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*Individual Variation of Form of the Brain of Triton
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riation of the Brain of Urodela.*

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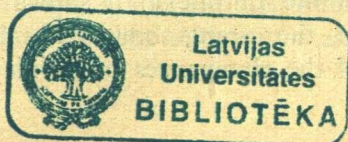
(From the Institute of Comparative Anatomy and Experimental Zoology of the Latvian University, Riga.
Director: N. G. Lebedinsky).

Individual Variation of Form of the Brain of *Triton cristatus* Laur. and its Relation to the Specific Variation of the Brain of Urodela.

By
Emma Nelmanis.
(With 54 Illustrations).

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I. Review of literature and introduction.

The brain of the higher animals, especially that of man is known to be often subject to morphological variation, with regard to size, form, convolutions and weight.

After *J. P. Karplus* (1921) certain variations of the human brain occur repeatedly in the same family so that such variations are subject to heredity. There are variations of the human brain specific to entire nations.

R. Weinberg (1905) in his researches on the brains of Poles states that they possess peculiarities which distinguish them from brains of other nationalities, as for instance a stronger development of the general cerebral mass. The form of the brain in general is characterized by the author as follows: „Was die allgemeine Form der Polenhirne betrifft, so deutet der encephalometrische Ausdruck des Verhältnisses zwischen grösster Länge und Breite in ähnlicher Weise auf eine gewisse Verbreitung der Dolichocephalie unter zahlreichen Brachyencephalen, wie dies die Kraniologie bezüglich der Schädel und die Kephalmetrie bezüglich der lebenden Bevölkerung dartut. Der von oben gesehene Umriss des Gehirns zeigt wie beim Schädel die Form eines Ovoids, welches beim männlichen Geschlecht fast immer regelmässig erscheint, bei dem weiblichen Geschlechte eine eklatante Verschwächigung, entsprechend der Region des Stirnhirnes aufweist.“

Of exceptional interest are the variations of the brain in the different human races when compared with that of the European. *Klaatsch*, who investigated the skeletons of living and fossil human races, classifies them into two types: the eastern and the western type. In the human brain he also distinguishes an eastern and a western type, basing on his investigations of the orangoid and gorilloid characters. He states that the Malay and Negroes of central Africa differ in the following: in the Malay there can be traced an approach towards the orangoid state, whereas in the Negroes he sees an coincidence in the characters with the gorilla and chimpanzee (Cited after *Kurz*, 1924).

Kurz (1924) investigated the brains of the yellow race and corroborates *Klaatsch's* results as to the presence of characters of the eastern type. After previous investigations of the same author (1913), the brain of the yellow race is much more primitive than that of the European: it shows characters of the ape brain, in particular of the orang brain. In the brain of Negroes he found characters of the chimpanzes or gorilla type (*Klaatsch*).

In his work „Die Hirnwindungen einiger niederer Menschenrassen“ *B. Rawitz* (1927) says that he found similar features in the brains of Bushmen. Comparing their general morphology as well as their convolution with such in the European brain the author arrives at the following conclusion: „Die Betrachtung der Oberfläche der Buschmanngehirne zeigt einen so scharfen Gegensatz zur Oberfläche der Europäergehirne, wie man ihn sich gar nicht schärfer denken kann. Man muss geradezu sagen: Das Buschmanngehirn und das Europäergehirn haben nichts miteinander gemeinsam. Es herrscht zwischen ihnen ein solcher Unterschied, als ob beide Gehirnrassen Individuen angehörten, die zu völlig verschiedenen Klassen zu rechnen sind.“ And further: „Dagegen zeigen die untersuchten Gehirne der Buschmänner unstreitig viele Beziehungen zu den Gehirnen der anthropoiden Affen, wenn sie auch von diesen durch grössere Komplikation abweichen.“

The above cited investigations lead us to the following conclusions. The racial variation of the brain can be of such amplitude that the brains of different races can become quite unsimilar to each other, and they might show more resemblance to the brains of representatives of other families.

An asymmetry of form occurs rather frequently though the structure of the normal brain is symmetrical.

„Die beiden Hälften eines Gehirns pflegen einander im grossen ganzen ähnlich zu sein: das Gehirn ist gross oder klein, lang oder kurz, es hat breite oder schmale Windungen, zahlreiche oder spärliche Furchen, und zwar zeigt das Gehirn diese Eigenschaften sowohl rechts als links“, quotes *Karplus* (1921) speaking of the human brain. At the same time he finds its structure to be considerably asymmetrical.

Summarizing the results of his investigations on the right and left halves of the human skull and brain *Ingliss* (1925) concludes that the asymmetry of the hemispheres results from a predominance in the development of one hand over the other (right- or lefthandedness), so that in most people the left hemisphere is better developed.

Rasdolsky (1925) ascertains an analogical fact in animals. He presumes that the asymmetry in the brain not only of man but also of animals results from the predominance in the functions of one extremity. Much as the shape of an animal organism depends on the environment, the hemispheres of the brain are dependent on the motor centres which in their turn are influenced by outer and inner stimuli.

The brain varies also in size. There are cases on record when the brain is considerably under the normal size (microcephaly). It has been believed that the cause of such an underdevelopment is a premature synostosis of the sutures as a result of which the skull-capacity is reduced. In later times however this hypothesis has been disaffirmed as it was discovered that often such a diminished brain does not fill the cavity of the skull.

F. Marchand (1908) who investigated such a reduced brain is of the opinion that a premature synostosis of the sutures alters the shape of the skull and brain but that size and weight of the latter are hardly influenced by it.

J. Herrick (1924) describes the form of the brains in tailed amphibia (*Urodela*), as *Amblystoma tigrinum*, *A. punctatum* and *A. jeffersonianum*. This author compares the respective lengths of 11 prosencephala of *A. tigrinum*. The specimens originated from two different places, partly from Colorado and partly from Chicago. It proved that the prosencephalon of the Colorado specimens was larger than of those from Chicago. *Herrick* found also an asymmetry of the brain, one hemisphere not corresponding in length with the other.

Working on the brains of birds *W. Kuenzi* (1918) found that they vary in size as well as in shape. „Als besonders wichtig, ja ausschlaggebend für die ganze Morphologie haben zu gelten die Unterschiede in der relativen Grösse. Sie bedingen die gegenseitige Lagerung der fünf Gehirnteile in ihrem Wechsel, bedingen aber auch, neben der Grösse des Auges und einigen secundären Momenten, die Formenunterschiede der verschiedenen Gruppen. Eine Zunahme der relativen Grösse des Vorderhirns ändert seine eigene Form wie die der anderen vier Teile in bestimmtem Masse, zugleich aber auch die gegenseitige Lagerung aller fünf Abschnitte.“

Kuenzi ascertained also a considerable variation in the same species of bird as to the size of the brain. „Nur ausnahmsweise zeigen zwei Individuen einer Art für die gleichen Gehirnteile durchgehend die gleichen Indices, fast immer sind grössere oder geringere Differenzen vorhanden.“

On the influence of the sex on the variation of bird brains *Kuenzi* says the following: „Das Geschlecht ist ohne wesentlichen Einfluss auf die relativen Grössenwerte der Gehirnabschnitte.“

Investigating the bird brains with regard to the variation of shape *Kuenzi* concludes that „Die Formenunterschiede bei einer Art sind

im allgemeinen sehr gering“, so that they vary more in size than in shape. In conclusion, comparing the brains of *Dromaeus*, *Picus* and *Crocodylus Küenzi* says: „Ihre Betrachtung lehrt, dass der Unterschied zwischen *Crocodylus* und *Dromaeus* in mancher Beziehung geringer ist, als der zwischen *Dromaeus* und *Picus*, und dass morphologisch die Entwicklungsreihe des Vogelhirns mit vollem Recht an das Diapsiden-Gehirn angeschlossen werden darf.“ The differences between the brains of birds and reptiles can therefore in some respects be smaller than between certain species of birds.

