms, with air-bladder in early stages; (*Psettodes ?*), *Rhombus, Paralichthys.*
3. Bothoid type: slender rounded sinistral forms, with air-bladder in early stages; *Bothus, Arnoglossus.*
4. *Symphurus* type: slender elongated forms, with air-bladder in early stages. A very large group, with at least two sub-divisions; sinistral forms: *Symphurus, Cynoglossus;* dextral forms: *Solea, Synaptura.*

The first and the fourth groups are best suited for displaying the gradual development of the asymmetry, and, under these, naturally those forms which take the longest time to metamorphose; *e.g.*, *Platysomatichthys, Hippoglossus, Glyptocephalus, Symphurus.* The second and third groups are of special interest, by contrast with the first group, in showing the divergence caused by the presence of an air-bladder.

The metamorphosis is here taken to include all the changes occurring in the form of the fish, from the absorption of the yolk of the larva until the adult Flat-fish form has been attained. During this period, four more or less well-defined stages can be distinguished. Only the third and fourth stages are really distinctive of Flat-fishes, but the first two stages have the added interest, that normal fishes display similar phenomena, yet grow out of the incipient asymmetry.

Stage I: from absorption of yolk to appearance of fin-rays and beginning of ossification; asymmetry of abdominal organs. *Pleuronectes* 7–8 mm., *Drepanopsetta* and *Glyptocephalus* 4–7 mm., *Bothus* 5–8 mm.

Asymmetry may be present already in the egg, as Parker has shown, but this temporary, embryonic asymmetry has nothing to do with the permanent condition found in the Flat-fishes. The latter is a phenomenon of the pelagic life, and begins only when the yolk has been absorbed. As soon as the yolk-sac has disappeared, the young Flat-fish proceeds to form a coil in its intestine, and to display the first signs of asymmetry.

In all fishes which form a coil, the pyloric end of the stomach comes to lie on the left side of the median longitudinal plane; there the beginning of the large intestine is usually marked by two or more pyloric cæca. The large intestine always passes down on the left side, turns round, and ascends a short way in front of the descending portion; then changes into the thin-walled small intestine, which continues upwards, then backwards, across the pyloric end of the stomach to the beginning of the rectum.

The position, shape, and mode of growth of the coil are of importance. In the Pleuronectoid forms, those which take longest to metamorphose have the coil more in the middle of the cavity (figs. 37, 42, 61). A posterior coil is accompanied by more rapid metamorphosis unless an air-bladder is present. In the higher Teleosts, the coil is usually formed anteriorly in the cavity, with the air-bladder also placed anteriorly, a condition not found in the Flat-fishes.

A second distinctive characteristic is, that in Flat-fishes the coil is formed mainly in a longitudinal direction, thus clearly visible from the side, with a space between descending and ascending portions, which is filled with pancreatic tissue. In the normal Teleosts the coil is mainly transverse, and the fish becomes relatively broader in transverse section. When the coil is at all transverse in the Flat-fishes (*e.g.*, *Drepanopsetta*, *Glyptocephalus*), these forms take longer to metamorphose (figs. 43, 61).

In all the common Flat-fishes the coil increases in size mainly downwards, thus increasing the height or depth of the fish; in *Symphurus* the long coil develops lengthways outside the cavity, and thus reaches further back towards the tail than in any other group, a condition seen again in certain normal Teleosts (*cf.* figs. 94, 98).

Again, in the fourth type (*Symphurus* and *Solea*), the rectum is mainly horizontal; in the other types, as in the higher Teleosts (but not the advanced Gadoids), the rectum is mainly vertical. This amounts to a coil and a half, and the descending rectum, tending as it does from right to left, may have something to do with the development of the asymmetry in the caudal region.

In the Pleuronectoid group, as also in some exceptional forms of other groups, there is no sign of an air-bladder at any stage. In the groups where it occurs, the position of the air-bladder gives the first external sign that asymmetry is already present in the body, and has begun with the coiling of the gut. The air-bladder is always asymmetrically placed in the Flat-fishes.

Taking the most clearly marked cases, *Bothus* and *Arnoglossus*, when the yolk is almost absorbed the coil begins to form, and immediately above it, on the left side, a differentiation of tissue connected with the hind-kidney leads to the appearance of a small air-bladder (figs. 40, 41). This lies precisely over the descending arm of the coil, and later it lies on the left side of the developing hæmapophyses of the 7th to 9th abdominal vertebræ (ten in all). So long as the yolk-sac persists, there is no coil and no air-bladder.

In *Symphurus*, which also has closed hæmapophyses, the air-bladder is large and lies entirely on the left side. Here the connection with the kidney is still more distinct; sections show (figs. 84, 90) that it replaces, not merely displaces, a part of the left hind-kidney. The right and left head-kidneys develop in the normal position, but at the level of the fourth abdominal vertebra the duct of the left kidney passes over to the right side and fuses with the duct of that side. The space for the air-bladder begins at the crossing and extends along the left side to the hæmal spines.

Sections of *Rhombus* reveal that the air-bladder is also placed asymmetrically in this type (fig. 57); it begins about the 5th vertebra, lying more under the left process of the vertebræ as far as the 8th, where it becomes more median. The aberrant *Lepidorhombus* and its allies have no air-bladder. In *Solea*, lastly, the air-bladder is more on the right side; in *S. vulgaris* it is small and lies about half-way along the cavity mainly on the right side (fig. 79); in *S. lascaris* or *nasuta* it is very large and double, the anterior part more on the right side, posterior part median; in *S. variegata* there is no air-bladder.

A third noteworthy feature of this stage is the early development in certain forms of one or more elongated rays above the head. In the Bothoids, as soon as the air-bladder appears, a longitudinal splitting of the upper margin of the embryonic dorsal leads to the formation of a long "tentacle" anteriorly, which soon develops a thickened core (figs. 40, 41). *Symphurus* has three long distinct rays on the head at this time, increasing later to five (*cf.* Macrurids and *Trachypterus*).

In connection with these rays it may be noted that the Bothoids have the least breadth relative to height of any larval Flat-fish, whilst *Symphurus* has the most asymmetrical air-bladder and also free abdominal organs. In the latter form also a large amount of loose connective or lymphoid tissue develops on the head beneath the long rays.

In *Symphurus* another sign of the body asymmetry develops towards the end of this stage—the ventral or pelvic fins. They are asymmetrical from the beginning; the fin of the right side occupies a median position on the ventral line and its pubic cartilage extends backwards from the cleithra along the ventral margin under the gut. The left fin, however, is displaced to the side and remains rudimentary; its pubic cartilage is quite short, the posterior and larger portion being absent.

The pectoral fins are also peculiar in *Symphurus*. Where in the other forms they are simple membranous folds with a small cartilaginous base, here the cartilage is very large and club-shaped, with a narrow fringe of membrane.

The vertical fins are ray-less, with simple, diphycercal tail, until near the end of this stage. The mouth is horizontal. The musculature of the body is composed simply of the central system round the notochord. A thin muscular layer extends obliquely across the abdominal cavity from the posterior, upper part down to the base of the cleithra (figs. 37, 41, 42). The latter are as yet unconnected with the skull superiorly, the suprascapular and posttemporal not developing till a later stage.

Except in the Bothoids the cleithra are the only part of the fish which at present shows ossification; in the former, however, the supraoccipital spine and the parasphenoid are ossified (fig. 41). From the base of the cleithra a single paired muscle extends forward to the junction of the hyoid and branchial arches. Here the large ceratohyal (unsegmented ceratohyal and epihyal) is a prominent structure at this stage (fig. 42). The gill arches are also well developed, but the filaments are very short.

The geniohyoid muscle arises in the connective tissue under the hyoids, and continues forward a short distance to end in the skin-membrane, which forms the floor of the oral cavity. Anteriorly, the membrane encloses the articular cartilage, the sole representative at this stage of the mandibular rami. Laterally, the quadrate, symplectic and hyomandibular cartilages are well developed, but form a loose-jointed apparatus (fig. 42). There is no sign of preoperculum or pterygoids; thus, the pterygo-palatine arch is not yet developed. The premaxillaries with their ascending processes and the maxillaries can just be detected as thin hyaline rods. Of the cheek muscles only a thin layer is present, extending from the hyomandibular cartilage downwards and forwards to the head of the quadrate, where it ends in the oral membrane. The opening and shutting of the mouth is thus effected by muscles acting on the oral membrane in which the permanent arches are not yet developed.

A common feature of this stage, seen not only in Flat-fishes (figs. 36, 38, 42), but also in many normal Teleosts (fig. 99), is the distortion of the mouth and arches. The jaws may be wide open and drawn to one side, and the arches are retracted backwards and upwards. This phenomenon is most clearly seen in the Pleuronectoid* type and *Symphurus* (fig. 92).

Except in the third group there is no ossification in the head region, and the most striking thing is the small amount of solid structure in the skull; by comparison the visceral arches are much more developed (fig. 42). The skull is a hollow shell posteriorly, the parachordal cartilage extending only half way up the sides and posterior wall; thus, the roof is quite devoid of solid covering from the occipital wall forward. In the middle region there is only a narrow rod of cartilage below, the fused trabeculæ. Approaching the anterior margin of the eyes the rod widens out into the ethmoid plate, which forms a broader oral cavity below (figs. 46, 47).

* It is worthy of mention that KOEFOED figures a specimen of *Platysomatichthys* at the same early stage, and the asymmetry of the mouth is as clearly marked in his figure as in the present specimens.

There is no direct sign of asymmetry in the skull, but on comparing one form with another and with the condition in normal Teleosts we find considerable marks of disturbance in the ethmoid region, which reveal themselves as asymmetries in the next stage. The normal condition is for the trabecular cartilage to fold back and upwards anteriorly to form a tegmen over the forebrain. The only form in which any approach to this can be discerned is *Platysomatichthys* and this is the only form which shows definite olfactory capsules (fig. 46).

The lateral ethmoids are not yet developed, but loose chondroid tissue is present on each side of the ethmoid; from the posterior part of the tissue, behind the olfactory capsules, two distinct rods arise and run some distance backwards laterally to the forebrain (fig. 47). These are the developing supraorbital trabeculæ; they are quite short, equally developed, consisting of 10–12 chondroid cells each. They do not extend to the posterior margin of the eyes and thus as yet have no connection with the periotic capsules, which indeed are not yet developed.

These supraorbital trabeculæ, along which the dermal frontals develop later, play an important part in the development of the asymmetry in this region. Both WILLIAMS and MAYHOFF have evidently begun their investigations at a later stage, when the supraorbital trabeculæ were united with the developed periotic capsules and have thus failed to detect this symmetrical stage of the skull. It is possible, as MAYHOFF states, that the supraorbital trabeculæ may grow forward from the periotic capsule, but it is doubtful; certainly in *Platysomatichthys* the first growth is from the ethmoid region, and they seem therefore to be the remnants of a tegmen cranii.

STAGE II: Development of fin-rays in vertical fins; caudal fin heterocercal; ossification of jaws; initial asymmetry of ethmoid plate and parasphenoid. *Pleuronectes platessa* 9–10 mm., *Drepanopsetta* 7–10 mm., *Glyptocephalus* 8–12 mm., *Bothus podas* 9–12 mm., *Solea* 5–6 mm., *Symphurus* 10 mm.

The body of the Flat-fish can now be definitely distinguished from that of the great majority of the normal Teleosts; by the single dorsal and anal fins, slight thickness in comparison with depth and by the abdominal organs. The latter continue to grow downwards, causing a deep bend at the anterior end of the anal fin. Here the posterior abdominal wall in the first three groups is formed by a solid cartilaginous rod, now ossifying, which is sometimes called the first interspinal of the anal fin, but is here a separate structure developing before and independently of the fin. It is in reality a supporting rod connected with the descending rectum. Where the rectum is mainly horizontal in the beginning (*Symphurus* and *Solea*) the rod does not develop.

A large liver is now present behind the pectoral arch, lying wholly anterior to the coil of the gut in the Bothoids, but partly between the descending and ascending branches in the other groups, thus more on left side (figs. 42, 61, 76). In the Pleuronectoids a distinction can now be drawn between the forms which have a partly transverse coil and those which retain the more longitudinal one; the former (*e.g.*, *Drepanopsetta* and *Glyptocephalus*) though starting at a smaller size, are able to prolong the different stages so as to reach a much greater size than the latter (*e.g.*, *Pleuronectes*).

As the depth increases below, the height increases in the dorsal region, where the neural spines begin to show ossification. This increase in height is much greater in the forms with air-bladder, except in the case of *Symphurus* and *Solea*. In the Bothoids the dorsal fin grows rapidly forward to the snout and becomes attached there, firmly in *Bothus*, loosely in *Arnoglossus*. In the former, when the attachment is consolidated the long tentacle or ray above the head begins to disappear and so does the air-bladder (fig. 53), but in *Arnoglossus* both air-bladder and elongated ray are retained to a much larger stage (figs. 58, 59). This is a striking illustration of the function of the dorsal fin as a balancing organ or dorsal keel.

In the region of the head the changes are expressed in the down-bending of the skull on the vertebral column (notochord) and the up-bending of the jaws (figs. 43, 53; *cf.* 40, 41, 59). There is a clear correlation between the two phenomena. Both changes are associated with the ossification of the jaws and strengthening of the arches. With regard to the latter, the hyomandibular cartilage grows down alongside and over the posterior margins of the symplectic and quadrate, almost to the articular head of the latter, thus forming a stiffening rod to the earlier three-jointed arrangement (figs. 43, 59).

Meantime the pterygopalatine arch is being completed. From the anterior, upper border of the quadrate a nodule of cartilage, thin and pointed superiorly, grows up towards the eye and the dermal (frequently cartilaginous) palatine descends in front of the eye to become apposed to the anterior edge of the pterygoid cartilage; their asymmetry can already be detected; the left and the right are not in the same plane (fig. 76).

The dermal maxillaries and premaxillaries are now formed and the dentary of the mandibular forms round the symphysis and grows down over the ascending prong of the articular (fig. 43).

The ossification of the jaws and strengthening of the arches completely alters the appearance of the head; the extreme retraction and distorsion of the mouth is no longer seen and the jaws appear to become symmetrical. The hyoid and branchial arches now take up a more horizontal position, reaching forward close to the mandibular arch.

Meanwhile important changes are taking place in the anterior region of the skull. It was noted in the earlier stage that the growth of the ethmoid cartilage was different from the normal. This cartilage tends to grow forwards (maxillary prominence) and also upwards and backwards (mesethmoid) to form the tegmen for the forebrain. In the Pleuronectoids two groups can be distinguished; in the one (*Pleuronectes*) the ethmoid cartilage retreats on to the eyes and forebrain (figs. 43, 45), in the other (*Platysomatichthys*, *Glyptocephalus*) the forward growth continues for some time and a distinct snout is formed (fig. 61). This is connected with the more advanced asymmetry of the body in the former.

On examining entire specimens of the long-snouted forms we find that the ethmoid plate is now quite distinctly flexed to the left. Sections of the plate are not able to show this very clearly for the reason that the jaws are also asymmetrical; but further back, in a transverse section behind the eyes, thus in the weakest part of the skull, the asymmetry is readily seen. The dermal parasphenoid is now developing and in *Drepanopsetta* it is connected mainly with the left trabecular cartilage; in *Pleuronectes* the unpaired trabecula is continued further back and we find, that the trabecula itself is asymmetrical relative to the median plane of the brain, whilst the parasphenoid ossification is still further to the left (fig. 52).

At this stage, therefore, the pterygopalatine arches, the ethmoid plate and the basal axis of the skull are developing asymmetrically. The lateral ethmoids are just beginning to appear between the olfactory organs and the forebrain; the loose chondroid tissue round the latter is as before and laterally the slender supraorbital trabeculæ run backwards between the eyes as far as the upper anterior corners of the periotic capsules (sphenotic region) now well-developed. These trabeculæ consist of six to ten cartilage cells (increasing backwards) in a single vertical row and the interesting point is, that they are still almost symmetrical relative to the brain and of equal size. Thus little change has yet been made in the orbital region.

The condition in *Symphurus* requires special mention. The dorsal and anal fins in this type develop at once in their final positions; there is no posterior abdominal rod; the air bladder occupies the posterior half of the abdominal cavity on the left side; the caudal fin is only slightly heterocercal (fig. 92). There is very little ossification at any time but about 9–10 mm., the neural arches, pectoral arch and parasphenoid can be distinctly discerned (fig. 93). At the same period the jaws assume a more definite shape and a change can be noted in the position of the arches. The hyoid and branchial arches are drawn forward and a distinct snout is formed in front of the eyes. At this time also the ethmoid plate is seen to be asymmetrical and a kink is present in the ventral axis of the skull posteriorly where the parasphenoid joins the cranium. The most remarkable thing is, that the jaws now show a flexure to the right, where previously they were flexed to the left (*cf.* figs. 81, 92).

On examining the sections of a specimen about this stage we find that the anterior part of the caudal region is flexed in two directions, the upper part, neural spines and dorsal fin, bending over to the right, whilst the lower part bends to the left (fig. 85); thus, this part of the body has an appearance of rotation. The same appearance can be traced right forward to the head (figs. 82, 83); the dorsal part tends to the right, the ventral part to the left.

The Soles display slightly more ossification than *Symphurus* at this stage, and the most interesting point is that the caudal region, instead of showing a rotating appearance, is flexed above and below to the left, like the Pleuronectoids (*cf.* figs. 80, 74); in the abdominal region a reverse flexure is clearly seen (fig. 79); anteriorly the jaws are now flexed to the left. The skull, on the whole, still shows little sign of asymmetry.

The main impression given by these early stages of *Symphurus* and *Solea* is that the head is subject to varying flexures, first on the one side, then on the other (opposite sides in the two forms). At the same time the arches and jaws develop in an abnormal manner, compared with the normal Teleosts or the other Flat-fishes. Connected undoubtedly with this phenomenon is the very large amount of lymphoid tissue, both in the head and body of these forms.

Very similar phenomena to the above-described also occur in normal fishes, and it is of interest to note some cases, where the differences throw some light on the changes in the Flat-fishes. In *Trachypterus* at this stage the whole skull is depressed downwards and the jaws project upwards (fig. 99), so that there must be some difficulty for a time in the opening of the mouth. With the further development of the arches, however, the base of the hyoids is carried forward between the mandibular rami, thus enabling the mouth to be opened in the normal manner. But the skull remains permanently in the depressed condition and the jaws are very protractile. *Symphurus* comes nearest to this condition (fig. 92), but the skull returns later to a more horizontal position (figs. 93, 95) and a snout is formed where *Trachypterus* has none. The skull in the Bothoids is also strongly depressed and likewise recovers to some extent. The recovery is connected with the fact that the anterior part of the skull (ethmoid and parasphenoid axis) is flexed upwards again on the posterior part (figs. 75, 77, 93), and this is the case in all Flat-fishes.

In another Teleost the pectoral arch is drawn forward (fig. 98) when the jaws ossify and the skull is only slightly depressed. The same thing occurs in the Flat-fishes as a general rule, but here again it is sometimes retracted later, and this retraction is correlated with the forward growth of the abdominal muscles (fig. 45). When this occurs, towards the end of the second stage, the hyoclavicular muscles begin to show signs of rupture. In *Symphurus*, at a still later stage, it will be seen that the retraction of the pectoral arch is connected with the final changes in the metamorphosis (figs. 96, 97).

STAGE III: Lateral ethmoids developing asymmetrically, deflection of frontals; rupture of head muscles; opposing tendencies in body. *Pleuronectes* 10–14 mm., *Drepanopsetta* 10–30 mm., *Glyptocephalus* 13–over 50 mm., *Bothus* 13–30 mm., *Solea* 6–8 mm., *Symphurus* 12–18 mm.

The body now approximates to the adult form; the tail becomes homocercal (not in *Symphurus*); the posterior abdominal rod is bending forward below, so that the ventral contour of the body becomes more even. The pelvic fins are forming and begin to show their asymmetry. The distance between the abdominal rod and the pelvics becomes shorter, so that the abdominal organs are gradually becoming enclosed below by more solid structures. The marginal muscles have now fully developed, growing with the radialia and rays forward on the skull; the skull is now more under the influence of the dorsal fin. At the same time the pectoral arch has become attached to the skull by the growth of the suprascapular and posttemporal. Ventrally the abdominal muscles are growing forward over the cleithra, except in *Symphurus*.

This is the critical stage, from which apparently there is no return for the Flat-fishes. Other fishes show as much disturbance in the body and skull as has been present up to this stage; now changes follow one another in body, head, and skull, which are found nowhere but in Flat-fishes.

