the skull. As he gives the number of vertebræ as 21 it seems probable that in the preparation of the skeleton the first vertebra adhered to the cranium, and was then removed separately and perhaps lost.

Subfamily 2. *Caproinæ.*

Mouth extremely protractile; præmaxillary processes very long, separating the frontals and extending back beneath the supraoccipital; maxillary narrow, without supramaxillary; a broad subocular shelf. Spinous dorsal not shorter than the soft-rayed fin.

The Miocene *Proantigonia*, Kramberger, is closely allied to the recent *Capros*, Lacep.

LIV.—*The Origin and Evolution of the Teleostean Fishes of the Order Heterosomata.* By C. Tate Regan, M.A.

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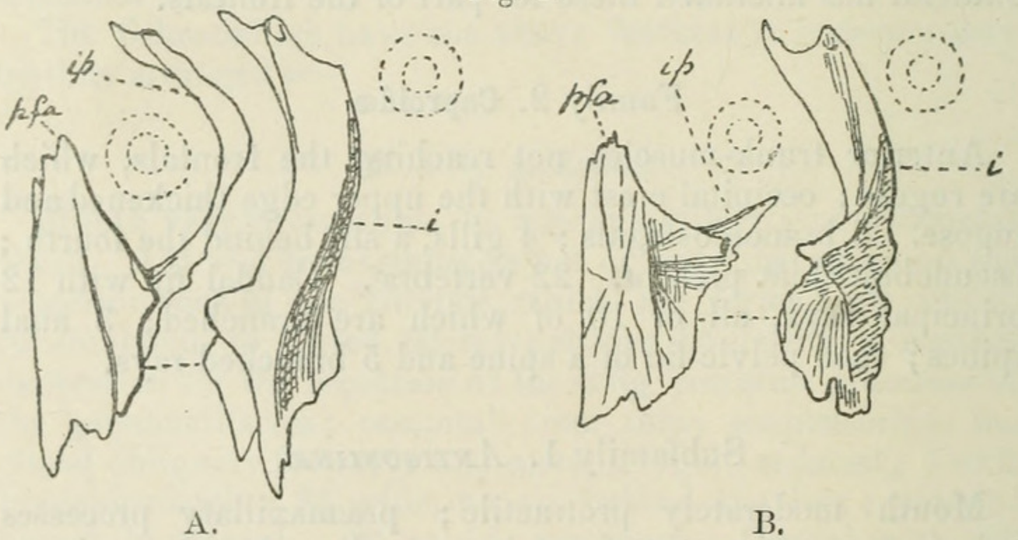
The Heterosomata, or Flat-fishes, differ from all other fishes in their asymmetry; both eyes are on one side, which is coloured, whilst the eyeless side is usually white.

Fig. 1.



Disarticulated frontal bones of (A) Halibut (*Hippoglossus hippoglossus*) and (B) Plaice (*Pleuronectes platessa*). (After Traquair.)

pfa, præfrontal articulation; *ip*, interorbital process; *i*, interorbital bar.

In the skull of all flat-fishes there is a bony interorbital bar mainly formed by the interorbital portion of the frontal bone of the eyed side, displaced outwards and downwards; the frontal of the blind side is broad and may send forward a process to share in the formation of the interorbital bar, but the main part of this bone in the orbital region is on the wrong side of its eye, although its relations are normal in other respects. The last-named fact leads one to suspect the correctness of Traquair's interpretation of this part of the frontal of the blind side, which he regards as a new process sent forwards to join the præfrontal in order to form a bar or bridge supposed to be requisite for the stability of the cranium.

Traquair's * elaborate descriptions and figures of the crania of several flat-fishes are most valuable, and his interpretation is in harmony with the often repeated statement that the migration of the eye causes or is caused by a twisting of the whole orbital region of the skull, and has been generally accepted; but recent embryological work does not, in my opinion, bear out this view. As is well known, flat-fish larvæ have the eyes on opposite sides and swim vertically, and at an early age one eye migrates round the top of the head to the other side, which is thenceforth uppermost.

