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SÉRIE *B*: SCIENCES NATURELLES (II)

CRACOVIE
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1930

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SÉRIE *B*: SCIENCES NATURELLES II

O ruchu i ciśnieniu krwi w tętnicach. — On the blood flow and the blood pressure in arteries.

I. Teoretyczne zbadanie własności kanjuli fotohemotachometru Cybulskiego. — Theoretical examination of the hydrodynamical properties of the tube of Cybulski's photohaemotachometer.

Mémoire

de M. **A. J. KLISIECKI**,

présenté dans la séance du 13. Janvier 1930, par M. A. Beck m. c.

Among the classical methods of blood flow measurement, there is one based on a very simple formula, expressing the velocity of the flow without any error, because the factors of the said formula can be exactly recognised. It is the Cybulski's[1]) method, outlined by Starling[2]).

When I calibrated Cybulski's metal-tubes possessing exactly known diameters, I observed, that the difference in the manometer are caused by some corresponding linear velocities, which are independent of the diameter of the tubes. E. g. the same difference of pressure in the manometer arises during the velocity of 313 mm. p. sec. in the tube of 4 mm. diameter, as in the tubes 3, 2, 1 mm. My attention was thus directed to an investigation of the properties of the Cybulski's tubes.

Every apparatus placed in the path of the fluid diminishes the latter's velocity and causes a change of pressure. Therefore, the velocities registered by such methods as Ludwig's (Stromuhr an dall its modifications), Cybulski's, Chauveau's etc. are not real. There must be made a difference between the velocity V_1

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[1]) N. Cybulski, Pflüg. Arch. XXXVII, 1885.
[2]) E. H. Starling, Principles of Human Physiology 1920, p. 933.
» — C. L. Evans » » » 1930, p. 772.

in a vessel under natural conditions (i. e. straight direction of the flow and the pressure depending only on the heart's work and peripheral resistance) and the diminished, secondary velocity V_2, appearing after the insertion of the apparatus, which changes the direction of the flow and the pressure in the examined place. The difference between V_1 and V_2 depend on the construction of the apparatus. E. g. the Stromuhr introduced into the rubber-tube in which water flows, in my experiments, changes the fall of pressure in it and the velocity in the following way:

Pressure before Stromuhr, mm. H_2O	Pressure behind Stromuhr, mm. H_2O	Velocity $\frac{Q}{r^2\pi}$
222	56	517 mm. p. sec. (V_2)

after removal of the Stromuhr the fall of pressure diminishes and the velocity increases

168	95	791 mm. p. sec. (V_1)

The Stromuhr more than doubles the fall of pressure. The ratio $\frac{V_1^2}{V_2^2} = \varrho$(canst) amounts to 2,4—3. I take into consideration the squares of the velocities, for V grows as the squares of numbers, which is peculiar to all angular bents. The factor ϱ cannot be determined exactly, because the loss of velocity is changeable, being dependent on the vortices evolved in every sudden enlargement and contraction of the fluid stream. If we multiplied V_2^2 by the factor ϱ we could calculate the V_1. This factor belongs to the original Stromuhr of the capacity of 29 cm. cubes, at the time when the water flows. The Stromuhr of another capacity and type (such as that of Huerthle, Tigerstedt, etc.) possesses, of course, another factor. By measuring the velocity of the blood instead of water, we shall naturally get a greater ϱ. Hence every type of Stromuhr has to be calibrated in order to find ϱ, by means of which as was explained we can calculate V_1. But this correction nevertheless was not taken into account.

The tube of Cybulski diminishes also the velocity, but as my experiments have shown, 1⁰ its loss is constant, 2⁰ and this loss is observable in the differential manometer as will be explained latter on; therefore we are able to determine directy, by means of a simple formula, the primary velocity V_1 without any calibration and without any factor.

The method of my investigations of the properties of this tube was as follows: By observing the pressures in the opened manometers RR_1 (fig. 1) inserted between the tube and the arms of the differential manometer, and the manometer M_1 immediately behind the tube, I investigated the properties of the differential manometer; then I examined the relation of pressures in the arm R and manometer M_0; afterwards I measured the resistance of the right angle $y = M_0 - R_1$; lastly the influence of this resistance on the primary velocity and pressure, which enabled me to come to the solution of the question.

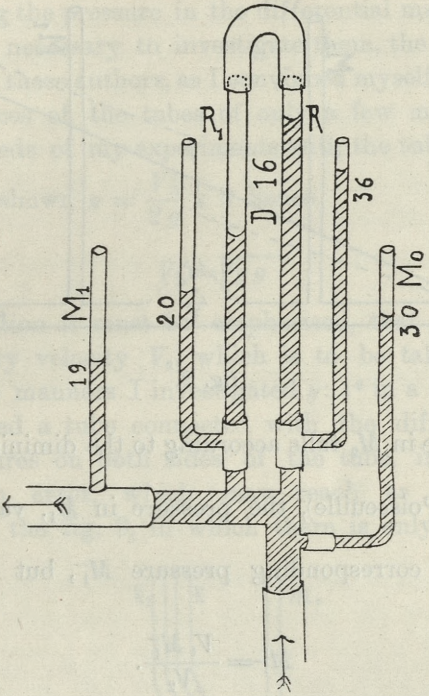

fig. 1.

A tube bent in a right angle, inserted into a rubber-tube of the same cross-section, causes a distinct local fall of pressure of the running water, for a distance of a few mm. and diminishes the primary velocity V_1, existing before insertion of the tube, to V_2:

$$V_1^2 = V_2^2\left(\frac{V_1}{V_2}\right)^2 ; \qquad V_2^2 = V_1^2\left(\frac{V_2}{V_1}\right)^2 \qquad 1)$$

Such is the influence of the right angle tube on the flow. The line of pressure fall (a) is changed by this tube in such a manner (b) as shows fig. 2.

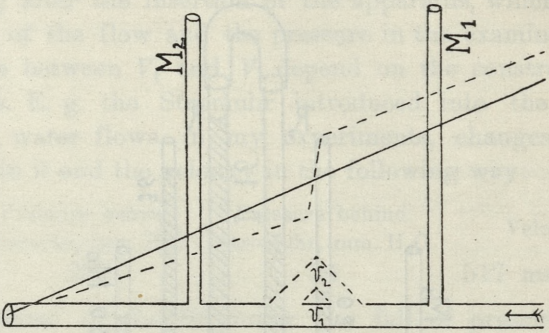

fig. 2.

The pressure in M_2 falls according to the diminished velocity V_2; $M_2^{\llcorner} = V_2 \frac{l}{r^2} k$ (Poisseuille), the pressure in M_1, varies directly as V_1 and as the corresponding pressure M_1^{-}, but varies inversely as V_2.

$$M_1^{\llcorner} = \frac{V_1 M_1^{-}}{V_2}. \quad (2)$$

E. g.	pressure in the manom. M_1		velocity mm. p. sec.
	before insertion of the tube	52 mm. H_2O	V 490
	after » » »	63 »	406

$$63 = \frac{490 \times 52}{406} = 62,7$$

$M^{\llcorner}$ pressure after the insertion of the tube
M^{-} » before » »

By means of the formulas 1), 2) we can calculate the real pressure M_1^{-}.

The resistance of the right angle-tube (y), was investigated by Weisbach, Montanari, Brightmores. According to Weisbach $y = \frac{V_2}{2g} \times 0,984$ for a tube with a diameter of 3 cm. (0,984 factor z); Montanari found $z = 1,536$ in the tubes of

1—4 cm. diameter; Brightmores for 7,6—10,2 cm. diameter $\mathfrak{z} = 1,17$. As the resistances of the tubes with diameters of a few mm. were not investigated, and as they play the most important part in producing the pressure in the differential manometer of Cybulski it was necessary to investigate them, the more so, as the factors found by these authors, as I convinced myself are not suitable for the resistances of the tubes of only a few mm. in diameter.

Some hundreds of my experiments with the tubes of 1—5 mm. diameter have shown $y = \frac{V_2^2}{2g} \times 2$ hence

$$V_2 = \sqrt{yg} \qquad (3).$$

In this equation it must be emphasised, that it is the diminished, secondary velocity V_2, which is to be taken into consideration. In two manners I investigated y: 1⁰ in a straight rubber-tube was inserted a tube connected with the differential manometer; the flexures on both sides of the tube, in this arrangement, cause an error, which may reach as much as 5⁰/₀. 2⁰ according to the fig. 3, in which there is only a right angle; this way is exact. The difference between the V_2 theoretically calculated by the formula 3 and practically estimated (by dividing the amount of the outflow by the cross-section) doesn't reach 1⁰/₀. The resistance y I read from the difference of mm. H_2O pressure in the manometer M_0 - R_1 (fig. 1).

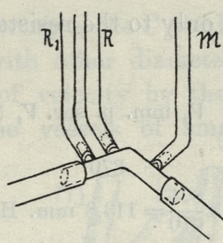

fig. 3.

E.g. y (M_0—R_1) mm. H_2O.	Q cm. cub. 30 sec.	$\frac{Q}{r^2\pi}$ mm. p. sec.	$V_2 = \sqrt{y \times g}$ mm. p. sec.
11	140	329	$\sqrt{11 \times 9812} = 328$
44		660	$\sqrt{44 \times 9812} = 657$
60		764	$\sqrt{60 \times 9812} = 767$

But if we close the manometer R (fig. 1, 3), the difference $M_0 - R_1$ in the same moment increases and becomes equal to the difference $R - R_1$, which is always greater than y. In the point of the tube attached to the manometer R becomes apparent an energy, which raises the pressure in this manometer above the pressure in M_0. In the case of clamping the R or using the tube to which can be attached only two manometers i. e. M_0 and R_1, this energy appears at the point M_0 and so increases the y. In order to measure exactly the y, we must, therefore, use the tubes with three manometers as in fig. 3.

What is the cause of the greater pressure in R as compared with the pressure in M_0? Comparison of the V_1 with V_2 shows, that the loss of the velocity of water, the stream of which is bent in a right angle, is constant, and the ratio $\frac{V_1}{V_2} = 1{,}2$ (factor μ). Thus the pressure in

$$R = V_2 \frac{l}{r^2} k + 2 \frac{V_2^2}{2g} \times \frac{V_1}{V_2}. \tag{4}$$

The pressure in R_1 is due only to the resistance $V_2 \frac{l}{r^2} k$ (Poisseille).

E. g. the pressure in manom.			V_2 mm. p. sec.	V_1 (after removal of the tube)
R	R_1	$M_0 - R_1$ (y)		
115	49	43	670	804

$$115 = 49 + 43 \frac{804}{670} = 113{,}8 \text{ mm. } H_2O.$$

In the point R is marked a change of a part of the kinetic energy into a static form, due to the loss of the velocity V_1. The pressure in R increases in direct ratio to $\frac{V_1}{V_2}$.