In all forms from *Solea* to *Pleuronectes* this stage is clearly marked externally by the rupture and re-formation of the hyocleithral connection. In the earlier stages there were first of all a single pair of muscles, then a second pair above the first, running from the base of the cleithra to the hyoid cartilages and branchiostegal membrane and in these stages already a thickening of the tissue between the muscles anteriorly indicated the nucleus of the urohyal bone, forming in its normal position. Soon after the pectoral arch has become attached to the skull and some time after the jaws have ossified, a break or discontinuity can be detected about halfway along the ventral edge of the muscles (figs. 43, 45). Following up the phenomenon through a series of specimens we see the upper part still maintaining its connection with the hyoid arch but not growing any larger or broader, whilst the lower, free part becomes more apparent and larger, forming a distinct break along the isthmus. Then in the clear space in front of this lower part chondroid cells appear, which rapidly set into a definite cartilaginous rod and thus the lower prong of the adult urohyal is formed, the central portion gradually receding towards the pectoral arch so that a curve or bay is formed anteriorly. The abdominal muscles are now spreading over the lower end of the cleithra and become part of the tissue round the lower prong. The latter is thus acted on directly by these muscles, whilst the upper, original part remains connected with the cleithra. Further, in the Rhomboid type the pelvic fins grow forward with the muscles, the left slightly in advance of the right, and become attached to the lower prong (fig. 75). In the Bothoid type only one pelvic, the left, grows forwards in this manner, the right not extending beyond the base of the cleithra. This forward growth of the pelvics is due to a secondary development of a large plate of cartilage, growing forward with the muscles from the innominate which remains behind the cleithra. This forward growth of the left pelvic is accompanied by a right flexure of the head (figs. 54, 56).

The rupture of the hyocleithral connection stands in the closest correlation with the ossification of the jaws and flexure of the ethmoid plate, which occur in the second stage. As already noted, the jaws have then become more vertical in position, whilst the hyoid and branchial arches have advanced forward at the base. If the latter were continued so far forward as to bring the base of the hyoids between the mandibular rami, the geniohyoid would still be able to function. But in the Flat-fishes, after the pectoral arch has become fixed to the skull, the line of the hyocleithral and geniohyoid muscles lies above the mandibular base and the mouth can hardly be opened with the original apparatus.

On the other hand, the hyocleithral muscle is not ruptured in *Symphurus* (fig. 95), and this is correlated with two conditions; the weakly ossified jaws remain more horizontal and the abdominal muscles do not grow forward beyond the cleithra.

The strengthening of the hyomandibular arch in the second stage is followed by the gradual appearance of the opercular bones; of these the first to ossify is the preoperculum, which forms along the cartilaginous rod already described (figs. 43, 59). At this time the cheek muscles show a great development, occupying nearly the whole space behind the eyes. Anteriorly they concentrate in the fibrous membrane which surrounds the oral cavity and continues forward round the articular bones below as well as the maxillaries above. These cheek muscles are now placed asymmetrically (figs. 44, 45). On the left side (*Pleuronectes*) the anterior attachment or insertion in the oral membrane extends higher up than on the right side and on the left side also some muscle strands continue forward and upward towards the head of the maxillary (fig. 45 *cm*); this maxillary slip is not present on the right side (fig. 44). Like the hyocleithral connection the oral membrane anteriorly has been subject to disturbance at the same time and presumably from the same causes.

Whilst these changes are taking place extra-cranially, extensive deformation is proceeding in the skull. It has been seen in the previous stage, that the dermal parasphenoid and ethmoid cartilage were developing asymmetrically, whilst the lateral ethmoids were just making their appearance. The principal feature of the present stage is the enormous increase in the ethmoid cartilage. Except in *Solea* and *Symphurus* its growth is rapid and everywhere asymmetrical; thus, the lateral ethmoids are asymmetrical from the beginning.

In *Glyptocephalus* the development of the asymmetry in the skull is so slow between 13 and 40 mm. that the changes are readily followed. Anteriorly, the lower jaw is seen to lie to the left (fig. 66), the left olfactory organ is higher than the right (fig. 67), and the left wing of the ethmoid is higher up and further back than the right. Below, the left palatine is higher than the right. The vomer is forming asymmetrically (at 34 mm.), and the parasphenoid, in addition to the left flexure of the earlier stage, shows a slight turning upward (fig. 69). This is associated with the turning of the ethmoids. Mesially, the interorbital membrane is still complete, and the anterior eye-muscles are inserted round it (figs. 64, 68). The fore-brain is still anteriorly between the eyes (fig. 70).

The supraorbital trabeculæ share the asymmetry of the developing ethmoid wings, but they remain of the same size (in other forms the left may be reduced at this stage; WILLIAMS). Anteriorly, the left trabecula is higher than the right (figs. 65, 69); further back it is seen to bend over towards its fellow even at 13 mm., and the only change at 34 mm. is, that both are bending more to the right.

The dermal frontals are forming already at 13 mm. whilst the ethmoids are developing asymmetrically. In the Pleuronectoids the frontals never form an arch over the eyes as in the Bothoids. The left frontal ossification is from the beginning more slender than that of the right, and, following the approximation of the supra-orbital trabeculæ, the two frontals are bent upwards to meet in a ridge on the top of the skull. At 34 mm. the right frontal has increased considerably, the left frontal has remained the same in extent but increased in density. Viewed from above, it is seen that the frontals simply bend over together to the right side (figs. 62, 63).

In *Pleuronectes*, however, the anterior part of the left frontal between the eyes does not develop, and the deflection takes place rapidly (figs. 49, 50). Connected with the difference between this form and *Glyptocephalus* are the conditions in the body.

In *Pleuronectes* the coil remains throughout more in a longitudinal than a transverse plane and the extension of the liver on the left side increases the disproportion on that side (fig. 73). In *Drepanopsetta* and *Glyptocephalus* (figs. 43, 61) the descending and ascending parts of the coil come to lie almost parallel to one another in the same obliquely transverse plane, thus leaving the posterior and upper part of the abdominal cavity empty.

The flexure of the caudal region is well seen in the sections of all Pleuronectoids at this stage (fig. 74); the upper and lower margins of the body tend to the left; thus, the adult condition is derived from the pelagic stages. Further forward, the dorsal part still remains to the left, but the abdominal organs and the pelvic fins are relatively to the right (fig. 71). Thus, the organs have a different tendency from the caudal region and posterior abdominal rod (*in* in figs. 56, 57, 73). And it may be noted, that the anterior abdominal muscles have not yet grown forward over the pectoral arch, nor is the hyocleithral muscle ruptured in *Glyptocephalus* at 34 mm. (fig. 61, *cf.* 44, 45).

In the Rhomboid and Bothoid forms, with an air-bladder, the dorsal half of the body tends to the right, and this right flexure can be followed forward on the skull (figs. 54, 56). The posterior abdominal rod (*in* in fig. 57) also tends to the right side when it bends forward, showing that the flexure is a longitudinal one and not merely transverse, and this condition is found again in the adult. But the abdominal organs, so long as they are free, and the lower part of the body are flexed to the left, as is seen in the position of the pelvics (fig. 56) and of the hyoids (figs. 55, 54; *cf.* fig. 50).

The changes in the skull of the Rhomboids follow essentially the same course as in the Pleuronectoids, but there are one or two interesting differences. In the first place, the trabecular cartilage and the ethmoid are more flexed than the dermal parasphenoid ossification (fig. 55); secondly, the frontal ossifications form round, not apposed to, the supraorbital trabeculæ; the same thing is found in *Limanda*. The ossification in the Rhomboids is sooner developed and stronger than in the Pleuronectoids, but the Bothoids are still more remarkable in this respect. The skull of the latter as well as the arches is strongly ossified in the second stage (figs. 54, 59), and the fish remains pelagic for a long period with a slight asymmetry in the skull, like *Glyptocephalus*. The asymmetry consists in the deflection of the parasphenoid axis, which takes place already in the second stage, and the raising of the right frontal slightly above the left. The frontals form a distinct dome above the fore-brain, thus a different kind of ossification from that seen in *Rhombus* (fig. 54).

As development proceeds, it may be noted that the brain, especially the forebrain, seems to rotate towards the eyed side, which means naturally that the skull is apparently rotating in the opposite direction (figs. 51, 56).

The deflection of the frontals means that the eye of the one side has a greater freedom of movement than that of the other side, but the condition in *Glyptocephalus* (figs. 63, 65) shows that the migration of the eye depends on something more than the bending of the frontals. This migration is due to the development of a special subocular tendon or ligament, first mentioned by MAYHOFF.

When the left frontal (in Pleuronectoids) bends to the right, the left palatine appears to be pressing the left ethmoid wing upwards and backwards (fig. 67). A concentration of the tissues under the left eye then takes place, and this can be followed from the posterior corner of the left lateral ethmoid backwards (fig. 68) to the lateral aspect of the skull below the left supraorbital trabecula. Posteriorly, the thickening consists of at least twelve rows of cells; on the right side there is a similar appearance, but only six cells, and further forward, under the right eye, it disappears. Throughout Stage III this concentration gradually increases, until the eye rests on it, as in a sling (figs. 55, 72).

In *Solea*, the development of the asymmetry proceeds along similar lines during this third stage. The frontals are flexed in the same way, and the subocular ligament gradually develops under the migrating eye. Extra-cranially, however, there are great differences. The dorsal flexure of the body, which may be on the opposite side during the earlier stages, now becomes definitely a flexure towards the eyed side, not eyeless, as in the previous types. The anterior part of the head seems, consequently, to be rotating (fig. 78). The hyoid arch below is also flexed to the future eyed side relative to the parasphenoid. Hence the asymmetry of the skull is brought about in a totally different manner. Examination of the entire specimens shows also that the articulations of the jaws and pterygopalatines have now become affected. The left premaxillary diverges from the right, leaving a distinct gap between (figs. 76, 77); the maxillary muscle of the blind side and the oral membrane appear to be ruptured at the same time, and the loose premaxillary becomes articulated at its lower end to the dentary of the mandibular (fig. 77). Further, the premaxillaries and maxillary cartilages are now depressed on to the head of the developing vomer, which is bending downwards, and the snout of the ethmoid begins to appear above. The pterygopalatine of the eyeless side (*ppt'*) is now much farther back than its fellow. Comparison of figs. 76 and 77 shows, indeed, that the whole of the upper part of the mouth (maxillaries and palatines) has come to the eyeless side, to such an extent that the dentary end of the pre-maxillary and pterygopalatine are beneath the migrating eye. It will be seen also, that in spite of these drastic changes externally, the skull is as yet comparatively little altered. Above, the dorsal fin is not yet overhanging the eye; below, the hyocleithral connection has just been ruptured, but the adult urohyal is not yet formed; the pelvic fins are just developing; the abdominal muscles do not as yet pass beyond the pectoral arch.

On the whole, *Solea* provides the best material for studying the action and effect of the extra-cranial forces operating on the skull. It is quite a different mode of asymmetrical development from that seen in the common forms.

STAGE IV: Migration of the eye; completion of metamorphosis.

The deflection of the frontals is not always synchronous with the migration of the eye; the former may be displaced quite early and the eye show a slight asymmetry, but something more than mere lateral deflection of the frontals is needed to complete the transference. A few examples will illustrate this.

	Frontal deflection begins at	Migration of eye completed.
S. vulgaris	7–8 mm.	8–9 mm.
Symphurus lactea	18	21
P. platessa	10	14–15
Drepanopsetta	10	over 30
Glyptocephalus	13	,, 60
Arnoglossus Rüppelii	12	,, 50
Bothus podas	12	,, 30

In specimens of *Glyptocephalus*, from 13 mm. onwards, a distinct gap is seen between the deflected frontals and the eye that is going to migrate (figs. 62, 63). Hence the connection between the deflection or "torsion" of the frontals and the migration of the eye is not a direct causal one; both are dependent on other factors.

The conditions in head and body preceding the transference of the eye are as follows. In the skull, the forebrain is still forward between the eyes, and the subocular ligament is still below the migrating eye (figs. 55, 70, 72). The jaws are more horizontal than vertical (figs. 45, 61); the hyocleithral connection is ruptured, but the adult urohyal is not yet formed, and the abdominal muscles have not yet grown forward over the pectoral arch. The abdominal organs are contracting, but still free below in great part; pelvic fins just appearing; abdominal rod beginning to bend forward (*cf.* figs. 61 and 45).

When the eye is definitely on the ridge (figs. 48–51), the forebrain has retreated into the cranium, the eyes are close together; the subocular ligament has grown up like a wall on the outer side of the migrating eye, and is ossified anteriorly and posteriorly. The interorbital septum is being ruptured anteriorly; the lower margin is deflected over to the subocular ligament, the insertions of the anterior eye muscles accompanying it, but the upper part is still attached to the cartilaginous lamina above (fig. 49). Thus, the fenestra in the interorbital septum of the adults is formed in the last stage of the metamorphosis.

Above the skull the dorsal fin has grown forward and bends to the left behind the eye (Pleuronectoids), where it rests on the posterior ossification of the subocular ligament (fig. 51). The jaws are becoming more vertical than horizontal (fig. 44), that is, the skull is foreshortened; the urohyal approximates to its final shape, the abdominal muscles are beginning to pass forward over the pectoral arch, the pelvic fins are well developed, the ventral wall of the abdomen is almost closed by the forward growth of the abdominal rod (fig. 44). When the metamorphosis is completed, the abdominal rod reaches the base of the pelvics, and the abdominal muscles are attached to the lower prong of the urohyal.

Regarding the ossifications in the subocular ligament, there can be no doubt they are of dermal origin, in so far therefore akin to the frontals. But anteriorly the ossification forms in the tissue connecting the lateral ethmoid and head of the palatine and is later, as we know from the adult condition, incorporated in the lateral ethmoid ossification to form the prefrontal. The posterior ossification might be considered part of the frontal ossification, since it develops in the place where the frontal would have been had it not been deflected, but it is nevertheless a fresh growth. Hence the "pseudomesial" bar which results from junction of the anterior and posterior ossifications is, on the whole, a new and special structure peculiar to Flat-fishes, as TRAQUAIR believed.

In the Rhomboids and Bothoids the subocular ligament develops under the same conditions as in the Pleuronectoids, but it ossifies sooner, in keeping with the earlier ossification as a whole in these groups. In *Solea* it is worthy of note that a similar thickening of the subocular tissue is also present under the right eye, though not so dense as on the left side; in one form, *S. azevia*, it also becomes partly ossified on the right side. It has been seen that these forms display alternating flexures of the body, accompanied by deformation of the skull and arches on both sides of the head; hence the subocular ligament on both sides.

The "subocular shelf" which is a fairly common feature among the advanced normal Teleosts, may be considered the nearest homologue of the pseudomesial bar of Flat-fishes and probably arises in the same way.

There are obvious signs that the eye does not move to its final position without some considerable amount of force. Not only is there a lateral transference, there is also a slight oscillation, forwards then backwards. Owing to the asymmetry of the lateral ethmoids the migrating eye is at first a little behind the other. As the subocular ligament develops and ossifies posteriorly, the eyeball moves forward on to the ethmoid cartilage and the anterior end of the dorsal fin grows down behind it posteriorly. The migrating eye is thus anterior to the other. The growth of the prefrontal ossification in front now presses it backwards and over to the other side into its final position, which is a little posterior to the other eye in the great majority of forms. The migration of the eye in Flat-fishes, which has been a puzzle for so long, can thus be referred to simple and natural causes.

In the Rhomboids the ossification of the skull is already far advanced in the previous stage ; in the Pleuronectoids it is most apparent in the fourth stage. The trabecular cartilage along the basal axis and in the frontal region disappears entirely, its place being taken by solid ossification. The ethmoid cartilage persists, however, and the only ossifications in this region previous to complete metamorphosis are the dermal parasphenoid and vomer. Neither the posterior descending processes of the lateral ethmoids nor the ascending processes of the parasphenoid are as yet developed.

In both the Rhomboids and the Pleuronectoids, therefore, the ossification of the skull is proceeding whilst the asymmetrical changes are in progress. The Bothoids show a remarkable difference in this respect. Here the skull is strongly ossified already in the second stage ; in particular the frontals have appeared below the supra-occipital ossification, which by that time projects forward in a sort of rostrum (fig. 53), seen only in this group, and the right frontal is slightly in advance or above the left. The frontal ossifications extend down on each side to meet the supraorbital trabeculæ and thus form a dome-shaped covering over the fore-brain (fig. 54). The conditions for the migration of the eye are thus very different in these forms and the matter is still further complicated by the forward growth of the dorsal fin. The ossified rostrum continues its growth forward and downwards, particularly in *Bothus*, until it nearly touches the ethmoid cartilage. The basal supports or cartilages of the dorsal fin then grow downwards to bridge over the gap. The first basal cartilage is very large ; in *Bothus* it becomes firmly attached to the upper margin of the right lateral ethmoid ; thus the skull and fin are asymmetrical relative to one another. This happens early and the balancing ray above then disappears along with the air-bladder, as already described. In *Arnoglossus* the first basal cartilage does not become united to the lateral ethmoid previous to metamorphosis.

In the latter form, when the first basal cartilage is about to rest on the ethmoid, the frontals are already bending over to the left. The basal cartilage is then seen for a short time to hang freely on the right side (fig. 58), and during this period the tissue between the skull and fin is ruptured and the right eye appears in the slit. The transit of the eye is here rendered easy by the frontals going to the left below whilst the dorsal fin is flexed to the right above. After the eye has passed, the anterior basal support settles down on the lateral ethmoid of the right side and the tissues fuse permanently.

In *Bothus* the skull is firmly ossified, and the first basal cartilage of the dorsal fin is permanently fixed long before the extra-cranial structures and the body have acquired their full asymmetry. When the final stage approaches and the subocular ligament is plainly seen under the right eye, the supraoccipital rostrum retreats, or the frontals grow forward, so that a wider distance separates the ethmoid and rostrum, the gap being finely bridged over by a number of basal cartilages balanced one on the other. The tissues in the gap split longitudinally to form an opening, and for a short time the right eye is able to see to the left or right side. Then the frontal of the right side gives way, and the right eye is rapidly pushed through the gap, as described by AGASSIZ. But the left frontal and prefrontal suffer no deflection, and the right eye is seen to lie freely without socket on the interorbital ridge (fig. 75). Later, a fibrous membrane appears round its base, and the eyes move further apart; it can then be seen that the right eye is being forced backwards and upwards under the basal supports of the fin by the growth of the prefrontal of the right side. Here again, it is worth noting, these final changes in the position of the migrating eye have arisen after the pelvic fins have developed, and the enclosure of the abdomen has taken place. The parasphenoid axis has been deflected when the young fish is about 13 mm. in length; the asymmetry of the body is not complete, and the eye does not migrate until the fish is over 30 mm.

In *Solea* the final changes in the skull are rapid and drastic. As mentioned, the jaws have assumed their final shape towards the end of the previous stage, whilst the skull is still in an early condition of asymmetry, and the changes along the ventral line, urohyal and abdominal region are still incomplete. The latter changes and the deformation of the skull take place practically at the same time. The dorsal fin also grows forward; the basal supports of the fin are long, slender, cartilaginous rods, the first starting from the second neural spine and passing right forward over the skull to a position just behind the eye; thus, the fin overhangs the eye. When the slender bones of the skull give way, the frontals protrude or bulge out to the right, and the ethmoid is bent up to meet the base of the overhanging fin; the parasphenoid axis is bent and twisted, and the eye is very rapidly carried over to the other side. This occurs in *S. vulgaris* about 8–9 mm., but *S. variegata*, which has no air-bladder, reaches 18 mm. before it is metamorphosed.

In some respects *Symphurus* stands to *Solea* as *Bothus* to *Arnoglossus* (or *Rhombus*); the dorsal fin is forward on the snout at an early stage, and the migrating eye has to find its way across under permanent structures. But there is a wide difference in the mode of transference; here the eye passes under the dermal frontals.

The structure of the dorsal fin above the head in *Symphurus* is somewhat similar to that in *Solea*. At 10 mm. already a short cartilaginous rod extends from the tip of the second neural spine forward over the skull as far as the mid-brain, where it rests on a second, longer rod of the same nature which curves forward to near the snout (fig. 93); at a later period after metamorphosis a third rod develops anteriorly. Thus, the dorsal part of the head is protected by a cartilaginous bridge of rods from the beginning, which means that the skull cannot be distorted in the same manner as in *Solea*. Above these rods are the five elongated soft rays of the dorsal fin.

