

TABLE OF STAGES OF THE NORMAL DEVELOPMENT OF
 AXOLOTL EMBRYOS AND THE PROGNOSTICATION OF TIMING OF SUCCESSIVE
 DEVELOPMENTAL STAGES AT VARIOUS TEMPERATURES

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Eggs and embryos of the axolotl are convenient subjects for various types of investigations. For this reason it was thought to be desirable to obtain for the axolotl, data on the relative duration of different developmental periods that would allow predictions of the times at which the different stages of development occur at various temperatures, and also to compare the temporal characteristics of axolotl development with those of other amphibian species.

This method of prognostication is based on the fact that in the middle zone of optimal temperatures the duration of different animal developmental periods changes proportionally (Dettlaff and Dettlaff, 1960, 1961; Dettlaff, 1964, 1976; Dettlaff and Rudneva, 1973). Such a proportionality has been established for the axolotl as well (Cate, 1956; Skoblina, 1963; Valouch et al., 1971). Therefore, by determining the duration of some one selected period at various temperatures and that of all the remaining ones at one constant temperature, it is possible to estimate the duration of different periods of development at various temperatures within optimal range.

The most convenient unit of the duration of development comparable in many animals is the duration of one mitotic cycle during the period of synchronous cleavage divisions - τ_0 (s. Dettlaff and Dettlaff, 1961; Dettlaff, 1976). In the axolotl it corresponds to the interval between the first appearance of the I and II cleavage furrows on the egg surface (Rott, 1973). The value τ_0 was determined at various temperatures by Skoblina (Skoblina, 1963, 1965) and the curve characterizing the dependence of the value of τ_0 from the temperature (sec. Fig. 1) was traced according to the averages of τ_0 for each temperature.

Thus in the present work we need only to determine the time of the onset of successive stages of development of the axolotl at one of the optimal temperatures and to express it in the number of τ_0 at the same temperature. When we began this work no tables of stages of the normal development for the axolotl were available. The practice of extrapolation of the stages proposed by Harrison for Ambystoma punctatum meets difficulties because after the end of neurulation the external morphological characters of embryos of these species differ considerably. For this reason we had to begin this work with the description table of the normal development of the axolotl. The paper of Schreckenberg and Jacobson (Schreckenberg and Jacobson, 1975) "Normal Stages of Development of the Axolotl Ambystoma mexicanum" was published when this work had already been essentially finished and the table of stages of the normal development of the axolotl were in press (Bordzilovskaya and Dettlaff, 1975). In the discussion we compared our data with the data of Schreckenberg and Jacobson (1975).

Materials and Methods

The eggs of the axolotl were taken for observation during the first 20-40 minutes after they had been laid. The observations were made under a binocular microscope. When the first appearance of the initial cleavage furrow on the animal pole was recorded and the eggs began to cleave in the interval of 3-5 or 10-20 minutes, the eggs were placed, several to a dish, and incubated in a Heppler ultrathermostat at 20°. The embryos were periodically observed to register the times at which the first embryos in every dish reached the subsequent stage. The stages have been designated in accordance with the numbering system proposed by Harrison for *Ambystoma punctatum*. In the complex of features characteristic for every stage (Harrison, 1969) those features were chosen which are common for embryos of both species. In addition, those stages which allow a distinction from the preceding one and a determination of the precise time at which it occurs were employed. The criteria of the later stages and their timing have been defined more accurately on fixed material. The fixation was done up to the stage 35, at first with an interval of 1/2 and one τ_0 , then - of 5 τ_0 , and the last stages - with a still greater interval - about 10 and 20 τ_0 with the orientation to some precisely definable features. From 3 to 5 portions of eggs that began to cleave a different times were fixed for every term. Stages which are transitional between different periods of development such as the beginning of gastrulation, the stage with a slitlike blastopore, and the closure of the neural folds, were defined on a greater number of eggs and with a greater repetition of observations. The investigation was carried out on the eggs of 5 females. Size indications in the descriptions of stages are the average of several measurements made as follows (see Fig. 1).