The theme of my investigations was to elucidate the individual variation of the shape of the brain in *Triton cristatus* and to compare it with the specific variation in the order *Urodela*.

For the choice of the theme and directions during the work I am indebted to Professor *N. G. Lebedinsky* to whom I wish to express my sincerest thanks.

II. Material and technique.

As material *Triton cristatus Laur.* was chosen on account of its large size and therefore large brain, better suited for preparation and study. The material consisting of 42 males and 48 females was collected in the vicinities of Sigulda and Bauska. The average length of the animals was about 13 cm, and they were fixed in a 10% and kept in a 4% solution of formaline. The comparative material was put at my disposal by the Institute of Comparative Anatomy and experimental Zoology of the University of Latvia. It consisted in specimens of different Urodela, as *Salamandra atra Laur.*, *S. maculosa Laur.*, *Diemictylus torosus Eschz.*, *D. viridescens Raf.*, *Triton palmatus helveticus*, *T. cristatus carelini* and *T. taeniatus L.*

For further preparation the head was separated, the muscles removed and the skull decalcinated during 24 hours in a 5% solution of nitric acid in alcohol, whereafter the skull was opened and the brain removed, to be preserved in 80% alcohol.

Some of the material was left unstained but the greater part was stained in total with borax-carmin. For the preparation of microscopic mounts the stained brains were submitted to a differentiation (10 ccm of 70% alcohol + 1 drop of hydrochloric acid) and afterwards embedded in paraffine at 48—50°. The thickness of the sections was 10 micr. The totally stained sections were counterstained with picric acid in solution. The sections of the unstained brains were stained after *Mallory's* method. The outline figures and drawings of the microscopic sections were prepared by myself by means of the drawing

after Mallory's method. The outline figures and drawings of the microscopic sections were prepared by myself by means of the drawing apparatus of Abbe and Eddinger. The other figures are executed by V. Krastiņ, student of the Latvian Academy of Arts. The terminology used in the present paper is explained on Fig. 1.

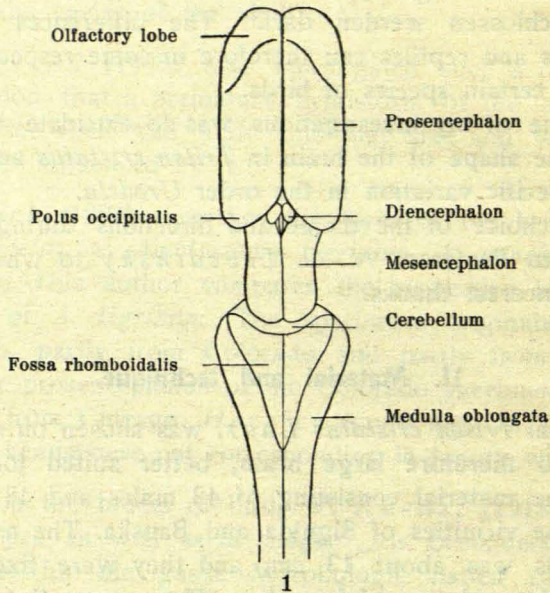


Fig. 1. — Brain of *Triton cristatus* from above.

III. Description of researches.

1. Prosencephalon or fore-brain.

a. Variation of length.

The measurements were taken relative to the width. The most frequent proportion is the following: hemisphere 3 to 3,5 times longer than wide (60 specimens. Sigs. 2, 4, 13, 14, 16, 17).

There also occur more extended hemispheres, in which the length exceeds the width by four times and even somewhat more (5 specimens. Figs. 8, 15, 21). There are also hemispheres which might be reckoned as long but in which the difference with the most frequent length than wide (60 specimens. Figs. 2, 4, 13, 14, 16, 17).

On the other hand there occur also short hemispheres which are only a little over twice as long as their width (1 specimen. Fig. 11). Other hemispheres are somewhat larger, but might be considered as short, their length exceeding width not quite 3 times (13 specimens. Fig. 10).

b. Variation of form.

In transverse section the surface of the hemispheres is dorsally more often convex (82 specimens. Figs. 23, 32). This can be observed at a macroscopic as well as a microscopic inspection of the sections (Figs. 36, 25).

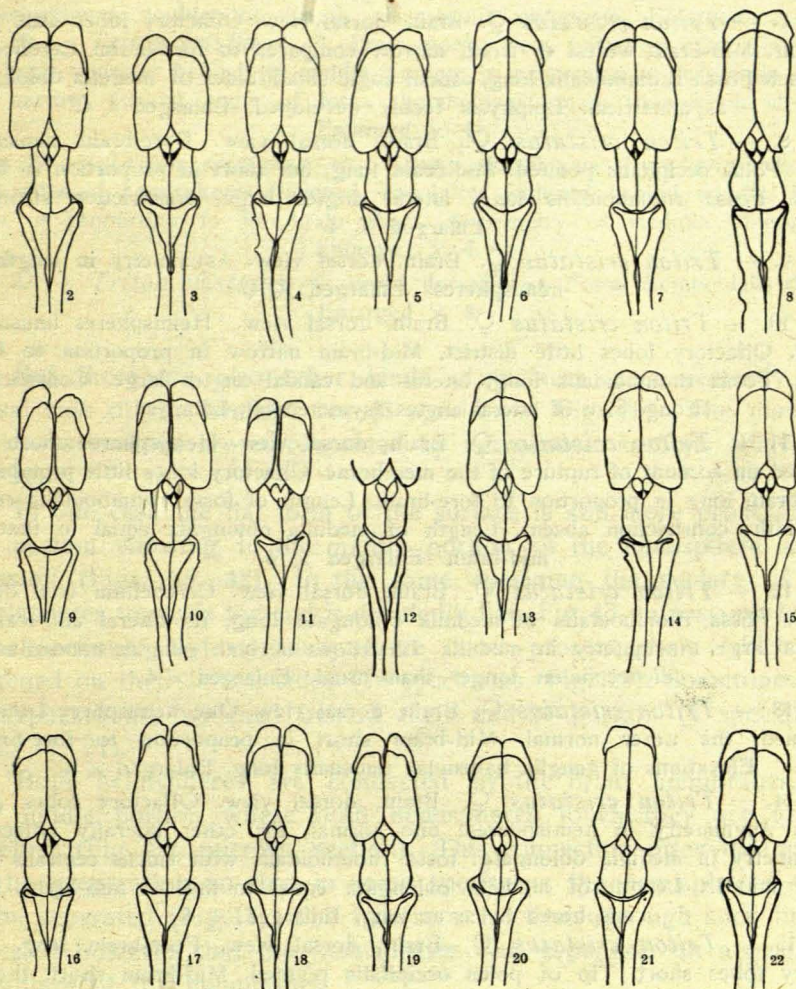


Fig. 2. — *Triton cristatus* ♀. Brain, dorsal view. Mid-brain long and narrow compared to fore-brain. Lateral angles of fossa rhomboidalis large. Enlarged $\times 4$.