Ventrally, the jaws and visceral arches are affected in the same manner as in *Solea*. The premaxillary of the right side becomes articulated to the dentary of the mandibular when the fish is about 18 mm. in length (*S. lactea*). At this time the abdominal organs begin to contract and the air-bladder begins to grow smaller. As in *Bothus* and *Arnoglossus* its contents appear to pass into the hind-kidney. Soon a definite retraction of the gut into the cavity takes place, and the balance of the fish is apparently upset. The space between the pectoral arch and the anal fin closes; the pectoral arch, instead of having a strong curve forward, is straightened out, thus affecting the hyocleithral connection. The latter does not rupture, however; for a short time the jaws assume a more vertical position than before (*cf.* figs. 96, 97). Whilst the jaws are vertical, the ethmoid plate with the vomer and anterior part of the parasphenoid is bent upwards and curved to the right (fig. 97). The right eye then suddenly retreats from the thick integument and disappears from the right side into the tissues of the head, emerging on the other side close above the left eye. The two eyeballs touch without sockets (fig. 95). One case has been recorded in which the migrating eye remained inside the tissues of the head (GARMAN).

The change in the frontal region can be followed both in the sections and the entire specimens. Comparing the sections of specimens at 10 mm. and 17 mm., a very great increase can be remarked in the density and amount of the muscular and lymphoid tissues above the skull (figs. 81, 86). At 17 mm. a clear space is beginning to appear just above the ethmoid, between the latter and the most anterior of the basal cartilages; these are being withdrawn from the skull and to the right side. The change in the frontals has now begun.

In the orbital region and posteriorly there is little disturbance at 10 mm.; at 17 mm. one can detect signs of the separation of the tissues. The supraoccipital spine and frontals are still together over the forebrain and eyes, but the former is breaking away from the lateral frontals, and the left frontal is raised slightly above the level of the right. The supraorbital trabeculæ are no longer continuous from the periotic capsules to the ethmoids; at the level of the eyes (fig. 87) they are seen to be in two portions, the upper connected with the dermal frontals above and the periotic capsules behind, the lower (*str'*) only with the ethmoids. It appears, therefore, that the posterior parts of the trabeculæ are being raised upwards with the ossifications, whilst the anterior parts remain in the skull.

A further interesting point revealed by the sections at 17 mm. is that a thickening of the tissues occurs above and behind the right eye similar to the subocular below (fig. 87); this is not seen in any other type, and obviously prevents the elevation of the eyeball. Hence the eye cannot migrate over the roof of the skull as in other forms.

At 18 mm. the separation of the supraoccipital and frontals can be seen in the entire specimens (fig. 96). The cartilaginous basal supports of the dorsal fin are present as usual, but an additional set of processes appears just above the skull, and these new processes are not cartilaginous but fibrous. Above there is a long process from the top of the cranium, which is clearly the supraoccipital spine. Further forward, just behind the eyes, two more dermal rods appear, joined together posteriorly, but separating above the eyes. The rod on the left side ends freely in front, just below the anterior basal support of the fin; the other passes forward to the right, and cannot be clearly followed beyond the right eye.

The same arrangement is present in the specimen with the eye sinking into the tissues (fig. 97), but here the right dermal rod can be made out to be attached to the lateral ethmoid in front, with the migrating eye beneath it. In the metamorphosed specimen (fig. 95) the right eye has come through under the dermal ossifications. The right ossification remains attached to the lateral ethmoid, the left is free; posteriorly they are united, but still at some distance from the supraoccipital. Here it will be noticed that the jaws have resumed their more horizontal position, and the parasphenoid axis has straightened out again.

From their position, mode of development, and character, membranous, not cartilaginous ossifications, it is clear that these dermal rods above the eyes are the frontals. The membrane in which they were forming has been drawn upwards posteriorly with the posterior part of the supraorbital trabeculæ (as indicated by the sections of the 17 mm. specimen), and has separated from the ethmoid, except at one corner on the right side, when the anterior end of the parasphenoid-vomer axis has bent upwards; the eye is forced through the tissues at the same time.

It serves, as confirmation of these phenomena, that the top of the adult cranium is open and unossified (fig. 20) with these dermal frontals exactly as in the metamorphosing and metamorphosed specimens. The only difference is, that the frontals appear to have grown back to join the supraoccipital, but this may be due to the formation of the dermal parietals in the uplifted membrane.

Theory of Metamorphosis: Symmetry and Balance.

The metamorphosis of Flat-fishes may be said to arise from an obliquity of growth superimposed on the ordinary course of development. Few parts develop in the normal manner or position. Unless we suppose them inherited, these peculiarities must have a direct cause or direct causes. One question is, therefore, whether the abnormal or oblique phenomena of development are so related to one another that direct causation can be deduced from their sequence. If so, what is the binding law of the causation; or, what theory will best describe the facts?

With regard to the relation between the phenomena, it is true that the asymmetry develops in a regular manner, just as if it belonged to the ordinary course of development, but if we compare the life histories of different species, we find that the progressiveness or rate of change from the normal depends upon recognisable factors (*cf. Pleuronectes* and *Glyptocephalus*, *S. vulgaris* and *S. variegata*). Secondly, the extreme asymmetry peculiar to Flat-fishes, viz., that of the skull, is invariably preceded by certain changes in the head and body. Hence the possibility of direct causation may be concluded. A brief survey of the facts, having the adult structure in mind as well as the development, will show how far this conclusion is justified and pave the way for a constructive theory.

The nature of the oblique growths or departures from the normal varies in the different regions. In the skull the changes are obviously due to pressure or stresses; apart from their tendency to grow, the structures are quite passive. The eye is not pulled into its new position by the frontals or its own muscles; it is demonstrably pushed over by the growth of the subocular ligament or the prefrontal. These again are constrained to grow obliquely by outside pressure. Where rupture of the tissues is apparent, it is not due simply to the structures growing apart; they are definitely forced apart (*e.g.*, frontals in *Bothus*, frontal and prefrontal in Pleuronectoids and Rhomboids, vomer and ethmoid in *Solea*). The parasphenoid, the trabecular and ethmoid cartilages are diverted from their ordinary longitudinal and vertical directions of growth, not by mutual pressure or internal interference, but by external forces. In fact, it is impossible to give a satisfactory description of the asymmetries of the skull without reference to the external pressure and compression. The ordinary course of development provides no motive force or forces for the disruptive changes we see in the skull of Flat-fishes.

Extra-cranially the oblique growth results from tension or strains; an active force or factor is discernible. For example, the upper jaw and structures connected therewith are pulled to one side (*e.g.*, in *Solea* and *Symphurus*) and the oblique tension is so great, that both the muscles conveying it and the structures under tension are displaced and may be ruptured (*e.g.*, cheek muscles on one side, separation of premaxillaries, loosening of palatine attachments, and re-formation of jaws in *Solea* and *Symphurus*). The base of this tension lies along the hyomandibular arch, which is not a fixed structure. Throughout metamorphosis this arch through its connections with the hyoid arch posteriorly and the articulars anteriorly, is affected by a more ventral tension acting from the pectoral arch on the lower jaw. During the third stage of metamorphosis the muscle conveying this ventral tension is also ruptured in many cases. The extreme points of resistance are here the tip of the lower jaw and the foot of the pectoral arch. These tend to approach each other; but during this stage the pectoral arch becomes attached to the skull by the growth of the suprascapular and posttemporal and offers more resistance to the tension. The jaws become more and more vertical in their slope until, one would think, the geniohyoid muscle cannot function. The hyocleithral connection is then ruptured and a new method of opening the lower jaw developed. In the cases where this does not happen, the pectoral arch is curved strongly forward and the lower jaw remains more horizontal (*e.g.*, in *Symphurus*).

From the adult structure of the arches and their position in sections of the young stages it is clear that this lower tension has acted obliquely when the structures are developing. The upper tension depends for its obliquity upon the lower; the former bears more directly on the skull, but its action alone would not cause the complete change that occurs in the skull. In the first two stages the ethmoid and trabecular cartilages are but slightly affected, and the main differences from the normal indicate only that pressure or compression is at that time preventing the cartilage from developing (*e.g.*, absence of tegmen cranii). The principal changes in the skull develop in the third and fourth stages (*e.g.*, lateral ethmoids, frontals, subocular ligament), when the lower tension is causing the rupture of the hyocleithral connection, that is, when there is an increasing difficulty in opening the jaws, as mentioned above. At this period the two tensions are operating together on the skull anteriorly, and this appears to be the essential, determining factor in the divergence of the Flat-fish skull from the normal. The subocular ligament, which develops in the tissues outside the skull, on one side only or on both sides (*Solea*), between the palatine-lateral ethmoid anteriorly and cranium posteriorly, may be regarded as a product of the tension. And the magnitude of the tension may be judged from the fact that the skull suffers deformation under it even when strongly ossified (*e.g.*, *Bothus*).

The principal changes in the skull and arches can thus be referred to the ventral mechanism of the head; the latter is more or less asymmetrical from the beginning, *i.e.*, when the structures are forming, and its asymmetry must be derived from some condition in the body. The asymmetries in the posterior region of the skull can also be referred to the conditions in the body, that is, this part of the skull is under the influence of tensions operating on the dorsal fin and superior pharyngeals (*cf.*, *ante* p. 87).

In the abdominal region the oblique growth of structures is also due to tensions in most cases, *e.g.*, flexure to one side of the neural and hæmal spines, dorsal and anal radialia and rays, pectoral arch and abdominal rod. That these abdominal tensions are stronger on the one side than the other, when the structures are developing, is shown in three ways; in sections of the early stages the abdominal rod and the vertebral spines behind it are seen to be growing towards the one side;

the adult structures here are asymmetrical; the growth of the pelvic fins, which lie across the tension, is impeded on the side of greater tension, according to the time of their appearance. The earlier they appear, the greater is their disturbance; *e.g.*, in *Symphurus*.

The growth forward of the abdominal muscles beyond the pectoral arch is also asymmetrical and seems to be connected with the rupture of tissues there. It follows upon the rupture of the hyocleithral muscle and does not occur in the cases (*e.g.*, *Symphurus*) where this does not happen. On the other hand, this forward growth is also seen in certain normal fishes, where apparently the hyocleithral connection is not disturbed, but these fishes also display a considerable amount of asymmetry in the adult structures.

As shown above, the sequence and nature of the asymmetrical changes point always to some anormal condition of the body, which can only mean that the balancing conditions are defective by comparison with those in other fishes.

The influence of the balancing conditions of the body on the development may be illustrated by some examples. Sinistral forms have almost invariably an air-bladder lying more or less on the left side; those without an air-bladder have a combination of sinistral and dextral characters. Dextral forms have either no air-bladder or the air-bladder more or less on right side. The balancing structures, air-bladder, dorsal and anal fins and pelvics all develop asymmetrically with respect to the vertebral column and the skull; even the column is asymmetrical, showing longitudinal curvatures. Throughout development variations in the rate of metamorphosis (judged by length) can be referred to differences in the balancing conditions of the abdominal region. The rate of change is most rapid in forms with an air-bladder on the right side (*Solea*), slowest in forms with a small air-bladder on the left side, or none at all. During development, before the abdominal cavity is enclosed below, the abdominal organs invariably show a flexure in the opposite direction to that of the abdominal rod and caudal region, whilst the dorsal part of the body has the caudal flexure as far forward as the skull. In the common forms, when the cavity is enclosed below, the dorsal and ventral parts of the fish have the flexure to the same side right forward to the mouth, and the metamorphosed specimens, like the adults, swim or lie on this side.

The connection between balance and flexure may be expressed simply in this way. If the organs or structures do not balance on each side of the longitudinal, vertical plane, there will be a greater flexion of the body to the one side than to the other; the longer the unequal flexion persists, and the greater its intensity, the greater will be its influence on the growing tissues; hence the flexures to one side (exemplified in the posterior abdominal rod, jaws and anterior end of the skull).

The range of influence of a defective balance at any part is determined by the shape or position of the muscles there. Unequal flexions arising in any part would not affect more distant parts (*e.g.*, mouth or tail) at least, not asymmetrically, without the direct assistance of the muscles. For example, the free abdominal organs may show for a long period a contrary flexure to that seen in the caudal region immediately behind. As the muscular system develops, the marginal sets are arranged in the shape of a double V about the vertebral column, the points being posteriorly. The first or inner set proceed backwards from the axis to the spines of the third or fourth vertebra behind; from there the outer set extend forward across the intervening spines to be inserted in the radialia corresponding to the original vertebra. Thus, a defective balance in the posterior part of the abdominal region affects the spines of the anterior caudal region as well, and it is here we find the first structural asymmetry in the body. When the posterior abdominal muscles operating on the anterior anal radialia develop, the abdominal rod in front of them begins to bend forward. This is the dominant characteristic in the body of Flat-fishes, not seen in normal fishes. At the same period the anterior abdominal muscles passing down to the foot of the cleithra and developing pelvics cause the pectoral arch to retreat. The abdominal cavity closes like a spring, and the asymmetrical flexure of the abdominal rod and caudal region joins up with the already present flexure of the arches and jaws.

In the earliest stage, when there are no body structures to display flexure, the presence of defective balance and unequal tension may be concluded from two separate phenomena. In the Pleuronectoids, which have no air-bladder (also in *Symphurus*, which has a very large asymmetrical air-bladder on the left side), the jaws and arches of the head show a flexure to the left; this flexure can be referred to unequal tension in the muscular strands passing down in the walls of the abdomen to the foot of the cleithra, and this unequal tension to defective balance in the posterior part of the abdominal region, which contains the asymmetrical coil of the gut on the left side. In the Rhomboids and Bothoids, however, with large, partly asymmetrical, or small wholly asymmetrical air-bladder, these early left flexures have not been seen, but the air-bladder is placed just above the coil of the gut. At this stage the balance here is not defective.

The phenomena of development, therefore, indicate that the oblique growths of the body and head and asymmetry of the skull arise from the defective balancing of the abdominal organs. The difficulty begins with the coiling of the gut. The Pleuronectoids, apart from the abdominal rod, have no extra balancing structures (except advanced *Glyptocephalus* in the head region), and the asymmetry develops quite regularly, the rate of change depending solely on the continued freedom ventrally of the abdominal organs. The asymmetry is impressed on the anterior caudal region and the jaws in the earliest stage, and this in the end overcomes the secondary balance acquired by the developing organs. That the latter plays an important part in delaying the junction of the two ventral asymmetries can be seen from a comparison of *Glyptocephalus* and *Pleuronectes*.

In the early stages the Rhomboids are distinguished from the preceding by the air-bladder and the earlier development of the abdominal rod; the height of the fish becomes greater; the balance of the fish is better to begin with. The first danger of asymmetry over, these fall into a second, which seems to be due to the secondary balance of the organs. The closed air-bladder under the vertebral axis becomes superfluous or excessive; the upper part of the trunk is persistently raised or inclined to the right relative to the lower part (seen in the adult structure, *e.g.*, in the parapophyses of *Rhombus*). A right flexure is thus impressed on the anterior caudal vertebræ and spines as they develop. In the absence of further balancing structures, this caudal flexure dominates the later development, just as in the case of the Pleuronectoids, but the abdominal rod does not bend so far forward here, the enclosure of the cavity being completed by one or two additional cartilaginous rods.

If the air-bladder could disappear at an appropriate moment, after serving as a counterbalance to the coil in the initial stage, it is conceivable that the structures would develop symmetrically and the vertical balance be maintained. Such cases possibly do occur; among the Flat-fishes, however, we see only the failures. *Bothus* comes nearest to success. This form has from the beginning an additional balancing organ in the shape of a long, stout ray anteriorly above the head. The height of the fish relative to its thickness becomes very much greater than in any other Flat-fish. The air-bladder and long balancing ray disappear together at 12—13 mm.; the dorsal fin is then firmly attached to the skull, thus forming a fixed dorsal keel. The skull becomes strongly ossified, so that in flexions of the fish the skull and dorsal part of the trunk move as one piece. In this condition the later stages of *Bothus* remain for a very long period; they are taken at all periods of the year. But the air-bladder has apparently been too late in its disappearance; when the dorsal fin becomes attached to the skull this has already been flexed to the right anteriorly. The base of the dorsal fin is also to the right of the mean longitudinal plane, which again may be referred to the influence of the air-bladder, as in the case of the Rhomboids. How near this form comes to the normal fish is shown by the fact that the left half of the skull remains normal.

In contrast to the above and in confirmation of this view regarding the part played by the air-bladder, we have the *Solea* forms, in which the air-badder is more or less on the right side. A possible explanation for the transference of the air-bladder to the right side in these forms will be given later, meantime it has to be noted that this position accentuates the left flexure caused by the coil of the gut. The fish turns over more rapidly than any other type, except in one instance (*S. variegata*), which has no air-bladder.

Having thus briefly indicated the parts played by the coiling of the gut, the air-bladder and abdominal organs in the balancing and asymmetry of the Flat-fish, it seems advisable to take a broader view and consider the conditions found in the normal fishes at the same time. If the theory put forward above is true, it implies that all fishes with a coil have had some difficulties in balancing, and these should be expressed in the structures; further, we should be able to see how they avoid a permanent asymmetry. Again, if the balancing conditions are precarious for the young Flat-fishes of the present day, it may be inferred that they have been so from the very beginning, when they and their nearest allies diverged from one another; hence a means of determining these allies.

In the early fishes the gut is long, without coil, and reaches nearly the whole length of the body and tail. So far as we know, the lower orders of the Teleosts have never fallen into asymmetry, and the comparatively long abdominal region is probably the explanation. The effects of any asymmetrical tendency are dissipated in that region before they can affect the skull. The balancing conditions in these early forms are aptly illustrated in a recent observation by TATE REGAN. A post-larval form, placed among the Stomiatidæ, has the terminal portion of the intestine very long and protruding, like a balancing organ, and supported by a cartilaginous rod. The gut has no coil and the other characters indicate a more primitive type than any Flat-fish. The author thinks that the chief effect of flexions of the tail would be to rotate the fish, the anal appendage serving as a fulcrum. Possibly, however, the long appendage impedes the rotating tendency.

Advance among the Teleosts has meant greater power to the tail without loss, rather with increase, of the absorptive area. The caudal region increases in size and various kinds of coil, or attempts at a coil, appear; the pelvics are moved forward; the nature and structure of the pectorals change; the air-bladder becomes a temporary or permanent balancing organ, without hydrostatic function; in some the abdominal organs remain unenclosed and protruding. The Flat-fishes have begun, that is, the balancing difficulties affect the head region, when the caudal region has obtained possession of more than half the total length. It is of interest now to note, that the rotating appearance of the caudal region is also present in what appears to be the earliest type of Flat-fish, but not in the other types.

The pelagic stages of this *Symphurus* type, representative of a very large family, are shown in figs. 92–94, 96, 97. The asymmetry is clearly indicated by the coil of the gut and the air-bladder, both on left side. The lower part of the caudal region is also flexed to the left, but the counterbalancing air-bladder flexes the dorsal part to the right; hence the caudal region has an appearance of rotating (figs. 85, 91). For a time these conflicting tendencies are warded off the skull, it may be supposed, by the long balancing rays dorsally, the heavy pedunculated pectorals and the pendulous abdominal organs, but the jaws and arches suffer from alternating flexures, leading eventually to dislocation. Then the long rays are reduced, the air-bladder disappears, the gut is reduced and withdrawn into the cavity, the pectoral arch is strongly retracted and the pectorals drop off. The vertical balance is utterly lost; the fish turns to the right anteriorly and the skull is very rapidly transformed, as described under the metamorphosis. It is worthy of special note, that the long gut after metamorphosis is coiled into a pocket along the hæmal spines of the one side, a condition found again only in the Soles.

It is a reasonable hypothesis, that the caudal region has a tendency to rotate in all similar forms, with elongated body and simple or slightly heterocercal tail and the diversity of the tail among the intermediate Teleosts speaks in its favour. The diphycercal form changes to many variations of the heterocercal; one lobe longer than the other like a boat with a single scull behind; long filamentous rays attached to the upper or lower lobe; both lobes large, sub-equal; or development of dermal plates along the body and loss of caudal fin; all attributable to unequal growth following upon uneqal tensions or flexions.

Retaining the primitive tail, however, the rotating tendency reveals itself in other ways, for example, in the unequal development of the dorsal and anal fins. One fin may be greatly reduced (Macruridæ) or absent (Halosauridæ); here the dorsal fin is affected. Or the anal fin may not develop, the dorsal fin remaining very large and reaching to the head (*Trachypterus*, fig. 99). Here we have one-half of the Flat-fish condition and, as a matter of fact, the fish is said to swim obliquely in the water and lie on its side at the bottom like a Flat-fish. But the skull has just managed to escape the final deflections by being bent down so far, that the compression of the jaws acts on the dorsal surface, with the result that the mouth is very protractile. In the Flat-fishes the anterior end of the skull is bent upwards again.