But the difference D in the Cybulski's differential manometer i. e. $R - R_1$ (fig. 1) is in such a relation to the velocity as the squares of numbers. It consists of y and μ^2 i. e. $\frac{V_1^2}{V_2^2} = 1{,}45$.

$$D = y \times \mu^2 = 2 \frac{V_2^2}{2g} \times \left(\frac{V_1}{V_2}\right)^2 = \frac{V_1^2}{g}. \tag{5}$$

Since this formula contains V_1^2, we are able to calculate the primary velocity in the vessel with the help of

$$V_1 = \sqrt{D \times g} \qquad (6).$$

nearly without errors, for D, in the physiological limits of the blood velocity, is 1 — 100 mm. long. By using this latter formula (6) the investigation of the blood circulation is much facilitated, for 1⁰ the calibration of the tubes, causing of course some errors, is unnecessary; 2⁰ the correction V_2 to V_1 is needless too.

The comparison of the primary velocity of the water according to $\frac{Q}{r^2\pi}$ with that according to $V_1 = \sqrt{R.g}$, shows an exact agreement:

E. g. The difference of the differ. manometer, mm. H_2O	$V_1 = \sqrt{R.g}$ mm. p. sec.	Outflow of water after removal of the Cybulski's tube cm. cub. (30 sec. Q_1).	$\frac{Q_1}{r^2\pi} = V_1$ mm. p. sec.
60	$\sqrt{60.9812} = 767$	166	762
29	$\sqrt{29.9812} = 533$	152	524
16	$\sqrt{16.9812} = 396$	400	396

This in an example referring to the Cybulski's tube with a diameter of 4,3 mm. In tubes with other diameters the result is the same.

The measurement of velocity by the help of the Cybulski's tubes especially in the vessels of small diameter (1—2) is not exact, because of flexures of the vessels on both sides of the tubes. In order to avoid this error (5%) I made a tube with two right angles (fig. 4). The ends aa are introduced into the vessel, mm are attached to the differential manometer, bb serve to the filling of the apparatus and measuring of pressure.

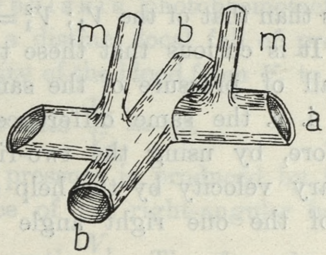

fig. 4.

The two-right-angle tubes cause a greater loss of the velocity of the fluid and they produce a more considerable local fall of pressure, than those with one angle. Fig. 5 shows the fall of pressures in one-right-angle tube and in a two-right-angle tube of the same bore.

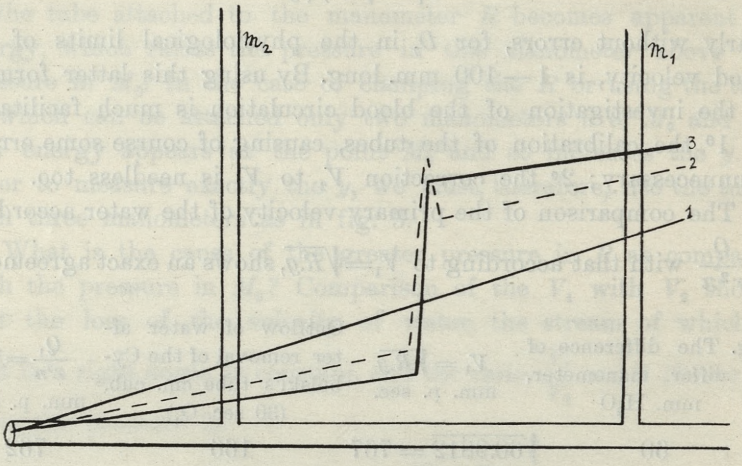

fig. 5.

1) the fall of pressure in a straight rubber-tube; 2) in the same rubber-tube after the insertion of one-right-angle tube; 3) after the insertion of two-right-angle tube.

The velocity in two-right-angle tube is marked as V_3; its square is twice less than that of the V_1; $V_1^2 = V_3^2 \times 2{,}1$; the factor 2,1 is μ^3, i. e. $1{,}2^3$. It is curious that these two-right-angle tubes produce a local fall of pressure of the same magnitude as the Cybulski's tube, i. e. the same difference in the differential manometer. Therefore, by using the two-right-angle tubes, we calculate the primary velocity by the help of the same formula as in the cause of the one right angle tube of Cybulski, $V_1 = \sqrt{D.g.}$

E. g. Two-right-angle tube ϕ 2,2 mm. D mm H_2O.	V_1 mm. p. sec.	Q cm. cub. 30 sec.	After removal of the tube, Q cm. cub. (30 sec.)	$\frac{Q_1}{r^2\pi} = V_1$ mm. p. sec.
30	$\sqrt{30.9812} = 543$	44 (Q_3)	62 (Q_1)	543
50	$\sqrt{50.9812} = 701$		80	700
82	$\sqrt{82.9812} = 897$	72	104	921

With reference to the increased pressure at the point before the two-right-angle tube, the squares of the pressures in the manometer M_1 before and after introducing the tube, are in an inverse ratio to the squares of the corresponding velocities:

$$\frac{M_1^{2\llcorner}}{M_1^{2-}} = \left(\frac{V_1}{V_3}\right)^2 \qquad (7).$$

With the help of this formula we can calculate the primary pressure at a point of the vessel, if we attach a manometer to the tube showing the primary velocity. This fact is important and very useful for the haemodynamic investigations as we see later.

In all these experiments I used water as a fluid. During the measurement of the velocity of the fluid, the viscosity of which is greater than that of water (e. g. blood) it is necessary to consider its relative viscosity. Generally, the formula for calculating the linear velocity of the fluid is

$$\text{Primary velocity} =$$
$$= \sqrt{\text{Difference in the differ. manom.} \times \text{gravity} \times \text{viscosity}}.$$

Conclusions.

The tube of Cybulski's photohaemotachometer introduced into a vessel causes a distinct local fall of pressure and diminishes the primary velocity of the blood from V_1 to the secondary velocity V_2 in a constant ratio $\frac{V_1}{V_2} = 1{,}2$.

The local fall of pressure is produced by two factors. One of them is the resistance of the right-angular bending of the tube (y), the second one the ratio $\frac{V_1}{V_2}$. The formula expressing the y possesses other factors than those found by other investigators (formula 3), therefore the difference of pressure in the differential manometer of Cybulski $D = \frac{V_1^2}{g}$.

Since the V_1 is expressed in D there is no need to calibrate the Cybulski's photohaemotachometer if we wish to determine the velocity of the blood in absolute measure. One has only to measure the difference of pressure in a graphic record and calculate $V_1 = \sqrt{D \times g}$; e. g. if $D = 10$ mm. then $V_1 = 313$ mm. p. sec.

In order to avoid the errors caused by twists of the vessel connected with the one-right-angle tube of Cybulski, I used a two-right-angle tube (fig. 4), the V_1 in which is to be determined in the same manner as in the former tube.

O ruchu i ciśnieniu krwi w tętnicach. — On the blood flow and the blood pressure in arteries.

II. Ruch krwi w aorcie. — The flow of blood in the aorta.

Mémoire

de M. ***A. J. KLISIECKI,***

présenté dans la séance du 13. Janvier 1930, par M. A. Beck m. c.

Our knowledge, regarding the movement of blood in this part of the vascular circuit which is inaccessible to the direct observation such as the capillary system, is scarce and inaccurate. The experiments of Nicolls[1]), based on the calculation of velocity from the difference (D) between the dynamic and static pressure by the formula $V = \sqrt{D \times g}$, have shown that the diastolic D in the aorta of a dog, was that of 12 mm. i. e. the velocity 346 mm. p. sec., and the pulse pressure had 9 mm. i. e. the systolic acceleration was 108 mm. p. sec. H. Elving and G. Wendt[2]) in the aorta abdominalis of the rabbit, found the amount of 43—16 and 35—13 cm. cub. passing p. minute and 1 kg. of weight of the lower part of rabbit trunk. Such a large variation of the blood flow in the latter investigations can't be admitted to be true in natural conditions; these changes were caused by the Tigerstedt's Stromuhr and clotting of the blood. As the flow of the fluid is, evidently, in some relation with the pressure, so in the vascular system generally there is parallelism between the velocity and blood pressure. The blood pressure shows three kinds of undulations systolic waves (I-order), respiratory waves (II-order) and Mayer's waves (III-order). We don't know what is the real relationship between the velocity of the blood and its pressure, especially if there are in the movement of the

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[1]) Journ. of Physiol. 1897. 20. p. 418.

[2]) Skand. Arch. f. Physiol. 1907, XIX, p. 119.

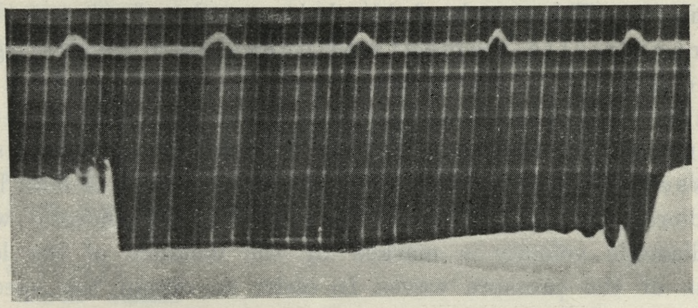
blood waves corresponding to those in the aortic pressure. My experiments had the object of explaining these and similar questions.

After incision in the mid-line of the abdomen of a narcotised dog, I prepared the lower part of the aorta abdominalis, and measured its external diameter with a calliper, then I tightened it by this instrument till the pulse below this place ceased beating, and I measured the thickness of the aortic wall. The difference showed the internal diameter. I tied the aorta and squeezed it with serre-fines on both sides 2 cm. far from the ligature. After the incision of the aortic wall I inserted the end »*a*« (see I. fig. 4) of the two-right-angle tube and filled it with Ringer-fluid. Then I cut the vessel between the ligature and the inserted end of the tube, and in the same manner I introduced the second end »*a*« of the tube. The cannulae »*mm*« of the tube were attached to the open differential manometer placed in front of the photographic camera of Cybulski. Finally I filled up the manometer with Ringer-fluid to a certain level and closed the manometer. In order to avoid the clotting of the blood I injected hirudin. The dog was placed closely under the manometer, so that it was connected immediately with the two right-angle tube, or exceptionally by a very short lead-tube or thick rubber-tube. In the experiments of Cybulski the dogs were placed 0·5—1 m. far from the manometer and therefore the changes of blood pressure which occurred in the tube, were not exact. The utmost shortening of the connection of the tube with the differential manometer, produces another aspect than that in Cybulski's photograms.