Williams † has studied the migration of the eye in *Pleuronectes americanus*; in the cartilaginous cranium there are two supraorbital bars, precursors of the frontal bones, connecting the lateral ethmoids with the otic capsules; preparatory to the metamorphosis there is a rapid resorption of the part of the supraorbital bar which lies in the path of the migrating eye, so that this bar becomes reduced to a forwardly directed process of the otic capsule and a backwardly directed one of the lateral ethmoid. The eye migrates between these two projections, and so approaches the supraorbital bar of the future eyed side; the eyes then move to their final position, causing a torsion of this supra-orbital bar, which also affects the ethmoid region; after the shifting is complete, ossification takes place.

From this account it seems that it is wrong to say that the two eyes are on one side as the result of the twisting of the orbital region of the skull, for the first step is a migration of one eye into the territory of its frontal bone, causing resorption of cartilage in the larva, and in the adult producing the effect that the orbital part of its frontal ossifies round it or even entirely outside it. The displacement of the frontal of the lower eye has enlarged the area of that of the

* Trans. Linn. Soc. xxv. 1865, pp. 263–296, pls. xxix.–xxxii.
† Bull. Mus. Comp. Zool. xl. pp. 1–57, pls. i.–v. (1902).

upper eye; but it seems wrong to speak of any part of the latter bone as a new formation, least of all that part which has the same position and the same relations (except to the eye) as it would have if the skull were symmetrical.

For a long time the flat-fishes were regarded as asymmetrical Gadoids, but in the latter the absence of spinous fin-rays, the large number of rays in the pelvic fins, and the indirect attachment of the pelvic bones to the cleithra may be regarded as primitive features, and it is probable that these fishes have evolved from generalized Iniomi, such as the Aulopidæ. In the Heterosomata, on the contrary, spinous fin-rays are present in *Psettodes*, the least specialized member of the order, the pelvic fins are never more than 6-rayed, and the pelvic bones are directly attached to the cleithra. *Psettodes* is simply an asymmetrical Percoid; about the first ten dorsal rays are spinous, the caudal has 17 rays, 15 of which are branched, and each pelvic fin is formed of a spine and 5 soft rays. The mouth, the skull (except for its asymmetry), the pectoral arch, and the vertebral column are all quite Percoid.

In other Pleuronectoids all the fin-rays are articulated, and in many of them the pelvic fins are 6-rayed, with the anterior ray simple. I am unable to confirm Boulenger's statement that an additional ray is present in *Hippoglossus*, and it is clear to me that the anterior pelvic ray of this and other genera with 6-rayed pelvic fins corresponds to the spine of *Psettodes*, and that the formation of joints in response to mechanical requirements has reconverted spines into articulated rays in the dorsal and pelvic fins of the Heterosomata, as in the case of the epaxial rays of the homocercal caudal fin *.

Thilo † and Boulenger ‡ consider that the Zeidæ are nearly related to the Heterosomata; I cannot find any anatomical evidence in support of this idea. I much more readily subscribe to Boulenger's view that the Upper Eocene *Amphistium* is allied to the symmetrical ancestor of the flat-fishes, for in my opinion this fish is a Percoid, which should probably be placed in the family Scorpididæ near the existing *Psettus*, or may perhaps be related to *Platax*. Thanks to the courtesy of Dr. Smith Woodward, I have been able to examine the two examples of *Amphistium paradoxum* in the British Museum. The caudal fin has 17 principal rays, 15 of which are branched, in addition to a few graduated rays above and

* Regan, Ann. & Mag. Nat. Hist. (8) v. 1910, p. 357.
† Zool. Anz. 1902, pp. 305-320.
‡ Ann. & Mag. Nat. Hist. (7) x. 1902, pp. 295-304.

below; the pelvic fin, preserved only in the Monte Bolca specimen, is formed of a spine and, in my opinion, 5 soft rays, for I cannot see a greater number inserted on the pelvic bone which lies uppermost, the outlines of which are fairly distinct.

Boulenger's restoration shows several features of *Psettodes* or *Zeus* rather than *Psettus* which I am unable to see in the fossils; thus he shows the lower jaw nearly as long as the head and the præoperculum vertical and scarcely curved, whereas the lower jaw appears to me only a little more than half the length of the head, and the præoperculum to have a distinct lower limb; also the origin of the anal fin is not so far forward in the actual fossils as it is in the restoration.

Bothus and *Solea* were already in existence in the Upper Eocene, and, indeed, the whole Upper Eocene fish-fauna is strikingly modern, so that there is no reason to regard *Amphistium* as ancestral to the flat-fishes on account of its occurrence in the Upper Eocene.