The Macrurids also begin with a close resemblance to the *Symphurus* type; long rays on head, pedunclated pectorals, long pelvics with pubic bars, elongated body and diphycercal tail; thus, a very similar balance. They end without the dorsal fin and with overhung mouth like the Soles. At the other end of the Acanthines the Gadoids retain a curious relict in the early stages; the coiled gut with anterior air-bladder does not end at the margin of the fin, but laterally at its base; thus, a higher centre of balance. Consequently, the flexions of the body are shorter and more rapid; separate fins develop and the movements are more of an undulating nature. The skeleton and body expand laterally, also the skull and head; nevertheless, these forms display asymmetry in the adult stages.

Among the Flat-fishes an advance from the *Symphurus* type is perhaps shown by *Solea*; caudal fin more strongly heterocercal with developing hypural plate and partially separated from the dorsal and anal; abdominal organs large but not protruding to the same extent, continued into caudal pocket after metamorphosis as in *Symphurus*; pubic bars short; pectorals with comparatively short peduncle, developing into small fins of the propulsive kind. The most significant difference is in the position of the air-bladder; instead of being wholly on the left side, it develops in part anteriorly, in part on the right side; in one case it has quite disappeared. There is no sign of rotation in the caudal region; the sections reveal a simple flexure to the left above and below (fig. 80); the rotating difficulty has been overcome.

As noted already, the combination of right air-bladder with left coil is, however, the worst possible for the balance of the body. As in *Symphurus* the head suffers from violent, alternating flexures and the jaws are dislocated as before. Owing to the absence of the dorsal balancing rays the skull shows more distortion and the hyocleithral muscle is ruptured to form the peculiar urohyal present only in these and the higher Flat-fishes.

The rotating tendency is not seen again in the caudal region among the Flat-fishes; apart from the air-bladder, its absence is correlated, firstly, with the development of the homocercal tail and separation of the latter from the dorsal and anal fins, and, secondly, with the great increase in depth of the body. With regard to the former, it is worthy of note that the homocercal tail is merely another variety of the heterocercal form, which serves the purpose of counteracting the rotating tendency of a tubular or rounded caudal region. Viewed in this light, considering also the differentiation in head and body it leads to, we should be reversing the order of nature if we believed that the homocercal tail could degenerate again to the diphycercal form.

In the earlier Teleosts, the extension forward of the rotating tendency of the caudal region has been checked by the abdominal position of the pelvic fins or side-keels. In *Symphurus* and many other forms these are connected with long cartilaginous pubic rods, which run backwards from the lower end of the pectoral arch along the ventral wall of the abdomen. These rods may also serve some balancing function. The pelvics are developed in connection with them by the growth of a small ossification ventrally (innominate), the position of which varies. The connection with the pectoral arch may be lost (possibly in the pelagic stages), and the pelvics remain posteriorly, or the posterior part of the bars disappears, sometimes with the pelvics. Even when the increasing proportion of the caudal region causes the pelvics to move forward, these pubic rods may persist, *e.g.*, in the adult of *Merluccius*, and traces of them occur in the more advanced Teleosts. They have been lost in *Solea*, possibly a derivative of the *Symphurus* type; how can we explain their reappearance in some of the more advanced Flat-fishes?

The primitive pectorals may also have their subsidiary balancing organ. In *Brotula*, for example, it is the post-cleithrum, which bends down and continues posteriorly along the ventral margin of the body (fig. 98). Here we have a broader fish from side to side, and the whole appearance suggests a balancing system different yet not remote from that of *Symphurus*.

The advanced forms of Flat-fishes seem far removed from the *Symphurus* and *Solea* types. They begin with a different shape and structure, show a different mode of balancing, and end with a different type of asymmetry. The body is more compressed and higher, abdominal organs by comparison short, with closer coil, and contained mainly within the cavity; posteriorly, the cavity has a thickened wall, sometimes definitely cartilaginous, which develops later into a large balancing organ; the tail forms a large homocercal plate. The abdominal organs never grow backwards along the caudal region before or after metamorphosis, and their increase in size takes place downwards along with the posterior abdominal rod. The coil is a coil and a half, the rectum being obliquely vertical from right to left side. In the normal Teleosts the coil is more in a transverse plane.

The disturbance of the head is brought about by longitudinal flexures, which can be detected soon after the coil is formed. The flexures are impressed on the growing vertebræ and spines of the body, a characteristic hitherto supposed to be of secondary origin (*cf.* figs. 33, 74). So long as the posterior abdominal rod remains vertical or nearly so, the fish is able to maintain its balance; the abdominal organs themselves serve as balancing organs. The head is affected as in *Symphurus* and *Solea*, but not so violently nor in the same way; the rami of the one side are pulled backwards and upwards; the jaws become more vertical; the cheek-muscles are partly ruptured on the one side; the hyocleithral muscles are also ruptured; the parasphenoid-vomer axis is deflected to the one side, the lateral ethmoids and frontals to the other side.

A sidelight on the importance of the abdominal organs in the balance of the fish is given by *Glyptocephalus*. Though starting from a smaller size than *Pleuronectes*, this form is able to maintain its vertical balance to a length of over 60 mm., longer than any other Flat-fish. The abdominal organs are arranged in a tightly coiled, pendant mass in the middle of the cavity (fig. 61). When this has been formed, the balance is maintained even when the dorsal and ventral axes of the skull show a gradually increasing deflection. At the same time some differences from the other forms arise in the head region; the base of the curved urohyal articulates with the left cleithrum, showing the direction of the asymmetry and the strain of the hyo-clavicular connection; the rami of the jaws develop equally, and the maxillary muscle persists on the right side, showing that the counterbalancing tendency of the abdominal organs has also had its effect on the arches of the head.

This latter phenomenon furnishes an explanation of reversed specimens, common, for example, in *Pleuronectes flesus*, also of the anomalous forms *Lepidorhombus* and its allies, which have dextral characteristics, and are yet sinistral. In *Lepidorhombus*, indeed, the posterior abdominal rod shows quite distinctly the double flexure (fig. 26).

The remaining Flat-fishes, the Rhomboids and Bothoids, have a greater height, more rounded shape, and greater extension of the fins posteriorly and anteriorly, and possess an air-bladder in the early stages—mainly on the left side above the coil of the gut. The Rhomboids have a similar structure to the Pleuronectoids, open parapophyses, thus thicker body, and the asymmetry develops along similar lines, but the principal flexure is to the right and the fish becomes sinistral.

The Bothoids are of wafer-like thinness (fig. 54) and have closed hæmapophyses. The long pubic bars are present as in *Symphurus*, but the pelvics show a secondary growth far forwards. The correlation between air-bladder and dorsal fin, which has a long balancing ray in this group, is very clearly seen, as already indicated. In related forms (*Arnoglossus*) the keel is imperfect, and the balance during the pelagic stages is maintained by the air-bladder and abdominal organs.

A great shrinkage of the abdominal organs occurs in all forms towards the end of metamorphosis when the cavity is being enclosed below. At this period the conflict is going on which ends in the formation of a new urohyal or the retraction of the pectoral arch, and the jaws take up a more vertical position, permanently or temporarily. It is probable that the fish are unable to feed for some time.

The changes accompanying the migration of the eye signify a total loss of balance; in the body the abdominal rod and vertebral spines are permanently flexed more or less distinctly to the blind side; in the head the jaws and arches are more to the blind side of the median longitudinal plane; in the skull the deflection of the frontals to the one side is more than counterbalanced by the deflection of the ventral axis to the other side, and the growth of the subocular bridge. The principal mass of the body is thus on the blind side. In *Pleuronectes*, for example, the neural and hæmal spines, dorsal and ventral margins of the body, jaws, arches and even the head as a whole (fig. 34), are all to the blind side of a median, longitudinal plane through the spinal column. As a rule, the young fishes gradually sink down through the water as development proceeds, just as is the case with the normal Teleosts, but in some cases (*Drepanopsetta* and *Pleuronectes*) the bottom is reached before the metamorphosis is completed. Some, like *Rhombus* and *Glyptocephalus*, remain in surface waters some time after they are metamorphosed; others, again, seem able to live pelagically even when adults (*Platysomatichthys*, *Lepidorhombus* and the Top-knots, and probably *Psettodes* and *Bothus*).

That these fishes swim on the side after metamorphosis has, therefore, nothing to do with the demersal habitat as such; it is due to lack of proper balance just as in the case of *Trachypterus*. And in this connection it may be noted that the lateral line system of the blind side is relatively weakened, sometimes totally destroyed by the changes in the head region. The fish swims and lies on its side because it must, not because it has learnt to do so.

It is therefore quite erroneous to think that the Flat-fishes have become flat through living on the bottom; not only the flatness, but all the family, generic and specific characteristics are developed during the pelagic stages. We can see, for example, how the *Solea* sub-family may have been differentiated from the *Symphurus* type by alteration of the balance and by structural changes arising therefrom during the pelagic life. It has yet to be shown that any changes, specific or otherwise, have arisen or can arise from the demersal life.

Normal Teleosts similar to the Bothoid and Rhomboid types of Flat-fishes show a great deal of asymmetry in various ways; externally in dermal plates or spines, and internally in curvatures of the spinal column. The question is, however, how the skull escapes the asymmetry.

The fundamental structures of these higher forms are: broad or deep body, homocercal tail, large abdominal rod, not curving forward or only slightly, cavity not enclosed below; pelvics behind the cleithra in the beginning and with six rays; dorsal and anal fins reaching to the tail. The head naturally may be variable.

Owing to the wealth of the Percomorphi and the great probability that the Bothoid and Rhomboid types are from separate stocks, these characters are not quite sufficient to detect the closest resemblance in balance among the normal Teleosts. The hyocleithral connection, hyoid arches, presence or absence of pubic bars and postcleithra, position of air-bladder in pelagic stages require further study. We can recognise developments from similar stocks (*e.g.*, *Psettus* on the Bothoid line, *Zeus* on the Rhomboid line), but these are not the originals.

The best example of the organisation and balance of the Rhomboid type is *Stromateoides*. In addition to the fundamental characters, this form in the early stages shows a marked affinity to a postlarval Rhomboid in shape, coloration, air-bladder, even to the spines on the opercular bones (fig. 101), but there are two important differences. In front of the nearly vertical abdominal rod are the long pelvics, projecting backwards from the cleithra; dorsally, the dorsal fin does not reach the head. These, however, are just the differences required in the balancing conditions; this might be an arrested or earlier phylogenetic stage of *Rhombus* before the secondary pelvics were developed. Later, the dorsal fin in *Stromateoides* gains connection with the head, not by growing forward, but by the development of a long stout bone from the skull to the beginning of the fin. A dorsal keel is thus formed, the whole framework is now more rigid, preventing deflections of the skull, and the vertical balance is maintained. The abdominal rod grows no further forward and the pelvics drop off, indicating the presence of a tension along the ventral margin of the abdomen, similar to that which precedes the loss of the pectorals in *Symphurus*.

This example also illustrates the meaning of the spines and spinous rays in the advanced Teleosts. Both spinous and jointed rays are only capable, as a rule, of a vertical movement, but the latter are easily bent to one side and thus do not afford the same resistance to the extension of persistent flexures from the body to the head. Hence in all these advanced Teleosts, with depth at least twice as great as breadth, the abdominal region is provided with spinous rays always in the dorsal fin above, and very frequently also in the anterior part of the anal fin—thus, where the flexures are most apparent in the Flat-fishes. And it may be considered certain that the nearer the spinous rays approach the head and the larger they are anteriorly, the nearer have the flexures of the abdominal region come to affect the skull.

Frequently the head itself develops balancing structures in the form of large spines on the opercular bones, changing often to offensive weapons (Weevers and Sea-scorpions, etc.). These are also present in the advanced Flat-fishes (small in *Rhombus*, very large in *Ancylopsetta*), and even the skull itself may have spinous protuberances (otocystic spines, *Lepidorhombus*, etc.).

There is only one known case of spinous rays occurring in the dorsal fin of a Flat-fish—*Psettodes*. The early life-history of this form has still to be ascertained, but one can see from the structure that its mode of balancing must be different from that of any other Flat-fish.

THE ORIGIN OF FLAT-FISHES.

The observations discussed in the preceding pages enable the question of the origin of Flat-fishes to be approached from a broader basis than has hitherto been available. Many endeavours have been made to locate these fishes. In the early days of systematic ichthyology they were placed near the Gadoids. GILL suggested that they were allied to the Trachipterids; AGASSIZ placed them near the Chætodontidæ and Scorpididæ; HOLT hinted at an affinity with the Chætodontidæ, or even with the Zeidæ. There was something more than mere superficial resemblance in these suggestions, but the comparative study of the structure was needed to make them definite theories.

In 1902, BOULENGER and TATE REGAN showed the remoteness of the Gadoids (at least from the common Flat-fishes), and BOULENGER definitely associated the Zeidæ and Amphistium (a fossil form from the Upper Eocene) with the Flat-fishes in one division of the Acanthopterygii under the name of Zeorhombi. In the same year THILO made a detailed comparison of the structure of *Zeus* with the Rhomboids, and came to the conclusion that they belonged together. In BOULENGER'S view, Amphistium was the prototype of the Flat-fishes, and at the same time a near relative of the living Zeidæ.

His comparative studies of Teleostean osteology led TATE REGAN in 1910 to remove Amphistium from the Zeidæ and place it with the "Percoids"; further, one of the Flat-fishes, *Psettodes*, was regarded as "simply an asymmetrical Percoid." In a later paper (1913), the Flat-fishes are noted as offshoots from the Percomorphi. This means that *Psettodes* is considered to be the first of Flat-fishes, and that the remainder have been derived from it or from advanced Teleosts such as the Percoids.

It is worthy of note that these comparisons are with the structure of the adult Flat-fishes. That is, the authors assumed that the extensive differences in structure in the order of Flat-fishes have arisen after the asymmetry and demersal habitat had been obtained. This does not seem a reasonable assumption; it would mean that the same parallel changes in fundamental structure can take place in two different media, in passive, asymmetrical, demersal fishes as in active, normal, pelagic fishes.

The distinctive characters of *Psettodes* are: (1) spinous rays in fins; (2) supra-maxillary; (3) toothed palatines; (4) two post-cleithra on each side.

These are advanced Teleostean characters, however, found in no other Flat-fish. And, as a matter of fact, *Psettodes* stands quite isolated, not merely as a separate genus or family, but even as a separate sub-order; yet only one species is known.

Psettodes also possesses primitive characters: (1) dimorphism of optic chiasma; (2) urohyal a simple plate; (3) no abdominal balancing rod; (4) tri-segmented radialia posteriorly.

The combination of primitive body characters with advanced head characters is not very remarkable; the connecting links are the postcleithra and spinous rays anteriorly (also articulation of urohyal with basibranchial). The vertical balance has been maintained longer in the stock from which *Psettodes* has sprung, and has enabled the advanced characters to be acquired. But the combination is singular among the Flat-fishes.

The isolation of *Psettodes* stands in marked contrast to the abundance of another type of Flat-fish, which is known to be ancient as Flat-fish, possesses more primitive characters than *Psettodes*, and has many more advanced Flat-fish relatives. This is the *Cynoglossus* type, of which *Symphurus* seems at present to be the most primitive representative. It has none of the advanced characters of *Psettodes*, but, in addition to the latter's primitive characters, it has: (5) pectorals with primitive pterygium, lost on metamorphosis; (6) pelvics (four rays) arising early in ontogeny; (7) pubics extending back under gut; (8) homocercal plate of caudal fin not developed; (9) vertical fins continuous; (10) slight ossification of skull and body.

Add to these the primitive type of metamorphosis, arrangement and size of abdominal organs, structure of opercular bones, and it becomes evident that *Symphurus* belongs to a stock far more primitive than *Psettodes*.

In reality, *Symphurus* is more nearly related to the Macrurids and Trachypterids, as shown in the preceding section. The mouth and head structures, even the pectoral arch, are not so valuable for tracing these phylogenetic relations as the body, since the balance of the latter determines the shape of the former. Thus, the fundamental characters, elongated caudal region with simple tail, pubic bars extending back under the longitudinally coiled gut, horizontal rectum, elongated dorsal rays on head—balancing round the same, slender, vertibral column, present a uniform picture in all three. In the *Symphurus* type the early asymmetry of the body affects the pelvic fins; in the others the growth of the dorsal or anal suffers most. The skull is transformed in a different manner; in the Trachypterids it is strongly depressed with protractile jaws; in the Macrurids a snout is formed and the jaws are pulled backwards; in *Symphurus* (and *Solea*) we have signs of both and the skull is deformed.

Psettodes has quite a different balance to begin with; the absence of pubic bars, presence of post-clavicular bars, caudal region with homocercal plate, caudal fin distinctly separated from vertical fins, presence of spinuous rays; these indicate an advanced stage on a different line of evolution. Its supposed resemblance to the Percoids and distinctness from other Flat-fishes have a simple explanation; it is the most recent addition to the ranks of the Heterosomata. Its indeterminate character, sinistral or dextral, as well as the structure of the mouth and cheek-muscles, indicate that it is a near relative of some present-day genus of normal Teleosts, *e.g.*, of *Lichia* among the Carangidæ.

The primitive nature of *Symphurus* is illustrated by a comparison with *Solea*. The fundamental structure and the type of asymmetry remain the same, but changes have been rung on the balancing appendages—before the acquisition of the demersal habitat. Thus, the confluence of the vertical fins is broken; caudal fin develops a homocercal plate; abdominal organs in great part contained within the cavity; radialia of vertical fins bi-segmented; pectorals with definite fin-rays; pelvics more defined in shape and position, but with loss of pubic bars; abdominal muscles grow forward over the pectoral arch and urohyal is forked; jaws more vertical and skull greatly foreshortened; air-bladder on right side.

The Soles and Cynoglossids, however, form an immense family and more information is wanted, especially of the development, before it can be definitely said that they have come from one single stock. *Achirus*, for example, is a deeper form with a breach in the interorbital septum as in *Lepidorhombus* and its allies and in some normal fishes, and it has a single, large bone bounding the posterior wall of the abdominal cavity. The American authors are probably right in regarding it as representative of a distinct family.

Theoretically there is no reason why the Flat-fishes should have had only one origin. On the contrary, the tendency to asymmetry is widespread among the Teleosts and the diverse arrangements of the apparently symmetrical fish are simply the means whereby the Teleostean stock has been able to balance itself in different ways at different levels of phylogeny. The air-bladder, the position and structure of the fins give clear evidence of the efforts to maintain a vertical balance; the position and shape of the skull and visceral arches, whether deformed or not, indicate the effects of the struggle. When an organ fails to serve its purpose in one position, it may move or be moved to another even during ontogeny or, with change of function and balance, be entirely discarded, *e.g.*, ventral fins in *Bothus* and *Rhombus*, pectoral fins in the Cynoglossids, disappearance of dorsal balancing ray and air-bladder in *Bothus*, forward growth of dorsal and anal fins in all the advanced forms.

One of the most prominent balancing structures in certain groups of normal fishes is the posterior abdominal rod, which partakes in the asymmetry of the caudal region. This structure is not present in the two primitive types already mentioned. Are we to suppose that this structure—an advanced Teleostean structure—has been acquired, then later discarded in one and the same group of fishes, under the same peculiar conditions of life?

It seems more reasonable to believe that this structure has come directly from other orders, it may be several, which have maintained their vertical balance into a later phase of phylogenetic development. Then the change of balance and form involved in the increasing depth, with formation of the abdominal rod, produced a disturbance of the pre-existing conditions which in some cases led to the development of special structures connected with the balancing of the body (*e.g.*, spinous processes or rays, in Stromateoides, Antigonia, Zeidæ, Psettidæ), and in other cases led to great changes in the head and skull (*e.g.*, Gerridæ, Chætodontidæ).

In support of this contention we have the remarkable form *Bothus*. Here the pelagic stage is already ossified, both head and body, with a well-defined rostrum like some permanently vertical Teleosts; then the change to asymmetry is only partial, the adult is half normal, half Flat-fish. The structure of the vertebræ and skull is distinct from that of the Rhomboid and Pleuronectoid forms, and more nearly resembles that of the *Psettidæ*. Further, from it we can derive more confirmed Flat-fishes, *e.g.*, *Arnoglossus*.

Again, the Rhomboids and Pleuronectoids do not form a homogeneous group. They are very similar in asymmetry, vertebræ and fins; yet the mode of ossification of the skull is different in the two groups, and there is a fundamental distinction in the structure of the olfactory organ. *Rhombus* has probably come from the same stock as the Zeidæ.