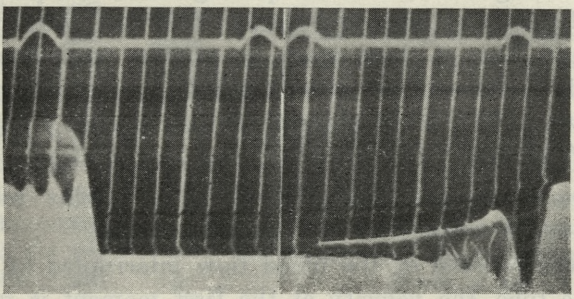
The diameters of the two-right-angle tubes used in my experiments were of 0·3—0·6 cm and their M_1 (»wirksame Masse«) 45—75. Glass-tubes of the differential-manometer were of 0·3 cm. bore; they were filled up with Ringer-fluid to a level of 20—25 cm. The M_1 of one glass-tube of the manometer connected with the t. r. a. tube (as used for measurement of blood-pressure), varied in the limits 330—440; the arrangement for measuring of blood-motion had a M_1 of 611—783. The period of vibration (Schwingungsdauer) T, investigated in a manner described by O. Frank (Tigerstedt, R. Hdb. d. physiol. Methodik 1913) is as follows:

the different.-manom. connected with a t. r. a. tube of 0·6 cm. bore 37—48/sec.
» » » » » » » 0·3 » » 24—40/sec.

The vibrations were produced under the pressure 110—150 mm. Hg. (fig. 1 a, b).



1 a. Period of vibration (figure of merit) of the **Cybulski**'s differential-manometer attached to the two-right-angle tube of 0·3 cm. bore: 25—47/sec.



1 b. Period of vibration of the same manometer with the t. r. a. tube of 0·6 cm. bore: 45/sec. 110—150 mm. Hg. of pressure. Horizontal line time in 0·2 sec., vertical lines time registered by the Gartens wheel.

The assertion of O. **Frank**, that the differential manometer of **Cybulski** is not suitable for measurement of blood movement in arteries, cannot be accepted.

I calculated the velocity from the difference of the levels in the differential manometer, marked on the photogram with the white upper and lower lines (see fig. 3 b of the velocity and pressure in the a. saphena, enclosed in the part IV of this paper). A glance at the photogram convinces us, that the waving of the upper and lower lines has the same character, and is similar to the pulse pressure line marked by an elastic manometer. Almost at the same time both levels rise in consequence of the growth of the pressure during the systole, afterwards fall, according to the ebb of the blood to the capillary vessels; during the fall of pressure in the manometer is manifested a dicrotic wave. and then there is a farther fall of pressure during the further period of diastole. The speed of blood in each of those three characteristic moments of pressure, possessing the same aspect in both arms of the differential manometer, is expressed by the distance of both levels. Therefore the velocity in the time of systole is expressed by the distance of the tops of waves of both levels, the dicrotic velocity by the distance of the two dicrotic waves, the diastolic velocity is marked by the distance of the lowest points of the pressure waves. In order to obtain the speed in mm. p. sec. it is necessary to measure the distance of both levels at some definite moment, (to take into consideration the possible decrease or magnification of the photogram in the photo-camera) and to calculate the primary velocity, i. e. that, with which the blood would flow if there were no angular resistances of the tube which measures the speed, according to the experimental formula $V_1 = \sqrt{D \times g}$ (D distance of both levels, g gravity).

E. g. if the length of both levels during systole amounts to 20 mm., the V_1 in this moment is 443 mm. In this way we get the mean speed, average of the axial movement.

After the renewal of the blood flow interrupted by the insertion of the tube, the velocity at the first moment is very great, reaching sometimes 1200 mm. p. sec.; then it decreases and becomes stabilized. The initial velocity after the renewal of blood flow in the aorta is always considerably greater than the latter owing to the anemia of extremities, and lasts till the flow in the extremities returns to its usual state.

It is known that between the abdominal aorta and the vessels of the extremities there exist numerous collateral arteries. It was proved that after the ligation and cutting of the aorta just above the a. iliacae, the paralysis of the hind limbs within two days or so entirely disappeared, and sometimes even no paralysis was observed, only a weakness lasting a few days. On the other hand the ligation of the end of abdominal aorta and of its seven lateral branches situated above this place and among them of the two arteries supplying the muscles of the thigh, caused a complete paralysis of hind extremities. The tying of the aorta above the renal caused death in 2—36 hours [1]).

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[1]) Coenen- Wiewiorowsky, Beitr. z. klin. Chirurgie 1911, LXXV, 325.

During the insertion of the tube into the abdominal aorta the blood flow towards extremities is entirely arrested, as one must for some time close the aorta on the length of several cm., and that is why the initial speed in the aorta exceeds so distinctly the speed which follows after some minutes.

Experiments.

1) Dog 8 kg. weight, narcotized by morphium-ether; in the aorta abdom. tube 3,5 mm. bore was introduced. Pulse-rate 180, respirat. 22.

velocity:

systol.	dicrot.	diastol.	respir. wave
464	490	454	1.
464	**500**	**484**	
480	524	480	
495	533	490	
495	528	485	
490	515	475	
478	512	461	
475	495	459	
464	495	454	
475	505	464	3.
475	**519**	**480**	
519	542	500	
528	542	500	
524	533	495	
495	524	480	
490	519	485	
480	510	470	
	etc.		

The average diastolic veloc. 493 mm. p. sek.
systolic acceler. 22 «
dicrotic « 35 «

The linear velocity of blood stream is quickest in the time of dicrotic wave, according to that the amounts of blood passing the cross-section of the aorta in time unit are the greatest in this moment of heart's-period.

The respiratory linear waves are placed on the longer waves (III-oder) which change the movement in this experiment at about 50 mm. p. sec.

The explanation of the fact the that diastolic movement is greater than the systolic one in some heart's-periods of respiratory waves (fat print) we shall find in the experimen 8.

2) 12. IV. 1925. Dog 4,5 kg. weight, narcotized by veronal-natrium. Aorta abdomin. 3 mm. bore. Pulse-rate 96, respiration 16.

velocity:

systol.	dicrot.	diastol.	respir. wave
331	348	276	5.
357	384	305	
378	392	313	
377	384	297	
355	363	287	
333	339	275	

In the respiratory wave 9 which is the top of III-order wave the velocity is greater to 100 mm. p. sec. On the fig. 2 is

377	399	313	7.
406	423	349	
409	420	331	
392	411	320	
399	418	331	
392	411	320	
426	432	355	9.
426	432	363	
432	443	406	
467	475	398	
467	467	384	
432	443	362	
426	437	362	

The average diastolic velocity is 341 mm. p. sec.
systolic acceler. 48 «
dicrotic « 66 «

graphically shown the behaviour of I-, II-, and III-order waving of the bloodstream.

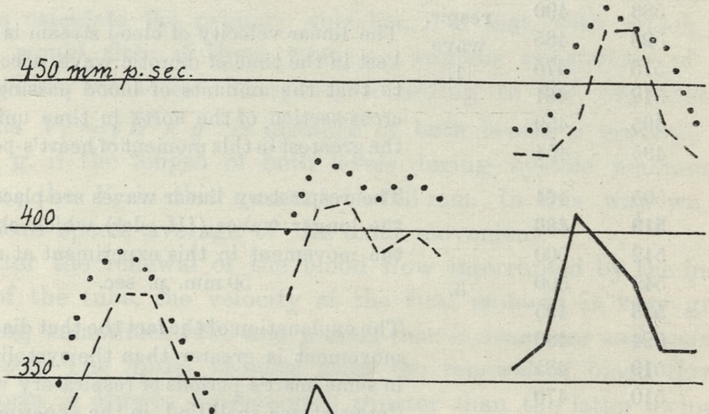

fig. 2.

Continous line: diastolic velocity.
Dashed « : systolic acceleration.
Dotted « . dicrotic acceleration.

3) 16. VI. 1925. Dog 7,2 kg. weight, narcotized by veronal-natrium. Pulse-rate 102. Aorta abdom. of 3,5 mm. bore.

The average diastolic velocity 431 mm. (4,13 cub. cm./sek.)
systolic acceleration 37 «
dicrotic acceleration 180 «

4) 19. VI. 1925. Dog 9 kg. weight, narcot. by veron.-natr. and ether. Aorta abdom. of 4 mm. bore.

The initial speed of the blood overreaches 1 m. p. sec. After a minute

velocity:

systol.	dicrot.	diastol.	
741	748	741	passive extension and flexion of the hind limbs cause immediately a distinct augmentation of motion.
757	757	741	
754	760	741	
754	760	748	
760	760	748	
760	770	754	
767	774	760	

in the 14th heart's-period

systol.	dicrot.	diastol.	
813	828	810	
831	860	851	
866	877	869	the growth of velocity belongs at first to the diastolic and dicrotic values, therefore the systolic motion becomes smaller or equal to diastolic one; it proves that the peripheral resistance is diminishing.
885	891	872	
880	896	880	
899	913	902	
910	914	891	
896	914	905	
918	929	918	
929	926	929	from this heart's-period commences a fall of velocity, and the systolic motion begins to be quicker than the diastolic one.
931	910	894	
896	908	891	
899	908	894	
896	896	877	
880	885	863	
869	864	846	
846	840	820	

in 87th second the movement was such:

systol.	dicrot.	diastol.
475	485	454

second passive movement of hind limbs accelerates the motion in 16 heart's-periods:

systol.	dicrot.	diastol.
792	804	783 mm. p. sec.

The average diastolic velocity in this experiment 531 mm. p. sec.
systolic acceleration 20 «
dicrotic « 30 «

5) 6. VII. 1925. Dog 9,5 kg. weight, narcot. by veron.-natr. and ether. The bore of aorta abdomin. 3,5 mm.

The diastolic velocity 591 mm. p. sec.
systolic acceleration 30 «

6) 6. VII. 1925. Dog 10 kg. weight, narcot. as above. Bore of a. abdomin. 4 mm.

The diastolic velocity 606 mm. p. sec.
systolic acceler. 33 «

7) I. IX. 1926. Dog 7 kg. narcot. by veronal-natr. Bore of a. abdom 3,5 mm.