The drawings of external morphological features of the successive stages of development were made by means of drawing apparatus. Both the drawings and the definitions of diagnostic features for every stage were prepared by N.P. Bordzilovskaya.

Times at which the different stages occur are determined on more advanced embryos in every portion which provides, as experience has shown (Dettlaff and Dettlaff, 1961; Zubova, 1962; Ignatieva, 1974), more precise and better reproducible results. However, since with axolotl embryos taken from natural layings it is difficult to have many simultaneously fertilized eggs or to provide a very great repetition of the observations, we can say only conditionally that the values in our table are indeed obtained on the more advanced embryos.

To obtain the relative characteristics of duration of different periods of development (τ_n/τ_0) the time from the appearance of the initial cleavage furrow on the egg surface to the onset of corresponding developmental stage (τ_n in minutes) is divided by the value τ_0 (in minutes) at the same temperature. At 20°C τ_0 (unpublished data of Skoblina) this parameter varies from 87 to 93 minutes. In our calculations we admit that τ_0 is equal to 92 minutes. Table 1 shows the time from the appearance of the first cleavage furrow to the corresponding stage in hours and minutes and in the number of τ_0 (τ_n/τ_0). In brackets the variability of the value τ_n/τ_0 is shown for embryos from different portions of a spawning.

With a small interval of time between the successive stages the individual differences in the stage's duration in different embryos of one and

the same term of fertilization usually exceed this interval. For that reason we failed to show for several stages designated on fixed material the duration of time intervals between these stages because they are found simultaneously in portions fixed in the near terms, (in the table they are marked by an asterisk).

Discussion

Since the drawings and the description of the embryo of Ambystoma punctatum served to distinguish the stages of development of the axolotl, we first needed to examine the extent to which the stages of development of A. punctatum and the axolotl designated by the same number correspond to each other, and where essential species differences are in the structure of embryos of both species. One part of the diagnostic features for each stage indicated in Table 1 is common for both A. punctatum and the axolotl. The principal difference connected with the specific features of the structure of embryos consists of the following: In axolotl embryos the gill swelling, hyomandibular, hyobranchial and branchial furrows and fin fold become apparent at the earlier stages; the angles of the mouth also form earlier. On the contrary the limb buds develop much later than in A. punctatum. In these species the size and the shape of the head region also differ at the same stages. Finally, in the axolotl the primordia of balancers fail to develop.

In our tables the structure of embryos of A. punctatum and the axolotl do not coincide at stage 8 (the embryo of A. punctatum is younger) and it is difficult to identify stage 9 from the features indicated in Harrison's table without a time parameter. For the axolotl, in the period of gastrulation we distinguish a greater number of stages (see Table 2). The beginning of gastrulation in the axolotl (Stage 10) corresponds in A. punctatum, if we examine the pictures, also to stage 10. But if we take into account the description, it corresponds to stage 10-. The stages corresponding to our stage 10 1/2 and stage 12 differ from the table of Harrison. Stage 10 3/4 in axolotls correspond to stage II in A. punctatum. At stage 12 1/2 the axolotl embryo is somewhat younger than the embryo of A. punctatum. Our stage 13- corresponds to stage 13, and stage 13 to stage 13+. The remaining stages, as already stated, generally correspond. Unfortunately, the Harrison's table lacks an indication of the stage at which hatching of the embryo from the membranes occurs. Thus, stage 41 of our table can not be compared.

It is also worthwhile to compare the stages determined here with those published by Schreckenber and Jacobson (Schreckenber and Jacobson, 1975). Since they oriented their data to the table of Harrison, a very great difference between our stages of axolotl development should not be found. This is not, however, always the case because it is sometimes difficult to see in photographs the exact features that served for us as the diagnostic ones, and those authors did not mention all of these features in their description, or indicate them on later stages. In certain cases Schreckenber and Jacobson deviate from the stage numbering of Harrison. Thus, the stage of beginning of gastrulation has N 9 but not the N 10 or 10-, and the stage of slit-like blastopore - N 14 but not the N 13. As far as we can judge, stages indicated by Schreckenber and Jacobson and by us correspond to each other as follows (see also Table 2): they coincide to the stage 7 inclusive, however at stage 8 (Schreckenber and Jacobson) the embryo is younger than the embryo of our stage 8. That stage lasts

