On the Morphogenesis of the Epithelial Hypophysis of the Tailed Amphibia.

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With 14 Text Figures.

I. Introduction.

The hypophysis of urodeles has been morphologically studied by many authors such as Haller ('98), Burckhardt ('91), Stendell ('14), and others. But works on its morphogenesis are rare. Recently Atwell ('18, '21) studied the morphogenesis of the hypophysis of amphibia, and made special observations on his so-called *pars tuberalis*, on its development and its relation to the other epithelial and neural lobes.

My present study is based upon observations on the development of the hypophysis of some Japanese tailed amphibia.

The terminology of the various lobes of the amphibian hypophysis is manifold. In this paper I have used the following names: *pars tuberalis* (Atwell), *pars intermedia* (Atwell), *pars anterior* (Atwell's anterior lobe proper), and *pars neuralis*.

II. Material and technique.

In my research I have used nine series of *Hynobius nebulosus* and six series of *Onychodactylus japonicus*.

The fixatives employed were Formol, Formol-alcohol, Formol-bichromate and Formol-Müller's fluid. The smaller materials were imbedded in paraffin, the others in celloidin. They were cut into sections 15–30 mikron thick.

The staining employed are as follows: Borax-carmin, Eosin-hematoxylin and Weigert's Iron-hematoxylin-bulk-stain.

The wax plate reconstructions were performed after Born-Peter's and Suzuki's methods and the models were constructed at a magnification of 33–66 diameters.

III. Descriptions.

1) 13 mm. larva of *Hynobius nebulosus* (Fig. 1).

Fig. 1 shows the wax plate reconstruction of a 13 mm. larva of *Hynobius*.

The hypophysis lies in this stage close to the infundibulum and its form is generally square, it prolongs lateralward, these parts on both sides are called pars lateralis, which become afterwards the pars tuberalis, but I cannot find any distinct grooves at the side, as Atwell ('21) described on a 12 mm. larva of *Amblystoma punctatum* (Fig. 1).

Fig. 1. Ventral view of a waxplate reconstruction of the hypophysis of a 13 mm. larva of *Hynobius*. $\times 66$. Caudal end is below.

The pars intermedia lies ventral to the infundibulum and caudal rather than dorsal to the pars anterior. In the midsagittal section of the wax reconstruction, the pars intermedia is projected especially dorsalward, and the development of that lobe in this stage is rather well, while the pars anterior is not so well differentiated.

The pars tuberalis is not yet seen in this stage.

2) 20 mm. and 22 mm. larvae of *Hynobius nebulosus* (Fig. 2, 3).

In the 20 mm. larva the pars tuberalis is not well developed, while in the 22 mm. larva this lobe is clearly differentiated and elongates oralward. Fig. 2 shows the ventral view of the wax plate reconstruction of a 22 mm. larva. The pars lateralis projects very much lateralward.

Fig. 2. Ventral view of a waxplate reconstruction of the hypophysis of a 22 mm. larva of *Hynobius*. $\times 50$.

As fig. 3 shows, the shape of the midsagittal section of this model is triangular, the dorsal projection of the caudal part of which is the pars intermedia and is rapidly developed in this stage. It lies caudal to the infundibulum.

Fig. 3. Midsagittal section of a waxplate reconstruction of the hypophysis of a 22 mm. Hynobius. $\times 50$.

The pars anterior is situated ventral to the pars intermedia and infundibulum, although its development is not so well represented.

3) 24.5 mm. larva of *Hynobius nebulosus* (Fig. 4).

Fig. 4. Ventral view of a waxplate reconstruction of the hypophysis of a 24.5 mm. larva of *Hynobius*. $\times 50$.

As fig. 4 shows, the left pars tuberalis is strangely not well differentiated, while the right is very well developed. The body of the hypophysis has as a whole a triangular shape.

The development of the pars intermedia is remarkable, so that this lobe is to be seen from the ventral side. It is situated dorsal to the pars anterior, at some distance from its caudal extremity and close to the caudal end of the pars neuralis, and ventral to the infundibulum.