The diastolic velocity 478
systolic acceler. 42
dicrot. « 82

8) 25. IX. 1926. Dog 12 kg. weight, narcotized by ether. Aorta abdom. of 4,2 mm. bore.

velocity:

systol.	dicrot.	diastol.	
485	533	**515**	respir. vave 1.
560	748	**907**	
672	774	**718**	
649	728	**657**	
626	693	618	
551	577	495	
460	536	**515**	2.
564	724	**672**	
653	754	**688**	
649	741	**686**	
642	693	610	
542	560	492	
464	560	551	
586	649	**618**	16.
626	792	**741**	
780	840	776	
760	834	767	
741	810	738	
679	721	630	
586	642	602	

The respiratory waves are very deep. In the commencement of resp. waves the diastolic motion is greater than the systolic, which happens if the peripheral resistance distinctly decreases. The decrease of peripheral resistance is caused by the distention of arteries by the rising blood-pressure after each inspiration; after cessation of distention the systolic motion is greater than the diastolic; it occurs at the end of respiratory waves.

The average diastolic velocity 646 mm. p. sec.
« systolic motion is less 20 « than the diastolic
« dicrotic acceleration 56 « p. sec.

9) 4. X. 1926. Dog 26 kg. weight, narcot. by ether, bore of aorta abdomin. 6 mm.

The diastolic velocity 546 mm. p. sec.
systolic acceler. 30 «

10) 12. XII. 1926. Dog 20 kg. weight, narcot. by veronal-natrium, bore of aorta abdominalis 4,5 mm.

velocity:

systol.	dicrot.	diastol
454	485	445
460		475
454		480
464		485
470		490
500		
	520	515 in the 3 rd. sec.
610		594 in the 7 th. sec.

After one passive movement of hind limbs the motion increases in this manner as in the 4 th experiment, i. e. the diastolic movement is greater than the systolic up ot this moment when the motion begins to stabilize or to diminish. The pulse-rate was constant all the time of observation, it was 132.

The average diastolic velocity 445 mm. p. sec.
systolic acceler. 10 «
dicrotic « 40 «

11) 14. XII. 1926. Dog 8 kg. weight, narcot. as above, bore of aorta abdom. 3,5 mm. Pulse-rate 228—234; the respiratory-waves and dicrotic acceleration are absent.

The diastolic velocity 432 mm. p. sec.
systolic acceler. 20 «

12) 15. XII. 1926. Dog 8,5 kg. weight, narcot. by morphium-scopolamin; pulse-rate 180; bore of aorta abdomin. 4 mm.

The diastolic velocity 245 mm. p. sec.
systolic acceler. 40 «
dicrotic « 30 «

13) 16. XII. 1926. Dog 20 kg. weight, narcot. by morphium and ether. Bore of aorta abdom. 5,6 mm.

The diastolic velocity 640 mm. p. sec.
systolic acceler. 54 «
dicrotic « 100 «

As one may see from the experiments as to blood-motion there are in the aorta the same changes of its movement as in the blood-pressure: heart's-waves (I-order), respiratory waves (II-order), and III-oder.

1) The systolic acceleration of the heart's-waves rapidly increases to its maximum in this moment when the amount of blood thrown out by the heart makes its appear in the examined part of the aorta, and as it ebbs away, the velocity gradually diminishes. After systole dicrotic acceleration appears at the same moment as appears the dicrotic wave in pulse-pressure. The pressure and speed gradually diminish as the heart continues its diastole and the blood constantly ebbs to the tissues. The lowest pressure and smallest speed are at the end of the diastole i. e. just before the next systole. The dicrotic acceleration causes that in spite of one heart-beat in each heart-period, there are two influxes of the blood to the arteries, and in the time of dicrotic waves usually even more blood flows through the cross-section, than during the systole. That is the expression of the work of the maintenance of circulation between the heart and aorta, relatively the whole pulsating vascular system, through which an equal and constant blood-current in the tissues is maintained. As a rule usually the smallest velocity of blood is at the end of diastole, the greater during the systole, the greatest during the dicrotic wave. Similar to the blood-pressure tracings, it happens that this regular character of heart-velocity waves is changed by the sudden decrease or increase of the amplitude of accelerations, or disappears or increases the dicrotic acceleration; — as well as in the linear velocity waves are deviations from this most generally met type. This usual type is connected with a certain blood pressure. If the pressure exceeds a certain limit, the amplitude of linear velocity waves diminishes, and instead of a normally considerable systolic acceleration there are small speed-oscillations; during a great fall of pressure caused by the relaxation of the vessels the amplitude grows, the systolic accelerations become very considerable in relation to the small diastolic velocity, as the blood in a shorter time and in greater quantities than before, ebbs to the capillaries. As the dicrotic wave and its position on the pulse wave depend on blood-pressure, so the dicrotic acceleration changes its place and size with the changing of blood pressure. In a low pressure, caused by dilatation of vessels the dicrotic wave and its acceleration are to be found lower than usually, nearer to the

end of the diastolic part of the pulse wave, because the ebb of the blood is quicker and facilitated; in this case the dicrotic acceleration is smaller than the systolic. When the ebb of the blood to capillaries is more difficult, the dicrotic wave is to be found higher than in normal conditions; its acceleration is greater than the systolic one. If the blood pressure falls below the normal level necessary for the presence of dicrotic wave, the latter one and its acceleration of blood movement disappear. So in general outlines according to photograms, the principles of the quality of the dicrotic acceleration manifest themselves.

The average diastolic speed of the blood in the aorta is 500 mm. p. sec. (in limits 245—640). The average systolic acceleration 45 mm. p. sec. (9—132), the dicrotic one 71 mm. p. sec. (26—180).

The velocity, expressed by the distance of the lowest points of the upper and lower pulse tracings, I considered as diastolic velocity. This velocity should be however calculated as a mean velocity from the distances of several points on the whole part of tracings which follows the dicrotic wave. Similarly I calculated the systolic and dicrotic acceleration. But the mean values are not so important as it would seem, because the velocity is not constant, but changing in great limits, showing the II^{d} and IIIrd- order velocity waves. E. g. The extreme systolic acceleration expressed by the manometric difference in the top of pulse wave is 510 mm. p. sec. (exp. 16) and the mean systolic acceleration 495 mm. p. sec.; the diastolic velocity 480 mm. p. sec. Thus the systolic acceleration is only 15 by this calculation instead of 30 mm. The numbers of the mean dicrotic acceleration would be a little smaller, because of the shorter time of the duration of the dicrotic wave and not such a steep fall. Of course the mean dicrotic acceleration would be also by this calculation greater than the systolic, as usually happens. The described changes of pulse velocity were noticed in the metal tube. But if we would take into account the pulse changes of the cross-section of the aorta and greater arteries, we should find almost a steady linear stream of blood, with minute small linear systolic and dicrotic accelerations, or even in some conditions without them.

2) The linear blood velocity waves of the II-order are caused by and dependent upon respiratory movements of the chest. Their size and persistence depend on the frequency of chest-movements. They don't appear during very frequent respiration. They are also missing if the action of heart exceeds a certain maximal limit, since the heart cannot, owing to highly shortened duration of diastole, be

filled enough. The inspiratory acceleration is simultaneous with the inspiratory growth of pressure and similarly to it appears later than the inspiration. In my experiments, on the top of the respiratory-waves the velocity augmented thus: the diastolic velocity 40—180, systolic acceleration 40—180, dicrotic acceleration 33—196 mm. p. sec.

3) The III-order velocity-waves comprise 3—9 respiratory waves. On the top of these waves there is a general acceleration of velocity of 50—100 mm. p. sec. The investigation of the cause of this phenomenon requires special experiments, as one has, besides the velocity, to measure the pressure as well.

These experiments confirm, that the linear blood velocity in the metal tube inserted into the aorta, is subject to the same changes as blood pressure. This velocity performs heart's oscillations, respiratory, and III-order oscillations. The blood-waves after systole do not show such a sharp decrease as it is stated again by some investigators, but on the contrary after the systole, i. e. at the time of dicrotic wave, the movement is the quickest.

Conclusions.

In the abdominal aorta of a dog the velocity of blood in the diastole amounts to 500 mm. per second (250—640), in the systole it undergoes an acceleration of 45 mm. per second (9 130), and at the time of the dicrotic wave of pulse-pressure it becomes 70 mm. per second quicker than in diastole. Hence through the cross-section of the abdominal aorta there flows in the dicrotic period in 24 hours 10—120 litres more of blood than in the systolic period. If for any reason the pulsation of the aorta and other big arteries is getting worse, the dicrotic acceleration is also smaller and the heart is much more burdened in supplying the tissues with any required amounts of blood. The dicrotic acceleration as well as the dicrotic wave of pulse-pressure is one of the characteristic signs of the movement of liquids in elastic tubes. The dicrotic acceleration protracting the influx of the liquid, contributes to the uniform outflow. The dicrotic acceleration and dicrotic wave of pulse-pressure are present, of course, also in a rubber-tube suitable in conditions.

Besides these heart waves (first-order waves) there exist in the aorta respiratory waves (second-order), which cause an oscillation of 50 mm. per second. They are synchronous with these of blood-pressure respiratory waves. Also the third-order waves are present in the motion of blood, containing 3—9 respiratory waves. They change the movement periodically to 100 mm. per second.

O ruchu i ciśnieniu krwi w tętnicach. — On the blood flow and the blood pressure in arteries.

III. Ruch krwi w dużych tętnicach. — The blood flow in the big arteries.

Mémoire

de M. ***A. J. KLISIECKI***,

presenté dans la séance du 13. Janvier 1930, par M. A. Beck m. c.

The former measurements of blood flow do not enlighten us as to the relation of the flow in the aorta to that in its branches, because there were not investigated in this regard the aorta and arteries in the same animal. It seemed also necessary to investigate the arteries by the help of such modified method of Cybulski in order to compare the results with those of the former investigators.

Dogiel measured the blood flow with the Ludwigs Stromuhr in the carotid artery and femoral artery simultaneously and found in two experiments the speed of blood flow in the carotid 4 - 5 times greater than in femoral artery; in another experiment the speed inversely in femoral artery was 2—4 times greater than in the carotid. Volkmann found in the carotid artery of a horse 254—220 mm. p. sec., in that of a dog 205—387. The blood movement after Vierordt in the femoral artery is 128—233. Tschuevsky in the carotid and femoral artery of a dog found 78—385 mm. p. sec. With reference to the pulse velocity:

Volkmann found systolic 297—303 and 215—127 diastolic velocity
Chauveau » » 570—400, dicrotic 180—250, and 120—190 diastolic velocity.
Cybulski » » 500—200, dicrotic 464—180, and 290—19 diastolic velocity.
Huerthle in the carotid artery found 600 syst. 130 dicrotic, 37 diastolic veloc.
and » » femoral » » 840 » 260 » 92 » »

(It is given aproximately, as far as I could make it out from diagrams 4, 5[1]).

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[1] Pflueg. Arch. 1923, CC, p. 46.