according to their 18°C data for 8-16 hours and ends at stage 8+ which corresponds, as one can see from the terms, to the stages 9 and 9 1/2 in our table. Stage 9 corresponds to stage 18, stage 10- to stage 10 1/2, stage 11 to stage 10 3/4. Stages 12 coincide in both tables; stage 13 corresponds to our 12 1/2 (if it is not the beginning of the neurulation but rather a small yolk plug); stage 14 corresponds to our 13 and stage 14+ to our 14; stages from 15 to 20 in general coincide: stages 21 and 22 externally coincide with our stages, however from the description embryos at these stages (S and J) are somewhat younger. Stage 23 and stage 24 coincide in the number of somites. Stage 25 differs from our stage 25, and by the head curvature corresponds to our stage 27. The period of forming of the head curvature both in our table and in Harrison's table is divided in a greater number of stages. Our stages 25 and 26 do not coincide. Their stage 26 corresponds to our stage 28, and stage 27 (after picture) - to stage 29 in our table.

It is not possible to identify stages 28 and 29 in the table of Schreckenberg and Jacobson either by their pictures or by the description of our stages. Stages 30, 31, 32 and 33 according to their shapes of embryos seem to correspond in general to ours. Since their stage 37 has such features as the beginning of heart pulsation, the definitive straightening of the body and the appearance of the primordia of external gills, it corresponds to our stage 35; stage 35 of Schreckenberg and Jacobson characterized by the appearance of chromatophores resembles our stage 35. For stages 36 and 37 the precise differences are not indicated. They are similar to our stage 36. Stage 38 after the structure of gills corresponds, in our table, to stage 37, and the stage 39 - to our stage 38. Our stages 34, 38 and 40 are not included in the table of Schreckenberg and Jacobson. The stage of hatching in their table is stage 40 and in ours - stage 41. Thus in our tables and theirs the stages 1 - 7, 15 - 24 and 30 - 33 more or less coincide. The numbering of other stages in the table of Schreckenberg and Jacobson differs not only from ours but also from Harrison's.

We also tried to compare our data on the timing of different stages of development. For this reason we recalculated the duration of more or less coinciding stages in the number of τ_0 (at 18°C $\tau_0 = 105$ min, s. Fig. 1) the time in hours pointed out by Schreckenberg and Jacobson at $18^\circ \pm 0.5$ for the transition of the first embryos to the next stage. It was taken into account that Schreckenberg and Jacobson counted off the time from the laying of the egg. In our studies we counted from the appearance in the animal region of the cleavage furrow 1, i.e. about by $2.5 - 3 \tau_0$ later. A satisfactory coincidence of the relative characteristics was obtained for some more distinct and soon passing stages: for the beginning of gastrulation, the stage of slitlike blastopore, several stages of neurulation - stage 16 and 20, and also for stage 23, 30 and 37 (38 after Schreckenberg and Jacobson). The stages of hatching 40 after Schreckenberg and Jacobson and our 41, on the contrary, differ by a very great intervals of time (about $85 \tau_0$!). Because of this the embryo at the stage 40 (after Schreckenberg and Jacobson) is considerably older than the embryo at the stage of the beginning of hatching.

For the period of cleavage and gastrulation our data agree fairly well with the data obtained earlier by Skoblina (1963) at 18° and 22°, and the data of Cate (1956) for 16°, 18°, 22° and 23° recalculated by Skoblina in the number of τ_0 and just so to the date of Valouch et al. (Valouch et al., 1971) for the period of cleavage at 18° - 23°. Beyond these temperatures the ratio τ_1/τ_0 begins to change. In the interval 26° - 28° with the rising of temperature τ_0 at first ceases to shorten and then even lengthens, which is evidence of the

