

The So-called Labial Cartilages of *Raia clavata*.

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With Plate 6.

GEGENBAUR (1872), in his classical work on "Das Kopfskelet der Selachier," describes (l. c., p. 216), in *Raia* (species not given) and *Raia vomer*, two cartilages which he considers to be the homologues of the labial cartilages of Selachii. In *Raia* (species not given), which is the one first described, one of these two cartilages is shown lying definitely nearer the anterior end of the ventral surface of the snout than the other cartilage, and, doubtless because of this, the former cartilage is called the anterior upper labial and the other the posterior upper labial. The so-called anterior labial lies, however, farther from the symphysis of the upper jaw and farther from the upper edge of the mouth than the so-called posterior one, and if the mouth were terminal it would be the posterior instead of the anterior cartilage. Doubtless because of this, Gegenbaur says (l. c., p. 218) that it is evident that the so-called anterior upper labial of the Batoidei corresponds to the posterior upper labial of the Selachii, and the posterior upper labial of the Batoidei to the anterior upper labial of the Selachii. The posterior (oral) edge of the posterior labial is shown (l. c., Pl. 17, fig. 1) in contact, its full length, with the palatoquadrate; its anterior (aboral) edge is said to be bound to the posterior (oral) edge of the anterior

labial; and the lateral (absymphysial) end of the latter cartilage is said to be in contact with the palatoquadrate. There is accordingly no space either between the adjoining edges of the two cartilages, or between their posterior (oral) edges and the palatoquadrate, and the nasal groove (Nasenrinne) must accordingly lie either wholly lateral (absymphysial) to both labials or external to them.

In *Raia vomer* the posterior labial is said to be overlapped externally, in its middle portion, by the broad lateral (absymphysial) portion of the anterior labial, the latter labial thus not here having the markedly anterior and aboral relations to the other labial that it has in *Raia* (species not given). It however has the same absymphysial relations to that cartilage. The nasal groove (Nasenrinne) is apparently shown (l.c., Pl. 16, fig. 7) lying between the lateral (absymphysial) ends of the two labials, but it is said that both labials lie, in part, in the nasal flap, and hence necessarily external to the nasal groove, as will be later fully explained. The anterior labial is referred to, both in the figure and in the text, by the index letter *L*, while in *Raia* (species not given) that letter refers to the posterior labial.

In *Rhinoptera*, Gegenbaur says (l.c., p. 219) that there are, in addition to a cartilage that corresponds strictly to the so-called anterior upper labial of *Raia*, two small cartilages found near the angle of the gape of the mouth which together form a rudimentary labial arch similar to the arch formed by the posterior upper and the single lower labials of the *Selachii*. The presence of this posterior pair of labials in *Rhinoptera* is said by Gegenbaur to definitely confirm his already expressed conclusion that the other labial of *Rhinoptera* must be the anterior upper one. But it also evidently proves, if correct, that the so-called anterior upper labial of *Rhinoptera*, and hence also the corresponding labial of *Raia*, must be the homologue of the similarly named labial of the *Selachii* and not of the posterior one; which is in direct contradiction to the positive statement made on p. 218 of his work and already above referred to.

On a still later page of his work (l.c., p. 222) Gegenbaur says that the first (anterior) labial of selachians corresponds to the premaxillary bone of teleosts and the second (posterior) labial to the maxillary bone of those fishes, and as he includes both the Selachii and the Batoidei in the term selachians (Selachier), and as he makes no qualification whatever of the statement, it evidently implies that the so-called anterior and posterior labials of both these sub-orders of the Plagiostomi are homologous, which is again in direct contradiction to his positive statement made on p. 218.

T. J. Parker (1884) gives a figure of these labials in *Raia nasuta* which somewhat resembles Gegenbaur's figure of them in *Raia vomer*, but the so-called first labial of Parker's descriptions, which is Gegenbaur's anterior labial, is so long that it crosses the opening of the mouth and overlaps externally the mandible. This labial is said to support the corresponding flap of the fronto-nasal process, while the second labial, Gegenbaur's posterior one, is said to lie in a fold of skin external to the naso-buccal groove. But as there is no fold of skin external to the naso-buccal groove excepting only the flap of the fronto-nasal process, this labial is thus here said to also lie in that flap.

W. K. Parker (1878) also gives figures and descriptions of these labials in *Raia maculata* and *Raia clavata*, but they differ so radically from Gegenbaur's and T. J. Parker's figures and descriptions that there is no possibility of comparison.