In Chauveau's experiments the systolic acceleration amounts to 372 - 100% of the diastolic velocity. Such a systolic acceleration is to be found in the arteries of a horse owing to the slow pulse-rate. The numbers shown by Huerthle refferring to the dog, are not real, in normal conditions; a systole could accelerate the blood stream at 1520 - 813% of its diastolic value only during faradisation of the vagus nerve. The Hürthle's diastolic velocity on the contrary is unusually small. After Cybulski the systolic acceleration is 34—73% of the diastolic velocity. My experiments show that the changes of blood-movement depending on the heart are in the limits 8—20%.

Experiments.

14) 9. XI. 1924. dog 16 kg weight, narcotized by morphium-scopolamin.
In the right catorid artery velocity:
diastol. 533 - 672, systol. 551—686
In the femoral artery diastol. 649—679, systol. 686—734

15) 3. I. 1925. dog 10 kg weight, narcotized by veronal-natrium.

In the femoral artery (bore of 2,2 mm.)			In the carotid left (3 mm. bore)		
velocity			velocity		
systolic	diastolic		systolic	diastolic	
542	495		689	672	
542	524		714	700	
556	524		734	714	
594	565		748	728	
610	577	respir. wave 1.	754	728	respir. wave 2.
622	586	—	752	714	
626	594		741	714	
626	594		734	693	
626	594		714	579	
614	569		700	664	
606	560		689	664	
594	560				
610	602		569	542	
642	626		569	551	
664	649		586	560	
679	653		586	560	
690	564	respir. wave 4.	590	560	respir. wave 3.
692	657		581	546	
679	642		581	546	
672	645		573	551	
660	610		569	511	
642	602		560	546	
626	602		569	546	

The III-order waves containing 8—10 respiratory waves change periodically the motion of blood at 100 mm. p. sec.

The average diastolic velocity in femoral artery is 601 mm. p. sec.
» systolic acceleration » 24 »
» distolic velocity in carotid artery is 646 »
» systolic acceleration » 26 »

16) 20. I. 1925. Dog 28 kg weight, narcot. by veronal-natrium, pulse-rate 180, respiration 18.

In the right carotid (3 mm. bore) the diastolic velocity 500 mm. p. sec.
systolic acceler. 85 » »

The III-order waves possess the size of 130 mm. p. sec.

4) 19. VI. 1925 (vide part. II, exp. 4).

In the left femoral artery diastolic velocity 570 mm. p. sec.
stystolic acceler. 24 »
dicrotic » 15 »

The passive movement of hind limbs increases the motion in such a manner:

velocity			
systol.	dicrot.	diastol.	
464	454	432	
475	454	432	
454	443	420	
475	432	402	
443	464	443	
505	524	510	
560	555	524	
551	515	495	
515	524	505	in the 2nd sec. after movement
551	542	515	
551	569	551	
700	683	668	in the 5th sec.
693	690	675	
700	683	668	
693	674	664	
686	668	649	
672	657	642	
664	646	649	
642	626	610	
630	614	602	
626	610	594	
618	602	585	
610	590	573	
598	586	569	
586	572	560	in the 11th sec.

7) (vide part II, exp. 7) in the carotid artery (2 mm. bore)
the diast. veloc. 590 mm.
systol. accel. 40 »
dicrot. » 48 »

8) (vide part II, exp. 8) in the femoral artery (2 mm. bore)
the diast. veloc. 650 mm.
syst. accel. 62 »
dicrot. » 30 »

13) (vide part II, exp. 13) in the femoral artery (2,5 mm. bore)
the diastol. veloc. 614 mm. p. sec.
systol. accel. 120 »

17) 18. XII. 1926. Dog 7,5 kg weight, narcotized by urethan, pulse-rate 108; respiration 12.

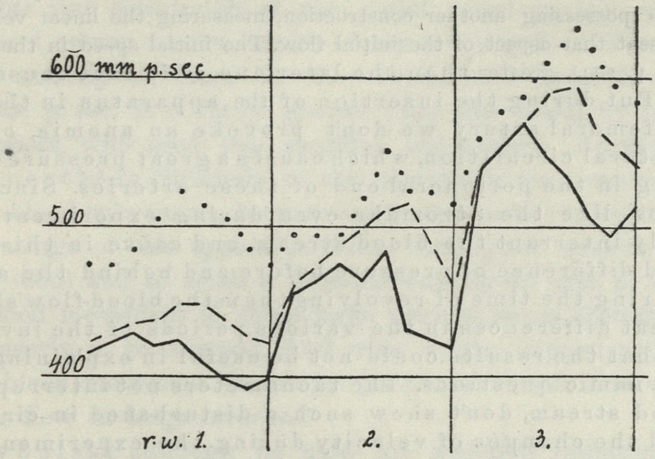
In the right carotid (2,5 mm. bore)

velocity			
systol.	dicrot.	diastol.	
443	475	432	
454	475	443	
470	480	459	
485	505	443	respir. wave 1.
495	524	447	
495	515	420	
475	505	396	
454	485	384	
443	475	396	
460	495	454	
475	495	464	
485	495	475	
500	520	464	respir. wave 2.
510	551	485	
515	524	432	
485	524	426	
464	515	420	
533	560	537	
555	577	551	
569	586	569	
590	610	546	
594	634	533	3.
573	618	505	
551	594	495	
542	586	515	

In the right carotid artery the average diastol. veloc. 509 mm. p. sec.
systol. acceler. 34 »
dicrot. » 62 »

In the femoral artery the diastol. velocity 595 mm. p. sec.
systol. acceler. 54 »
dicrot. » 58 »

The fig. 1 shows graphical aspect of the ascending part of III-order wave.



Continuous line: diastolic velocity. Dashed line: systolic acceleration. Dotted line: dicrotic acceleration r. w. 1, 2, 3: respiratory waves (II-order)

The speed in the peripheral arteries in the first moment after the renewal of blood-flow, stopped for the time of the insertion of the tube, is the same as in the later stages, or increases gradually. Experiments in which dogs, after having had the two carotid or vertebrals arteries ligated, did not show any deviations from the normal state of dogs, and even where the ligation of both carotids and vertebrals didn't cause seemingly any harm, prove how well is developed the lateral circulation in the head and in the lower extremities[1]). In connection with it stands the question of the speed after an anemia of short duration. In Dogiel experiments in which he used Ludwigs Stromuhr, the initial great amount of blood-flow in a short time diminished greatly and the average quantities of blood flowing through the carotid constantly changed so, that in one minute they fell to one half and afterwards rose again. The causes of this fact one tries to see in the influence of the anemia during the insertion of the Stromuhr. The anemia must paralyse the peripheral vessels and diminish their tonus owing to the increase of CO_2; therefore the initial speed after the renewal of blood flow is increased till the vessels get back their tonus. Nikolaides observed that such a dilatation appears more often in femoral than carotid artery. Tschuevsky states that the increase of speed after anemia in the carotid amounts to 40%, in the femoral on an average to 100%; besides the stopping of flow for 17–30 sec. doubles

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[1]) Coenen-Wiewiorowski l. c.

the speed in normal conditions, but after dissection of the nerves anemia lasting 15—55 sec. causes either a very insignificant acceleration or none.

This is a characteristic sign, that only those investigators observed such changes of blood-flow, who used apparatuses constructed like the Ludwigs Stromuhr (Dogiel, Nikolaides, Tschuevsky). On the contrary the »tachometers« possessing another construction, measuring the linear velocity, didn't present that aspect of the initial flow. The initial speed in the aorta (1000 mm. p. sec.), greater than the later one is in fact caused by anemia. But during the insertion of the apparatus in the carotid or femoral artery we don't provoke an anemia, owing to the lateral circulation, which causes a great pressure even pulsating in the peripheral end of these arteries. Since apparatuses like the Stromuhr even during experiments periodically interrupt the blood stream, and cause in this way a marked difference of pressure before and behind the apparatus during the time of revolving them the blood-flow shows such great differences in the various periods of the investigation, that the results could not be useful in explaining the haemodynamic questions. The tachometers not interrupting the blood stream, don't show such a disturbance in circulation, and the changes of velocity during the experiment are caused only by the heart, respiration and III-order linear waves. The initial speed in the carotid and femoral artery in my experiments was never greater than the later one, but on the contrary smaller or equal to the later speed. The same relation of the initial speed to the later I observed after the closing of the carotid artery for some seconds.

E. g. the velocity of the blood in the carotid artery before closing was 675, systolic acceleration 4 mm. p. sec. For the time of 10 sec. I closed the artery just behind the tube, after releasing the clip the speed from 0 increased in such a manner in the successive heart beatings:

systole	diastole
0	0
209	276
348	377
420	432
480	491
513	524
544	544
564	569
614	610
628	632
653	663
668	663
671	663

The statement of Tschuevsky, that after a short anemia there is an increase of the blood speed in the carotid and femoral artery is right only in cases of real anemia caused by closing of the aorta or the binding round of the whole extremity.

After this description of the initial speed in the peripheral arteries I return to the results of my investigations. The average linear velocity of blood in the carotid and femoral artery is 610 mm. p. sec. It is thrice greater than that found by other investigators, who used less sensitive apparatuses. Among others the Huerthle's Stromuhr is also unsuitable for measurement of linear blood movement, because the linear velocity calculated from the tracings of this apparatus shows such great systolic acceleration (600) and so small a diastolic velocity (37 mm. p. sec.) that the blood movement in these large arteries seems during the diastole nearly to be stopped. And what might happen to the diastolic blood movement in smaller peripheral vessels if we assumed such a flow in large arteries?

Cybulski although he used his sensitive fotohaemotachometer for some purposes found the velocity like other investigators. 1° His tube caused twists of the vessels which diminished the speed. 2° the differential-manometer was placed 1 metre aside of the tube, what diminished the difference. 3° He used thick glass-tubes the diameter of which was approximately marked. 4° The difference in the photograms was not properly measured. Namely the diastolic difference was measured from the lowest diastolic point of the upper pulse-tracing to the highest point (systolic) of the lower tracing; the systolic difference was measured from the highest (systolic) point of the upper tracing to the before-dicrotic point of the lower tracing. Only the dicrotic difference was correct (see Starling Principles of Hum. Physiol. p. 934). The cause of the measurement in this manner was, that the second cannula of the tube, connecting the seconde arm of the manometer was placed too far from the right angle, and the pressure changes in it came too late in view, i. e. the systolic pressure on the upper tracing corresponded to the diastolic pressure in the lower tracing. In my photograms the pulse-waves appear practically simultaneously, and I consider as diastolic difference the distance of both diastolic points of waves, similarly the systolic and dicrotic difference. 5^0 Cybulski, as all other investigators calculated the secondary but not the primary linear velocity.