damaging action of these temperatures upon the early stages of cleavage (see Fig. 1). The duration of the later and less sensitive periods of development at these temperatures continues to shorten and as a result of this the values of τ_n/τ_o decrease compared with their values at the optimum temperatures (Dettlaff and Dettlaff, 1961; Skoblina, 1963). At the low temperatures (10° see Cate, 1956), on the contrary, the process of gastrulation lengthens disproportionately and the fusing of neural folds is retarded. Thus, the value τ_o at different temperatures (Fig. 1) and the ratio τ_n/τ_o (Table 1) can be used for the prognostication of the timing of different stages of development only in the middle zone of the optimum temperatures for the development of the axolotl where the duration of different periods of development changes proportionally with the change of temperature. Herewith one should take into account that the variability of the term of transition to the next stage for the different embryos usually constitutes not more than 10% of the total duration of the period.

To compare the duration of the corresponding developmental periods in various species of amphibia it is necessary to determine for each of the compared species the τ_n/τ_o at one of the optimum temperatures for its reproduction. In various species of Acipenser, Rana (Dettlaff and Dettlaff, 1961) and Salmo (Ignatieva, 1974) it was shown that, in the closely related species, the relative duration of the developmental periods of the same name is similar or even identical. It is possible to expect that this holds true for various species of Ambystoma; especially A. mexicanum and A. punctatum. But for the latter, unfortunately we have no data for such a comparison. The comparison of the absolute duration of the developmental periods of the same name in various species of Ambystoma at either temperature (Schreckenber and Jacobson, 1975) can have only a very restricted value, since even in the most closely related species, the limits of favorable temperatures for reproduction do not coincide and as a consequence the relation between the duration of developmental periods of the same name is different at different temperatures.

Actual data
Stages of normal development of *Ambystoma mexicanum*
(incubation at 20°C)

Table I

N of Stages	Time from the cleavage furrow I		Features, size, in mm
	In hours and minutes	In number of τ_0	
1	2	3	4
1			Freshly laid fertilized egg in membranes Egg diameter without membranes - 1.85 - 2.00 mm
1½			Activated egg, a broad perivitellin space formed. D = 2.0
2-	0	0	First appearance of the I cleavage furrow on animal pole. Beginning of time reckoning (picture fails). D = 2.0
2	65	0.72	2 cells. D = 2.0
3	2.40	1.7	4 cells. D = 2.0
4	4.12	2.7	8 cells. D = 2.0
5	5.22	3.5	16 cells. D = 2.0
6	6.45	4.5	32 cells. D = 2.0
7	8.26	5.5	64 cells. D = 2.0
8	16.06	10.5	Early blastula (Fall of mitotic index in animal blastomeres (Rott a. Beritashwili, 1974). D = 2.0
9	21.28	14	Late (epithelial) blastula. The surface is smooth.
9½	24.32	16	Beginning of morphogenetic function of nuclei (Ignatieva, 1972). D = 2.0
10	26.00	17	Early gastrula I. First signs of dorsal blastopore lip formation. D = 2.0
10½	32.10	21	Early gastrula II. Invagination continues. Blastopore is a slit going almost horizontally (one quadrant). D = 2.0
10 3/4	37.00	24	Middle gastrula I. Dorsal lip of blastopore forms a semicircle. D = 2.0