These several descriptions of the labials of the Batoidei are accordingly not clear, and I have, in connection with my present work on the cranial anatomy of *Chlamydoselachus*, examined these cartilages in such specimens of these fishes as I happened to have at my disposal. These specimens consisted of a single head of *Raia clavata*, two small specimens of *Raia radiata*, two small specimens of *Myliobatis*, and two partly dissected specimens of *Torpedo ocellata*. The head of *Raia clavata* was a fresh one, while all the other specimens had been long preserved in alcohol, and were not in good condition for this particular dissection.

In *Raia clavata* (Pl. 6, figs. 1-3) the posterior (oral) edge of the nasal flap of either side occupies about two-fifths of the distance from the angle of the gape to the symphysis of the upper jaw, and it covers a depressed region that will be referred to, in its entirety, as the nasal-flap furrow. The term nasal groove is avoided, because that term (*Nasenrinne*), as employed by Gegenbaur, would seem to refer to a lateral and deeper portion, only, of the entire furrow, as will be later fully explained. Between the nasal flaps of opposite sides the edge of the upper lip of the fish is deeply re-entrant, exposing the teeth and a considerable portion of the upper jaw. A well-marked furrow separates this part of the upper lip from the underlying upper jaw, and may be called the upper labial sulcus. Laterally, on either side, this sulcus runs into the mesial (symphysial) edge of the corresponding nasal-flap furrow, and the posterior (oral) edge of the nasal flap of either side accordingly appears as a direct continuation of the upper lip. It is, however, not a continuation of that lip, the lip and its related sulcus being prolonged a certain distance along the floor of the nasal-flap furrow, internal to the nasal flap, and there gradually vanishing, as shown in Pl. 6, fig. 2.

In the nasal flap, occupying approximately its entire posterior (oral) half and extending mesially (symphysially) somewhat beyond the base of the flap into the subdermal tissues between the upper lip and the nasal capsule, lies the cartilage called by Gegenbaur the anterior upper labial. This so-called anterior upper labial of my specimen, like the corresponding one in Gegenbaur's figure of *Raia vomer*, lies external to the so-called posterior upper labial and farther from the symphysis of the upper jaw than that labial, but not definitely anterior to it. It is, however, not a labial cartilage, as will be later shown, but a cartilage developed strictly in supporting relations to the nasal flap. It can accordingly be called the nasal-flap cartilage, which will sufficiently distinguish it from the *Nasenflügelknorpel* of Gegenbaur's descriptions, which latter cartilage also in part supports the nasal flap and is the *ala nasalis* of certain

English authors. J. Müller (1834) also did not consider this nasal-flap cartilage to be a labial cartilage, and he called it the inner Nasenflügelknorpel.

This nasal-flap cartilage of *Raia clavata* has the shape shown in the accompanying figures, and it is connected with what Gegenbaur calls the anterior process of the corresponding ala nasalis by the dermal and connective tissues of the nasal flap. At its anterior (aboral) corner there is, on one side of the head of my one specimen, a small and independent bit of cartilage. In about the middle of the postero-mesial edge of the cartilage there is a curved incisure, and slightly lateral to the bottom of this incisure, and parallel to the edge of the cartilage, there is a ridge on the internal surface of the cartilage. The mesial surface of this ridge is flat and slopes gradually to the edge of the cartilage, and, on either side of the incisure, it rests upon and is firmly bound to the posterior upper labial of Gegenbaur's descriptions, this contact with the latter labial being particularly large and strong anterior (aboral) to the incisure. The lateral (absymphysial) surface of the ridge is abrupt and curved, and forms the mesial (symphysial) boundary of the nasal-flap furrow, thus marking the base of the nasal flap. The nasal-flap cartilage thus extends mesially beyond the base of the nasal flap into the general tissues on the ventral surface of the head, but it in no place reaches or touches the palato-quadrato, being everywhere separated from it either by the so-called posterior labial cartilage or by the nasal-flap furrow. The incisure in the postero-mesial edge of the nasal-flap cartilage arches over the posterior (oral) end of a short section of the nasal latero-sensory canal (Garman, 1888) that is directed antero-posteriorly.