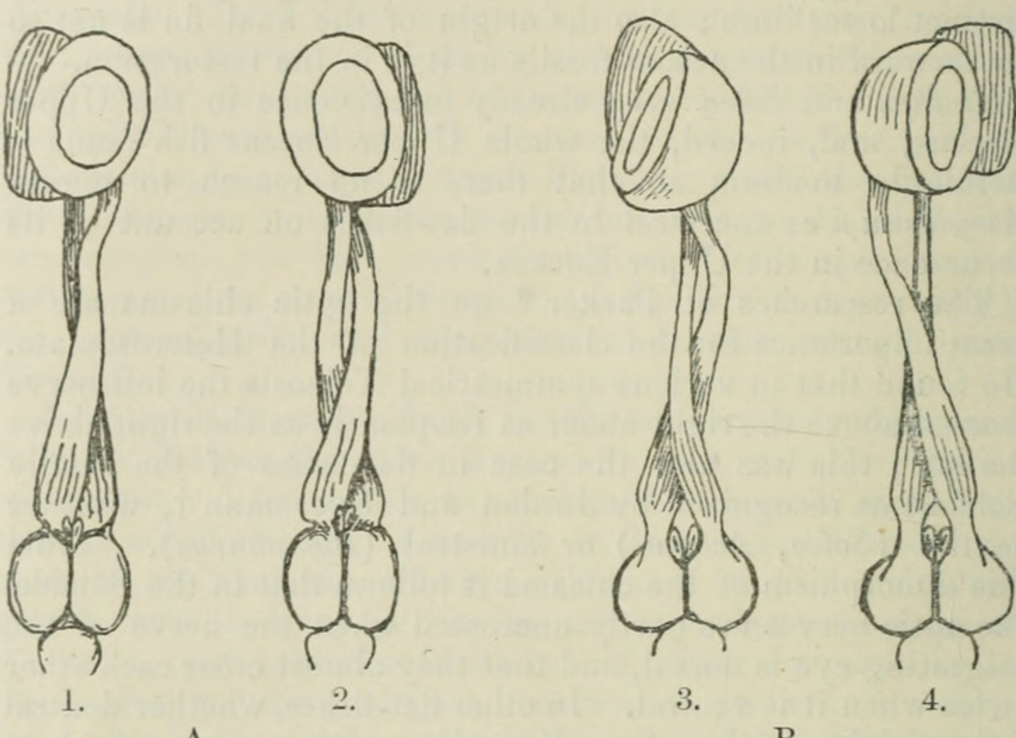
The researches of Parker * on the optic chiasma are of great importance for the classification of the Heterosomata. He found that in various symmetrical Teleosts the left nerve crossed above the right about as frequently as the right above the left; this was also the case in flat-fishes of the family Soleidæ as recognized by Jordan and Evermann †, whether dextral (*Solea, Achirus*) or sinistral (*Symphurus*). From this dimorphism of the chiasma it follows that in the Soleidæ the optic nerves are partly uncrossed when the nerve of the migrating eye is dorsal, and that they almost cross each other twice when it is ventral. In other flat-fishes, whether dextral (*Psettichthys*, *Atheresthes*, *Parophrys*, *Pleuronectes*, &c.) or sinistral (*Paralichthys*, *Platophrys*, *Citharichthys*, &c.), Parker found that it was always the case that the nerve of the migrating eye was dorsal, the only exception being in the case of reversed examples, *i. e.* sinistral members of dextral species or dextral members of sinistral species, in which that nerve was dorsal which was normally dorsal in the genus. In a few species of the Pacific coast of North America sinistral and dextral individuals are equally numerous; but in a species of a sinistral genus, such as *Paralichthys californicus*, the nerve of the right eye is always dorsal, whether the individual be sinistral or dextral; similarly, in a species of a dextral genus, such as *Platichthys stellatus*, the nerve of the left eye is dorsal. This monomorphism of the optic chiasma is obviously a specialization, which Parker considers has been

* Bull. Mus. Comp. Zool. xl. pp. 219–242 (1903).
† Bull. U.S. Nat. Mus. xlvii. pt. iii. pp. 2602–2712 (1898).

arrived at on account of its mechanical advantage, and he draws the deductions that the Soleidæ are a natural group and that they have evolved from more generalized flat-fishes than those with a monomorphic chiasma.