Fig. 3. — *Triton cristatus* ♀. Brain, dorsal view. Mid-brain widest behind middle portion. Enlarged $\times 4$.

Fig. 4. — *Triton cristatus* ♀. Brain, dorsal view. Olfactory lobes globular. Mid-brain short compared to fore-brain. Caudal angle of fossa rhomboidalis small. Epiphysis feebly developed. Enlarged $\times 4$.

- Fig. 5. — *Triton cristatus* ♀. Brain, dorsal view. Polus occipitalis much rounded. Asymmetry of medulla oblongata: sulcus centralis not through middle of fossa rhomboidalis. Epiphysis long. Enlarged $\times 4$.
- Fig. 6. — *Triton cristatus* ♀. Brain, dorsal view. One olfactory lobe stronger developed than other. Mid-brain widest behind middle portion, short compared to fore-brain. Asymmetry of medulla oblongata: sides of fossa rhomboidalis unequal. Enlarged $\times 4$.
- Fig. 7. — *Triton cristatus* ♀. Brain, dorsal view. Olfactory lobes little prominent. Mid-brain widest in front, narrow compared to fore-brain. Cerebellum distinct. Fossa rhomboidalis long, caudal angle small. Sides of medulla oblongata asymmetrical. Epiphysis feebly developed. Enlarged $\times 4$.
- Fig. 8. — *Triton cristatus* ♀. Brain, dorsal view. Fore-brain unusually long. Polus occipitalis pointed. Mid-brain long, but short in proportion to fore-brain. Fossa rhomboidalis long, lateral angles large, constriction strong. Enlarged $\times 4$.
- Fig. 9. — *Triton cristatus* ♀. Brain, dorsal view. Asymmetry in length of hemispheres. Enlarged $\times 4$.
- Fig. 10. — *Triton cristatus* ♀. Brain, dorsal view. Hemispheres unusually short. Olfactory lobes little distinct. Mid-brain narrow in proportion to fore-brain. Fossa rhomboidalis long, lateral and caudal angles large. Constriction strong. Size of lateral angles asymmetrical. Enlarged $\times 4$.
- Fig. 11. — *Triton cristatus* ♀. Brain, dorsal view. Hemispheres short, separated on account of rupture of the membrane. Olfactory lobes little prominent. Mid-brain long in proportion to fore-brain. Length of fossa rhomboidalis equal to width: constriction absent. Length of medulla oblongata equal to that of mid-brain. Enlarged $\times 4$.
- Fig. 12. — *Triton cristatus* ♀. Brain, dorsal view. Cerebellum well developed. Fossa rhomboidalis of medulla oblongata long, its lateral and caudal angles large. Asymmetry in medulla. Elevations of both ganglia habenulae in diencephalon longer than usual. Enlarged $\times 4$.
- Fig. 13. — *Triton cristatus* ♀. Brain, dorsal view. One hemisphere laterally flattened, the other normal. Mid-brain short in proportion to fore-brain. Elevations of ganglia habenulae unusually long. Enlarged $\times 4$.
- Fig. 14. — *Triton cristatus* ♀. Brain, dorsal view. Olfactory lobes globular. Asymmetry in hemispheres: one normal, the other laterally inflected. Asymmetry in medulla oblongata: fossa rhomboidalis with sulcus centralis not along middle. Length of medulla oblongata equal to that of mid-brain. Hemispheres twice as long. Enlarged $\times 4$.
- Fig. 15. — *Triton cristatus* ♀. Brain, dorsal view. Fore-brain long. Olfactory lobes short. Tip of polus occipitalis pointed. Mid-brain short, throughout of equal width. In proportion to fore-brain the mid-brain is short but wide. Hemispheres double the length of medulla oblongata. Enlarged $\times 4$.
- Fig. 16. — *Triton cristatus* ♀. Brain, dorsal view. Mid-brain wide in proportion to fore-brain. Fossa rhomboidales of medulla oblongata without constriction. Enlarged $\times 4$.
- Fig. 17. — *Triton cristatus* ♂. Brain, dorsal view. Hemispheres widened behind middle. Tip of polus occipitalis pointed. Fossa rhomboidalis of medulla oblongata strongly constricted. Enlarged $\times 4$.

Fig. 18. — *Triton cristatus* ♂. Brain, dorsal view. Olfactory lobes long. One hemisphere wider than the other, one laterally bowed outward the other inward. Mid-brain widened behind its middle portion. Fossa rhomboidalis short, its lateral angles small, lateral sides asymmetrical. Elevations of ganglia habenulae broad. Enlarged $\times 4$.

Fig. 19. — *Triton cristatus* ♂. Brain, dorsal view. Mid-brain long and wide in proportion to fore-brain. Length of fosse rhomboidalis equal to its width.

Hemispheres double the length of medulla oblongata. Enlarged $\times 4$.

Fig. 20. — *Triton cristatus* ♂. Brain, dorsal view. Olfactory lobes globular, Mid-brain widened behind its middle portion, in proportion to fore-brain long and narrow. Caudal angle of fossa rhomboidalis small, constriction strong, Enlarged $\times 4$.

Fig. 21. — *Triton cristatus* ♂. Brain, dorsal view. Fore-brain long, lateral sides of hemispheres flattened, the latter widened behind middle. Mid-brain in proportion to fore-brain short. Asymmetry of medulla oblongata. Enlarged $\times 4$.

Fig. 22. — *Triton cristatus* ♂. Brain, dorsal view. Fossa rhomboidalis short. Enlarged $\times 4$.

But there are also other kinds of surfaces, as a perfectly flat dorsal side of the hemispheres (3 specimens. Fig. 26). The macroscopic observations are corroborated by microscopic sections (Figs. 29, 30, 31).

In one case the flat form of the surface is still more pronounced, the section showing in the middle portion of the hemisphere a depression (Figs. 38, 42). In the same specimen the surface of the hemispheres towards the end is decidedly flat (Fig. 43, microscopic transverse section). Not unusually there occur prosencephala which are flattened on their lateral sides (12 specimens. Fig. 21). Sometimes the hemispheres are widened behind their middle portion (5 specimens. Figs. 17, 21).

Both hemispheres are connected by the brain membranes. In the middle portion where both hemispheres touch they are grown together (Fig. 29, microsc. section). This connection often disappears at the preparation so that in some specimens the hemispheres seem to be separated (Fig. 11). The transverse sections through such brains revealed however that the hemispheres had separated on account of a rupture of the membranes.

c. Olfactory lobes.

The most frequent shape of the olfactory lobes is the following: in transverse section they are somewhat more convex than the hemispheres, their ends are rounded, and their medial portion is shorter than the lateral (67 specimens. Fig. 3).

Variation of length in the olfactory lobes.