The posterior upper labial of Gegenbaur's descriptions above referred to, is the only labial found in either *Raia clavata* or *Raia radiata*, and it will accordingly be called, in the following descriptions, the upper labial, or simply the labial. It consists of two broad and approximately parallel portions connected by a narrow neck of cartilage which

extends from the middle of the mesial portion to the mesial end of the lateral portion. The mesial portion lies quite closely upon the palatoquadrate, but is separated from it by branches of the nervus trigeminus and other tissues. Its mesial end projects antero-mesially beyond the palatoquadrate. The antero-mesial end of the lateral portion of the labial lies against the posterior surface of the nasal capsule, the remaining portion lying external to the muscles of the region, but separated from them by tough connective tissues, the cartilage being bent in conformity with the shape of the underlying structures. The postero-lateral portion of this lateral portion of the labial lies immediately beneath the external dermis and parallel with it, and its posterior end lies at a considerable distance from the angle of the gape, separated from that angle by the bulging muscles of the region. The connective tissues in which it lies are attached to it, but it cannot be said that the cartilage runs gradually into ligamentous tissues that are continued into the mandible, as Gegenbaur says is the case in *Raia vomer*.

The narrow neck of cartilage that connects the mesial and lateral portions of the labial lies in the hollow between the aboral edge of the palatoquadrate and the posterior wall of the nasal capsule, and it is always somewhat bent or twisted. In my specimens of *Raia radiata* this twist is so pronounced that the primarily posterior (oral) edge of the cartilage is presented ventrally, the cartilage thus here lying, as Gegenbaur has said for *Raia vomer*, in a vertical position. The primarily external surface of the neck was thus, in these specimens, presented anteriorly instead of ventrally, and the nasal-flap furrow, having crossed the primarily posterior (oral) edge of the labial, had, anterior (aboral) to that edge, somewhat the appearance of lying on the internal rather than the external surface of the labial.

There were, in my specimen of *Raia clavata*, no special ligamentous attachments of the mesial (symphysial) end of either the labial cartilage or the nasal-flap cartilage to the ventral surface of the rostrum, such as Gegenbaur describes

in *Raia vomer*; this end of the labial of *Raia clavata* simply lying in dense connective tissues of the region, and the corresponding end of the nasal-flap cartilage lying upon and being firmly bound to it. On each side of the head the ventral edge of the posterior wall of the nasal capsule was partly membranous, and in this membrane there was a narrow and independent strip of cartilage. In the mesial wall of the capsule, near its ventral edge, there was a hiatus closed by membrane. One or more branches of the nervus trigeminus perforated the cartilage between the hiatus and the edge of the capsule.

The nasal latero-sensory canal was so named by Garman (1888) in his descriptions of these fishes, and is the antorbital portion of the main infraorbital canal of my descriptions of *Mustelus* (Allis, 1901). Running mesially across the external surface of the muscoli adductor mandibulæ and levator labii superioris, this canal reaches the lateral edge of the lateral portion of the labial cartilage immediately anterior to the point where that cartilage assumes a position parallel to the external surface of the head. The canal then crosses the external surface of this portion of the labial and reaches its mesial edge, where it continues onward and reaches and traverses the narrow neck of cartilage that connects this lateral portion of the labial with its mesial portion. Having reached the mesial portion of the labial the canal turns abruptly posteriorly (orally) and crosses the external surface of this part of the labial, lying close to its lateral edge. When the canal reaches the postero-mesial edge of the labial it traverses the incisure in the mesial edge of the nasal-flap cartilage and then turns abruptly antero-mesially along the postero-mesial edge of the labial; and continuing in that direction it joins its fellow of the opposite side in the median line to form the median canal of Garman's descriptions. The canal lies internal to the nasal-flap furrow, and internal also to the nasal-flap cartilage, and in no part of its course does it enter any part of the nasal flap. It lies everywhere external to the labial cartilage and is firmly attached to

that cartilage, but, excepting where it crosses the mesial portion of the labial, there is no noticeable groove to mark its course. In my specimens of *Raia radiata*, because of the marked twist in the neck of the labial, the canal there has markedly the appearance of lying on the internal rather than on the external surface of the labial. In *Raia clavata* some of those branches of the nervus buccalis lateralis that innervate the organs of the canal perforate the labial, but most of them pass over the anterior (aboral) edge of the labial and then turn posteriorly (orally) across its external surface. They always lie internal to the nasal-flap cartilage.

In *Raia batis* Ewart (1892) shows two loops in the nasal latero-sensory canal. No such loops were found in *Raia clavata*, and it is probable that they are exaggerated in Ewart's figure, the loops simply representing points where the canal follows bends or twists in the labial such as I find in *Raia radiata*.