There are good reasons for believing, therefore, that the Flat-fishes are a composite group of Teleosts derived from several different sources. One of these is very primitive in time, the *Symphurus* type, giving rise to the large family of Cynoglossids and Soles, and has been formed from some stock much earlier than the Acanthopterygians. Other types, certainly the Bothoid, probably also separate Rhomboid and Pleuronectoid types, have been added later, from intermediate stocks on the way to the Acanthopterygians; *Psettodes* is quite a modern addition.

General Summary.

1. Consideration of the adult structure of Flat-fishes reveals that rotation of the orbital region of the skull cannot be the beginning of the asymmetry. The asymmetries of the skull are correlated with asymmetries in the jaws, visceral arches, and muscles opening and closing the mouth. The structures of the body are also asymmetrical, and it is shown that the latter condition must be primary, not secondary to the condition of the head and skull. Two distinct types of asymmetry can be detected in the adult structure, the characteristics of the one being the reverse of those of the other.

2. The metamorphosis arises from an inherent asymmetry in the abdominal organs. Various arrangements of the coil of the gut and air-bladder indicate how the balance of the body is effected. The symmetrical structures, vertebral spines, fins, arches, and jaws all develop asymmetrically, so that the balance of one stage is not the balance of the next. As the jaws and pterygopalatine arches ossify, their asymmetry is communicated to the skull; the lateral ethmoids, developing asymmetrically, force the frontals to bend in the opposite direction to the deflection of the parasphenoid. The jaws take up a more vertical position and for a time the mouth cannot open; in *Symphurus* the axis of the skull and the jaws return nearly to their earlier positions,

as also the pectoral arch; in all other groups the muscles opening the mouth are ruptured and a new and special urohyal bone is formed. During this time the abdominal organs shrink considerably in size and the cavity becomes enclosed below by asymmetrical structures. The vertical balance is now completely lost; the fish is heavier on one side than on the other. During the strain on the skull, a thickening of the tissues leads to the formation of a subocular ligament under the eye of the flexed side, and it is this ligament which forces the eye to follow the deflected frontals to the other side; later, it ossifies and becomes the pseudomesial bar, the homologue, perhaps, of the subocular shelf of normal Teleosts. In *Symphurus* the ligament is formed round the eye, which is forced through the tissues of the head under the dermal frontals.

The early signs of the same asymmetrical tendencies are seen also in normal Teleosts; the asymmetry, however, is diverted from the skull by different arrangements of the structures, *e.g.*, bending down of the skull or jaws, and development of dorsal spines.

3. With regard to Origin, the conclusion is reached that the Flat-fishes are not a homogeneous group. *Symphurus* represents the earliest origin and has sprung from a stock which has given rise, amongst others, to the Macrurids and Trachypterids. The *Bothus* type is related to the Psettidæ; the Rhomboids have a near relation in *Stromateoides*, and *Zeus* is an advanced relative; the Pleuronectoids are distinct from both. *Psettodes*, the "Percoid," appears to have sprung from a different line of evolution, and is a modern accession to the ranks of Flat-fishes.

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Lettering used in Figures.

(Dashed letters on the figures refer to eyeless side.)

a, 1st abdominal vertebra.
ab, air-bladder.
al, alisphenoid of eyed side.
ar, articular.
b, basioccipital.
bs, breach in interbranchial septum.
chy, ceratohyal.
cl, primordial cartilage of interorbital septum.
cm, cheek-muscles.
cpb, cartilaginous pubic bar.
e, ethmoid.
em, entrance to anterior eye-muscle canal.
ep, epiotic of eyed side.
ex, exoccipital of eyed side.
f, frontal of eyed side.
fn, fenestra in interorbital septum.
g, gut.
gh, glossohyal.
gm, geniohyoid muscles.
hf^1, sphenotic fossa for hyomandibular.
hf^2, facet on pterotic for ditto.
hh, hypohyals.
hs, hæmal spine.
i, interoperculum.
in, posterior abdominal rod.
io, interorbital bar.
ios, interorbital septum.
lc, lachrymal.
le, lower eye.
lo, lower orbit.
m, mesentery.
me, mesethmoid process.
na, remnant of neural arch of 1st abdominal vertebra.
ns, nasal sac.
o, ovary.
of, olfactory foramen of eyed side.
og, olfactory groove of eyed side.
op, opisthotic of eyed side.
p, prootic of eyed side.
pa, parasphenoid.
pem, posterior eye muscles.
pf, prefrontal of eyed side.
pk, posterior kidney.
ppt, pterygopalatine.
pr, parietal of eyed side.
pt, pterotic.
pt^2, fossa for lower head of posttemporal.
ptc, postcleithrum.
q, quadrate.
r, rectum.
rem, position of attachment of anterior eye muscles.
s, sphenotic of eyed side.
sl, subocular ligament.
so, supraoccipital.
sph, superior pharyngeals.
ss, supraoccipital spine.
str, supraorbital trabecula.
str′, lower part of ditto after separation.
ub, urinary bladder.
ug, urinogenital canal.
uh, urohyal.
uo, upper orbit.
v, vomer.
vf, pelvic fin.
x, position of insertion of anterior eye muscles.

EXPLANATION OF PLATES.

Plate 4.

Figs. 1–5 show the varying degrees and varying position of the primary flexure of the skull.

Fig. 1.—*Pleuronectes platessa L.*, from lower aspect. n.s.
Fig. 2.—*Arnoglossus imperialis* (Rafin.), from lower aspect. 2/1.
Fig. 3.—*Solea nasuta* (Pall.), from lower aspect. 2/1.
Fig. 4.—*Solea vulgaris* Quens., from lower aspect. n.s.
Fig. 5.—*Platysomatichthys hippoglossoides* (Walb.), from lower aspect. n.s.

Figs. 6 and 7 illustrate the asymmetry of the posterior region of the skull in the first group of Flat-fishes.

Fig. 6.—*Lepidorhombus megastoma* (Don.), posterior aspect. 2/1.
Fig. 7.—*Platysomatichthys*, posterior aspect. n.s.
Fig. 8.—*Solea vulgaris*; from upper aspect; skull as a whole deflected to eyed side.
Fig. 9.—*Platysomatichthys*; upper aspect.
Fig. 10.—*Solea nasuta*; from eyed side; great distorsion in frontal region and at junction of parasphenoid and basioccipital.
Fig. 11.—*Solea vulgaris*; from eyeless side; peculiar position of vomer and olfactory foramen.

Plate 5.

Fig. 12.—*Bothus podas* (Delar.), male; from eyed side. 2/1. *xx*, a membranous area where migrating eye first rested before being pushed upwards and backwards by prefrontal of eyeless side (*pf'*).
Fig. 13.—*Bothus podas* (Delar.), seen from above. 2/1.
Fig. 14.—*Bothus podas* (Delar.), eyeless side. 2/1.
Fig. 15.—*Bothus podas* (Delar.), lower aspect. 2/1. The seeker indicates olfactory canal, quite distinct from eye-muscle canal (*em*).
Fig. 16.—*Bothus podas* (Delar.), posterior aspect. 2/1.
Fig. 17.—*Bothus podas* (Delar.), upper aspect after removal of prefontal of eyeless side (2/1); upper orbit opens directly into cranial cavity.
Fig. 18.—*Bothus podas* (Delar.), eyeless side after removal of prefrontal of eyeless side (*a*); *b*—frontal of eyeless side; *c*—frontal of eyed side. 2/1.
Fig. 19.—*Symphurus lactea* (Bonap.); from eyed side. 6/1. Frontals separated from skull.
Fig. 20.—*Symphurus*, from upper aspect; 6/1. Cranial cavity covered only by a thin membrane.
Fig. 21.—*Bothus*, viewed from in front (n.s.); unequal rami of jaws.

Fig. 22.—*Solea*; pterygopalatine arch; mesethmoid pointing to eyed side; vomer to eyeless. n.s.

Fig. 23.—*Pleuronectes;* pterygopalatine arch; mesethmoid and vomer pointing to eyeless side. n.s.

Fig. 24.—*Solea;* upper and lower jaws; mandibular longer on eyed side; premaxillary articulated to dentary on eyeless side. n.s.

Fig. 25.—*Platysomatichthys;* first caudal vertebra with posterior abdominal rod (*in*) inclined to eyeless side.

Fig. 26.—*Lepidorhombus;* anterior view of abdominal vertebræ, showing double deflection of abdominal rod. n.s.

PLATE 6.

Fig. 27.—*Lepidorhombus;* dissection of ventral mechanism opening the mouth; curved urohyal, breach in interbranchial septum, abdominal muscles passing forward to lower prong of urohyal. n.s.

Fig. 28.—*R. maximus,* L.; urohyal. n.s.

Fig. 29.—*S. vulgaris* QUENS.; urohyal. n.s.

Fig. 30.—*Synaptura*; simple urohyal, not hooked. n.s.

Fig. 31.—*Cynoglossus;* simple urohyal, not hooked. n.s.

Fig. 32.—*Rhombus maximus* L. Vertebral column to show longitudinal flexures of abdominal region; to eyeless side on caudal vertebræ, then to eyed side anteriorly. n.s.

Fig. 33.—*P. platessa* L. Section through abdominal region, front view, showing flexure to eyeless side dorsally and ventrally, and also longitudinally. 1/2.

Fig. 34.—*P. platessa* L. Head strongly flexed to eyeless side.

Figs. 35 to 42 represent the first stage in the metamorphosis of Flat-fishes; coil of gut just formed on left side; air-bladder above it also on left side (40, 41); asymmetry of jaws.

Fig. 35.—*Hippoglossus.* 12 mm. × 7. Jaws beginning to ossify.

Fig. 36.—*Hippoglossus.* 10 mm. × 10. Showing persistent flexure to side of coil; jaws asymmetrical.

Fig. 37.—*Platysomatichthys.* 18 mm. × 18; coil in middle of cavity.

Fig. 38.—*Platysomatichthys;* primitive jaws strongly flexed to left.

Fig. 39.—*Glyptocephalus,* 8·2 mm. × 10.

Fig. 40.—*Bothus,* 5 mm. × 12; air-bladder above coil; balancing dorsal ray.

Fig. 41.—*Arnoglossus laterna* WILL.; 4·5 mm. × 20. Beginning of Stage II; periotic capsule not completely formed; supraorbital trabeculæ above eye; ethmoid plate flexed to right side; supraoccipital and parasphenoid ossified.

Fig. 42.—*Drepanopsetta platessoides* FABR.; 7 mm. × 30; primitive jaws strongly flexed to left side.

Fig. 43.—*Drepanopsetta platessoides* FABR.; 10 mm. × 20. Secondary supports of jaws formed; asymmetry of orbital region beginning.

PLATE 7.

Fig. 44.—*Pleuronectes*; 14 mm. × 15. Stage IV; frontals deflected; migrating eye beyond anterior end of dorsal fin; enclosure of abdominal cavity nearly complete; urohyal forming; no maxillary muscle on eyed side.

Fig. 45.—*Pleuronectes*; 12 mm. × 15. Stage III; subocular ligament developing (*sl*); hyocleithral muscles ruptured; maxillary muscle on eyeless side.

Figs. 46, 47.—*Platysomatichthys*; 18 mm. × 20. Stage I. Olfactory capsules well-developed; jaws asymmetrical; ethmoid plate and basal axis of skull slightly asymmetrical.

Figs. 48–51.—*Pleuronectes*; 14 mm. × 20. Stage IV. Subocular ligament developing compels eye to move over to right side; fenestra forming in inter-orbital septum and eye muscles being carried over to left side (49).

Fig. 52.—*Pleuronectes*; 9 mm. × 20. Stage II. Section posterior to eyes; beginning of left flexure of parasphenoid.

Fig. 53.—*Bothus*; 10 mm. × 10. Air-bladder and dorsal balancing ray about to disappear; skull depressed.

Fig. 54.—*Bothus*; 25 mm. × 15. Section through eyes; upper part of head to right, lower part to left; eyes only slightly asymmetrical.

Figs. 55–57.—*Rhombus*; 17 mm. Ossification of frontals round supraorbital trabeculæ (55); flexure of pelvics to left, dorsal fin to right side (56); air-bladder slightly to left side, dorsal and ventral margins to right side (57).

Fig. 58.—*Arnoglossus*; relation of migrating eye to dorsal fin, which is not attached to lateral ethmoid until after metamorphosis.

Fig. 59.—*Arnoglossus*. Stage II; ossification of head and body; frontals slightly asymmetrical.

Fig. 60.—*Rhombus*; 6 mm. × 15. Beginning of Stage II; jaws to right.

PLATE 8.

Fig. 61.—*Glyptocephalus*; 34 mm. × 4. Abdominal organs arranged in tight, transverse coil, thus serving as a balancing organ, so that fish remains in a vertical position long after skull is asymmetrical.

Fig. 62.—*Glyptocephalus*; head viewed from above.

Fig. 63.—*Glyptocephalus;* 42 mm. × 5. Increasing deflection of frontals, but migrating eye not yet begun to move; abdominal cavity not yet enclosed.

Figs. 64, 65.—*Glyptocephalus* at 13 mm. Slight asymmetry of ethmoid, and left frontal and supraorbital trabecula higher than right.

Figs. 66–70.—*Glyptocephalus* about 34 mm. Lower jaw to left, but rami equal (66); palatine higher on left (67); parasphenoid strongly to left, and left lateral ethmoid higher than right (68); left supraorbital trabecula higher than right but not reduced (69, 70).

Fig. 71.—*Glyptocephalus.* Section through pectoral arch; dorsal fin flexed to left; pelvic fins, under influence of counterbalancing tendency of abdominal organs, flexed to right.

Figs. 72–74.—*Pleuronectes,* 12·5 mm. Stage III or beginning of Stage IV; frontals deflected (72); adult convexity of right side of body and flatness of left side already conspicuous (73, 74) though fish still pelagic.

Fig. 75.—*Bothus;* metamorphosis just completed; migrating eye resting temporarily on frontal of eyed side; jaws nearly vertical; adult urohyal formed.

Fig. 76.—*Solea vulgaris,* Quens. 8 mm. × 20. Large abdominal organs; air-bladder on right side; jaws strongly asymmetrical under influence of left flexure; palatine of left side (*ppt′*) well behind that of right side; left premaxillary being pulled backwards away from right.

Fig. 77.—*Solea* sp., 9 mm. × 20. More advanced than 76; no maxillary muscle on blind side; premaxillary articulated with dentary; ethmoid snout beginning to form.

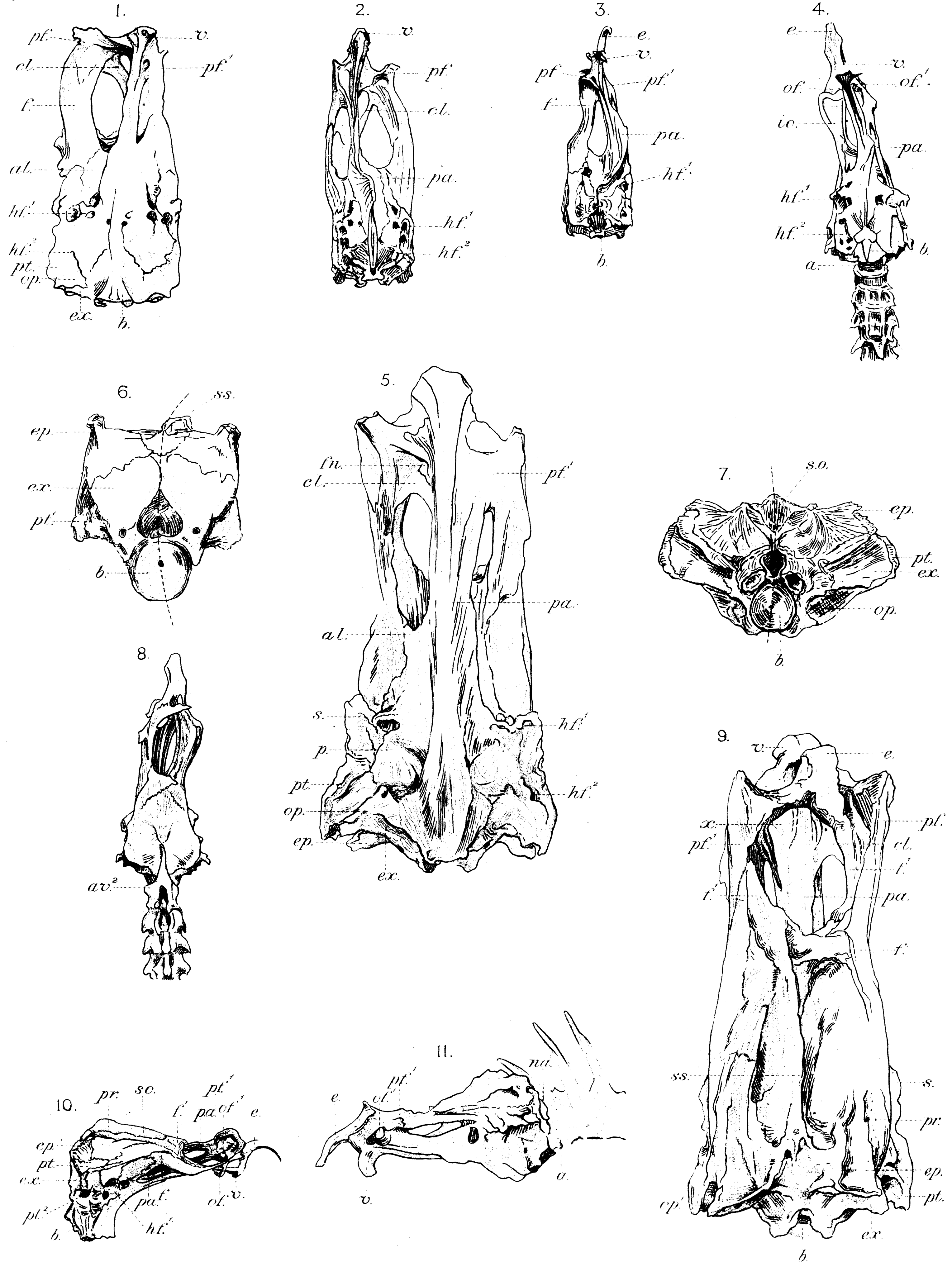
Plate 9.

Figs. 78–80.—*Solea vulgaris,* Quens., 6 mm. Slight asymmetry of skull, but jaws drawn to left (78); air-bladder on right side (79); dorsal and ventral margins of caudal region flexed to left (80), thus an advance on rotating tendency of *Symphurus* (*cf.* figs. 85, 91).

Figs. 81–85.—*Symphurus lactea* (Bon.); 9 mm. Skull slightly asymmetrical (81–83); dorsal fin strongly flexed to right; large air-bladder on left (84); rotating appearance of caudal region (85).

Figs. 86–91.—*Symphurus,* 17 mm. Large amount of lymphoid tissue; dorsal fin now flexed to left on head and abdominal region; disturbance of frontals and supraorbital trabeculæ preparatory to separation from skull (87); air-bladder becoming smaller (89, 90); rotating tendency still present in caudal region (91).