The length of the olfactory lobes is very variable in proportion to the total length of the prosencephalon. In some cases the olfactory lobes occupy about one half of the total length of the fore-brain (1 specimen. Fig. 18). But on the other hand there are specimens the olfactory lobes of which are so short as to occupy little more than a quarter of the former (2 specimens. Fig. 15).

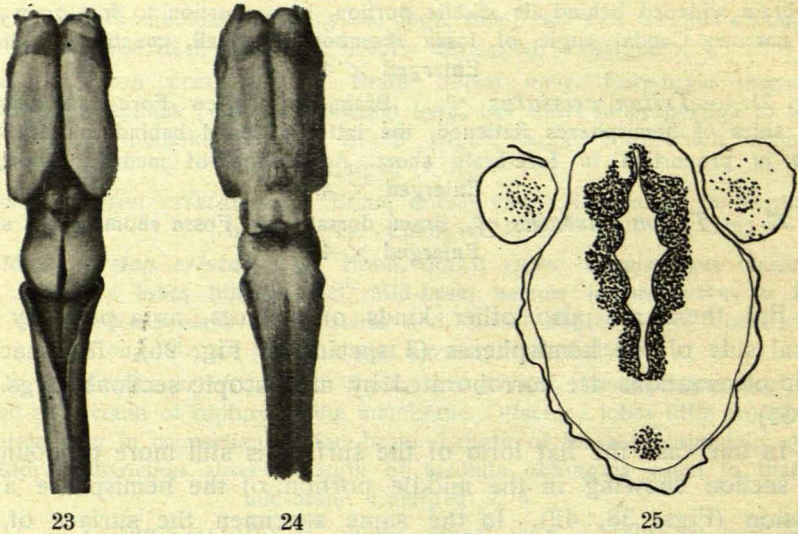


Fig. 23. — *Triton cristatus* ♂. Brain, dorsal view. Fore- and mid-brain wide. Lateral angles of fossa rhomboidalis large. Elevations of both ganglia habenulae broad, epiphysis long. Enlarged $\times 6$.

Fig. 24. — Same brain as on fig. 23, ventral view. Enlarged $\times 6$.

Fig. 25. — Same brain as on fig. 23, transverse section through polus occipitalis. Enlarged $\times 28$.

Variation of form.

The bulges at the ends of the olfactory lobes already mentioned can be so considerable that they appear convex (21 specimen. Figs. 4, 14, 20). There are however cases when this bulging is so insignificant that the lobes are but little set off from the general form of the fore brain (24 specimens. Figs. 4, 10, 11).

In the brain of *Anura* the olfactory lobes are fused, but in *Triton cristatus* and *Urodela* in general they are quite independent from each other, notwithstanding that they are often firmly joined. From a macroscopic inspection it is difficult to judge of their mutual independence but microscopic sections show this quite indisputably (Fig. 28).

d. Polus occipitalis.

The polus occipitalis — the caudal portion of the prosencephalon — is in its most frequent form somewhat tapering and rounded behind (68 specimens, Fig. 38), but there are many aberrations from this shape. It can for instance be acutely pointed at the tip (1 specimen, Fig. 8), or be less markedly pointed (15 specimens, Figs. 17, 15). But there occurs also the opposite case, the polus occipitalis being rounded (5 specimens, Figs. 5, 10).

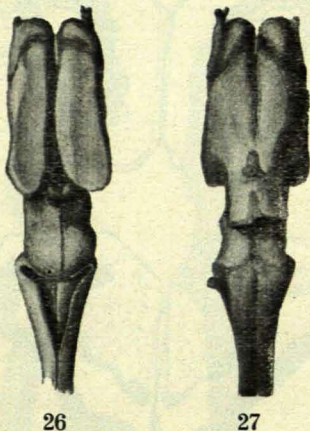


Fig. 26. — *Triton cristatus* ♀. Brain, dorsal view. Surface of hemispheres flat. Fossa rhomboidalis short, caudal angle large, former without constriction. Medulla oblongata and mid-brain of equal length: hemispheres twice as long. Enlarged $\times 6$.

Fig. 27. — Same brain as on fig. 26, ventral view. Enlarged $\times 6$.

e. Asymmetry of the prosencephalon.

Both hemispheres are not always equal. There are cases when one of them is longer (1 specimen, Fig. 9), or wider than the other (3 specimens, Fig. 18).

With regard to the form a difference between both hemispheres of the same fore brain can also be observed (6 specimens). It occurs that one of the hemispheres is laterally convex whereas the other is instead concave (Fig. 18), or is neither the one nor the other (Fig. 14). One hemisphere can be concave laterally on the outer side whilst the other is of the normal shape (Fig. 13). Asymmetry can also be observed in the olfactory lobes, one of them being stronger developed than the other (1 specimen, Fig. 6).

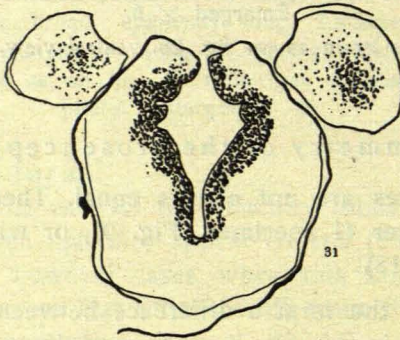
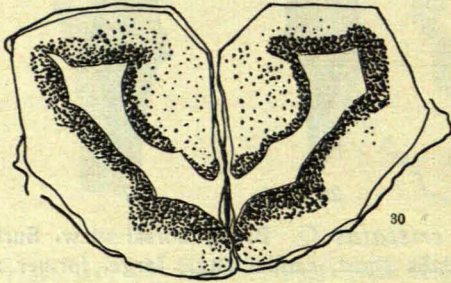
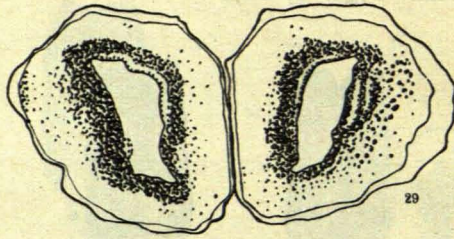
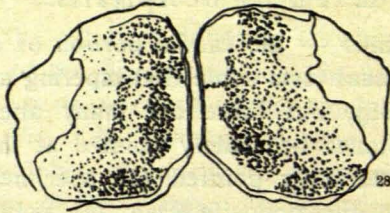


Fig. 28. — Same brain as on fig. 26. Transverse section through olfactory lobes, showing their independence from each other. Enlarged $\times 4$.

Fig. 29 and Fig. 30. — Same brain as on fig. 26. Transverse sections through fore portion of hemispheres. Enlarged $\times 4$.

Fig. 31. — Same brain as on fig. 26. Transverse section through pole occipitalis. Dorsal surface of hemispheres flat. Enlarged $\times 4$.

2. *Mesencephalon, or mid-brain.*

a. Variation of size.

In the mid-brain also many variations might be found as to its size. Sometimes it is twice as long as its width (16 specimens. Figs. 8, 2, 38), whilst in other cases its length surpasses the width but inconsiderably (20 specimens. Figs. 15, 4). The most frequent is a medium form in which the length is by about one-half larger than the width (53 specimens. Figs. 3, 6, 9, 10, 12, 18, 19).