In my specimens of *Myliobatis* the nasal-flap furrows are so wide (deep) that they nearly meet in the median line, a narrow "frenulum" (Gegenbaur) there alone separating them. In correlation with this extension of the nasal-flap furrows the nasal-flap cartilages have been carried toward the median line, and are there separated from each other by only a narrow space in which lies the small median bit of cartilage that Müller (1834) describes as the "Träger der Nasenflügelknorpel." The nasal-flap cartilage, called by Müller the inner Nasenflügelknorpel, has the triangular shape shown by that author in his figure of *Myliobatis aquila* (l. c. Pl. 9, fig. 13), but it is more deeply fimbriated in my specimens than shown by Müller. The ala nasalis is as shown in Müller's figure. The nasal-flap furrow lies internal to both these cartilages. The nasal latero-sensory canal runs internal to the nasal-flap furrow, and then outward and forward (aborally) in the frenulum to meet and fuse, in the median line, with its fellow of the opposite side. In one of my specimens the canal is enclosed in the ventral edge of a strip of cartilage that has

somewhat the position of the narrow strip found along the ventral edge of the posterior wall of the nasal capsule in *Raia clavata*, and already described. In the other specimen the canal is enclosed in an independent tubule of tissue that has a semicartilaginous appearance. In *Trygon tuberculata* Gegenbaur describes (l. c., p. 220) and figures what would seem to be a strictly similar tubule, but it is said by him to be a rod; and although he says that this so-called rod is of fibro-cartilage, he nevertheless considers it to be the homologue of the anterior upper labial of his own descriptions of *Raia* and *Myliobatis*, which latter labial is said to be of hyaline cartilage. The lateral portion of this tubular or rod-like cartilage of *Trygon* is shown, in Gegenbaur's figure, lying definitely internal to the ala nasalis, and it seems as if it must accordingly lie, as does the latero-sensory tubule in my specimen of *Myliobatis*, internal also to the nasal-flap furrow. If such be the case it cannot be a nasal-flap cartilage, or so-called anterior labial, of this fish. It probably contains, in both *Trygon* and *Myliobatis*, a remnant of the upper labial of the present descriptions. If not, then that upper labial is entirely wanting in my specimens of *Myliobatis*, as it was in those examined by Gegenbaur. The cartilage described by Gegenbaur, in *Myliobatis*, as the posterior upper labial I could not find in my specimens.

In *Torpedo ocellata* I find the nasal flap much less long, antero-posteriorly, than the flap of *Myliobatis*, this being due, as Gegenbaur has said, to the nasal capsules lying nearer the anterior edge of the mouth. The nasal flap is supported by a marked prolongation and development of the ala nasalis, similar to the prolongation of that cartilage in *Myliobatis*, but there is no indication of a separate nasal-flap cartilage. The frenulum is supported by a small median Träger der Nasenflügelknorpel, as in *Myliobatis*, and the posterior (oral) end of this little cartilage is strongly attached by connective tissues to the adjoining mesial (symphysial) ends of the palatoquadrates of opposite sides. No upper labial cartilage was found, and a cord of connective tissue lying internal

to the nasal-flap furrow alone represented the aborted nasal latero-sensory canal.

Certain of Gegenbaur's statements regarding the labials of the Raiidæ and their relations to the nasal flap may now be considered. In *Raia* (species not given), Gegenbaur says, as already stated, that the oral edge of the anterior labial is in contact with and bound to the aboral edge of the posterior labial, and that the lateral (absymphysial) end of the anterior labial is in contact with the palatoquadrate. Of *Raia vomer* he says (l.c., p. 216), that the posterior labial, where it bends posteriorly along the external surface of the muscoli adductor mandibulæ and levator labii superioris, "gelangt dadurch mit seiner Fläche an die hintere resp. obere Fläche des vorderen Knorpels, den er mit seinem Endabschnitte seitlich überragt." This statement certainly implies that the lateral ends of the two so-called labials of *Raia vomer* are in contact, as they had previously been said to be in *Raia* (species not given), but the figure given of *Raia vomer* apparently shows the nasal-flap furrow (Nasenrinne) lying between them; and it certainly shows the lateral end of the posterior labial lying internal to the nasal furrow. On p. 219 Gegenbaur says: "Wenn wir bei *Raja* erfahren, dass Labialknorpel in die mit der Bildung der Nasenfurche zusammenhängende Nasenklappe gelangen, in deren nicht bedeutende seitliche Zipfel sie einragen, so folgt daraus, dass bei einer medialen Verbreiterung des labialen Endes der Furche die Labialknorpel von ihrer Lagerung vor dem Oberkieferknorpel gelöst werdenmüssen. Indem die lateralen Zipfel der Klappe auf eine grössere Strecke hin von der Unterfläche des Kopfes sich trennen, kommen die Labialknorpel mehr oder minder vollständig in die Klappe zu liegen. . . . Je mehr die beiderseitigen Nasenklappen gegen die Medianlinie zu frei werden, um so mehr werden die Labialknorpel in sie eintreten." And on p. 226 he says: "Die beiden oberen Labialknorpel kommen ins Velum zu liegen. Der zweite obere Labialknorpel wird aber nicht immer vollständig vom Velum umschlossen. Ein Theil davon