With reference to the pulse-linear velocity, there are three distinct moments: the diastolic, systolic and dicrotic.

In the diastole the velocity is 592 mm. p. sec. (448—734), in the systole there is the velocity 642 (525—734). Thus the systolic acceleration is only 50 mm. p. sec., less than that formerly found.

The velocity during the dicrotic wave was first remarked by Chauveau, who found such a form of a pulse velocity waves in the carotid of a horse:

	systol.	dicrot.	diast.
	570	180	120
	400	250	190
Cybulski in a carot. of a dog	262	272	211
	199	180	131

Cybulski's assertion is important, that the dicrotic acceleration may exceed the systolic; in the carotid it is 2% quicker, in the femoral artery it is as a rule 13% smaller than the systolic. In my experiments the dicrotic acceleration in the upper part of femoral and catorid artery does not exceed the systolic so constantly as it does in the aorta. In the dicrotic elevation the speed of the blood in some experiments was greater to 30 mm. p. sec. than in systole. In another experiments the average dicrotic accelerations was smaller to 10 mm. p. sec. than the systolic one. The size of dicrotic acceleration is dependent evidently on the tonic state of peripheral vessels. In the time of relaxation of vessels e. g. after movement of hind limbs, the dicrotic acceleration — if it was smaller than the systolic one, becomes greater than that; after cessation of the tonic changes the dicrotic acceleration becomes again smaller than the systolic one.

Lortet with the help of Chaveau's haemodromograph noticed the respiratory waves velocity, while Hering and Vierordt observed them by the method of infusion. Cybulski was the first who submitted concrete figures concerning these changes. And so in the carotid artery of a dog in the time of inspiration the velocity amounted to 305 and that of expiration to 368 mm. p. sec. In the femoral artery 338 and 449 mm. p. sec.

Cybulski remarks too, that the greatest acceleration is in the middle of expiration, the smallest is at the end of expiration or in the beginning of inspiration. The changes of velocity, in short, are delayed in the same way in relation to the respiratory movements as the respiratory waves of blood-pressure. Similar respiratory changes are present in my photograms. In the carotid the systolic acceleration at the end of inspiration amounts to 65, the diastolic to 50 mm. p. sec. In the femoral artery inspiratory systolic acceleration is 42, diastolic 24 mm. p. sec., in another exp. 74 and 77 mm. p. sec. Generally the systolic acceleration increases in a greater degree by inspiration than the diastolic, for the heart is better filled up with blood. Sometimes however both accelerations are equal in those cases when simultaneously with the increase of pressure, peripheral arteries are being distended. After tracheotomy Cybulski stated the diminution or complete disappearance of both respiratory accelerations.

Besides the heart and respiratory waves there are in these arteries as well as in the aorta, long, III-order, velocity waves. The average diastolic velocity at the top of such a wave is increased by 100, and the systolic by 120 mm. p. sec.

Comparison of the speed in aorta with that in its branches.

In some of my experiments I investigated the speed in aorta and in one of the arteries, carotid or femoral. The time between both investigations amounted to 30—45 minutes. The comparison of the speed in these two locations of the vascular system of the same dog confirms the supposition of R. Thomé[1]), that in the I-order arteries of the aorta the linear speed ought to be greater than in the aorta, as the cross-section sum of those branches is smaller than that of the aorta, and therefore a certain quantity of blood passing the lower aorta at a given time, must pass quicker through these branches.

	velocity			
	systol.	dicrot.	diastol.	average
Exp. 1. IX. 1926. In the aorta	520	560	478	519
» left carotid	630	638	592	620

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[1]) Pflüg. Arch. 1900, LXXXII, p. 496.

		velocity			
		systol.	dicrot.	diastol.	average
25. IX. 1926.	In the aorta	621	702	646	656
	» femoral.	708	685	652	681
16. XII. 1926.	In the aorta	649	750	640	666
	» femoral.	734		614	672
18. XII. 1926.	In the aorta	500		640	475
	» right carot.	543	571	509	541
	femoral	649	653	595	632
19. VI. 1925.	In the aorta	550	559	531	546
	» femoral.	594	585	569	582

The relation of the speed in the aorta and its branches may sometimes seem not to be so evident owing to the periodic II- and III-order waves which are not of the same size. In spite of that the average speed in these arteries is greater than in the aorta. One must add that the cause of it may be not only the smaller cross-section sum of these arteries, because I have found the same phenomenon in the peripheral small arteries and their branches, the cross-section sum of which is, on the contrary, greater.

Conclusions.

In the femoral and carotid artery of a dog the velocity is 600 mm. per second (509—664), the systolic acceleration 50, the dicrotic acceleration 55—60, but often the latter does not exceed the former or is smaller. The respiratory waves are changing the movement for 20 – 70, and the third-order waves for 100 mm. per second.

In the lower part of the femoral artery the velocity is 450 mm. per second (270—500), like that in the aorta, the systolic acceleration is 48; the dicrotic acceleration is here rarely greater than the systolic (10 mm.), usually smaller. The respiratory changes of the blood movement are 50 mm. per second (10—45) and third-order waves 30 mm. per second.

In the aorta the velocity is smaller than in femoral or carotid artery (500 and 600 mm. per second), according to the hypothesis of R. Thomé.

O ruchu i ciśnieniu krwi w tętnicach. — On the blood flow and the blood pressure in arteries.

IV. Ruch krwi w małych tętnicach. — The blood flow in small arteries.

Mémoire

de M. ***A. J. KLISIECKI,***

présenté dans la séance du 13. Janvier 1930, par M. A. Beck. m. c.

In the calculation of the speed of the blood from the difference of pressures after $V_1 = \sqrt{D \times g \times \eta}$, we must take into account the relative viscosity of blood. It is known that the viscosity of the fluid depends also on the cross-section and length of the tube; that is why two liquids flow with like speed in broad and short tubes, whereas in narrow tubes is observed a difference in speed because of the difference in viscosity. When measuring the speed ot blood from the differences of pressure in the tube inserted into the blood-vessel, we are concerned here with the viscosity, as it is in it that there arises the difference which is the base of our calculation.

In the tubes of 6—2 mm. diameter, long 30—15 mm., the outflow of water and blood is practically the same, i. e. there is no difference in viscosity between water and blood, with the exception of the 2 mm. diameter, during the speed not exceeding 450 mm. p. sec. Therefore in the calculation of blood movement in the aorta and greater arteriers I knowingly passed over the viscosity of blood; and I calculated the speed as if we had water in place of blood. But blood moves unlike water in tubes of a small diameter. Here we see distinct differences in the outflows of blood and water under the same conditions. Notwithstanding the same manometer-differences, the blood in small tubes flows with a smaller speed than water, owing to a greater viscosity. In order to know how much smaller is the speed of blood than the corresponding manometer-difference, one had to find the relative viscosity by comparing the speed of blood and water. The apparatus consisted of a Mariotte-flask connected by a broad rubber-tube with the tube supplied with the differential-manometer. Both were dipped into water of 39° C. I passed the fluid with different speeds and got the amounts running out with the secondary velocity V_2 (diminished by the re resistance of two right-angles). I directed the tube then at 90°, and the liquid not passing through the right-angles flowed through the straight tube with the primary velocity V_1. Acting in this way I controlled the data submitted in the preceding article, reffering to the same questions of the relation of the V_2 to V_1, as well as to the formula of measuring the V_1 with help of the two right-angles tube. The said control confirmed entirely my views on that matter. I compared the speed of blood with that of water in various bores and the relative viscosity of blood I drew in the diagram (Fig. 1). On the abscissa is marked the linear velocity in mm. p. sec. (in the physiological limits), on the ordinate the viscosity of the blood η i. e. $\frac{Q \text{ blood}}{Q \text{ water}}$. The numbers in the curves denote the bore of the tubes. The direction of the lines shows that the relative viscosity of blood diminishes with the increase of the speed more and more, and finally reaches the viscosity of water, $\eta = 1$. The character of the change of viscosity depends on the bore of the tubes. In bore of 2 mm. the running blood is as viscous as water during the speed of 450 mm. p. sec.; at the same speed in the 0,5 mm. bore the viscosity is 0,68, and in limits of the blood velocity of a dog never reaches 1. The curves are essentially similar. From 0 – 100 mm. p. sec. the increase of curves is rapid, in greater speeds gradually slowing down. The way of 0,38 mm. bore is different, though the relation of the bore to the length is the same as in the 0,5 mm. and the factor of length has no importance whatever. It seems to prove that in the tubes of this and smaller bores, there must be a much greater loss of energy than in the broader tubes. Therefore by measuring the velocity in small vessels we must take into consideration also the viscosity of the blood as, owing to the greater viscosity of the blood there is a greater fall of pressure in the manometer than when water would flow in the same conditions. In order to find the real velocity, one has to multiply the velocity calculated from the differences of the manometer by corresponding relative viscosity. E. g. blood flowing through the tube 0,5 mm. bore inserted into the vessel, produces the difference of 12,5 mm. To this difference corresponds the linear velocity of water 350 mm. p. sec. and the velocity of blood amounts to 350 × 0,6 = 210 mm. p. sec. In the tube with 2 mm. bore at the velocity of 500 mm. p. sec. to which corresponds the difference of 25,5 mm. there is no necessity of taking into account the viscosity of blood, since at this speed shown by the diagram the blood is as viscous as water and the energy of its movement produces the same difference of pressure as water would produce in the same conditions. The same applies to the tube of 1,66 bore and dif-

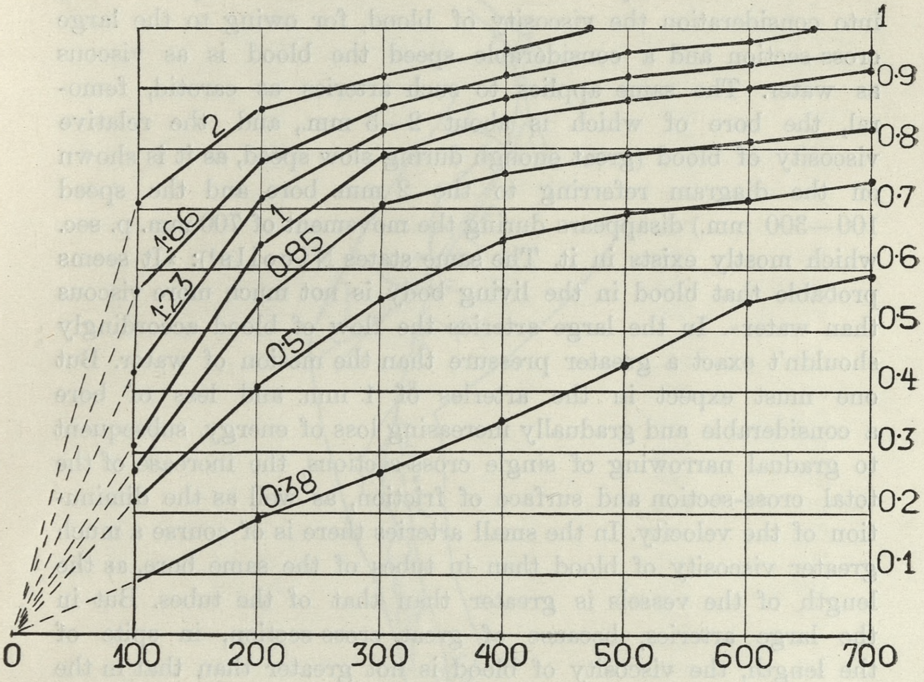

Fig 1.