1	2	3	4
11	38.30	25-26	Middle gastrula II. Blastopore is three quadrants of circle. Lateral lips of blastopore formed, ventral lip only marked by pigment accumulation. Yolk plug reaches maximum diameter, $d = 1.2$ mm; $D = 2.0$
11½	40-42	27-28	Late gastrula I. Blastopore forms a circle. Invagination continues, yolk plug decreases, $d = 0.6$ mm; $D = 2.0$
12	47.30	31	Late gastrula II. Blastopore has an oval or circular form. Size of yolk plug: 0.40×0.45 ; $D = 2.0$
12½	49-51	32-34	Late gastrula III. Closing oval blastopore. Size of yolk plug: 0.15×0.20 mm; $D = 2.1$
13-	50.30-54	33-35	Stage of slitlike blastopore. Boundaries of neural plate are still not distinct
13	55-56.30	36-37	Early neurula I. Blastopore is a narrow vertical slit. Groove in the midline of the neural plate. Boundaries of neural plate are outlined but neural folds are not yet elevated above the surface of the embryo. The dorsal side is slightly flattened. $D = 2.1$
14	58.15	38	Early neurula II. Neural plate is broad. Neural folds are outlined and begin to raise above the surface in the head region. Embryo becomes slightly elongated. Length = 2.2; Breadth = 2.0
15	59.50	39	Early neurula III. Neural plate has the shape of a shield. Neural folds are raised and bind all the regions of the neural plate. $L = 2.25$; $B = 2.1$
16	63	41	Middle neurula II. Neural folds become higher, the spinal region of neural plate narrows, the neural plate becomes sunken. $L = 2.25$; $B = 2.1$
17	64.30	42	Late neurula I. Neural folds higher especially in the head region. Further narrowing and deepening of the neural plate both in the head and in the spinal regions. Hyomandibular furrow limiting the mandibular arch is outlined (yet very slightly). The segmentation of mesodermal material begins. 2 pairs of somites formed. $L = 2.35$; $B = 2.0$

1	2	3	4
18	66	43-44	Late neurula II. The neural plate is deeply sunken. Neural folds are developing and are especially high in the head region where three expansions (still yet very slight) corresponding to fore, middle and hind brain vesicles are outlined. The neural folds of spinal region are about to come into contact. Hyomandibular furrow becomes more marked. 2 pairs of somites. L = 2.4; B = 1.9
19	69.00	45	Late neurula III. Neural folds are coming in contact throughout but yet do not fuse. Brain curvature is quite distinct in profile; fore, middle and hind brain vesicles are also distinct. The swelling of optic vesicles are outlined. Hyomandibular furrow becomes deeper. 3 pairs of somites. L = 2.7; B = 1.7; Height = 2.1
20	70.30	46	Late neurula IV. Neural folds fused in spinal region. In brain region they are only in contact. Optic vesicles are distinct and increasing. Grooves in ectoderm appear at the level of the hindbrain. Very slight swelling of the future gill region is faintly marked. Mandibular arch becomes prominent. 4 pairs of somites. L = 2.7; B = 1.5; H = 1.7
21	72	47	Neural folds are completely fused. The hind boundary of gill region becomes more distinct. Pronephros begin to outline (very slight swelling). 4 pairs of somites. The ventral side of embryo is a lightly concave line; the head region (from the level of mandibular arch) is somewhat downwardly curved. The dorsal side is a semicircle; occipital and parietal brain curvatures become apparent.
22	73	48	The gill region and the pronephros are now more distinct. The tail bud is outlined (but still very slightly). 5-6 pairs of somites. The ventral side of the embryo becomes more concave in relation with a greater curving downward of the head. L = 2.8; B = 1.4; H = 2.3
23	74.00	48.5	The primordium of the ear outlined as a shallow depression in ectoderm in the region above the future hyoid arch. In the dorsal region of the gill swelling the hyobranchial furrow appears outlining the boundary between the hyoid arch and the branchial arch I.