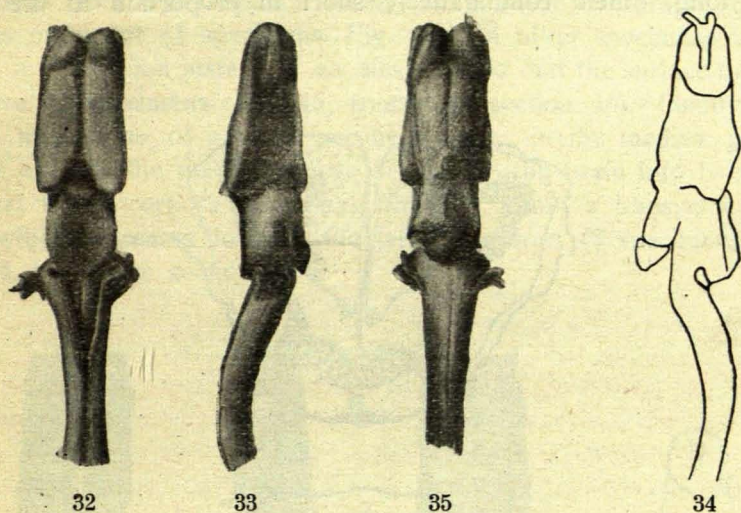


Fig. 32. — *Triton cristatus* ♀. Brain, dorsal view. Mid-brain wide in proportion to fore-brain, its dorsal surface flat. Longitudinal groove obsolete in front portion. Lateral angles of fossa rhomboidalis small, constriction also small. Asymmetry in medulla oblongata: sulcus centralis not along middle of fossa rhomboidalis. Elevations of both ganglia habenulae broad. Enlarged $\times 6$.
Fig. 33 and Fig. 34. — Same brain as on fig. 32, in profile. Medium outward bending of medulla oblongata. Enlarged $\times 6$.

Fig. 35. — Same brain as on fig. 32, ventral view. Enlarged $\times 6$.

The width of the mid-brain is not the same throughout its whole length. In most cases it is widest about the middle of the mid-brain (47 specimens. Figs. 3, 5, 8, 9, 13, 19, 32, 15), so that it widens towards the middle, and attenuates behind. There are however exceptions. The mid-brain can be widest in front and tapering behind (3 specimens. Fig. 7), or on the contrary it is attenuate in front and widens behind the middle (14 specimens. Figs. 2, 6, 18, 20). There are also brains without any widened portion, equally wide

throughout their whole length, and rounded at the very tip (25 specimens. Figs. 15, 38). From a comparison of the mid-with the fore-brain it results that the following proportion is dominating: the mid-brain is about half the size of the fore-brain (58 specimens. Figs. 10, 22, 18, 23, 32).

But there occur considerable digressions from this proportion. The mid-brain can be larger than half the size of the fore-brain (15 specimens. Figs. 4, 6, 8, 13, 15, 21), or it can be smaller (16 specimens. Figs. 11, 19, 20, 45). It results that some mid-brains are rather long, others comparatively short in proportion to the fore-brain.

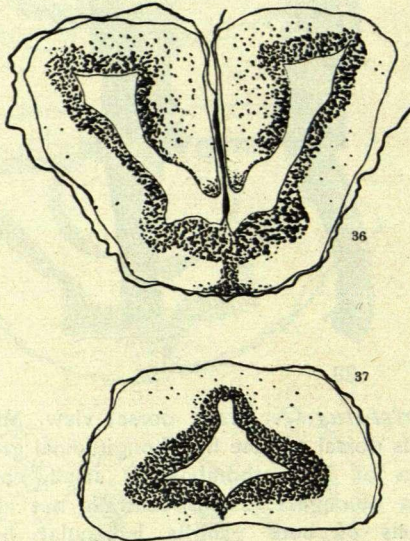


Fig. 36. — Same brain as on fig. 32. Transverse section through hemispheres, showing convex surface of these. Enlarged $\times 28$.

Fig. 37. — Same brain as on fig. 32. Transverse section through mid-brain, showing flattened surface of mid-brain. Enlarged $\times 28$.

The same can be said of the relative width of the fore- and mid-brain. There are cases when a wide fore-brain coincides with an also wide mid-brain (6 specimens, Figs. 23, 45), but there happens also the contrary, the fore-brain being wide, and the mid-brain narrow (8 specimens. Figs. 2, 7, 10, 20), or the mid-brain wide, and the fore-brain narrow (10 specimens. Figs. 15, 16, 19, 32).

b. Variation of form.

The most frequent form is the following. In the fore portion of the mid-brain its surface is situated lower than that of the hemispheres, but in its middle portion or somewhat before it the former bulges more strongly, its surface becoming, when viewed in transverse section, more convex, and sometimes it bulges to an extent that it exceeds the hemispheres. When viewed from above the mid-brain is rounded behind (81 specimens. Fig. 47, transverse section through normal a mid-brain). There are however considerable deviations from this dominant form, and in some mid-brains the surface is quite flat (4 specimens. Fig. 32). In other specimens it even forms a depression instead of an elevation, so that the surface becomes concave (2 specimens. Fig. 45, transverse section 46). Finally there occur mid-brains of a quite peculiar shape: in the median portion, where extends the median groove separating the brain into two lobes (optical lobes, corpora bigemina), there is found a transverse elevation which decreases towards the lateral portions (2 specimens. Figs. 38, 44, transverse section).

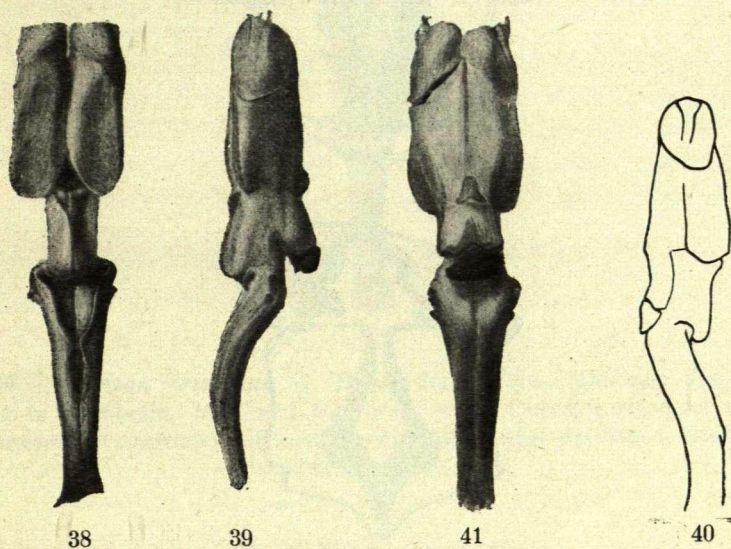
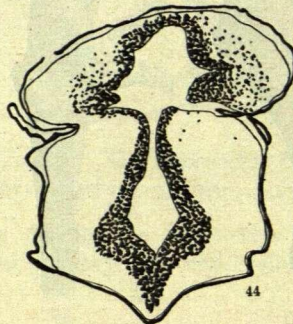
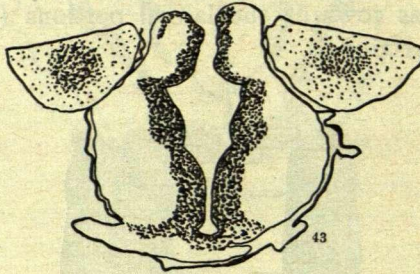
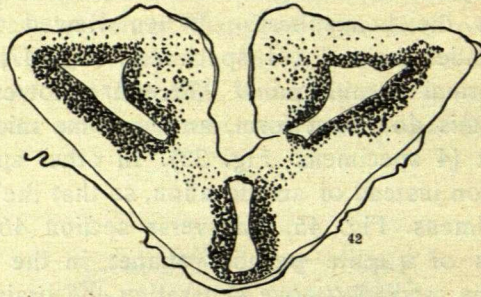