The pars anterior is much less developed compared with the pars intermedia, and is covered by the latter lobe.

4) 32 mm. and 35 mm. larvae of *Hynobius nebulosus* (Fig. 5, 6. a, b, c).

All three lobes of the hypophysis are well developed and lie close to the infundibulum, especially the pars tuberalis grows remarkably oral- and lateralward. The left pars tuberalis is slender and seems like a cylinder, while the right

presents the form of a triangular plate, which connects with the oral portion of the anterior lobe by its one border (Fig. 5).

Fig. 5. Ventral view of a waxplate reconstruction of the hypophysis of a 35 mm. larva of *Hynobius*. $\times 50$.

The pars intermedia is situated dorsal to the anterior lobe and covers the latter in such a manner that the former lobe is to be seen from the ventral side, the midportion of the pars intermedia is thin, each lateral part is thick and is elongated near the caudal extremity of the pars anterior. Its greatest dimension is from side to side (Fig. 6).

The pars anterior is situated under the ventral surface of the pars intermedia.

Fig. 6. (a, b, c). Transverse sections of the hypophysis of a 35 mm. larva of *Hynobius*. $\times 80$.

5) 100 mm. adult *Hynobius nebulosus* (Fig. 7).

In this stage the enlargement of the pars anterior is more especially apparent on each side than its craniocaudal development, therefore the transversal dimension is larger than that of the craniocaudal, the entire shape of this gland is oval

excluding the pars tuberalis (Fig. 7). Though the cephalic portion of the pars anterior is situated close to the infundibulum, the caudal portion is not in contact with the latter, as the case is in larval stage, for this portion is elongated caudalward.

Fig. 7. Ventral view of a waxplate reconstruction of the hypophysis of a 100 mm. adult *Hynobius*. $\times 33$.

The pars intermedia lies dorsal to the pars anterior having close contact with each other, and its cephalic end touches the caudal end of the pars neuralis. The enlargement of the pars intermedia is not so considerable as in larval stages, therefore we can not observe this lobe from the ventral side.

The pars tuberalis is very much flattened and has an oval shape in this stage, its roots are situated near the median line of the cephalic end of the gland, not on each side. The pars tuberalis is separated by a peculiar deep incisure from the lateral portion of the anterior lobe (Fig. 7).

6) 25 mm. larva of *Onychodactylus japonicus* (Fig. 8, 9).

The best developed portion in this stage is the pars tuberalis, then the pars intermedia, the pars anterior represents the least differentiated part of the hypophysis (Fig. 8).

Fig. 8. Ventral view of a waxplate reconstruction of the hypophysis of a 25 mm. larva of *Onychodactylus*. $\times 33$.

The gland lies close to the infundibulum and the very small portion of its caudal extremity is elongated and lies remote from the caudal end of the infundibulum (Fig. 9).

The pars intermedia is situated close to the caudal end of the pars neuralis, a short distance from the caudal end of the pars anterior and on its dorsal surface.

Fig. 9. Midsagittal section of a waxplate reconstruction of the hypophysis from a 25 mm. larva of *Onychodactylus*. $\times 66$.

Fig. 9 shows the midsagittal section of the model, its dorsal prominent portion makes a top of the pars intermedia, therefore its dorso-ventral dimension is very considerable, but the dimension from side to side is much greater than that of the former, so that the pars anterior is covered by this lobe and we can see a small lateral portion from the ventral surface of the hypophysis.

7) 53 mm. larva of *Onychodactylus japonicus* (Fig. 10).

The two bud-like processes, pars tuberalis, of which the right is much smaller than the left, are well developed. The most differentiated lobe in this stage is the pars intermedia.

Fig. 10. Ventral view of a waxplate reconstruction of the hypophysis of a 53 mm. larva of *Onychodactylus*. $\times 33$.