Fig. 92.—*Symphurus lactea.* 6 mm. × 13. Stage I; flexure of visceral arches and jaws to left (later to right); protruding abdominal organs, large air-bladder on left side; simple tail.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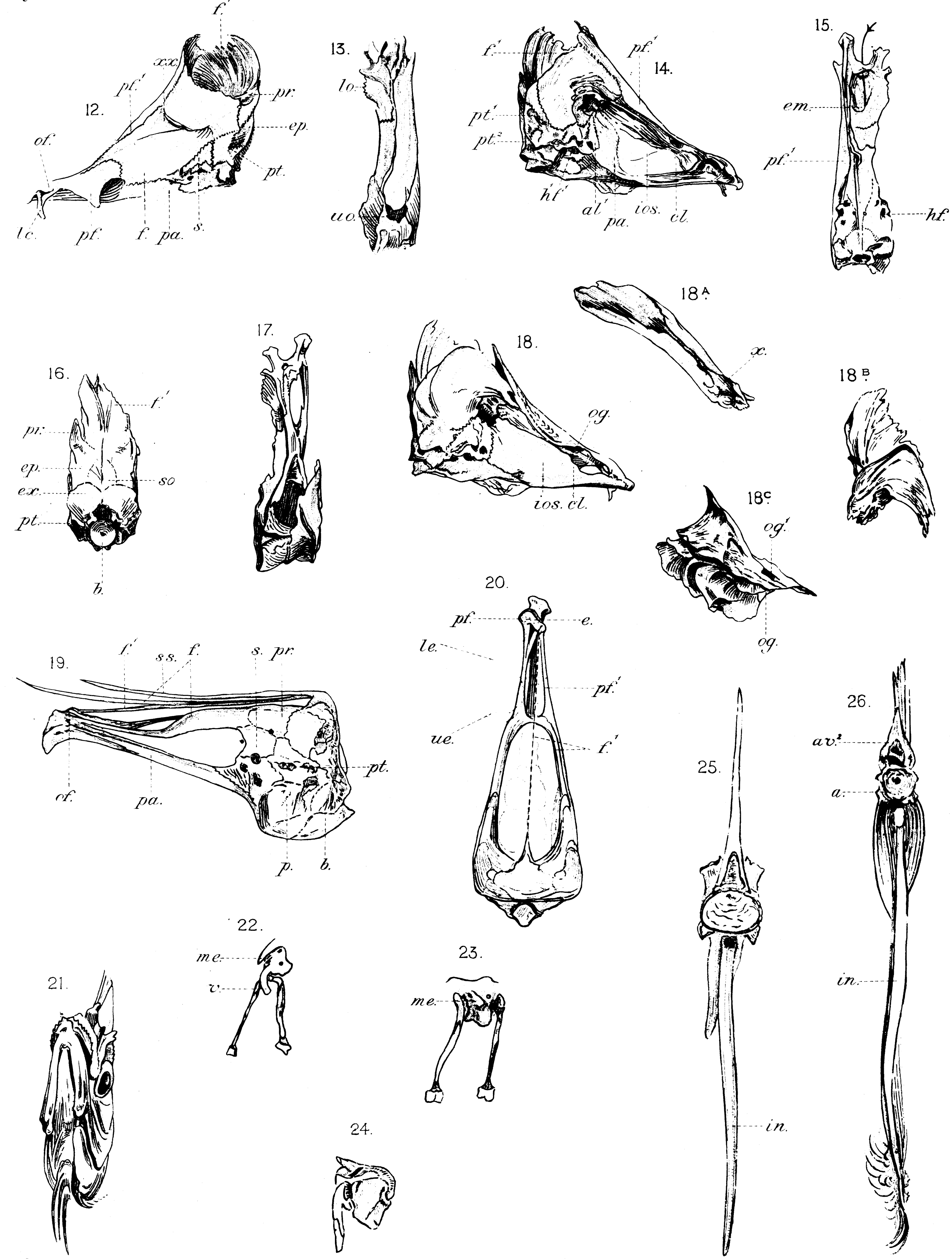
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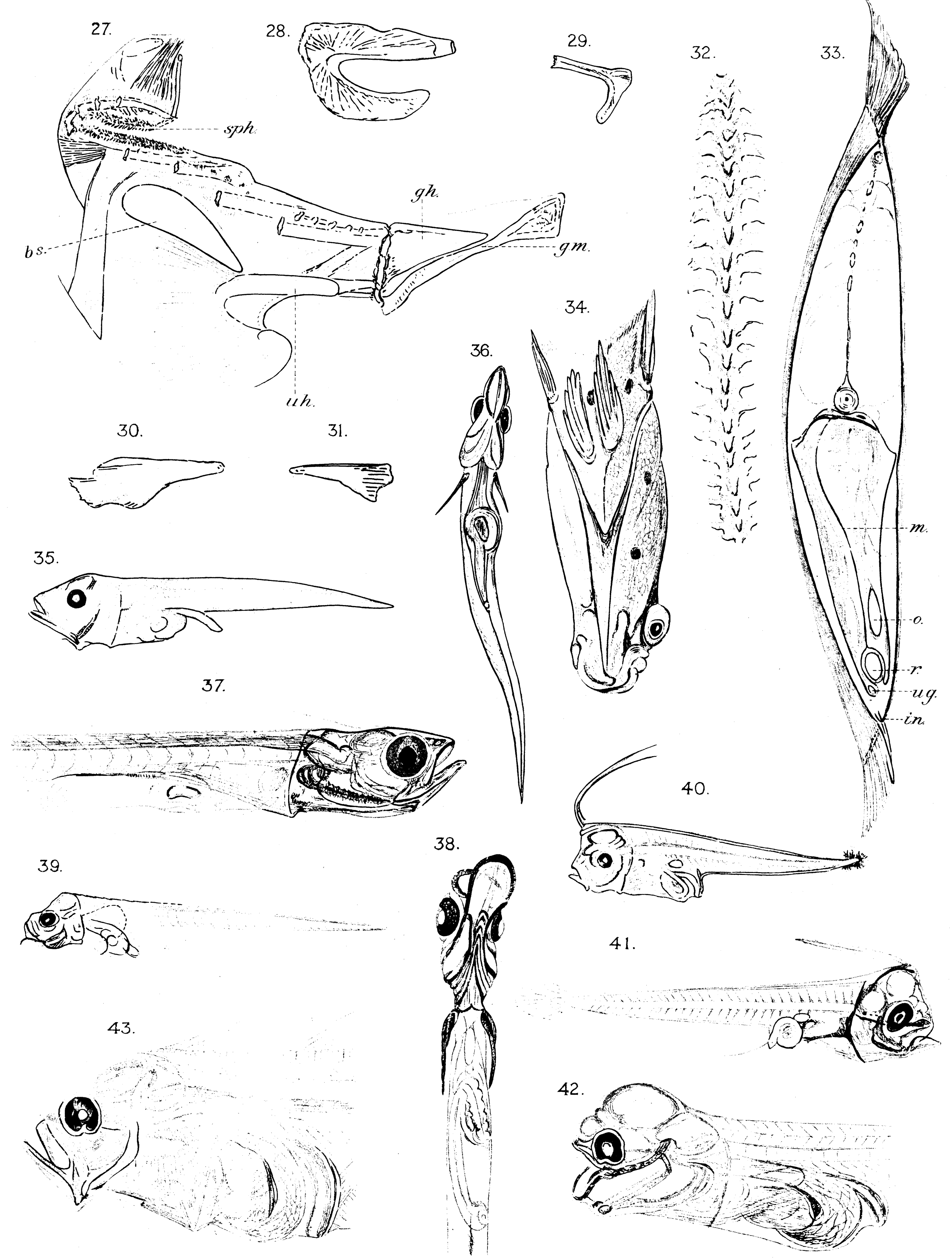
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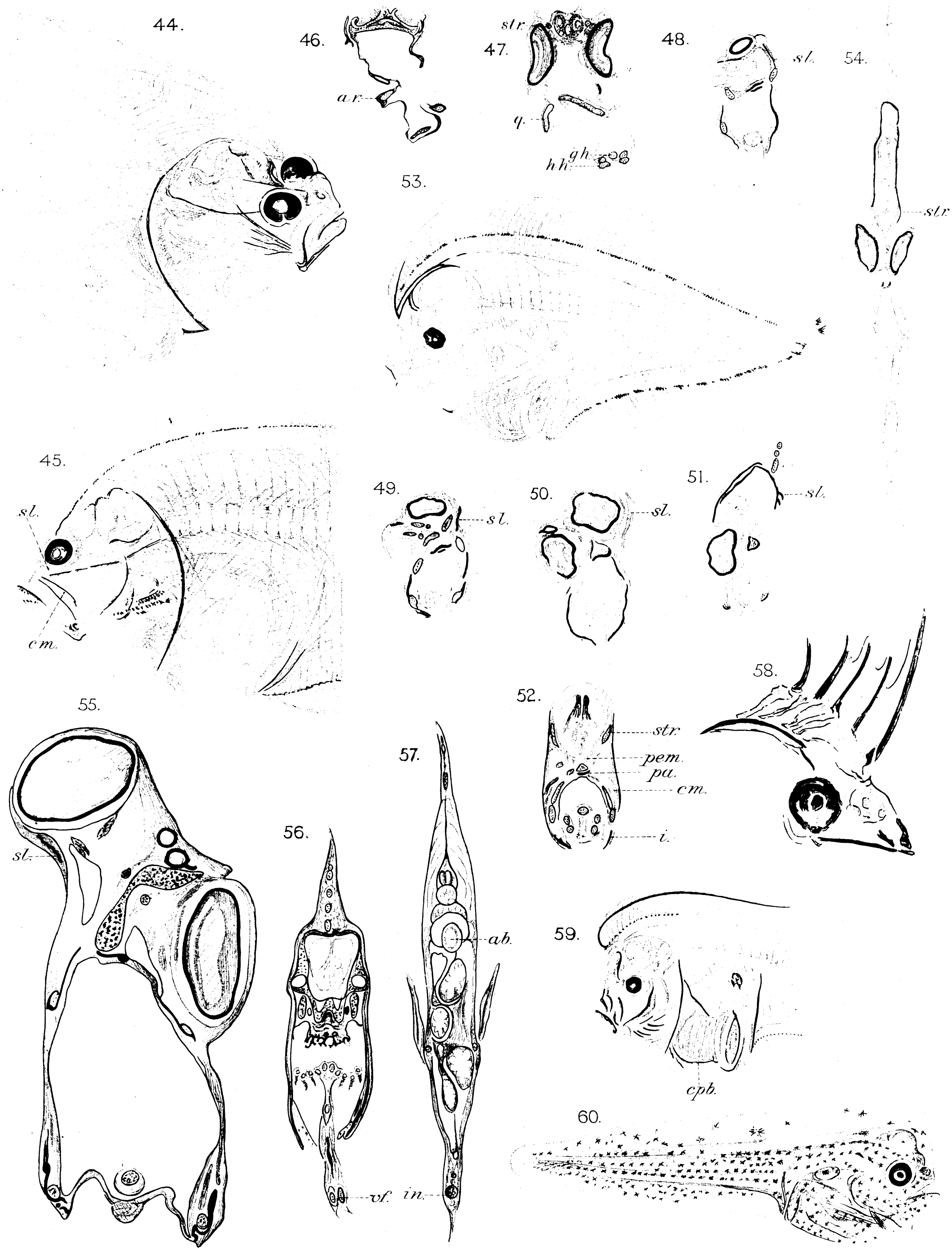

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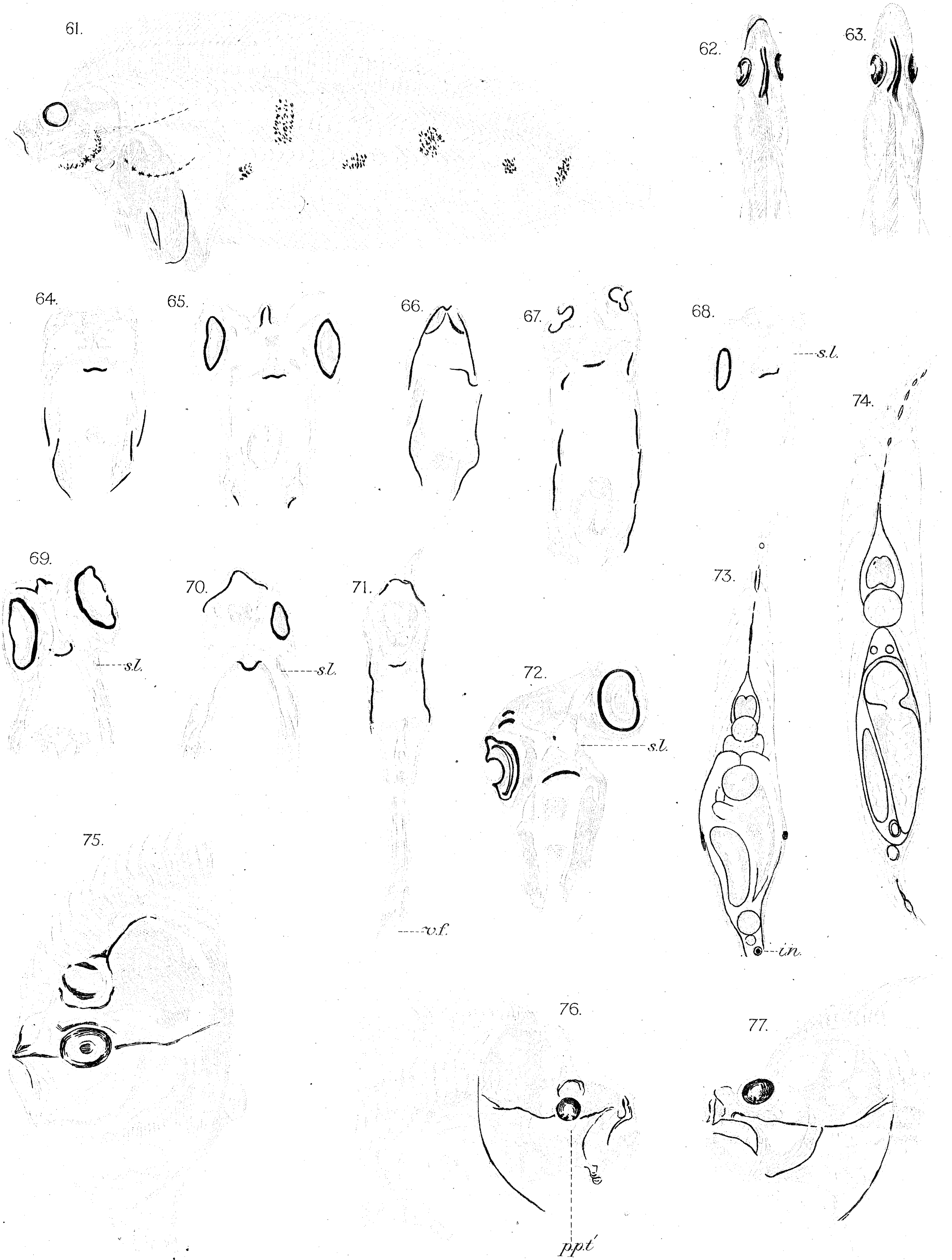

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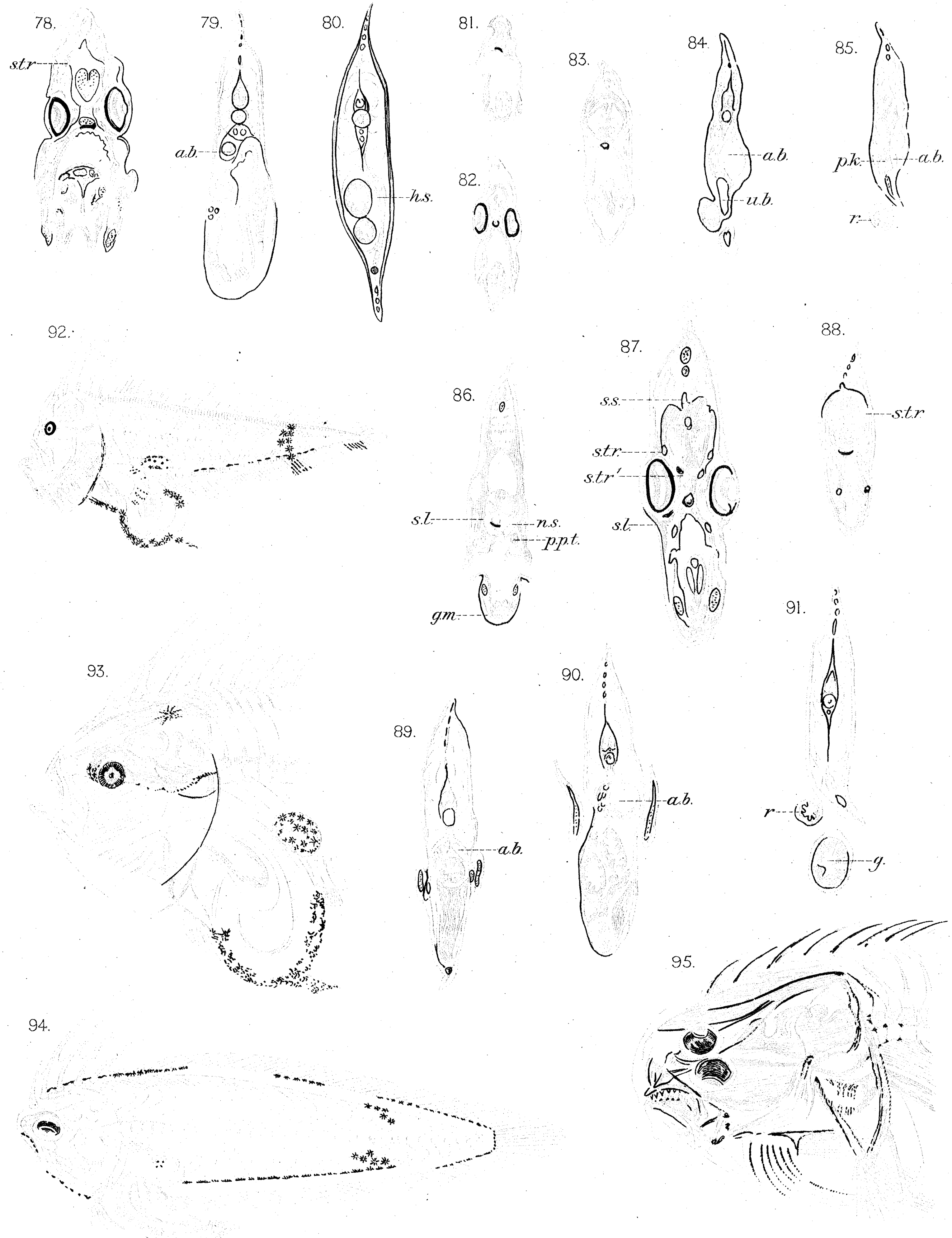

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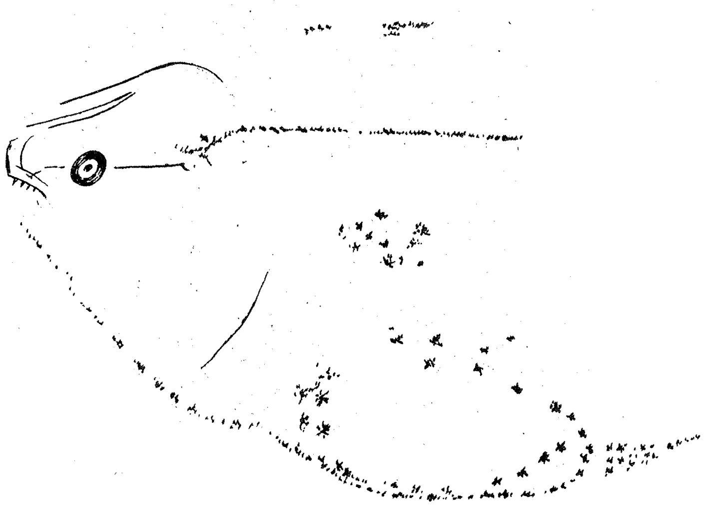

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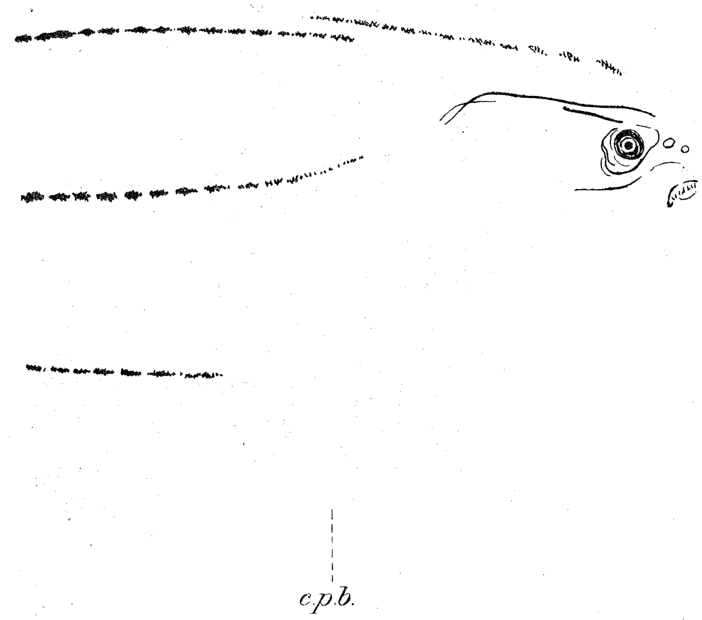

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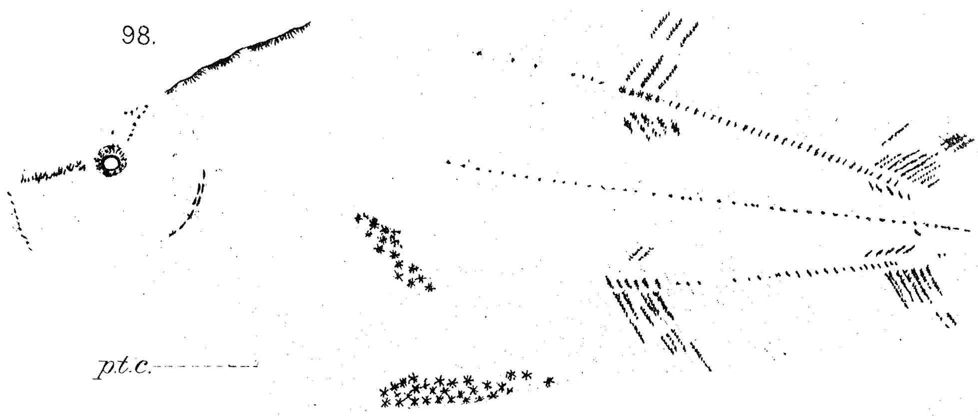

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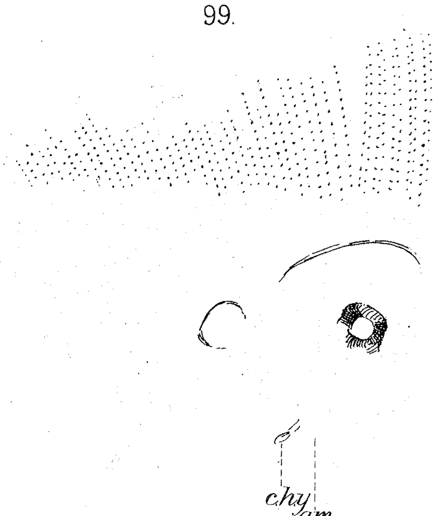

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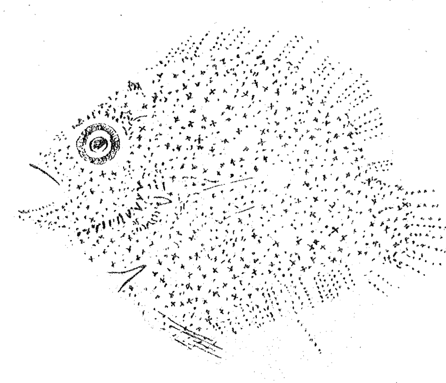

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Fig. 93.—*Symphurus lactea.* 10 mm. × 20. Anterior basal supports of dorsal fin (cartilaginous) developed; body strongly asymmetrical; only right pelvic developed.