Fig. 38. — *Triton cristatus* ♀. Brain, dorsal view. Dorsal surface of hemispheres depressed. Mid-brain long, equally wide throughout its length with oblique sides. Fossa rhomboïdalis long, caudal angle large, constriction strong. Epiphysis long. Enlarged $\times 6$.

Fig. 39 and Fig. 40. — Same brain as on fig. 38, in profile, showing strong bent of medulla oblongata. Enlarged $\times 6$.

Fig. 41. — Same brain as on fig. 38, ventral view. Enlarged $\times 6$.

The longitudinal groove of the mid-brain is usually visible all along its extension, and among all the brains I investigated in one only it became obliterated in the frontal portion, i. e. before the middle (fig. 32). In his paper „*Untersuchungen am Hirn und Geruchsorgan von Triton und Ichthyophis*“ *Burckhardt* (1891) asserts



- Fig. 42. — Same brain as on fig. 38. Transverse section through hemispheres, their dorsal surface bent inwards. Enlarged $\times 28$.
- Fig. 43. — Same brain as on fig. 38. Transverse section through *polus occipitalis*. Dorsal surface of hemispheres flat. Enlarged $\times 28$.
- Fig. 44. — Same brain as on fig. 38. Transverse section through mid-brain, showing surface of mid-brain with longitudinal elevation in middle and oblique lateral sides. Enlarged $\times 28$.

that a sulcus dorsalis is present in adult animals only. In the case above mentioned the feeble development of the median groove is therefore presumably connected with a retardation of growth.

3. Cerebellum.

The cerebellum in *Triton cristatus* is little developed and forms a small transverse ridge which often is hidden under the mid-brain (38 specimens) but can also project from below the latter and so become conspicuous (42 specimens, Fig. 7). It protrudes but rarely more strongly and then takes the shape of a more conspicuous formation towards the fossa rhomboidalis of the medulla oblongata (10 specimens, Fig. 12).



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Fig. 45. — *Triton cristatus* ♀. Brain, dorsal view. Mid-brain long in proportion to fore-brain. Mid- and fore-brain wide. Dorsal surface of mid-brain bent inwardly. Constriction of fossa rhomboidalis feebly developed, lateral angles unequal. Enlarged $\times 4$.

4. Medulla oblongata.

a. Variation of size of the fossa rhomboidalis.

The fossa rhomboidalis is widest in its fore portion and produces lateral angles on each side. In its very front part it becomes much narrower, and as far as the middle of its length — more often even farther behind — it gradually attenuates, and here bows me-

dially so as to form a kind of constriction of the fossa rhomboidalis and terminates caudally in an extended angle. The most frequent proportions of the fossa rhomboidalis are the following. The total length exceeds the width of the fore portion, or often somewhat less (50 specimens. Figs. 3, 4, 17, 32): the fore lateral angles are very small, in fact so insignificant as to form but a small slit (47 specimens. Figs. 15, 45): the caudal angle is much pointed and often also forms but a small slit (57 specimens. Figs. 8, 15, 23, 45)

Not only the size of the fossa rhomboidalis is variable but also the angles just mentioned. In proportion to its widest, the front portion, the length of the fossa rhomboidalis exceeds the former by usually considerably over one half (24 specimens. Figs. 7, 8, 10, 12, 38). but it might be also smaller (8 specimens. Figs. 18, 21, 22, 26), and even equal to the width of the fore part (5 specimens, Figs. 11, 19). It can be said that in general the shape of the medulla oblongata corresponds with the shape of the fossa rhomboidalis. There are therefore relatively long or short medullae oblongatae.

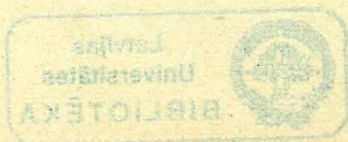
With regard to the fore lateral angles of the fossa rhomboidalis their size is variable and often deviates from the usual acute type. They can, as to the degrees, be considerably enlarged (16 specimens. Figs. 2, 3, 8, 10, 12, 23) or, on the contrary reduced to a minimum (26 specimens. Figs. 18, 21, 32). The caudal angle can also be either large (10 specimens. Figs. 10, 12, 26, 38), or in other cases small to an extent as to form but a narrow slit the sides of which sometimes fuse, so that the angle disappears altogether (22 specimens. (Figs. 4, 7, 20, 21).

b. Variation of shape in the fossa rhomboidalis.

The contraction of the fossa rhomboidalis occurs in most brains considerably behind the middle of the latter (55 specimens), in some however it is pushed forward almost to the middle of the fossa (7 specimens. Fig. 7, 10, 38). The medially directed bendings produced by the constriction are also variable. Usually they are of medium size and distinct (62 specimens. Figs. 18, 19): but there are cases when they are more sharply pronounced (13 specimens. Figs. 38, 8, 10, 17, 20), or on the contrary hardly perceptible (11 specimens. Figs. 32, 45), or even entirely absent, i. e. the fossa rhomboidalis has no constriction whatever (3 specimens. Figs. 11, 16, 26).

c. Asymmetry in the medulla oblongata.

Just as the other parts of the brain the medulla oblongata is symmetrical in its structure. A longitudinal groove, the sulcus cen-



tralis, running across the middle of the fossa rhomboidalis divides the latter into a right and a left half, which are symmetrical (84 specimens). But there are also cases of asymmetry. So the sulcus centralis instead of going through the middle of the fossa can be dislocated to one or the other side (4 specimens. Figs. 5, 14, 32). The asymmetry of the sulcus centralis is partly called forth by an asymmetry of the sides of the medulla oblongata, i. e. by a stronger development of one of them which therefore occupies a larger portion of the fossa rhomboidalis, and sometimes overlaps the sulcus centralis in its caudal part.