tritt manchmal lateral über das Velum hinaus in den Boden der Nasenrinne, die er dann noch lateral mit begränzen hilft. Dem Nasenvelum gehört somit streng genommen nur der eine vordere, obere Lippenknorpel an."

These several statements of Gegenbaur's certainly definitely affirm that both the anterior and the posterior labials of either side of *Raia* enter into some part of the corresponding nasal flap, and they are apparently both said to extend into the tip of the flap. This is, however, evidently impossible, in so far as the so-called posterior labial is concerned, for in both *Raia clavata* and *Raia radiata*, which cannot differ markedly in this respect from *Raia* (species not given) and *Raia vomer*, the nasal-flap furrow lies definitely between the lateral portions of the two so-called labials, and it would necessarily continue so to lie however much the furrow might be reduced, or be extended mesially. The mesial edge, or bottom, of the furrow marks, or rather determines, the base of the corresponding nasal flap, and the so-called posterior labial could not possibly enter any part of that flap, as the flap is found in my specimens, nor could it enter into a velum formed by the fusion, in the median line, of two such flaps. Gegenbaur's several statements, above referred to, are accordingly certainly incorrect.

The nasal flap of *Raia* and the other non-electric rays is said by Gegenbaur to be derived from the much smaller and quite different nasal flap found in most of the *Selachii*, the *Scylliidæ* being said to present several intermediate stages in the process of development. A nasal velum is said to be formed in *Myliobatis*, in certain others of the non-electric rays, and also in certain of the *Selachii*, by the fusion, in the median line, of the nasal flaps of opposite sides. In the electric rays the method of development (*Genese*) of the velum is said (l. c., p. 221), to be totally different from that in the non-electric rays, the inference accordingly being that the vela in these two groups of fishes are equivalent but not homologous structures. This will be further discussed

after considering the intimately associated nasal-flap furrow and naso-buccal groove.

The nasal-flap furrow, as I have used that term, is the entire space that lies in the angle between the nasal flap and the underlying external surface of the dermis of the ventral surface of the head. The lateral (absymphysial) portion of this space is in *Raia clavata* deepened, and this depressed portion, beginning immediately mesial (symphysial) to the angle of the gape, runs at first anteriorly (aborally) and then turns antero-mesially to fall into the postero-mesial portion of the nasal pit. This deepened portion of the entire furrow thus forms a marked groove in the dorsal (internal) wall of the furrow, and it will be referred to hereafter as the naso-buccal groove, this term being taken from T. J. Parker's (1884) descriptions of this fish. Parker, however, used this term to designate, not the naso-buccal groove alone of my descriptions, but the entire nasal-flap furrow.

Gegenbaur says of the nasal groove of his descriptions (l. c., p. 224): "Durch den geschilderten Vorgang der Velumbildung werden nicht bloss die Nasenklappen dem Munde genähert, sondern die von der Klappe bedeckte Räumlichkeit dehnt sich dabei von der Nasengrube her gegen den Mundrand zu aus und bildet eine flache oder tiefere Rinne, die von der anderseitigen durch ein verschieden breites Frenulum getreunt ist, oder auch bei bedeutender Kürze jenes Frenulums mit derselben zusammenfliesst. Eine solche Einrichtung kann als eine Weiterbildung des bei den zuletzt aufgeführten Scyllien bestehenden Verhaltens gelten. Sie findet sich bei *Chiloscyllium*, ähnlich auch bei *Stegostoma*, bei denen die ziemlich tiefe Rinne zum Mundwinkel herabführt. Entfernter vom Mundwinkel führt sie bei *Crossorhinus* zum Munde, indem sie den Rand der Oberlippe durchbricht."