Parker did not examine *Psettodes.* I find that in two sinistral examples of this monotypical genus the right nerve is dorsal in one, ventral in the other ; this establishes that

Fig. 2.



Dorsal views of anterior parts of brains with cerebral hemispheres removed, showing eyeballs, optic nerves, and optic lobes. (After Parker).

A. *Paralichthys californicus*, sinistral species, with nerve of right eye dorsal. 1, sinistral individual ; 2, dextral individual.

B. *Platichthys stellatus*, dextral species, with nerve of left eye dorsal. 3, sinistral individual ; 4, dextral individual.

the chiasma is dimorphic, and it appears to me that in all probability the presence of sinistral and dextral individuals in equal numbers is primitive and is of another nature from the phenomena observed in some species of *Paralichthys* and *Platichthys.*

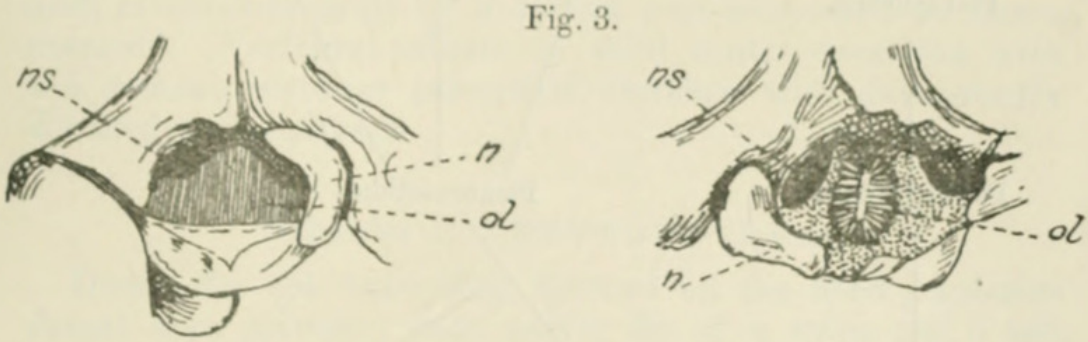
Kyle * has written a valuable paper on the classification of the Heterosomata, and has used some new characters without

* Rep. Fisheries Board Scotland, xviii. 1900, pp. 335–368, pls. xi.-xii.

quite appreciating their full importance. Adopting Jordan and Evermann's two families, Pleuronectidæ and Soleidæ, he has found that in the former the nasal organ of the blind side has accompanied or followed the eye in its migration, and lies nearly on the edge of the head, whereas in the latter the nasal organs are placed symmetrically; this confirms Parker's ideas as to the Soleidæ, and I may mention that, although in *Psettodes* the nasal organs are not quite symmetrical, they are very nearly so.

Kyle has also found that in *Psettodes*, the sinistral Pleuronectoids, and the Soleidæ the olfactory laminæ radiate from

Fig. 3.