- 24 80 52 Ear pit becomes more distinct. The hyobranchial furrow continues to lengthen running to the ventral side. The pronephric swelling is clearly outlined and not only the pronephros itself are well seen but the beginning of the pronephric duct also: 8-9 pairs of somites. L = 3.0; B = 1.35; H = 1.85
- 25 83 54 The gill swelling continues to increase, the hyobranchial furrow lengthens further. The branchial furrow I appears (still faintly outlined) in the dorsal region of the gill swelling. The tail bud continues to be small. 9 pairs of somites. The body of the embryo continues to lengthen, the ventral side becomes more concave, the head protudes more downwardly. L = 3.25; B = 1.45; H = 2.0
- 26 84.30 55 Ear pit is quite distinct. The branchial furrow I becomes more marked and longer. The whole gill region is a considerable, distinctly outlined swelling, the height of which is accentuated by a deep groove formed between the developing pronephros and the gill region. Pronephric duct is seen along 6 somites. The primordium of the olfactory organ appears as a tubercle in the anterior part of the head. The tail bud gradually increases. The body of the embryo is stretched, the head is curved down. 10-11 pairs of somites. L = 3.25; B = 1.45; H = 2.0
- 27 86 56
(54-59) The branchial furrow II appears in the dorsal part of the gill swelling (still very faintly marked). 12 pairs of somites. L = 3.35; B = 1.6; H = 1.85.
- 28 92.30 60
(57-63) Further stretching of the body of embryo. Maximum downward curvature of the head is shown. The olfactory pit is distinctly outlined in front of the eye. 14 pairs of somites. L = 3.55; B = 1.6, H = 1.75
- 29 97 63.5-64 The straightening of the body of embryo begins but that can be seen only by somewhat less curvature of the head. The tail bud increases. 16 pairs of somites. L = 4.2; H = 1.75
- 30 102 67
(65-68) The straightening of the head curvature continues and the dorsal curvature of the body reduces. The body elongates and the tail bud becomes greater. The fin fold appears for the first time. The dorsal fin fold begins on the level of the 14th somite. L = 4.5; H = 1.65

1	2	3	4
31*	109	71 (69-74)	19 pairs of somites. In the region of the lens primordium a groove appears. The branchial furrow III becomes apparent in the dorsal part of the gill region. The dorsal fin fold begins on the level of the 12th somite. L = 4.7; H = 1.7
32	113	74	20 pairs of somites. The dorsal fin begins on the level of 10th somite. L = 5.0; H = 1.7
33*	113	71	21-22 pairs of somites. The dorsal fin begins on the level of the 8th somite. L = 5.25; H = 1.6.
34	115	75	24-25 pairs of somites. The dorsal fin begins on the level of the 7th somite. L = 5.5; H = 1.6
35	122	80	From this stage on the body axis from the hind-brain to the tail base is quite straight. Three external gills show as nodules on the surface of gill swelling. The lateral line reaches to the 6th somite. The dorsal fin begins on the level of the 5th somite. The first chromatophores appear and also heart pulsation begins. The somites are now difficult to count. L = 6.25; H = 1.6
36	130	85-98	External gills have the form of short sprouts directed to the side from the gill swelling. L = 7.1; H = 1.7
37*	177	115	Gills elongate and push ventroposteriorly. The limb buds fail. L = 7.5; H = 1.7
38*	178	114-132	In the gills the filament sprouts appear as nodules, two in each gill. The primordium of operculum becomes visible as a fold upon the hyoid arch. At this stage both rudiments of operculum do not yet reach the midline. The limb buds are still slightly outlined. L = 7.9; H = 1.8
39	220	144	The gill I has 2 pairs of filament sprouts, the gills II and III - 3 pairs. The gills cover the limb buds. Both rudiments of operculum almost approach the midline. The angles of the mouth begin to show. L = 9.0; H = 1.9
40	240	157	The gills become longer and the number of filaments increases: on the gill I are 4 pairs of filaments on the gills II and III - 6-7 pairs of filaments. Both rudiments of operculum join at the midline. The angles of the mouth are marked more distinctly. The limb buds form small tubercles. L = 9.3; H = 2.1

41	265	173-177	The gills continue to elongate. The number of filaments increases; filaments also become longer. The mouth is distinctly outlined. The lateral line 2 runs on the flank toward the limb bud and passes around it on the ventral side. The forelimb buds are still small tubercles. At this stage hatching begins. L = 10.0; H = 2.2
42	296	193	The gills reach far from the level of the forelimb buds. The mouth is completely outlined but is not broken through. L = 10.5; H = 2.1
43	342	223	The breaking through of the mouth or the mouth is already open. L = 11.3; H = 2.3

Comparison of stages of development of embryos of A. punctatum and A. mexicanum in the tables of Harrison (1969), Bordzilovskaya and Dettlaff (1975) and Schrecken- berg and Jacobson (1975)

<u>A. punctatum</u>		<u>A. mexicanum</u>		<u>A. punctatum</u>		<u>A. mexicanum</u>
Harrison	Bordzilovs- kaya, Dettlaff	Schrecken- berg, Jacobson	Harrison	Bordzilovs- kaya, Dettlaff	Schrecken- berg, Jacobson	
1	1	1	19	19	19	
-	2-	-	20	20	20	
2	2	2	21	21	21	
3	3	3	22	22	22	
4	4	4	23	23	23	
5	5	5	24	24	24	
6	6	6	25	25	-	
7	7	7	26	26	-	
8	-	8	27	27	25	
-	8	-	28	28	26	
9?	9/9,5	8+	29	29	27	
10/10-	10	9	-	-	28?	
-	10,5	10	-	-	29?	