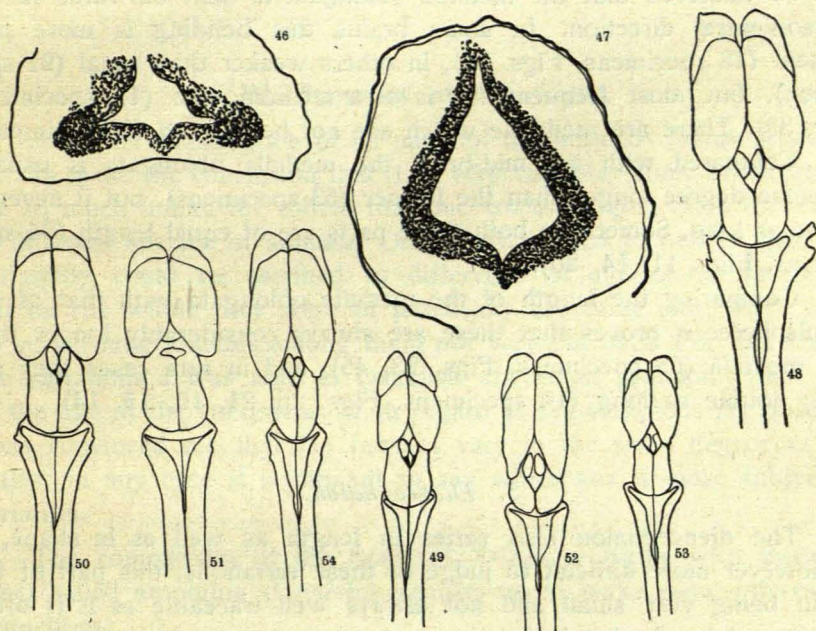


Fig. 46. — Same brain as on fig. 45. Transverse section through mid-brain. Dorsal surface of mid-brain bent inwardly. Enlarged $\times 28$.

Fig. 47. — *Triton cristatus*. Transverse section through mid-brain. Dorsal surface of usual, normal shape. Enlarged $\times 28$.

Fig. 48. — *Diemictylus torosus*. Brain, dorsal view. Enlarged $\times 4$.

Fig. 49. — *Diemictylus viridescens*. Brain, dorsal view. Enlarged $\times 4$.

Fig. 50. — *Salamandra atra*. Brain, dorsal view. Enlarged $\times 4$.

Fig. 51. — *Salamandra maculosa*. Brain, dorsal view. Enlarged $\times 4$.

Fig. 52. — *Triton palmatus helveticus*. Brain, dorsal view. Enlarged $\times 4$.

Fig. 53. — *Triton taeniatus*. Brain, dorsal view. Enlarged $\times 4$.

Fig. 54. — *Triton cristatus carelini*. Brain, dorsal view. Enlarged $\times 4$.

An asymmetry of the sides of the medulla oblongata occurs rather often, and the fore lateral angles of the fossa rhomboidalis are of different length (5 specimens. Figs. 10, 45). The bendings at the constriction of the fossa rhomboidalis can be larger on one side and smaller on the other (7 specimens. Figs. 3, 7, 12, 18); on one side the bending can be present, and wanting on the other (3 specimens. Figs. 6, 23).

d. Comparison with other parts of the brain.

In profile, when compared with the other parts of the brain, it can be observed that the medulla oblongata is bent outwards in the dorso-ventral direction. In some brains this bending is more prominent (18 specimens. Figs. 39), in others weaker than usual (21 specimen), but most frequently it is of a medium size (44 specimens. Fig. 33). There are medullae which are not bent at all (3 specimens).

Compared with the mid-brain the medulla oblongata is usually in some degree longer than the former (63 specimens), but it never is twice as long. Sometimes both these parts are of equal length (24 specimens. Figs. 11, 14, 26).

Comparing the length of the medulla oblongata with that of the hemispheres it proves that these are always considerably longer than the medulla (68 specimens. Figs. 23, 45), and in rare cases they are even double as long (19 specimens. Figs. 26, 21, 19, 15, 14).

5. *Diencephalon.*

The diencephalon also varies in length as well as in shape, it is however more difficult to judge of these variations, this part of the brain being very small and not always well traceable as it is often overlapped by the hemispheres.

In front the diencephalon shoves between the ends of the hemispheres and behind into the mid-brain. Its fore part consists of the plexus chorioideus medius, which was removed as to permit of a better view on the paired prominence formed by the thickened wall of the ganglia habenulae. In the median portion of the diencephalon is found the bladder-like epiphysis. Each half of the paired prominence of the ganglia habenulae is as a rule oval, i. e. longer than wide. There occur however cases when each half is much more extended in length (35 specimens. Figs. 12, 13), and others when each half is much wider and the oval shape less pronounced (26 specimens. Figs. 18, 23, 32).

The epiphysis is in general elongated and situated in the median portion of the diencephalon. It starts between the halves of the paired prominences of the ganglia habenulae and shoves itself wedge-like into the mid-brain between the prominences of the lobi optici. The epiphysis is sometimes more extended than usual and intrudes rather far between the paired prominences of the ganglia habenulae (32 specimens. Figs. 23, 38, 5).

There occur also diencephala of small size which are feebly developed in spite of all other parts attaining a full development (4 specimens. Figs. 4, 7).

IV. Summary of the results.

After the examination of all parts of the brain of *Triton cristatus* we can make the conclusion that it is very variable. Some of the brains are so much unlike the others that one could imagine them to belong to different species of animals. One might be led to believe that this variability could be ascribed to difference of age of the specimens but on the whole they were of practically the same size: there were no very young animals among them nor very old ones. For this reason the variations I was able to establish are in all probability not due to the age of the specimens. With regard to sex-variations my observations convinced me that the females vary in the same degree as the males: in any case it is difficult to say which sex is more subject to variation.

The comparison of the brain of *Triton cristatus* with those of other tailed amphibia (*Urodela*) enables us to make some interesting deductions.

The brain of *Triton cristatus* is very similar to that of *Salamandra atra* in the proportions of the different parts as well as in shape (Figs. 22, 50).

On the other hand the brain of *T. cristatus* is in its proportions quite unlike that of *Salamandra maculosa* (Fig. 51). The hemispheres in the latter species are comparatively much abridged, the length ratio of the midbrain to the length of the hemispheres is much larger than in the brain of *T. cristatus*. The brain of *Diemictylus torosus* (Fig. 48) is likewise much similar to that of *T. cristatus*: the fore-brain and mid-brain correspond even completely in both with regard to size and shape, and only the shape of the fossa rhomboi-

dalis which in *D. torosus* has a strong, sometimes even confluent, constriction which in *T. cristatus*, though present, occurs less often, serves as a sufficiently typical differentiating character between these two genera.

In *Burckhardt's* (1891) paper we read the following passage on the proportions of the brains in different species of *Urodela*. „Es standen mir erwachsene Exemplare von *Triton alpestris*, *cristatus*, *taeniatus*, *helveticus* und dem amerikanischen *viridescens* zu Gebote. Von diesen fünf Species zeichnet sich die letztere dadurch aus, dass das Mittelhirn und Zwischenhirn zusammengenommen an Volumen dem Vorderhirn gleichkommen: auch ist hier das Mittelhirn zu zwei Corpora bigemina vorgewölbt. Das andere Extrem ist durch *Triton helveticus* vertreten, eine Art, bei welcher das Vorderhirn das Mittel- und Zwischenhirn beinahe um das doppelte übertrifft. Zwischen diesen beiden Gegensätzen bilden die drei übrigen Species Übergänge, und zwar so, dass *Triton cristatus* sich an *helveticus*, *alpestris* und *taeniatus* an *viridescens* anlehnen.“ Thus after *Burckhardt* the brain of *Triton cristatus* differs from those of *T. taeniatus* and *T. viridescens* usually very considerably. From the comparison of some of the brains of *T. cristatus* investigated by myself with such of *T. taeniatus* and even *Diemictylus viridescens* it results however that precisely the parts of the brain mentioned by *Burckhardt* can with regard to size and shape correspond in all three species (Figs. 16, 49, 53). Some brains of *T. cristatus* are much alike to that of *Triton palmatus helveticus* (Figs. 52, 15), only that in the latter species the length of the mid-brain is small in comparison to the length of the hemispheres, whereas on the other hand the diencephalon is somewhat longer. The form of the brain, especially that of the medulla oblongata and the hemispheres, coincides with the shape in *Triton cristatus* ,(after *Burckhardt* also the proportions of size are the same in the two species). Some brains of *T. cristatus* are much resembling to that of *T. cristatus carelini* (Figs. 54, 4); the proportions can entirely correspond, and sometimes coincides also the pointed tip of the polus occipitalis (Fig. 8), peculiar to *T. cristatus carelini*.