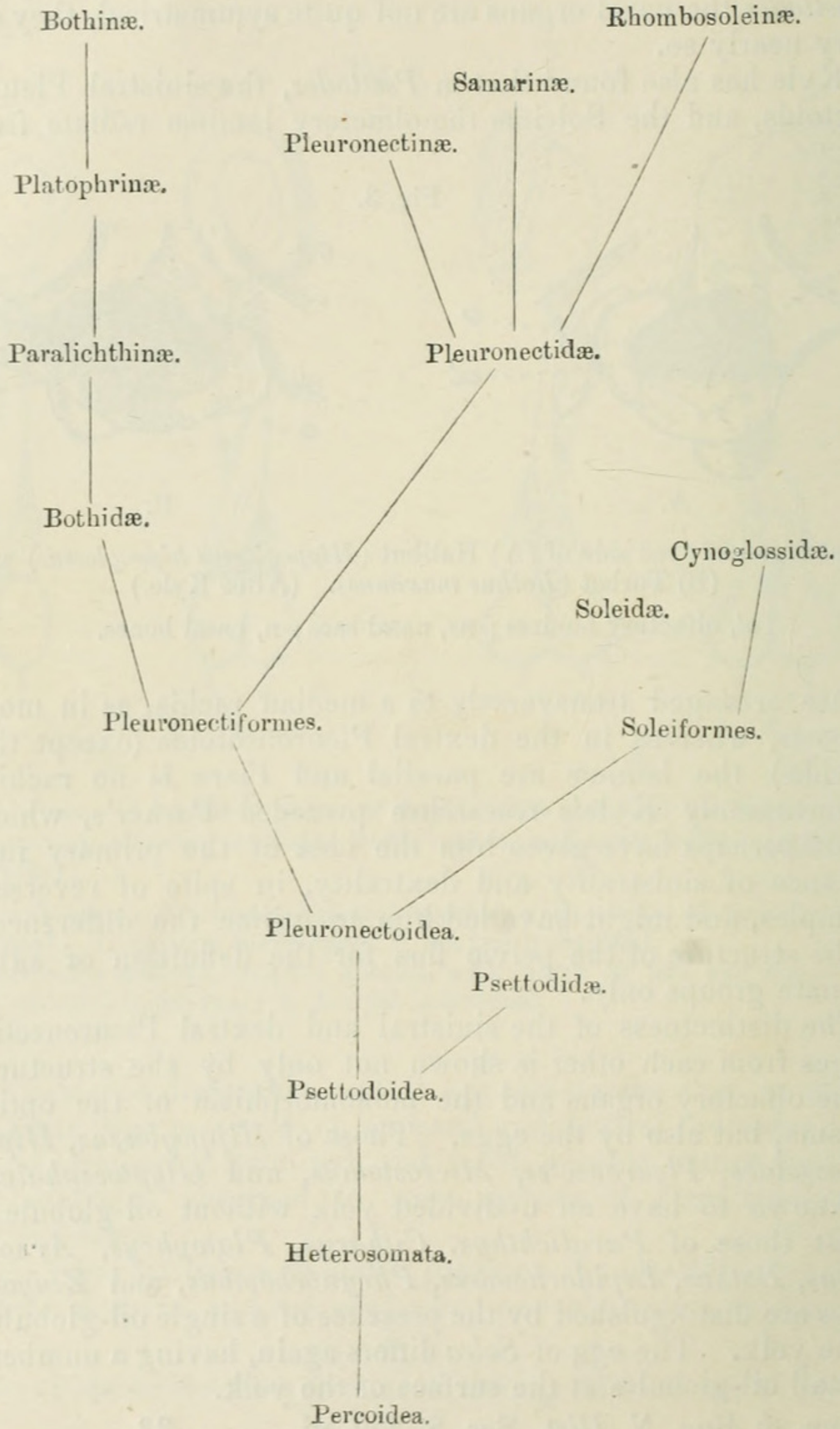
Nasal organ of eyed side of (A) Halibut (*Hippoglossus hippoglossus*) and (B) Turbot (*Bothus maximus*). (After Kyle.)

ol, olfactory laminæ; *ns*, nasal sacs; *n*, nasal bones.

or are arranged transversely to a median rachis, as in most Teleosts, whereas in the dextral Pleuronectoids (except the Soleidæ) the laminæ are parallel and there is no rachis. Unfortunately Kyle's researches preceded Parker's, which would perhaps have given him the idea of the primary importance of sinistrality and dextrality, in spite of reversed examples, and might have led him to utilize the differences in the structure of the pelvic fins for the definition of subordinate groups only.

The distinctness of the sinistral and dextral Pleuronectiformes from each other is shown not only by the structure of the olfactory organs and the monomorphism of the optic chiasma, but also by the eggs. Those of *Hippoglossus*, *Hippoglossoides*, *Pleuronectes*, *Microstomus*, and *Glyptocephalus* are known to have an undivided yolk without oil-globule; whilst those of *Paralichthys*, *Citharus*, *Platophrys*, *Arnoglossus*, *Bothus*, *Lepidorhombus*, *Phrynorhombus*, and *Zeugopterus* are distinguished by the presence of a single oil-globule in the yolk. The egg of *Solea* differs again, having a number of small oil-globules at the surface of the yolk.

I venture to think that it is fairly certain that from some form not very unlike *Psettodes* the two groups typified by the plaice and the sole have arisen, and that each of these has split into two series, a sinistral and a dextral. These conclusions are embodied in the following classification, and may be expressed diagrammatically thus :—



Order HETEROSOMATA.