The "Räumlichkeit" or "Rinne" here described by Gegenbaur is evidently the entire nasal-flap furrow of my descriptions, but several others of Gegenbaur's statements seem quite definitely to make the term apply only to the naso-buccal groove. In a footnote on p. 218 he says:

“*Scyllium* besitzt keine Nasenfurche”; and this notwithstanding that there is a well-marked nasal-flap furrow in certain of the *Scylliidae*, and that in his own figure of *Scyllium canicula* a so-called “Nasenrinne” is indicated by index letters. On p. 217 he says: “Denkt man sich an der Vorderfläche des Oberkiefers einen sich bedeutend verbreiternden Labialknorpel gelagert, so wird derselbe, da die Flächenvergrößerung nicht gegen den Mundrand zu stattfinden kann, nach vorn zu sich ausdehnen müssen und wird mit der Bildung einer von der Nasengrube zum Mundwinkel führenden Nasenfurche median von derselben zu liegen kommen.” On p. 218 he says: “Auf die Nasenfurche lege ich hierbei grösseres Gewicht als auf die Nasenklappe, denn durch den Verlauf der ersteren zum Mundwinkel ist die Zutheilung der bezüglichlichen Knorpel zu dem zwischen beiden Nasenfurchen gelegenen zur Nasenklappe sich differenzierenden Abschnitte des Integumentes zu erklären.” And on p. 224 he says: “Diese Nasenrinne oder Nasenfurche erscheint unter den Rochen allgemein verbreitet. Sehr ausgeprägt ist sie bei den *Rajae*, meist gerade zum Mundwinkel herabziehend. Durch eine mediale Verbreiterung erfährt die Rinne eine Abflachung, und beiderseitige Rinnen können vor der Mundöffnung zusammenfliessen, was bei einer geringeren Ausbildung des Velums, wie z. B. bei manchen *Rhinobatiden*, fast zu einem Verschwinden der ganzen Einrichtung führt. Aus demselben Grunde ist auch bei *Trygon* die Rinnenbildung schwer zu erkennen und eben so bei *Myliobatis*. Die ganze Erscheinung erlangt bei diesen den höchsten Grad ihrer Ausbildung und zwar in einem das Verhältniss bei den *Rajae* weit überschreitenden und es damit unkentlich machenden Masse.”

In all these several quotations the so-called nasal groove (Nasenrinne) is evidently considered to be a groove that runs primarily from the nasal pit to the angle of the gape of the mouth, and the appearance of this groove is apparently conceived to precede the differentiation of the nasal flap. There is, however, no slightest indication in any of the many

fishes described by Gegenbaur of such a groove existing independently of the nasal flap and its related nasal-flap furrow, and it is quite certain that the groove is simply a secondary differentiation of the furrow. Such being the case the nasal-flap furrows of all the Plagiostomi are strictly homologous structures, and this is the conclusion that Luther (1909) arrives at from physiological considerations. A continuous nasal velum would then be formed if the furrows of opposite sides were to coalesce in the median line by the complete or partial breaking through of the intervening frenulum. There is, however, no indication whatever, in any of my specimens, that this frenulum is ever broken through, for even in *Myliobatis* the oral edge of the frenulum forms a part of the upper lip of the fish and not a part of the nasal flap of either side. The nasal-flap furrows of opposite sides are here certainly in communication with each other beneath the velum, but it is through the intermediation of the small persisting median section of the upper labial sulcus and not because of the coalescence of the furrows. I am accordingly convinced that a complete velum, extending across the median line, must, if ever found, be formed by the coalescence of the opposing mesial edges of the nasal flaps of opposite sides in fishes where those flaps have been prolonged beyond the oral edge of the upper lip; and this would seem to be confirmed by the conditions that I find in a small specimen of *Scyllium*.

In this small specimen of *Scyllium*, which I am quite certain is *Scyllium canicula*, I find the nasal flaps of opposite sides so much more developed than those shown in Gegenbaur's figure of this fish that it would seem as if the two fishes could not be of the same species. The flaps of opposite sides are separated by a small median incisure which extends to the oral edge of the frenulum, that edge certainly representing a small persisting median portion of the upper lip. There is accordingly no complete velum in my specimen of this fish. Such a velum would, however, be formed if the adjoining edges of the incisure were to fuse, and this is

apparently what does take place in older specimens, for Günther (1870) says of this fish: "The nasal valves confluent, without cirrus, forming together a simple broad flap in front of the mouth, the posterior edge of the flap being nearly free, not interrupted in the middle."