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Legends to Figures

Fig. 1. Scheme of measurements.

Fig. 2. Dependence of the duration of one mitotic cycle in the period of synchronous cleavage divisions (τ_0) from the temperature in axolotl (after Skoblina, 1965).

Tables I - VI. Stages of the normal development of axolotl embryos *Ambystoma mexicanum* (drawings of N.P. Bordzilovskaya). Numbers of drawings refer to the corresponding stage numbers. an - animal pole view; veg - vegetal pole view; d - dorsal view; ven - ventral view; t - tail region view. Drawings without designations - embryos viewed from the side.

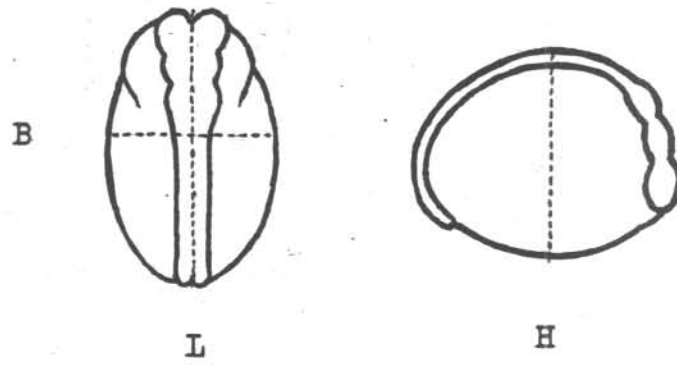


Fig. 1

L - length
 B - breadth
 H- height

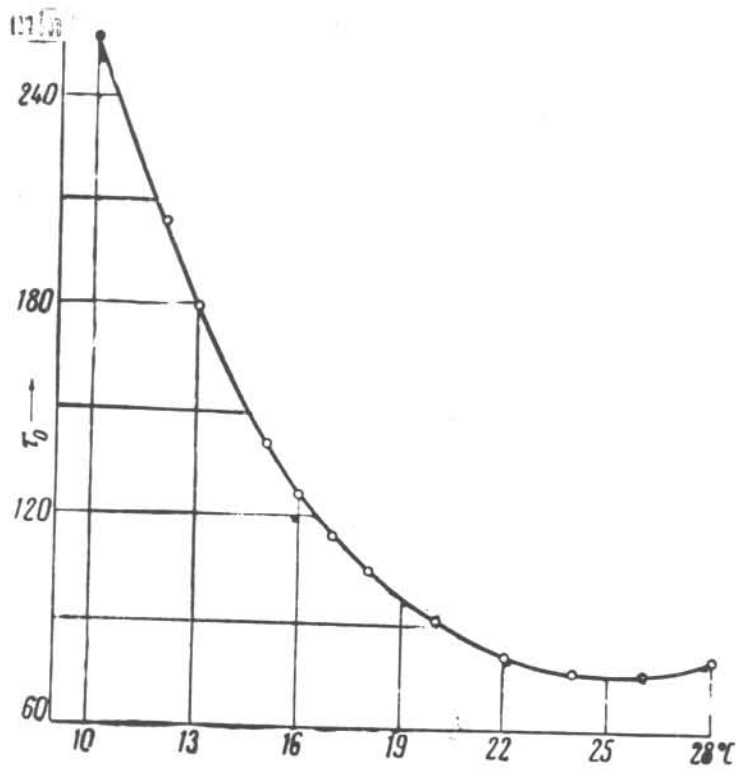


Fig. 2