Asymmetrical, with both eyes on one side. Body strongly compressed, with the præcaudal region short; dorsal and anal fins long; caudal fin with 17 principal rays (15 branched) or fewer; pelvic fins 6-rayed or less, thoracic or jugular, with the pelvic bones directly attached to the cleithra. Air-bladder absent in the adult. Mouth more or less protractile, bordered above by the præmaxillaries only. Parietals separated by the supra-occipital; interorbital bar mainly formed by the frontal of eyed side; frontal of blind side extending to præfrontal external to upper eye; no orbito-sphenoid. Pectoral arch attached to skull by a forked post-temporal; no mesocoracoid. Vertebral column of solid centra coossified with the arches; posterior præcaudal vertebræ with downwardly directed parapophyses.

Suborder 1. PSETTODOIDEA.

Dorsal fin not extending forward on the head; anterior dorsal rays spinous; each pelvic fin of a spine and 5 soft rays. Maxillary with a well-developed supra-maxillary bone; palatines toothed; urohyal normal, the lower edge scarcely curved. Two post-cleithra on each side. Vertebræ 24 (10+14). Species with sinistral and dextral individuals equally numerous and with the optic chiasma dimorphic.

Family 1. **Psettodidæ**.

Pelvic fins nearly symmetrical in form and position, posterior to the cleithra. Mouth large, with strong pointed teeth; jaws and dentition equally developed on both sides. Nasal organ of blind side scarcely higher than the other; olfactory laminæ arranged transversely to or radiating from a central rachis. Præcaudal parapophyses downwardly directed and united to form closed hæmal arches; pectoral radials well developed.

A single species, *Psettodes erumei*, ranging from West Africa to China. It has no gill-rakers, and the strongly toothed mouth is larger than in any other flat-fish; this is evidently a predaceous fish, which probably lies on the bottom concealed from its prey, and then darts out, swimming rapidly for a short distance by lateral movements of the tail. Probably it has retained so many Percoid features because it has not adopted progression by undulating movements of the body and marginal fins to the same extent as other fishes of this order.

Suborder 2. PLEURONECTOIDEA.

Dorsal fin extending forward on the head at least to above the eye; all the fin-rays articulated; each pelvic fin of 6 or fewer rays. No supramaxillary bone; no palatine teeth; lower edge of urohyal deeply emarginate, so that the bone appears forked. On each side a single post-cleithrum or none. Vertebræ never fewer than 28 (9+19).

Division 1. *PLEURONECTIFORMES.*

Mouth usually terminal, with the lower jaw prominent; præoperculum with free margin. Nasal organ of blind side near edge of head. Optic chiasma monomorphic, the nerve of the left eye in dextral forms and that of the right eye in sinistral forms always dorsal. A post-cleithrum; ribs present.

Family 1. **Bothidæ.**

Sinistral, except for reversed examples in certain species. Nerve of the right eye always dorsal. Olfactory laminæ arranged transversely to, or radiating from, a central rachis. Egg with a single oil-globule in the yolk. Pectoral radials present.

Subfamily 1. *PARALICHTHINÆ.*

Pelvic fins short-based, supported by the pelvic bones and situated behind the cleithra, either symmetrical or with the fin of the eyed side nearly median in position. Vertebræ 33–41 (9–12+24–30); most or all of the parapophyses in the præcaudal region downwardly directed, united or connected by bridges to form closed hæmal arches; caudal vertebræ without transverse apophyses.

Principal genera:—*Tephritis, Verasper, Hippoglossina, Lioglossina, Xystreurys, Paralichthys, Pseudorhombus, Ramularia, Ancylopsetta, Notosema, Gastropsetta, Cyclopsetta, Syacium, Azevia, Citharus, Citharichthys, Thysanopsetta, Etropus,* from tropical and temperate seas.

In most the mouth is moderately large, with the jaws and dentition nearly equally developed on both sides; but in the small-mouthed *Etropus* the jaws of the blind side are curved and are much more strongly toothed than those of the eyed side.

I have examined the skeletons of *Paralichthys* (vertebræ 10+24), *Pseudorhombus* (10+27), *Citharichthys* (11+28), and *Syacium* (10+25).

Subfamily 2. *Platophrinæ.*

Pelvic fin of blind side short-based ; pelvic fin of ocular side elongate, extending forward to the urohyal, supported by a cartilaginous plate placed in advance of the cleithra. Vertebræ 37–43 (9–10 + 27–33) ; parapophyses in præcaudal region connected or united as in the Paralichthinæ ; caudal vertebræ with well-developed transverse apophyses.

