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THE EPI-BRANCHIAL PLACODES OF AMEIURUS.*

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The study of the epi-branchial placodes of Ameiurus was taken up with the object of ascertaining to what extent they enter into the composition of the cranial nerves in this group of Teleosts.

The catfishes with their enormously hypertrophied system of gustatory nerves ought to have these placodes correspondingly prominent during embryonic development if they are concerned in the origin of the communis portions of the cranial ganglia.

Ameiurus has proven to be an unusually favorable type and a study of the development of its epi-branchial placodes suggests the idea that possibly the extremely divergent accounts given in the literature of these structures may be due to the choice of unfavorable types for study.

The extent to which communis fibres enter into the composition of the cranial nerves varies greatly even among the teleosts. There is probably a corresponding variation in the distinctness with which the placodes may be traced in the early development of those types in which the system is reduced. At any rate they are far more prominent and easily followed in Ameiurus than they seem to be in any other form described.

Aside from working out the details of their origin the following queries have been kept more or less constantly in mind:

(1) Do the cells derived wholly or in part from the placodes really become the communis ganglia of the adult?

(2) Are the placodal portions of the cranial ganglia pure—i. e., are the communis ganglia derived exclusively from the

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placodes or they do contain cells derived from the neural crest or the mesectoderm?

(3) Are the placodes in their early growth and at the time of their origin proportionate in size to the communis ganglia of the adult?

(4) Is there any evidence that the placodes arise in response to a stimulus furnished by the neural crest portion of the cranial ganglia, as has been stated, or is there any evidence that they may be in part or wholly endodermic in origin?

(5) Lastly, if they are of pure ectodermic origin do they give rise to both general and special visceral fibres or only to special visceral fibres?

A brief description of the origin of the placodes will answer several of these queries.

In Ameiurus the placodes appear serially from anterior to posterior on the hyoid and first four true gills, none being developed on the fifth.

They arise in the ectoderm just dorsal and posterior to the gill slit at the time when the endodermic evagination comes into contact with the ectoderm.

Their presence is first indicated by a thickening of the ectoderm; this is followed by a period of active mitosis in the ectodermic thickening and a proliferation of cells into the mesoderm of the corresponding gill bar: This proliferated mass pushes its way posteriorally and dorsally and finally becomes detached from the skin which later assumes its normal thickness.

The proliferated masses especially in the IX and first two divisions of the X nerves are quite definite in outline and stain much darker than either the ectoderm from which they arose or the mesoderm. This difference in staining seems to be due to the amount and character of the intercellular substance. In the VII nerve the placode is so large and the proliferation of cells so rapid that in its earlier stages at least it is not so definite in outline as those of the IX and X, but in all cases from the time the proliferation begins the cell mass is easy to follow.

The size of the mass proliferated is apparently proportionate to that of the communis ganglia of the adult being largest in the VII nerve and much smaller in the IX and first two diivsions of the X.

The placode of the fourth true gill combines so closely with a neural crest portion that I am unable to compare it with the others.

All these ganglia of placodal origin have been followed up to a stage where the roots and chief trunks of the nerves are formed and there can be no doubt except in the third division of the X that they give rise to the communis ganglia of the adult.

As to whether these placodes may possibly be partly endodermic in origin or not can be answered in the negative without any hesitation. The relations in the VII are somewhat confused owing to the rapid proliferation of cells which seems to push the ganglion forward into contact with the endoderm but I believe this placode is also purely ectodermic.

The important question to be determined here is of course, whether these placodal masses contain cells derived from the neural crest or from the mesectoderm.

They certainly do not arise in Ameiurus in response to stimuli furnished by the contact of neural crest cells with the skin. There are no neural crest cells that can be distinguished as such, that come into contact with the skin where the placodes arise except in the third division of the X nerve.

If the placodes arise in response to any stimulus furnished by the embryo, it is much more probable that it is the stimulus derived from the contact of the endodermic evagination that forms the gill slit.

The contact of this evagination which occurs even in the VII nerve is coincident with or closely associated with the appearance of the placode and while there may be no causal relation it is a striking fact and may be fundamental.