The nasal flaps of all of the Plagiostomi, whether Selachii or Batoidei, are accordingly simply folds of the dermal tissues of the internasal portion of the snout, this internasal portion of the snout being presented more or less ventrally according to the greater or less development of the rostrum and the correlated configuration of the head. If the mouth were terminal and the nasal apertures disposed as in *Amia* and most of the Teleostei, this internasal region would lie on the dorsal surface of the snout, and the relations, anterior and posterior, would be the reverse of what they are in *Raia*. In the Batoidei the nasal flap always lies external to the nasal section of the latero-sensory canals, and the nasal-flap cartilage, which lies in large part in the flap, also always lies external to that canal, and external also to the nervus buccalis lateralis. In most Selachii the nasal flap lies wholly aboral to the nasal latero-sensory canal, that is, on the opposite side of the canal to the labial cartilages; but in my specimen of *Scyllium* it lies external to the canal, as it does in the Batoidei. In *Chlamydoselachus* both labials lie oral to the suborbital latero-sensory canal but internal both to the third group of ampullæ of Merritt Hawkes' (1906) descriptions and to those branches of the buccalis that supply those ampullæ; the labials thus lying morphologically internal to the suborbital canal. In *Mustelus* (Allis, 1901) the labials have similar relations to the latero-sensory canals, ampullæ, and related nerves. In my specimen of *Scyllium* the anterior end of the single upper labial (Gegenbaur, 1872) lies directly internal to the latero-sensory canals at the point where the nasal canal joins the suborbital canal; and, in *Stegostoma tigrinum*, Luther (1909) says that the rostral (external) surface of the anterior labial is grooved to lodge the nasal canal.

The so-called anterior upper labial of Gegenbaur's descrip-

tions of the Batoidei, the nasal-flap cartilage of the present descriptions, can not accordingly be the homologue of either of the labial cartilages of that author's descriptions of the Selachii, and it is apparently a fibro-cartilage developed wholly in supporting relation to the nasal flap. Sections of it show the interior of the cartilage a mass of fibrous strings running gradually, toward the exterior on either side, into hyaline cartilage.

The nasal-flap cartilage of *Raia* thus not being the homologue of either of the labials of the Selachii, the single upper labial of the former fish might represent either one of the labials of the latter fishes. I am, however, strongly inclined to believe that it represents both the labials of the latter fishes, here secondarily connected by a narrow neck of cartilage; the mesial and lateral portions of the labial of *Raia* representing, respectively, the anterior and posterior labials of the Selachii. The general shape and disposition of the cartilage favours this view, and this composition of the labial would offer a possible explanation of the peculiar course of the nasal latero-sensory canal. The labials, in the Selachii, lie either oral or internal to the nasal latero-sensory canal, as just above explained. In *Raia* the labial lies in large part aboral to the canal, and, in acquiring this position, the two parts of which I consider the labial to be composed have necessarily pushed against and carried with themselves those branches of the nervus buccalis lateralis that supply the organs of the related portion of the canal. This push on the nerves would naturally tend to displace the canal, but the mesial section of the canal was held in place by the attachment of the nasal-flap cartilage to the lateral end of the anterior labial. The lateral portion of the canal was not so held in place, and would in consequence be carried aborally by the pull of the nerves, and these nerves, becoming more or less enveloped in the pushing edge of the labial, would be found perforating the cartilage in the adult. The sharp bend actually found in the canal would thus be accounted for. The relations of the nerves to the mesial

portion of the labial, in *Raia*, and the relations of the canal itself to the lateral portion of the labial are both against the view that these cartilages are developed in direct relation to the canal, but the cartilage of *Raia* is nevertheless evidently of fibro-cartilaginous origin, for sections of it show certain fibrous strings in the interior of the cartilage. They are, however, much less numerous than in the nasal-flap cartilage.

Gegenbaur considered the anterior and posterior upper labials of his descriptions of the *Selachii*, and their assumed homologues in the *Batoidei*, to be cartilages that served as groundwork (*Grundwerk*) on which the premaxillary and maxillary bones, respectively, of the *Teleostei* were developed. My work has as yet offered nothing decisive either in favour of or against this view, in so far as it applies to the two labials of the *Selachii* and the one upper labial of the present descriptions of *Raia*, but the relations of the labial of *Raia* to the branches of the *nervi buccalis* and *trigeminus* favour the view that its two portions may represent the two bones of the *Teleostei*. There is, however, doubt as to which part of the labial represents the maxillary and which the premaxillary. The nasal-flap cartilage, Gegenbaur's anterior labial, can not, however, represent either of the two bones of the *Teleostei*. Its general position, in *Raia*, and its relations, in *Myliobatis*, to the so-called *Träger der Nasenflügelknorpel*, strongly suggest that it may represent the ascending process of the premaxillary bone of the *Teleostei*, and that the *Träger der Nasenflügelknorpel* may represent the rostral cartilage of certain of those fishes.