ference 37 mm. (velocity 600 mm. p. sec.), while in the tube 1 mm. bore the viscosity of blood $\eta = 1$ is only in the speed of 700 mm. p. sec. The abdominal aorta of a dog possesses bore between 3—6 mm., and the velocity of blood 500 mm. p. sec. The calculation of the velocity of blood in the aorta doesn't require taking into consideration the viscosity of blood, for owing to the large cross-section and a considerable speed the blood is as viscous as water. The same applies to such arteries as carotid, femoral, the bore of which is about 2—3 mm., and the relative viscosity of blood (great enough during slow speed, as it is shown on the diagram referring to the 2 mm. bore and the speed 100—300 mm.) disappears during the movement of 700 mm. p. sec. which mostly exists in it. The same states Nicolls[1]): »It seems probable that blood in the living body is not much more viscous than water«. In the large arteries the flow of blood accordingly shouldn't exact a greater pressure than the motion of water. But one must expect in the arteries of 1 mm. and less of bore a considerable and gradually increasing loss of energy, subsequent to gradual narrowing of single cross-sections, the increase of the total cross-section and surface of friction, as well as the diminution of the velocity. In the small arteries there is of course a much greater viscosity of blood than in tubes of the same bore, as the length of the vessels is greater than that of the tubes. But in the large arteries, because of great cross-section, in spite of the length, the viscosity of blood is not greater than that in the corresponding tubes. According to these facts the blood-pressure and velocity in the arteries of 0,5—0,3 mm. bore, have to fall considerably. In what degree this haemodynamic principle is valid, we shall state after the examination of the blood pressure-gradient and velocity in central and peripheral arteries. We have no knowledge of the blood movement in small vessels not very far from capillaries as to the linear velocity. We should like to know about this part of the vascular system also from an other standpoint; whether there are I-order, II-order and III-order velocity waves, how great is there the dicrotic acceleration etc.

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[1]) Journ. of Physiol. XX, 411, 1896.

I examined the velocity in these series of investigations only in the arteries of the hindlimb of a dog such as a. femoralis, a. saphena, r. plantaris (Fig. 2. After Ellenberger-Scheunert). In the femoral artery I always measured the motion just above branching of a. saphena, because the upper part of that artery is known from my former investigations. In the following researches I measured the flow in one or two places simultaneously. I calculated the bore of the vessels by subtracting from the external diameter the thickness of the wall, seeking a place corresponding to the section of the tube in question.

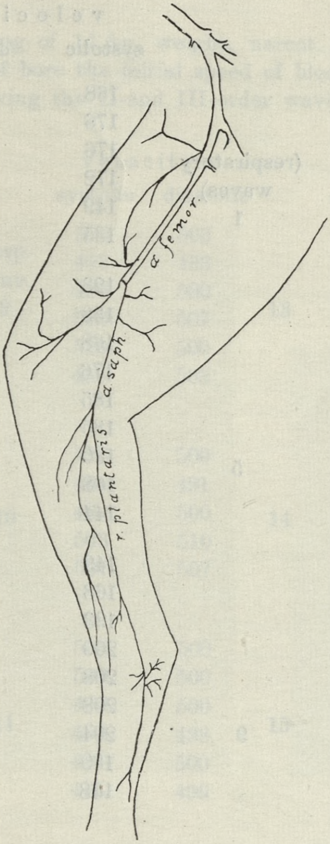

Fig. 2.

Experiments.

1) 7. X. 1926. Dog of 16 kg. weight, narcotized by veronal-natrium.

Puls 154, respiration 18 p. min. In the arteria saphena of 0,75 mm. bore

velocity		
systolic	diastolic	
216	208	
216	208	
216	204	
212	200	(respiratory waves) 1
208	193	
200	185	
193	175	
185	168	
168	158	
127	113	
135	132	
154	144	
160	149	
160	149	5
160	149	
158	144	
149	132	
139	123	
127	113	
132	132	
149	144	
158	154	9
160	154	
160	144	
144	127	
135	118	

at the end of experiment the pulse-rate 224, respir. 26.

velocity		
systolic	diastolic	
168	158	
176	168	
176	160	
172	144	(respiratory waves) 1
149	132	
135	123	
123	118	
139	135	
168	158	
176	168	
185	168	3
185	168	
180	154	
168	139	
144	123	
149	139	
168	168	
193	180	
200	193	
208	193	5
208	193	
204	180	
189	168	
168	149	

The average diastolic velocity in this experiment 152 mm. p. sec.
» systolic acceleration 12 »
The respiratory movements change the diastolic velocity at 10—60
» » » systolic acceleration 25—66
The III-order waves change the motion of the blood at 50 mm. p. sec.

2) 5. XI. 1926. Dog of 30 kg. weight, narcotized by veronal-natrium. In the lower part of a. saphena 0,75 mm. of bore, the diastolic velocity was 109 mm. p. sec., the systolic acceleration 11 mm., the pulse-rate 120. After-

wards the pulse-rate increased to 195 per minute also the diastolic velocity to 223 mm. p. sec., while the systolic acceleration diminished to 3 mm. p. sec.

The average diastolic velocity	200	mm. p. sec.
systolic acceleration	7	»
The respiratory changes of motion	10	»

3) 7. X. 1926. Dog of 14 kg. weight, narcot. by veron-natr. In the a. saphena 0,5 mm. of bore the initial speed of blood increases from 310 to 400 mm. p. sec., showing the II-and III-order waving:

velocity:			velocity:			velocity:		
systolic	diastolic		systolic	diastolic		systolic	diastolic	
405	405	resp. wav. 9	500	503	13	482	482	17
400	400		493	493		475	472	
397	402		496	500		468	470	
402	405		503	507		468	470	
405	405		510	500		468	472	
405	405		496	503		470	472	
405	405	10	496	500	14	470	470	18
402	402		496	491		461	461	
397	397		489	500		458	458	
409	420		503	510		454	458	
423	427		507	507		458	458	
430	441					458	461	
						461	458	
445	451	11	503	500	15	458	454	19
445	437		500	500		449	451	
450	485		496	500		448	451	
465	465		496	498		448	448	
461	468		496	500		451	451	
475	479		496	496		451	451	
475	479	12	493	493	16	451	448	20
493	503		390	490		440	440	
509	503		486	486		435	437	
500	507		486	486		435	437	
510	510		486	486		437	437	
517	507		486	486		440	440	
500	500					440	445	

The average diastolic velocity 410 mm. p. sec.

systolic acceleration 3 » sometimes completely disappears or the systolic movement of blood is even slower than the diastolic one; this fact is in connection with the pulsation of arteries.

The size of respiratory changes in linear movement in the systole is 11
in » diastole 9
» of III-order waves 70—100 mm. p. sec.

4) 12. I. 1928. Dog of 12 kg. weight, narcotized by veronal-natr. pulse-rate 120, respiration 48.

In the arteria saphena 0,56 mm. of bore

The average diastolic velocity	355 mm p. sec.
» systolic acceleration	22 »
» dicrotic »	8 »
The III-order waving	30 »

Fig. 3 a. The velocity of blood in the arteria saphena 0,56 mm. of bore; above the respiratory curve; time in seconds.

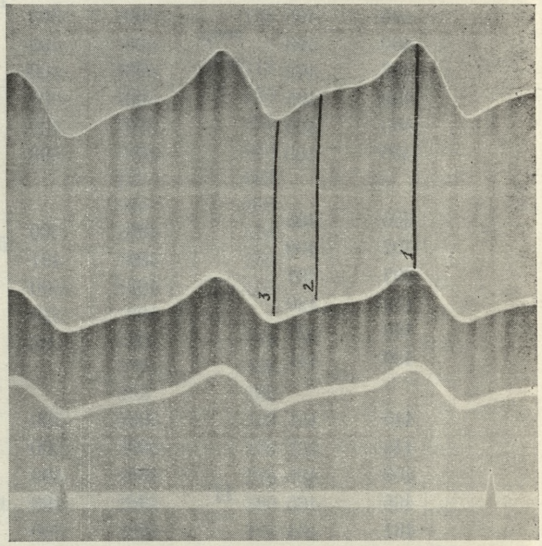

Fig. 3 b. The velocity of blood and its pressure in the arteria saphena 0,56 mm. of bore; 1) systolic acceleration, 2) dicrotic acceleration, 3) diastolic velocity. Below the pressure curve. Time in sec., line of zero pressure.

5) 17. I. 1928. Dog of 35 kg. weight, narcotized by veron.-natr. In the lower part of a. femoralis, just above branching of a. saphena, was inserted cannula 2 mm. of bore. In the arteria saphena cannula 1 mm. of bore, and in the ramus plantaris cannula 0,85 mm. of bore was introduced.

In the femoral artery the average diastolic velocity 550 mm. p. sec.
systolic acceleration 38 »

In the a. saphena the movement of blood at first was
in the diastole 500 (470—540)
after some minutes diminished to 370
the systolic acceleration was 70
dicrotic » 10

The respiratory systolic waving 14
diastolic » 10
The III-order waving 30—40 mm. p. sec.

Lastly I measured the movement in ramus plantaris, maintaining the circulation in the above two cannulas;

The diastolic velocity 407 mm. p. sec.
» systolic acceleration 58 »
» dicrotic » 7 »

The respiratory waving of diastolic velocity 20
» » » systolic acceleration 26
» III-order waving 30 mm. p. sec.

6) 19. I. 1928. Dog of 18 kg. weight, narcotized by veron-natr., pulse-rate 131, respiration 32. In the upper part of a. saphena was inserted the cannula 0,85 mm. of bore, in ramus plantaris in the region of calcaneus the cannula of 0,38 mm. bore was inserted. In the ramus plantaris the motion of blood is steady, in diastole it changes only to 0,5 mm. p. sec., the systolic acceleration is often not marked or very small usually 2 mm. p. sec. The respiratory and III-order waves are not present.