In the third division of the X nerve the neural crest mass comes into contact with the skin about the time the placode appears and the relation of the neural crest cells and of the placodal cells is so intricate that I have been unable as yet to separate them. This seems to me, however, to call for a different interpretation from the one mentioned above.

While there are no definite masses of neural crest cells added to the placodes except in the third division of the X nerve, it is much more difficult to be sure as to whether cells usually designated as mesectoderm may be incorporated with those derived from the placodes, particularly in the VII nerve.

The visceral portions of the IX ganglia and of the first two divisions of the X seem to be pure placodal ganglia.

In the VII where the placode is large and the proliferation of cells rapid the borders of the growing ganglion are not so definite and there may be a small portion of the ganglion that comes from the mesectoderm and is not derievd from the placode. It must, however, be very small. So that we can say for this type that the communis ganglia of the IX and the first two divisions of the X are practically pure placodal ganglia, that there is more doubt about the gerniculate ganglion, although even here the incorporated portion must be very small; while in the third division of the X there is a large neural crest portion which combines with the placodal portion so intimately that it is not possible to distinguish them.

As to whether the placodal portions of the communis ganglia give rise to special visceral fibres only, or to both special and general visceral fibres there is less certainty. The facts on which we may hazard a conclusion are as follows:

Every cranial nerve containing gustatory fibres comes from a ganglion which can be traced wholly or in part to an epi branchial placode. The VII, the cranial ganglion supplying by far the largest number of gustatory fibres comes from the largest epibranchial placode.

The X, the cranial ganglion supplying the largest general visceral component contains the largest neural crest element.

The smallest general visceral component is apparently in the VII nerve and there is possibly a small neural crest element in the gerniculate ganglion.

The IX nerve is most interesting in this connection. I am unable to find any neural crest cells in the communis ganglion of the IX nerve and Professor Herrick describes it as supplying taste buds throughout its whole area of distribution and makes no mention of its supplying general mucuos surfaces.

If this is true we have a pure special visceral or gustatory nerve coming from a pure placodal ganglion in the case of the IX, and a very reasonable deduction from this is, that the placodes give rise to that portion of the communis ganglion which supplies special visceral or gustatory fibres, the portion supplying general visceral fibres coming from the neural crest.

The latter is homologous then in origin with the general visceral ganglia of the cord, but differs from them in that it dissociates itself from the general cutaneous cranial ganglia and fuses with that derived from the placode.

The general cutaneous ganglia of the cranial nerves are quite distinct and there is even less excuse for confusing the cutaneous and visceral ganglion in the embryo than there is in the adult.

If the epibranchial placodes give rise to the gustatory portions of the communis ganglia, we must look on the gustatory nerves as comprising a special visceral system because they end in visceral centers in the brain, and not because of any similarity in origin of the general and special visceral ganglia or because of the method of distribution of the gustatory organs.

The ganglia are in no immediate sense related to general visceral ganglia in mode of origin, and the gustatory organs are highly specialized and may be mainly ectodermic in position so that I think the term special communis ought to be applied with central brain connections always in mind as the justification for the term and this seems to be generally done.

This generalization in regard to the origin of the gustatory fibres is too far reaching to be rendered safe by a study of one

type. Other teleosts in which the gustatory system is reduced as compared with Ameiurus, as well as Cyclostomes, Elasmobranchs and Amphibia must be studied with this particular point in view.

In other forms the neural crest element is apparently fairly constant in those nerves which contain gustatory fibres. The small size of the special visceral component and of the placodes in these types may account for the idea that the placodes arise in response to the stimulus furnished by the contact of the neural crest with the skin. The catfishes, however, are unique in the size of their placodes and of their special visceral component.

And if the IX ganglion should prove not to be a pure placodal ganglion and the IX nerve of the adult does supply general visceral surfaces, I still think the evidence very strong that the placodal portions of these ganglia give rise to the special visceral or gustatory fibres.

And the special visceral system bears the same relation to the general visceral that the Acustico-lateralis system bears to the general cutaneous.