Principal genera :—*Arnoglossus*, *Anticitharus*, *Chascanopsetta*, *Pelecanichthys*, *Scæops*, *Engyprosopon*, *Læops*, *Monolene*, *Trichopsetta*, *Platophrys*, *Lepidopsetta*, *Lophonectes*, from tropical and temperate seas.

In the small-mouthed *Læops* the jaws and dentition are unequally developed on the two sides, just as in *Etropus*.

I have examined skeletons of *Arnoglossus* (vertebræ 10 + 33), *Platophrys* (10 + 29), and *Lophonectes* (10 + 31).

Subfamily 3. *Bothinæ.*

Both pelvic fins elongate, extending forward to the urohyal, supported by cartilaginous plates placed in advance of the cleithra. Vertebræ 35–41 (9–12 + 25–31) ; parapophyses in precaudal region separate ; caudal vertebræ with well-developed transverse apophyses. Jaws and dentition equally developed on both sides.

Genera :—*Bothus*, *Lepidorhombus*, *Zeugopterus*, and *Phrynorhombus*, from the North Atlantic and Mediterranean.

I have examined skeletons of *Bothus* (vertebræ 11 + 25), *Lepidorhombus* (9 + 31), *Zeugopterus* (9 + 26), and *Phrynorhombus* (10 + 26).

Family 2. **Pleuronectidæ.**

Dextral, except for reversed examples in certain species. Nerve of the left eye always dorsal. Olfactory laminæ slightly raised, parallel, without rachis. Egg without oil-globules.

Subfamily 1. *Pleuronectinæ.*

Anterior part of dorsal fin posterior to nasal organ of blind side ; pelvic fins short-based, supported by the pelvic bones posterior to the cleithra, similar in form and symmetrical, or the fin of the eyed side median. Pectoral radials present ; hypocoracoids narrowed forward below. Vertebræ 35–65 (10–16 + 23–52) ; præcaudal parapophyses separate, divergent.

The principal genera may be arranged thus :—

A. Mouth large, with the jaws and dentition nearly equally developed on both sides. Vertebræ 40–50 (10–16 + 29–37).

Hippoglossus, *Atheresthes*, *Platysomatichthys*, *Hippoglossoides*, *Psettichthys*, *Eopsetta*, and *Liopsetta*, from arctic and northern seas.

B. Mouth small, asymmetrical, the jaws and dentition more developed on the blind side. Vertebræ 35–65 (10–14 + 23–52).

Pleuronichthys, *Parophrys*, *Isopsetta*, *Limanda*, *Pleuronectes*, *Platichthys*, *Microstomus*, *Glyptocephalus*, &c., from arctic and northern seas, with *Pœcilopsetta*, *Boopsetta*, and *Nematops*, from the Indo-Pacific.

I have examined specimens of *Hippoglossus* (vertebræ 16 + 34), *Hippoglossoides* (13 + 31), *Psettichthys* (10 + 32), *Pleuronectes* (10–11 + 24–30), *Parophrys* (13 + 24), and *Microstomus* (12 + 36–37).

Subfamily 2. Samarinæ.

Dorsal fin extending forward on snout either above or below nasal organ of blind side ; pelvic fins supported by the pelvic bones behind or below the cleithra, asymmetrical, that of the eyed side median and somewhat advanced. Pectoral radials present ; hypocoracoids expanded. Vertebræ 31 (10 + 21) ; præcaudal parapophyses united to form closed hæmal arches bearing the slender ribs at their extremities. Mouth symmetrical, with the jaws and dentition nearly equally developed on both sides.

Genera :—*Paralichthodes*, *Brachypleura*, and *Samaris*, from the Indo-Pacific.

Well distinguished externally from the Pleuronectinæ with symmetrical mouth by their form, the absence of a distinct caudal peduncle, the extension forward of the dorsal nearly to the end of the snout, and the asymmetrically placed pelvic fins, these three genera form a natural and well-marked group. *Paralichthodes* differs from the others in that the nostrils of the blind side appear below instead of just above the anterior part of the dorsal fin, and *Samaris* is distinguished by the more extended bases of the pelvic fins.

I have examined the skeleton in *Brachypleura*.