Fig. 94.—*Symphurus pusilla* (GOODE and BEAN). Specimen of 14 mm. in final stage of metamorphosis; clear space above eyes (*cf.* fig. 97).

Fig. 95.—*Symphurus lactea* (BON.). 21 mm. Specimen just metamorphosed. Migrating eye has come through under frontals; pectorals thrown off; pectoral arch drawn backwards.

PLATE 10.

Fig. 96.—*Symphurus lactea.* 18 mm. × 14. Frontals and supraoccipital separating from skull (*cf.* fig. 93) preparatory to migration of eye.

Fig. 97.—*Symphurus pusilla;* right eye disappearing under thick integument; ethmoid plate strongly bent upward; pectoral arch strongly retracted; eyeless side of fig. 94.

Fig. 98.—Brotulid. 18 mm. × 8. Similar mode of balancing to that of *Symphurus,* but post-cleithra assuming function of pubic bars; advanced type of pectoral.

Fig. 99.—*Trachypterus,* sp. 12 mm. × 9. Hyoid arch strongly retracted; skull depressed; premaxillaries growing up in front of skull; horizontal coil and abdominal pelvics represent possibly an earlier phylogenetic stage than *Symphurus.*

Fig. 100.—Blennioid. 30 mm. × 5. Very similar balance to that of *Symphurus,* but depressed skull indicates divergence.

Fig. 101.—Postlarval *Stromateoides.* 12·5 mm. × 5. Very similar balance to Rhomboid type of Flat-fishes; ventrals drop off later and skull becomes connected with anterior end of dorsal fin by means of a bony spine or rod.

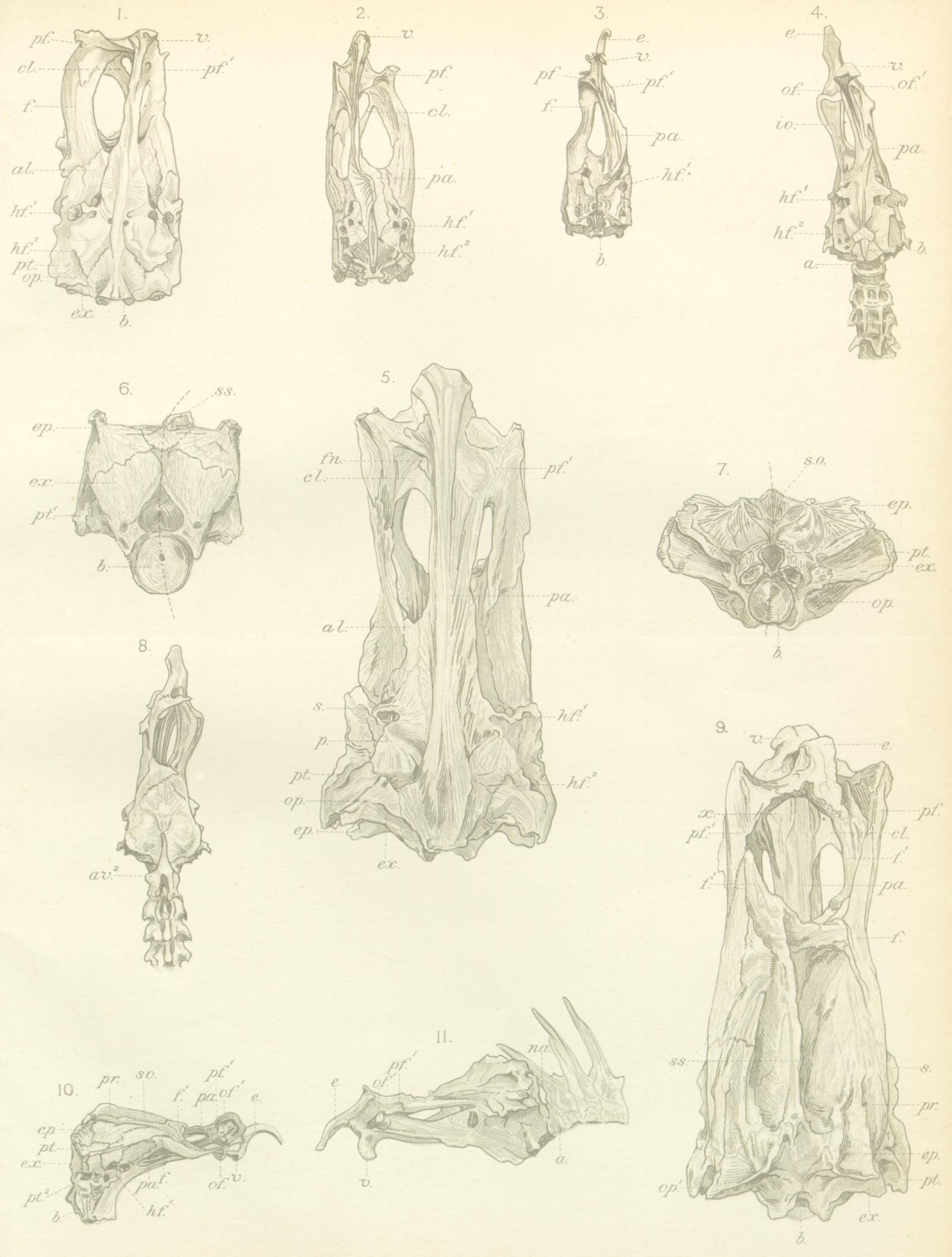

PLATE 4.

Figs. 1–5 show the varying degrees and varying position of the primary flexure of the skull.

Fig. 1.—*Pleuronectes platessa L.*, from lower aspect. n.s.
Fig. 2.—*Arnoglossus imperialis* (RAFIN.), from lower aspect. 2/1.
Fig. 3.—*Solea nasuta* (PALL.), from lower aspect. 2/1.
Fig. 4.—*Solea vulgaris* QUENS., from lower aspect. n.s.
Fig. 5.—*Platysomatichthys hippoglossoides* (WALB.), from lower aspect. n.s.

Figs. 6 and 7 illustrate the asymmetry of the posterior region of the skull in the first group of Flat-fishes.

Fig. 6.—*Lepidorhombus megastoma* (DON.), posterior aspect. 2/1.
Fig. 7.—*Platysomatichthys*, posterior aspect. n.s.
Fig. 8.—*Solea vulgaris ;* from upper aspect ; skull as a whole deflected to eyed side.
Fig. 9.—*Platysomatichthys ;* upper aspect.
Fig. 10.—*Solea nasuta* ; from eyed side ; great distorsion in frontal region and at junction of parasphenoid and basioccipital.
Fig. 11.—*Solea vulgaris ;* from eyeless side ; peculiar position of vomer and olfactory foramen.

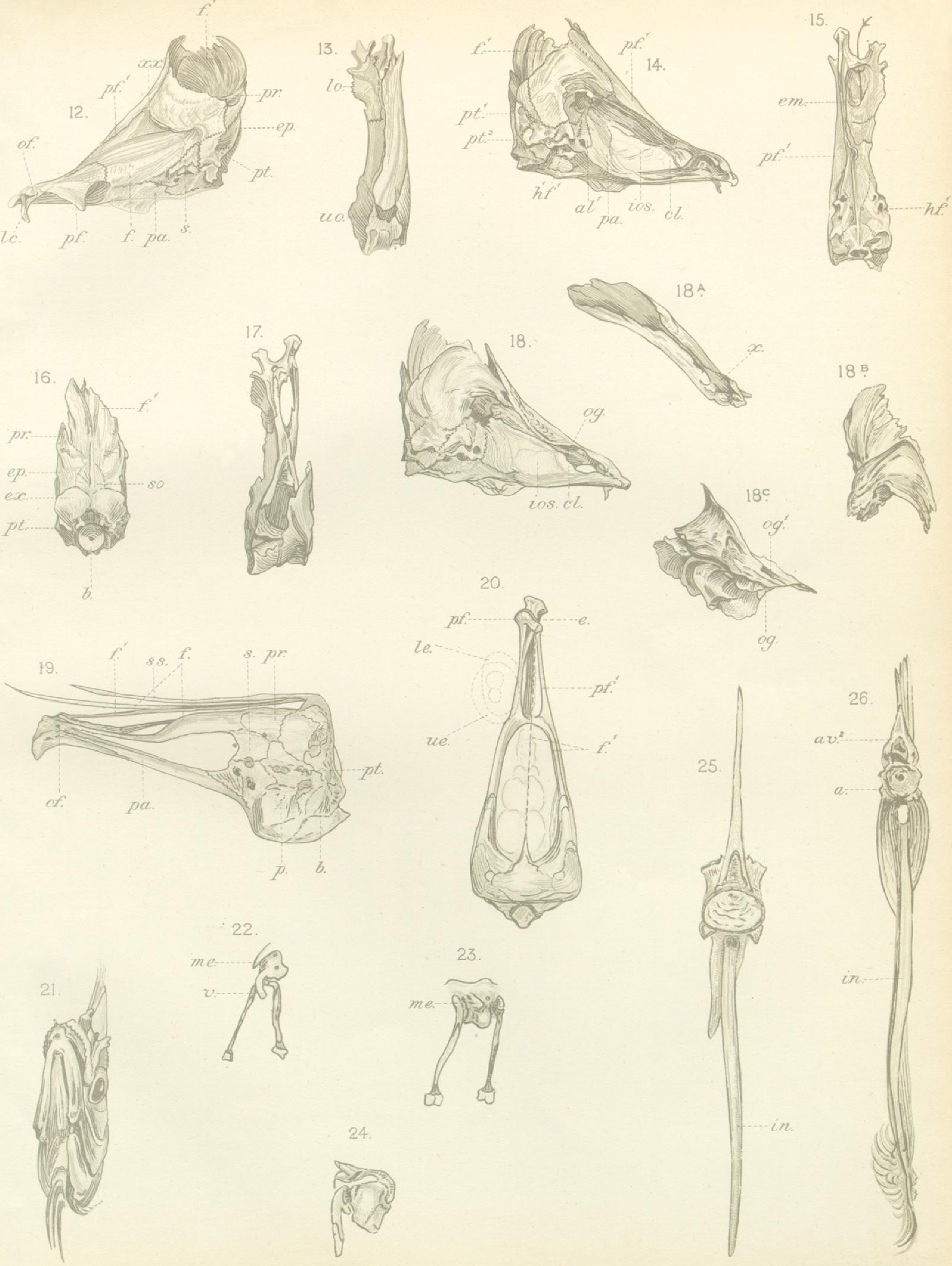

PLATE 5.

Fig. 12.—*Bothus podas* (DELAR.), male; from eyed side. 2/1. *xx*, a membranous area where migrating eye first rested before being pushed upwards and backwards by prefrontal of eyeless side (pf').

Fig. 13.—*Bothus podas* (DELAR.), seen from above. 2/1.

Fig. 14.—*Bothus podas* (DELAR.), eyeless side. 2/1.

Fig. 15.—*Bothus podas* (DELAR.), lower aspect. 2/1. The seeker indicates olfactory canal, quite distinct from eye-muscle canal (*em*).

Fig. 16.—*Bothus podas* (DELAR.), posterior aspect. 2/1.

Fig. 17.—*Bothus podas* (DELAR.), upper aspect after removal of prefontal of eyeless side (2/1); upper orbit opens directly into cranial cavity.

Fig. 18.—*Bothus podas* (DELAR.), eyeless side after removal of prefrontal of eyeless side (*a*); *b*—frontal of eyeless side; *c*—frontal of eyed side. 2/1.

Fig. 19.—*Symphurus lactea* (BONAP.); from eyed side. 6/1. Frontals separated from skull.

Fig. 20.—*Symphurus*, from upper aspect; 6/1. Cranial cavity covered only by a thin membrane.

Fig. 21.—*Bothus*, viewed from in front (n.s.); unequal rami of jaws.

Fig. 22.—*Solea*; pterygopalatine arch; mesethmoid pointing to eyed side; vomer to eyeless. n.s.

Fig. 23.—*Pleuronectes;* pterygopalatine arch; mesethmoid and vomer pointing to eyeless side. n.s.

Fig. 24.—*Solea;* upper and lower jaws; mandibular longer on eyed side; premaxillary articulated to dentary on eyeless side. n.s.

Fig. 25.—*Platysomatichthys;* first caudal vertebra with posterior abdominal rod (*in*) inclined to eyeless side.

Fig. 26.—*Lepidorhombus;* anterior view of abdominal vertebræ, showing double deflection of abdominal rod. n.s.

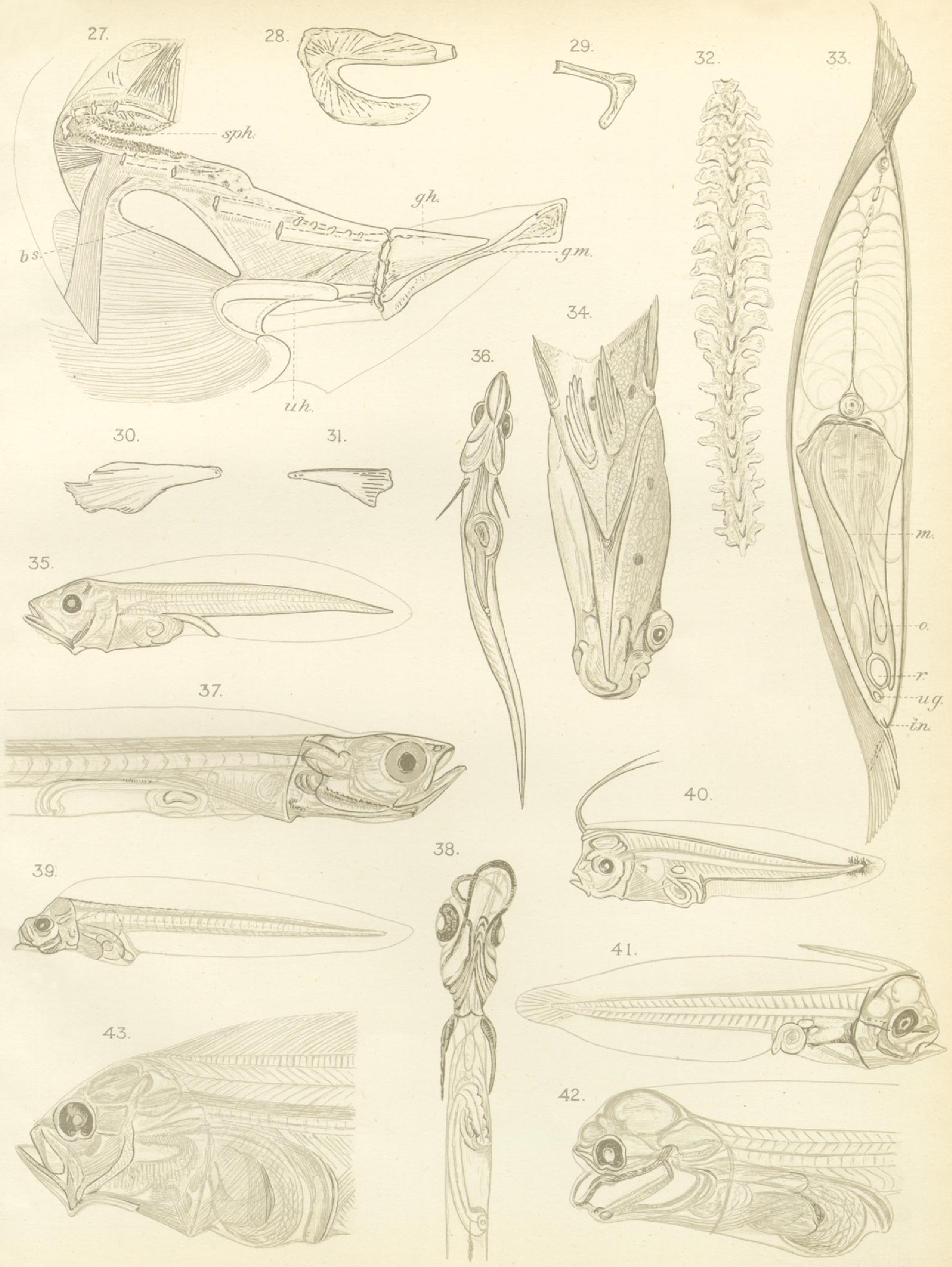

PLATE 6.

Fig. 27.—*Lepidorhombus;* dissection of ventral mechanism opening the mouth; curved urohyal, breach in interbranchial septum, abdominal muscles passing forward to lower prong of urohyal. n.s.

Fig. 28.—*R. maximus*, L.; urohyal. n.s.

Fig. 29.—*S. vulgaris* QUENS.; urohyal. n.s.

Fig. 30.—*Synaptura*; simple urohyal, not hooked. n.s.

Fig. 31.—*Cynoglossus;* simple urohyal, not hooked. n.s.

Fig. 32.—*Rhombus maximus* L. Vertebral column to show longitudinal flexures of abdominal region; to eyeless side on caudal vertebræ, then to eyed side anteriorly. n.s.

Fig. 33.—*P. platessa* L. Section through abdominal region, front view, showing flexure to eyeless side dorsally and ventrally, and also longitudinally. 1/2.

Fig. 34.—*P. platessa* L. Head strongly flexed to eyeless side.

Figs. 35 to 42 represent the first stage in the metamorphosis of Flat-fishes; coil of gut just formed on left side; air-bladder above it also on left side (40, 41); asymmetry of jaws.

Fig. 35.—*Hippoglossus.* 12 mm. × 7. Jaws beginning to ossify.

Fig. 36.—*Hippoglossus.* 10 mm. × 10. Showing persistent flexure to side of coil; jaws asymmetrical.

Fig. 37.—*Platysomatichthys.* 18 mm. × 18; coil in middle of cavity.

Fig. 38.—*Platysomatichthys;* primitive jaws strongly flexed to left.

Fig. 39.—*Glyptocephalus*, 8·2 mm. × 10.

Fig. 40.—*Bothus*, 5 mm. × 12; air-bladder above coil; balancing dorsal ray.

Fig. 41.—*Arnoglossus laterna* WILL.; 4·5 mm. × 20. Beginning of Stage II; periotic capsule not completely formed; supraorbital trabeculæ above eye; ethmoid plate flexed to right side; supraoccipital and parasphenoid ossified.

Fig. 42.—*Drepanopsetta platessoides* FABR.; 7 mm. × 30; primitive jaws strongly flexed to left side.