The pars intermedia lies close to the caudal end of the pars anterior. The

middle portion of this lobe is much thinner than the lateral portions, and these lateral portions are enlarged and look like a club on the transverse section. The pars anterior is covered from dorsal and from each lateral side by this lobe.

The cephalic portion of the pars anterior lies close to the infundibulum, and its development is poorer than that of the pars intermedia.

8) 64 mm. larva of *Onychodactylus japonicus* (Fig. 11, 12. a, b, c.).

All the three lobes are remarkably developed, and the pars intermedia and pars anterior are more distinctly differentiated than in the former stage.

Fig. 11. Ventral view of a waxplate reconstruction of the hypophysis of a 64 mm. larva of *Onychodactylus*. $\times 33$.

The pars intermedia covers the pars anterior from the dorsal side, and its caudal extremity is at some distance from the caudal end of the pars anterior, we can see its lateral portion from ventral.

Fig. 12. (a, b, c). Transverse sections of the hypophysis of a 64 mm. larva of *Onychodactylus*. $\times 80$.

The small anterior portion of the pars anterior lies ventral, close to the infundibulum, with its caudal extremity elongated caudalwards.

9) 83 mm. *Onychodactylus japonicus* (Fig. 13).

The best developed portion of the three lobes is the pars anterior, and this

lobe in this stage is elongated considerably caudalward. Its lateral dimension is also enlarged (Fig. 13).

Fig. 13. Ventral view of a waxplate reconstruction of the hypophysis of a 83 mm. larva of *Onychodactylus*. $\times 33$.

The pars intermedia has developed also remarkably, though compared with the former stages its development is much poorer. This lobe covers the pars anterior from the dorsal side.

The pars tuberalis is in this stage not so enlarged, so that it represents almost the same size as the former stage, the left is especially small.

10) Adult *Onychodactylus japonicus* (Fig. 14).

The pars anterior is very remarkably developed and elongated from side to side, so that the transversal dimension is the greatest of all, as in the adult *Hynobius*. The oral portion of this part lies ventrally close to the infundibulum,

Fig. 14. Ventral view of a waxplate reconstruction of the hypophysis of an adult *Onychodactylus*. $\times 33$.

but the caudal part is elongated caudalward and lies remote from the caudal end of the infundibulum.

The pars intermedia is not so well developed as in larval stages and is situated dorsal to the pars anterior, lying at some distance from the caudal end of the pars anterior, and close to the caudal end of the pars neuralis. Therefore we can not see this lobe from the ventral side.

The pars tuberalis is well developed compared with that of the adult *Hynobius*, its roots lie near the median line and are more slender and thinner than its oral portion, especially on the left side. It seems as if it was detached from this point.

IV. Summary and discussion.

1. The pars anterior (anterior lobe proper).

In the larval stage this lobe is not so remarkably developed as after the metamorphosis, near the metamorphic stage it develops rather rapidly. In accordance with the development this lobe is elongated caudalward, so that in adult stage the greater part of this lobe is not situated anterior to other lobes, but ventral to them. Its most developing stage is seen after the metamorphosis, and in adult stage this lobe represents the greatest of three lobes of the hypophysis.

In adult *Hynobius* and *Onychodactylus* the greatest dimension of this lobe is from side to side, and its shape oval.

Stendell ('14) described the phylogenesis of the hypophysis of the vertebrates as follows: "Während der Hauptlappen also an Grösse stetig zunahm, wurde der Zwischenlappen kleiner, ohne jedoch ein funktionsloses Organ zu werden" (S. 153-4).

I am of the opinion that the developmental relation of the pars anterior to the pars intermedia, i.e. much more diminution of the latter than the former, is to be seen equally, either phylogenetically or ontogenetically.