As a result of the comparison of brains of *T. cristatus* with those of other representatives of the order *Urodela* we might say the following. The amplitude of variation in form and proportions of the brain can be larger than in representatives of different species and even genera. The individual variation of the brain in *Triton cristatus* exceeds therefore sometimes the specific variation.

V. Theses.

1. The variation of the brain in *Triton cristatus* in the adult state is independent of the animal's age.
2. A sexual variation of the brain could not be ascertained.
3. The individual variation of the brain can sometimes exceed that of the specific variation.

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Triton cristatus Laur. smadzeņu individuālās formu svārstības, salīdzinot ar smadzeņu variabilitāti dažādās Urodela ģintīs.

Emma Nelmanis

Pēc visu *Triton cristatus* smadzeņu daļu apskatīšanas nākam pie slēdziena, ka tās stipri variē. Ir smadzenes, kas tik stipri atšķiras vienas no otrām, ka šķiet ņemtas no dažādu sugu dzīvniekiem. Par iemeslu šādai lielai smadzeņu variabilitātei varētu būt arī dzīvnieku vecums. Visi aplūkotie tritoni tomēr bija videja lieluma: mazu, nepieaugušu, tāpat arī lielu un vecu starp viņiem nebija.

Tā tad lielā smadzeņu variabilitāte domājams nav atkarīga no vecuma.

Attiecībā uz dzimumiem, jāsaaka, ka variācijas vienlīdz sastopamas, kā pie tēviņiem, tā pie mātītēm. Tādēļ arī grūti noteikti konstatēt, kurš dzimums būtu variāciju ziņā pārkāps par otru.

Salīdzinot *Triton cristatus* smadzenes ar citām astaino amfibiju — *Urodela* — smadzenēm, nākam pie interesantiem slēdzieniem.

Triton cristatus un *Salamandra atra* smadzenes, kā formas, tā arī atsevišķo daļu relatīvā lieluma ziņā, ļoti līdzīgas (zīm. 21, 49).

Turpretim no *Salamandra maculosa* smadzenēm (zīm. 51) *Triton cristatus* smadzenes atšķiras, sevišķi relatīvā lieluma dažādības dēļ. Salamandru hēmifaires stipri īsas; vidus smadzeņu gaņuma attiecība pret hēmifairu gaņumu stipri vien lielāka, kā pie *Triton cristatus* smadzenēm.

Tāpat atkal *Triton cristatus* un *Diemictylus torosus* (zīm. 48) smadzenes ļoti līdzinājas vienas otrām: lielās un vidus smadzenes pat pilnīgi atbilst, kā relatīvā lielumā, tā arī formas ziņā. Tikai *Diemictylus torosus* romboidālās bedrītes forma ir pārveidojusies, iegūstot stipru iežņaugumu. Šis iežņaugums, samērā reti, bet tomēr ir sastopams pie *Triton cristatus* smadzenēm (zīm. 38), un ir diezgan raksturīga atšķirība starp šīm divām ģintīm.

R. Burkhardts raksta par smadzeņu lieluma attiecībām pie dažādiem *Urodela* priekšstāvjiem sekošo:

„Es standen mir erwachsene Exemplare von *Triton alpestris*, *cristatus*, *taeniatus*, *helveticus* und dem amerikanischen *viridescens* zu Gebote. Von diesen fünf Species zeichnet sich die letztere dadurch aus, dass Mittelhirn und Zwischenhirn zusammengenommen an Volumen dem Vorderhirn gleichkommen; auch ist hier das Mittelhirn zu zwei Corpora bigemina vorgewölbt. Das andere Extrem ist durch *Triton helveticus* vertreten, eine Art, bei welcher das Vorderhirn das Mittel- und Zwischenhirn beinahe um das Doppelte übertrifft. Zwischen diesen beiden Gegensätzen bilden die drei übrigen Species Übergänge, und zwar so, dass *Triton cristatus* sich an *helveticus*, *alpestris* und *taeniatus* an *viridescens* anlehnen.“

Tā, pēc *Burkhardta* novērojumiem, *Triton cristatus* smadzenes no *Triton taeniatus* un *T. viridescens* smadzenēm parasti stipri atšķiras. Salīdzinot dažas no manis aplūkotās *Triton cristatus* smadzenes ar *Triton taeniatus* un pat *Diemict. viridescens* smadzenēm, iznāk, ka *Burkhardta* minētās smadzeņu daļas, kā relatīvā lieluma, tā arī formas pēc var dažos gadījumos pie visām 3 sugām sakrist (zīm. 16, 49, 53).

Dažu *Triton cristatus* smadzenes ir stipri vien līdzīgas *Triton palmatus helveticus* smadzenēm (52., 15. zīm.). Te tikai vidējo smadzeņu gaņums ir mazs, attiecībā pret hēmisfairu gaņumu, bet toties starpsmadzenes ir drusku gaņakas. Smadzeņu forma, it sevišķi hēmisfairu un gareno smadzeņu, sakrīt ar *Triton cristatus* smadzeņu formu. (*Burkhardts* arī atrod, ka šo divu sugu smadzenēs ir vienādas lieluma attiecības).

Ir arī tādas *Triton cristatus* smadzenes, kuņas līdzinājas *Triton cristatus carelinii* smadzenēm (54., 4. zīm.). Lieluma attiecības var pilnīgi sakrist, un dažreiz sakrīt arī hēmisfairas raksturīgā asā smaile *polus occipitalis* (8. zīm.).

Pēc šiem *Triton cristatus* smadzeņu salīdzinājumiem ar citu *Urodela* priekšstāvju smadzenēm, iznāk:

Smadzeņu formas un relatīvā lieluma variācijas pie vienas un tās pašas sugas var būt lielākas kā starp atsevišķu sugu, pat ģinšu priekšstāvjiem. Tā tad individuālā galvas smadzeņu variabilitāte var būt stiprāka par sugu smadzeņu variabilitāti.

Tezes.

1. Smadzeņu variābilitāte adultā stāvoklī nav atkarīga no dzīvnieka vecuma.
 2. Dzimumu variābilitāte smadzenēs netiek konstatēta.
 3. Individuālā galvas smadzeņu variābilitāte var būt stiprāka par sugu smadzeņu variābilitāti.
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