Fig. 43.—*Drepanopsetta platessoides* FABR.; 10 mm. × 20. Secondary supports of jaws formed; asymmetry of orbital region beginning.

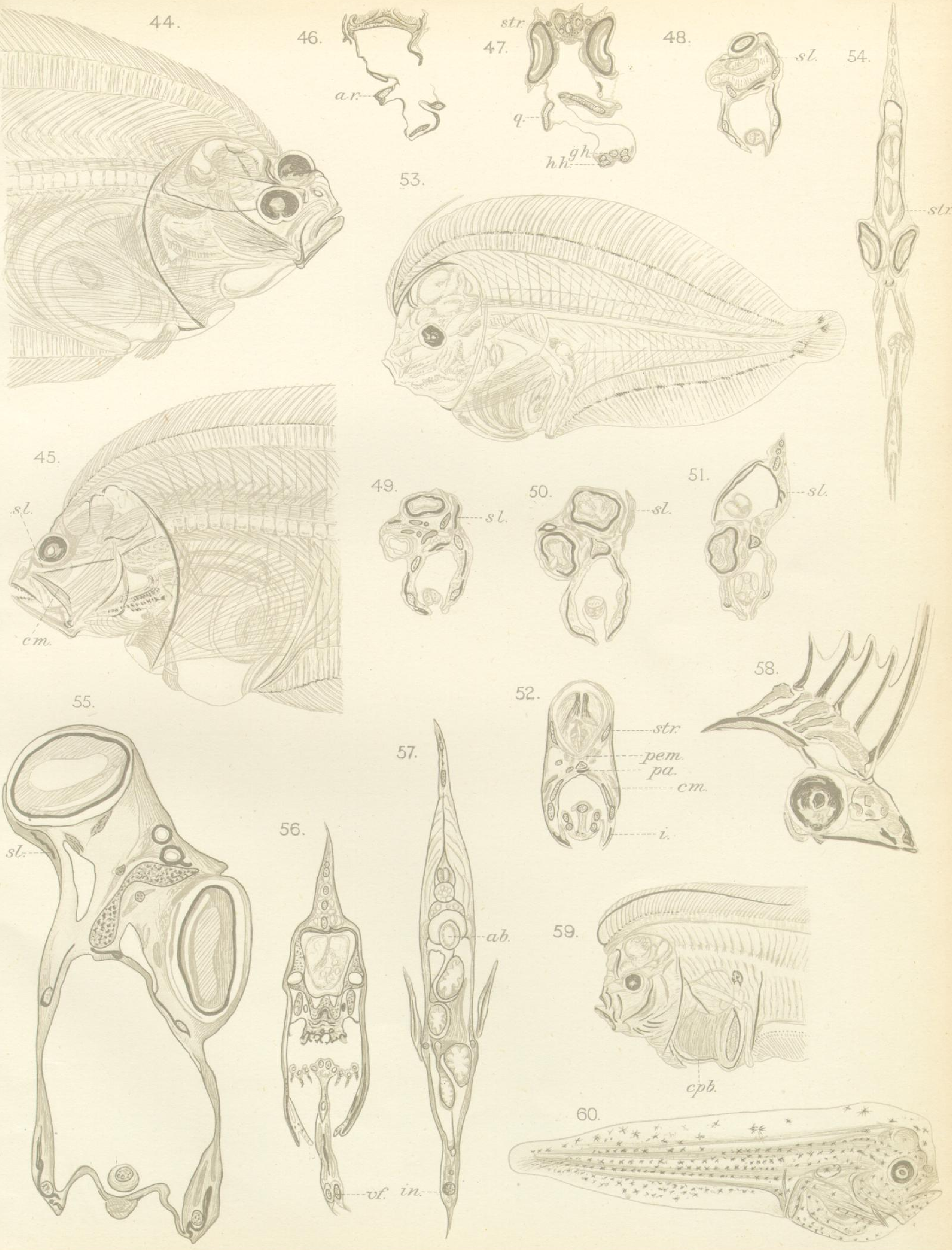

PLATE 7.

Fig. 44.—*Pleuronectes;* 14 mm. × 15. Stage IV; frontals deflected; migrating eye beyond anterior end of dorsal fin; enclosure of abdominal cavity nearly complete; urohyal forming; no maxillary muscle on eyed side.

Fig. 45.—*Pleuronectes;* 12 mm. × 15. Stage III; subocular ligament developing (*sl*); hyocleithral muscles ruptured; maxillary muscle on eyeless side.

Figs. 46, 47.—*Platysomatichthys;* 18 mm. × 20. Stage I. Olfactory capsules well-developed; jaws asymmetrical; ethmoid plate and basal axis of skull slightly asymmetrical.

Figs. 48–51.—*Pleuronectes;* 14 mm. × 20. Stage IV. Subocular ligament developing compels eye to move over to right side; fenestra forming in inter-orbital septum and eye muscles being carried over to left side (49).

Fig. 52.—*Pleuronectes;* 9 mm. × 20. Stage II. Section posterior to eyes; beginning of left flexure of parasphenoid.

Fig. 53.—*Bothus;* 10 mm. × 10. Air-bladder and dorsal balancing ray about to disappear; skull depressed.

Fig. 54.—*Bothus;* 25 mm. × 15. Section through eyes; upper part of head to right, lower part to left; eyes only slightly asymmetrical.

Figs. 55–57.—*Rhombus;* 17 mm. Ossification of frontals round supraorbital trabeculæ (55); flexure of pelvics to left, dorsal fin to right side (56); air-bladder slightly to left side, dorsal and ventral margins to right side (57).

Fig. 58.—*Arnoglossus;* relation of migrating eye to dorsal fin, which is not attached to lateral ethmoid until after metamorphosis.

Fig. 59.—*Arnoglossus.* Stage II; ossification of head and body; frontals slightly asymmetrical.

Fig. 60.—*Rhombus;* 6 mm. × 15. Beginning of Stage II; jaws to right.

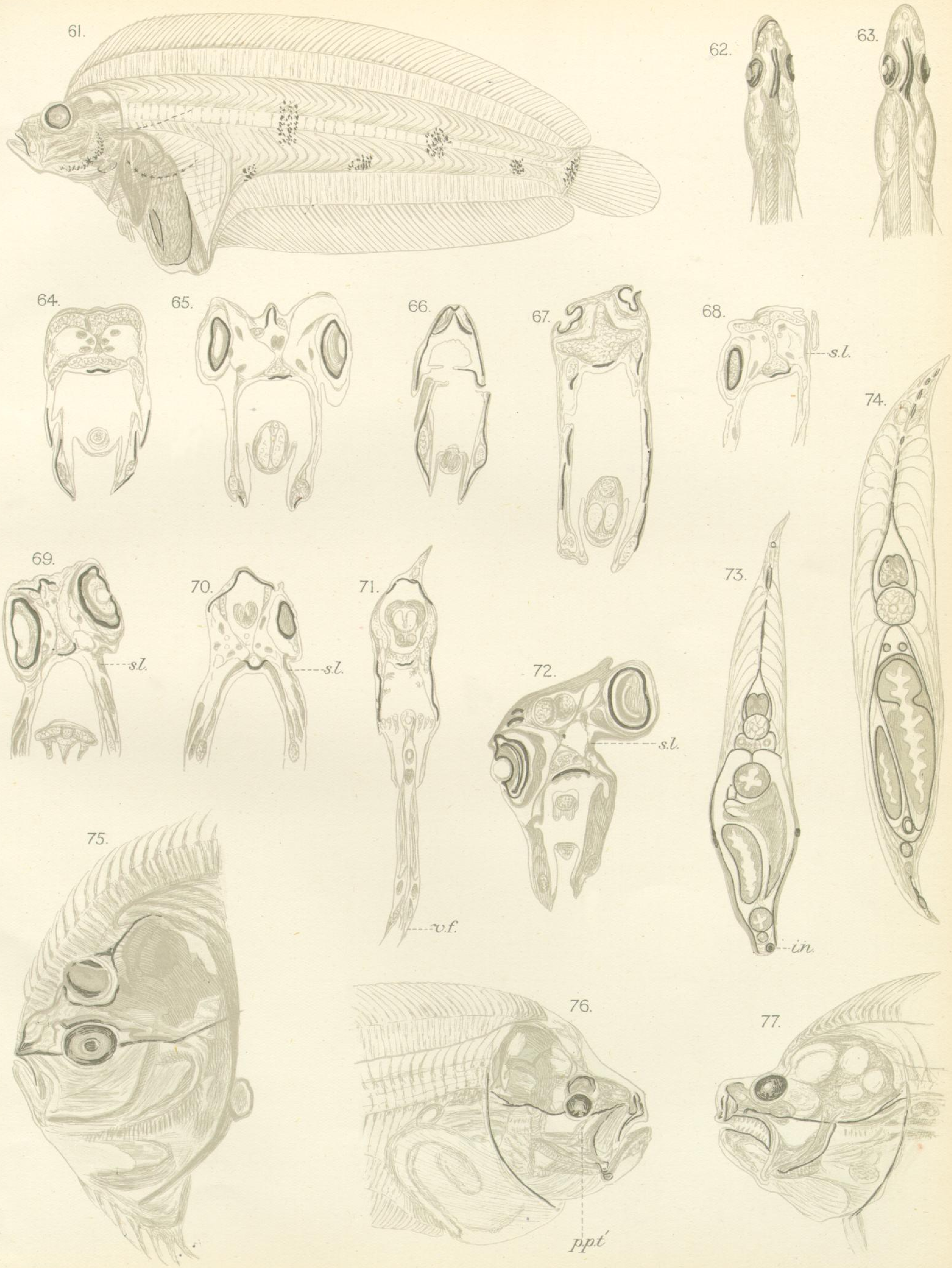

PLATE 8.

Fig. 61.—*Glyptocephalus;* 34 mm. × 4. Abdominal organs arranged in tight, transverse coil, thus serving as a balancing organ, so that fish remains in a vertical position long after skull is asymmetrical.

Fig. 62.—*Glyptocephalus;* head viewed from above.

Fig. 63.—*Glyptocephalus;* 42 mm. × 5. Increasing deflection of frontals, but migrating eye not yet begun to move; abdominal cavity not yet enclosed.

Figs. 64, 65.—*Glyptocephalus* at 13 mm. Slight asymmetry of ethmoid, and left frontal and supraorbital trabecula higher than right.

Figs. 66–70.—*Glyptocephalus* about 34 mm. Lower jaw to left, but rami equal (66); palatine higher on left (67); parasphenoid strongly to left, and left lateral ethmoid higher than right (68); left supraorbital trabecula higher than right but not reduced (69, 70).

Fig. 71.—*Glyptocephalus.* Section through pectoral arch; dorsal fin flexed to left; pelvic fins, under influence of counterbalancing tendency of abdominal organs, flexed to right.

Figs. 72–74.—*Pleuronectes,* 12·5 mm. Stage III or beginning of Stage IV; frontals deflected (72); adult convexity of right side of body and flatness of left side already conspicuous (73, 74) though fish still pelagic.

Fig. 75.—*Bothus;* metamorphosis just completed; migrating eye resting temporarily on frontal of eyed side; jaws nearly vertical; adult urohyal formed.

Fig. 76.—*Solea vulgaris,* Quens. 8 mm. × 20. Large abdominal organs; air-bladder on right side; jaws strongly asymmetrical under influence of left flexure; palatine of left side (*ppt′*) well behind that of right side; left premaxillary being pulled backwards away from right.

Fig. 77.—*Solea* sp., 9 mm. × 20. More advanced than 76; no maxillary muscle on blind side; premaxillary articulated with dentary; ethmoid snout beginning to form.

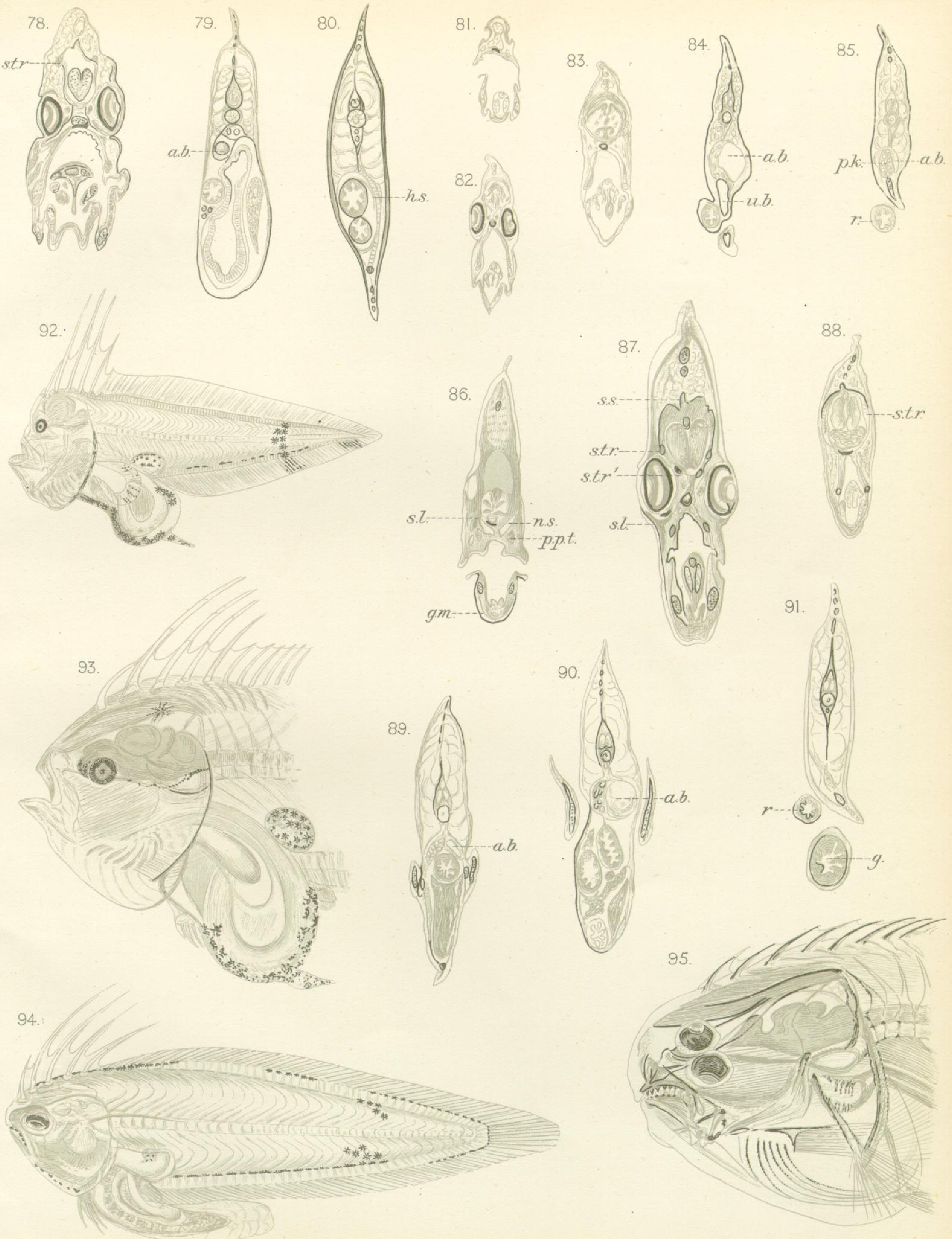

Plate 9.

Figs. 78–80.—*Solea vulgaris*, Quens., 6 mm. Slight asymmetry of skull, but jaws drawn to left (78); air-bladder on right side (79); dorsal and ventral margins of caudal region flexed to left (80), thus an advance on rotating tendency of *Symphurus* (*cf.* figs. 85, 91).

Figs. 81–85.—*Symphurus lactea* (Bon.); 9 mm. Skull slightly asymmetrical (81–83); dorsal fin strongly flexed to right; large air-bladder on left (84); rotating appearance of caudal region (85).

Figs. 86–91.—*Symphurus*, 17 mm. Large amount of lymphoid tissue; dorsal fin now flexed to left on head and abdominal region; disturbance of frontals and supraorbital trabeculæ preparatory to separation from skull (87); air-bladder becoming smaller (89, 90); rotating tendency still present in caudal region (91).

Fig. 92.—*Symphurus lactea.* 6 mm. × 13. Stage I; flexure of visceral arches and jaws to left (later to right); protruding abdominal organs, large air-bladder on left side; simple tail.

Fig. 93.—*Symphurus lactea.* 10 mm. × 20. Anterior basal supports of dorsal fin (cartilaginous) developed; body strongly asymmetrical; only right pelvic developed.

Fig. 94.—*Symphurus pusilla* (Goode and Bean). Specimen of 14 mm. in final stage of metamorphosis; clear space above eyes (*cf.* fig. 97).

Fig. 95.—*Symphurus lactea* (Bon.). 21 mm. Specimen just metamorphosed. Migrating eye has come through under frontals; pectorals thrown off; pectoral arch drawn backwards.

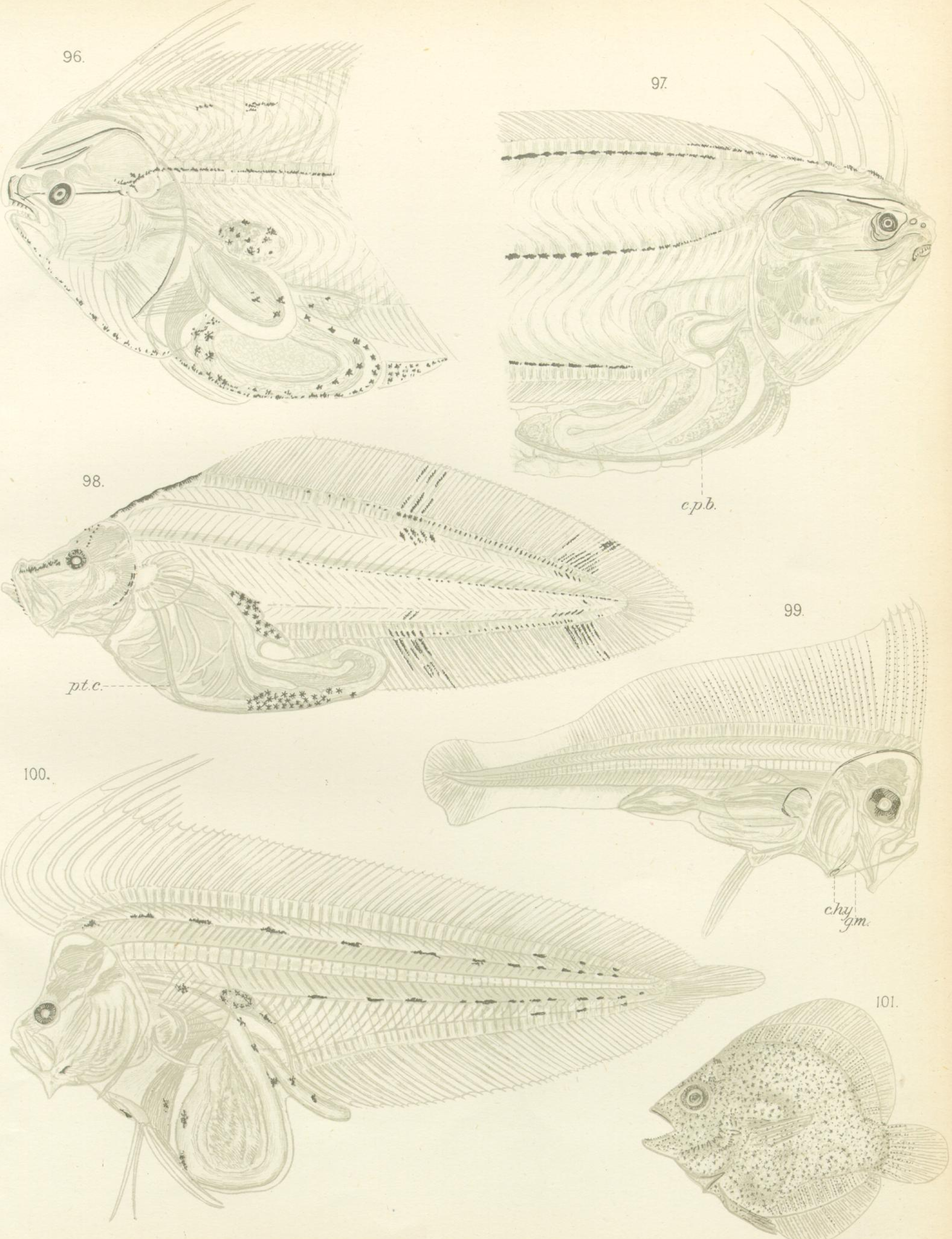

PLATE 10.

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