In two of my earlier works (1898, 1909) I came to the conclusion that the ascending process of the premaxillary bone of the *Teleostei* was primarily an independent bone, the so-called dermal ethmoid, which later fused with the premaxillary. This primarily independent bone was said to have been developed in protective relation to a line of latero-sensory organs, and to be found as such a protective bone not only in certain ganoids (*Amia*, *Polypterus*), but also in

Elops and probably also in *Belone*. In certain other Teleostei the corresponding bone, the supra-ethmoid of current descriptions, was said to underlie a line of surface pit organs that corresponded to the canal line in *Amia*. This supra-ethmoid bone was accordingly considered to be a bone of membranous origin that represented a deeper component of the canal-bearing bone of *Amia*, just as, in certain others of the canal-bearing bones of *Amia* and other fishes, there is an underlying membrane component apparently developed somewhat independently of the canal-bearing component. The conditions now found in *Raia* suggest that this supra-ethmoid bone of the Teleostei is represented in the nasal-flap cartilage of *Raia*. If this be so, the supra-ethmoid bone can not represent an underlying component of a canal-bearing bone, for the cartilage of *Raia* lies definitely external to the related canal. This origin of the supra-ethmoid bone from the nasal-flap cartilage might then account for the absence, in those fishes in which that bone is found, of the canal line found in *Amia*; for this cartilage, or bone, in sinking from the position which it has in *Raia* to that which it has in the Teleostei, would necessarily smother the underlying canal and ultimately lead to its complete abortion. The line of pit organs that overlies the supra-ethmoid bone in certain Teleostei would then be a secondary outgrowth from the end of the infraorbital canal line, and hence not the homologue of the cross-commisural canal line of *Amia* and the other fishes in which it is found. In *Amia*, *Polypterus*, and *Elops*, it is to be especially noted that the presence of a canal-bearing ethmoid bone is associated with the relation of the maxillary bone to the premaxillary that Sagemehl (1884) described as lateral, and that is said by that author to be found in only a few of the Teleostei. These two conditions may accordingly be related, but the want of proper material does not at present permit me to farther investigate it.

PALAIS DE CARNOLES, MENTON;

January 20th, 1916.

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EXPLANATION OF PLATE 6,

Illustrating Mr. Edward Phelps Allis's paper on "The So-called Labial Cartilages of *Raia clavata*."

INDEX LETTERS.

a. n. Ala nasalis. *a. n. a.* Anterior nasal aperture. *ant.* Antorbital cartilage (Parker), Schädelflossen-Knorpel (Gegenbaur). *f. n.* Fenestra nasalis. *m.* mouth. *md.* Mandibula. *n.* Nasal section of latero-sensory canal. *n. b. g.* Naso-buccal groove. *n. c.* Nasal capsule. *n. f.* Nasal flap. *n. f. c.* Nasal-flap cartilage. *n. f. f.* Nasal-flap furrow. *orb.* Orbital section of latero-sensory canal. *pn.* Pre-nasal section of latero-sensory canal. *p. n. a.* Posterior nasal aperture. *pq.* Palato-quadrata. *r. b.* Ramus buccalis lateralis. *r. mæ. t.* Ramus maxillaris trigemini. *so.* Suborbital section of latero-sensory canal. *sr.* Subrostral section of latero-sensory canal. *u. l. c.* Upper labial cartilage.

Fig. 1.—Ventral view of the snout of *Raia clavata*. On the right-hand side of the figure the dermis has been removed from the nasal flap so as to expose the ala nasalis, the nasal-flap cartilage, and the related sections of the nasal and pre-nasal latero-sensory canals.

Fig. 2.—The same; a deeper dissection. The nasal flap has been almost completely removed on both sides of the figure. On the left-hand side that part of the flap that contains the anterior process of the ala nasalis has been left and turned back so as to expose the nasal apertures and the nasal-flap furrow.

Fig. 3.—The same; a still deeper dissection. The nasal flap and the related portions of the latero-sensory canals have been removed on the right-hand side of the figure, exposing the ala nasalis and the upper labial cartilage. On the left-hand side these last two cartilages have been removed so as to expose the nasal capsule.



Allis, Edward Phelps. 1916. "Memoirs: The So-called Labial Cartilage of Raia Clavata." *Quarterly journal of microscopical science* 62, 95–114.

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