2. The pars intermedia.

According to Atwell ('21) the pars intermedia is developed from the dorsocaudal extremity of the early hypophysial fundament. In its adult position it lies caudal to the pars neuralis and dorsal to the pars anterior. In my specimens in earlier stage (13 mm. *Hynobius*) this lobe lies dorso-caudal to the pars

anterior. But near the metamorphic stage this lobe develops very remarkably, compared with the pars anterior, it covers the latter from dorsal and lateral side, and is situated at some distance from the caudal end of the pars anterior, and caudal to the pars neuralis.

In adult stage this lobe is not so well developed, compared with the pars anterior. It lies caudal to the pars neuralis and dorsal to the pars anterior, more distant than in larval stages from the caudal end of the pars anterior.

3. The pars tuberalis.

Recently Atwell ('21) described the tailed amphibia as follows: "The pars tuberalis develops from a pair of processes which grow forward from the remainder of the gland, these processes do not become detached to form separate epithelial plaques as in the anura, but maintain their connections with the anterior lobe throughout life."

According to his figures we recognize that the pars tuberalis grows oralward from each side of the cephalic end of the pars anterior not only in adult stage but also in larval stage.

In my specimens these two processes of this lobe develop from the lateral lobe and gradually grow oralward. Near the metamorphic stage they are well developed and raised from each side of the cephalic end of the pars anterior. But in adult stage they are not so enlarged compared with the pars anterior. They have their roots near the median line of the cephalic end of the pars anterior at some distance from each lateral end of the latter lobe.

In my case the developmental proportion between the pars anterior and the pars tuberalis is quite different in adult and larval stage: that is, the pars tuberalis is not so well developed in adult stage as in larval stage, while the pars anterior is remarkably elongated in adult stage.

Notwithstanding the fact, that their roots are much thicker than their cephalic portion in larval stage, they are very slender and thin in adult stage, as fig. 7 and 14 show. And it seems to me as if they can detach from this point, as is found in anura by Atwell, but I could not see the detached form in my two specimens.

Stendell ('14) says "Ob ihm (Pars tuberalis) funktionelle Bedeutung beizumessen ist, erscheint fraglich."

It seems to me that the pars intermedia and the pars tuberalis have some functional significance on the metamorphic phenomenon.

Woerdeman ('14) believes that the pars tuberalis (his "lobulus bifurcatus") becomes progressively less important as the vertebrate scale is ascended.

I think that the developmental relationship of this lobe between the adult and larval stage, i.e. the developmental proportion of this lobe to the pars anterior is greater in larval stage than in adult stage, is the same either phylogenetically or ontogenetically.

V. Conclusion.

1. In the tailed amphibia the epithelial hypophysis consists of three parts: the pars anterior, the pars intermedia, and the pars tuberalis.

2. In adult stage the pars anterior is the main bulk of the gland and lies caudal and ventral to the infundibulum.

3. The pars intermedia develops remarkably rapidly near the metamorphic stage, and in its adult condition it lies caudal to the neural lobe and dorsal to the pars anterior.

4. The pars tuberalis develops from a pair of processes, which grow oralward from the remainder of the gland. In the larval stage the roots of these processes are situated on the cephalic lateral end of the pars anterior, but in adult stage these roots come near the median line and they are more slender and thin compared with their cephalic parts. It seems to me that the processes can detach themselves from the main bulk of the hypophysis, as Atwell ('18) observed it in anura.

The development of this lobe is seen to be remarkable up to the stage of its metamorphosis, but after the metamorphosis it does not develop so well.

5. Judging from these observations I am of the opinion that the hypophysis of *Hynobius nebulosus* and *Onychodactylus japonicus* forms the transverse type between the anura and the other urodela.

6. The developmental relationship between the pars anterior, the pars tuberalis and the pars intermedia of the urodela, i.e. the deficient development of the two latter parts compared to the former after the metamorphosis, is to be seen equally, either phylogenetically or ontogenetically.

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Abbreviations in Figures.

- Pa. Pars anterior.
Pi. Pars intermedia.
Pl. Pars lateralis.
Pn. Pars neuralis.
Pt. Pars tuberalis.
B. Brain.
Inf. Infundibulum.
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