Subfamily 3. *Rhombosoleinæ.*

Dorsal fin extending forward on snout above nasal organ of blind side; pelvic fins formed as in the Platophrinæ, that of the eyed side median, extending forward to the urohyal, supported by a cartilaginous plate in advance of the cleithra; that of the blind side small or sometimes absent. No pectoral radials, the rays inserted on the hypercoracoid; hypocoracoids narrowed forward below. Vertebral column formed as in the Pleuronectinæ, the præcaudal parapophyses not united. Mouth asymmetrical; jaws of the blind side strongly curved, those of the eyed side toothless.

Genera:—*Rhombosolea*, *Ammotretis*, and *Peltorhamphus* from Southern Australia and New Zealand, with *Oncopterus* from Patagonia.

I have examined the skeleton in *Rhombosolea* (vertebræ 10+21) and *Peltorhamphus* (9+27).

Division 2. *Soleæiformes.*

Mouth small, terminal, subterminal, or inferior, the lower jaw never prominent; jaws of the blind side toothed, strongly curved, the convexity of the lower fitting the concavity of the upper; jaws of the eyed side not or but feebly toothed; præopercular margin not free. Nasal organs symmetrical in position; olfactory laminæ arranged transversely to or radiating from a central rachis. Optic chiasma dimorphic, the right or the left nerve dorsal without reference to dextrality or sinistrality. No post-cleithrum; no pectoral radials, the rays inserted on the hypercoracoid; hypocoracoid reduced; pelvic fins supported by the pelvic bones, which are dependent from the lower extremities of the cleithra, which do not reach the ventral profile; præcaudal parapophyses united or connected by a bridge to form closed hæmal arches; no ribs.

Family 1. **Soleidæ.**

Dextral. Caudal fin separate or not; pectorals often present; both pelvic fins usually developed, but that of the blind side sometimes vestigial or absent, that of the eyed side sometimes median, with extended base. Vertebræ 28–57 (9–10+19–48).

Principal genera:—*Solea*, *Synaptura*, *Æsopia*, *Achirus*, *Pardachirus*, *Liachirus*, *Gymnachirus*, *Apionichthys*, mostly from the sandy shores of tropical and temperate seas ; many species enter rivers and some are permanently fluviatile.

I have examined skeletons of *Solea* (vertebræ 9–10 + 31–41), *Synaptura* (9 + 41–48), *Achirus* (9 + 20), *Pardachirus* (10 + 27), and *Liachirus* (10 + 23). *Achirus* is certainly generically distinct from *Solea*, but there are no structural characters which entitle it to rank as the type of a distinct subfamily, as in Jordan and Evermann's classification.

Family 2. Cynoglossidæ.

Sinistral. Vertical fins confluent ; no pectorals ; pelvic fin of blind side present, 4-rayed, median in position, that of eyed side displaced upwards and reduced, or entirely wanting ; pelvic bone of the reduced or absent fin much smaller than the other. Vertebræ 47–65 (9–10 + 38–56).

Principal genera :—*Symphurus*, *Paraplagusia*, *Cynoglossus*, from tropical and temperate seas.

I have examined skeletons of *Symphurus* (vertebræ 9 + 40), *Paraplagusia* (9 + 43), and *Cynoglossus* (9 + 56). The skeleton is strikingly similar to that of the Soleidæ, and there can be no doubt that the two families are closely related ; as in *Achirus* and other Soleid genera without pectoral fins, the coracoid bones are absent.

LV.—*New* Unionidæ *from East Asia*. By Dr. F. Haas, Senckenberg Museum, Frankfurt-a.-M.

In preparing a continuation of Küster's Monograph of *Unio* in the 'Martini-Chemnitzsches Conchyliencabinet' I examined a large number of shells, which, for the greater part, belonged to the Senckenberg Museum or were purchased from Messrs. Sowerby and Fulton, Kew, and Mr. H. Rolle, Berlin. The East-Asiatic Unionidæ of the Zoological Museum of Berlin were also at my disposal. Among all these shells I found the following new species and subspecies, the types of which, with the only exception of *Nodularia undulata*, belonging to the Berlin Museum, are in the collection of the Senckenberg Museum, and which I shall figure in my monograph mentioned above.

1. *Nodularia denserugata*, sp. n.

Shell elongate-elliptical, rather solid and inflated, rounded