E. g. velocity:

systolic	diastolic
48,7	48,0
48,7	48,0
48,7	48,0
48,7	48,0
48,7	48,0
50,3	48,0
48,7	48,7
48,7	47,6
50,3	48,0

etc.

In the arteria saphena the diastolic velocity was 360 mm. p. sec.
systolic acceleration 20 »
dicrotic » 8 »

After 25 seconds the motion begins to accelerate, and in 4,5 seconds during 10 heart's-beats the diastolic velocity increased to 424
while the systolic acceleration decreased 13
and dicrotic » 5

The following numbers represent this change of blood motion:

	velocity:		
systolic	dicrotic	diastol.	respiratory wave
381	367	362	11
381	375	367	
381	371	362	
383	374	364	
383	371	367	12
381	375	367	
381	367	362	
375	371	367	
385	383	383	13
397	391	385	
400	388	383	
400	394	391	
408	426	408	14
420	417	414	
429	420	420	
429	429	426	15
436	436	433	
441	436	431	
446	438	438	
446	446	446	16
451	448	441	
453	443	443	
	etc.		

The heart does not cause this change of the movement, because with the greater increase of speed the systolic acceleration diminishes. If this change took place in consequence of a greater heart-work and the vessels were not dilated, the greater output of the heart would cause a greater systolic acceleration indeed. The increasing velocity shown in the above numbers is due to the dilatation of peripheral vessels. In the moment of dilatation of a greater part of these vessels, the diastolic velocity suddenly increases and simultaneously in a considerable degree the systolic acceleration diminishes or disappears (e. g. the end of the respiratory wave 13 and the beginning of 14). In the case when the diastolic velocity during at least one or two following heart-beats does not change, the systolic acceleration gains its former size (13). The evidence of those changes is somewhat obscured by the respiratory waves. This sort of change of the speed is one of the criteria for the differentiation of the heart-output changes from those of the cross-section of peripheral vessels. In this place of photogram the pulse-rate didn't change and was just as at the beginning of the experiment, 131 p. minute.

Five minutes later the other place of photogram shows the average diastolic velocity 414, systolic acceleration 26, the dicrotic one 9 mm. p. sec.; the pulse-rate 126, respiration 32 p. minute. After another interval of some minutes the third part shows the velocity 300 mm. p. sec., the systolic acceleration 24, the dicrotic one 5. Generally in the course of about 10—20 minutes the motion varies greatly, 360, 424, 300 mm. p. sec.

The average diastolic velocity in this experiment
in the a. saphena 360 mm. p. sec.
systolic acceleration 20 »
dicrotic » 10 »
respiratory » 8 »
III-order waves possess the size of 30 »

7) 9. V. 1928. Dog. 28 kg. weight, narcotized by veronal-natrium; in the femoral artery the cannula 3,5 mm. of bore, in a. saphena the cannula 0,56 mm., 17 cm. away below the former; pulse-rate 120, respiration 40.

In the femoral artery the diastolic velocity was 509 - 470
the systolic acceleration 15 (5—20),

in some instances it disappears completely, and the diastolic velocity in these heart-beats is the greatest. This phenomenon is due to the great respiratory waves of pressure and movement of the blood; also the dicrotic acceleration is changeable; it is greater than the systolic one only in one or two consequent heart-beats of a respiratory wave, but with this exception it is as great as the systolic or a little smaller; on an average the dicrotic acceleration amounts to 15 mm. p. sec.

The diastolic velocity in the a. saphena simultaneously measured was 316, the systolic acceleration only 4 mm. p. sec.

8) 10. V. 1828. Dog 8 kg. weight, narcotized by veronal-natrium.
In ramus plantaris I found the diastolic velocity 120
the systolic acceleration 2
Then I examined the movement in a. saphena (0,85 mm. bore)
in which I observed the diastolic velocity 226
systolic acceleration 22 mm. p.

after some minutes the blood movement diminished to 151
while the systolic acceleration was 29

Finally (not interrupting the blood stream in this artery)
I returned to the ramus plantaris and found there only 40 mm.
with a systolic acceleration to 5 » ;
at the end of this experiment the velocity increased to 98 »

The average diastolic velocity in a. saphena 188 mm. p. sec.
systolic acceleration 25 »
respiratory systolic changes 45 »
» diastolic » 34 »

The average diastolic velocity in r. plantaris 75 mm. p. sec.
systolic acceleration 3 »
respiratory changes 3 »

E. g. velocity in r. plantaris (0,38 mm. bore)

systolic	diastolic
55,3	51,5
53,2	49,3
51,5	49,3
49,3	41
47	45,6
45,5	43,2
43,2	41
etc.	
43,2	41
47,1	38,8
47,1	38,8
41	38,8
etc.	
at the end	
97,7	93,5
100	97,7
104	102,9
106,8	102,9
107,8	104

(numbers chosen from different points of photogram).

9) 18.V.1928. Dog 17 kg. weight, narcotized by veronal. In the arteria femoralis tube of 2 mm. bore, 10 cm. below in the arteria saphena the tube of 0,56 mm. bore. The motion of blood was simultaneously registered. The respiration was quick, irregular, pulse rate 200 p. minute. The relation of the blood movement in these two arteries was as follows:

In the first part of photogram in the a. femor.

in the a. saphena 206, the blood flow is steady, sometimes are apparent heart's waves without acceleration of the motion.

systolic	dicrotic	diastolic	
454—485	454—495	420—485	
after some minutes in the second part of photogram			
443—448	432—495	432—464	243—248
in the third part of photogram			
505—524	505—537	475—505	170—173
the vagus nerve was stimulated, after cessation of stimulation			
573—606		551—581	260 mm. p. sec.
at the end of experiment			114 »

The average diastolic velocity in a. femoralis 497 mm. p. sec.
» systolic acceleration 17 »
» velocity in the a. saphena 200 »

10) 19. V. 1928. Dog. 15 kg. weight, narcotized by veronal-natrium. Tube of 0,85 mm. bore put into the a. saphena, and that of 0,38 mm. bore introduced into the r. plantaris. In both arteries the motion was simultaneously registered.

In the a. saphena			
systolic	dicrotic	diastolic velocity	in the r. plantaris
425	425	396	381 mm. p. sec.
417	417	388	
417	417	388	
410	410	380	
410	410	380	
417	417	388	
417	417	388	

in this moment vagus nerve was stimulated, after cessation of stimulation
218 130 100 155—166

The average diastolic velocity in a. saphena 250 mm. p. sec.
systolic acceleration 30 »
dicrotic acceleration 30 »
diastolic velocity in r. plantaris 270 »

From the hydrodynamic point of view it is a paradox, that the linear velocity in a vessel is greater or equal to that in its branch. As we shall later see it is due to the pulsation of arteries. Concerning the amounts of the blood passing trough the cross-section, through the a. saphena in a given time flow 224 mm. cub. p. sec., with an average velocity of 400 mm. p. sec., and through the r. plantaris, with the average velocity of 381 mm. flow 43 mm. cub. p. minute, i. e. one fifth of the former amount. That seems to prove that the amounts of blood in various arteries are directly proportional to the cross-sections of the latter, but not the linear velocity to the squares of radius, as it is in a non-pulsating system of tubes.

11) 22. V. 1928. Dog 16 kg. weight, narcotized by somnifen and urethan. In the a. saphena in the middle of its length the cannula of 0,56 mm. bore was introduced.

The diastolic velocity 126 mm. p. sec.
systolic acceleration 15 »
(after injection of histamin the movement of blood increased to 350).

13) 26. V. 1928. Dog 32 kg. weight narcotized by veronal.
In the a femoralis 3 mm. bore the diastolic velocity was 270
systolic acceleration 60

In the a. saphena, 10 cm. away below the former, 1,2 mm. bore
the diastolic velocity 300
systolic acceleration 57
In the r. plantaris (0,7 mm. bore) the blood pressure 75—66 mm. Hg.

It is seen from these experiments that generally speaking as we pass outwards towards the periphery the linear velocity of blood is getting gradually smaller. But in details we meet with big differences in various sections in diverse experiments, and even in some experiments the linear velocity undergoes spontaneously considerable changes in various periods of time. The decrease of velocity towards peripheries is not so schematic as in the non-pulsating system, in which the loss of velocity in singular branches is proportional to the increase of the sum of the cross-sections. Several simultaneous measurements of linear velocity in some arteries and their branches, show us somewhat unexpectedly, that the blood movement in the branches in spite of the increase of the sum of cross-sections, can be quicker or equal to the linear velocity in the arteries (e. g. exp. 5, 10, 13).

Altogether the average linear velocity in the femoral artery of a dog just above the a. saphena amounts to 450 mm. p. sec. (270 – 550). In its branch, arteria saphena to 257 mm. p. sec. (107—410). In the ramus plantaris with 0,38 mm. diameter, in two experiments to 67 mm., in exp. 9 to 270 mm. p. sec.; in the same branch with 0,85 mm. diameter of a dog, weight 35 kg, the velocity was 400 mm. p. sec.

In what way, then, does blood fluctuate in that part of vascular system? The systolic heart's waves being large in the aorta, a. femoralis and generally in the arteries of a greater cross-section are diminishing towards periphery. E. g. in the exp. 7 the systolic acceleration in the femoral artery amounts on an average to 15, in the a. saphena 4 mm. p. sec.; in the exp. 6 in a. saphena (0,85 mm. bore) the systolic acceleration is 20, in r. plantaris (0,38 mm bore) 0,4 mm. p. sec. In the arteries above 0,5 mm. bore the size of the systolic acceleration greatly depends on respiration. However it happens that, on the contrary, the systolic accelerations in the branch are greater than in the artery itself. E. g. in the experiment 5 the systolic acceleration of the a. femoralis is 38 mm., this one of a. saphena 70, and this one of r. plantaris 58 mm. p. sec.

Another acceleration of the blood, the dicrotic one, in the aorta as a rule greater than the systolic one, in the upper part of a. femoralis not always surpasses the systolic, and in the lower part of this artery it is generally equal to them or smaller. Only during deep enough respiration on the tops of respiratory-waves the dicrotic acceleration exceeds the systolic one. In the arteria saphena the dicrotic acceleration is not very distinct, and in the ramus plantaris is never to be seen. Just as in the aorta and upper femoral artery, so in the lower part of this artery and in its small rami (a. saphena, r. plantaris) the linear motion of the blood doesn't produce any oscillations or disturbances which could confirm the presence of the peripheral reflexion with its influence on motion and blood pressure. The reflected waves are seen in the aorta and big vessels only during the stimulation of the vagus nerve at the time of very rare heart beats, but in pulse rate above 40 p. minute they disappear and the motion shows throbs coming only directly from the heart.

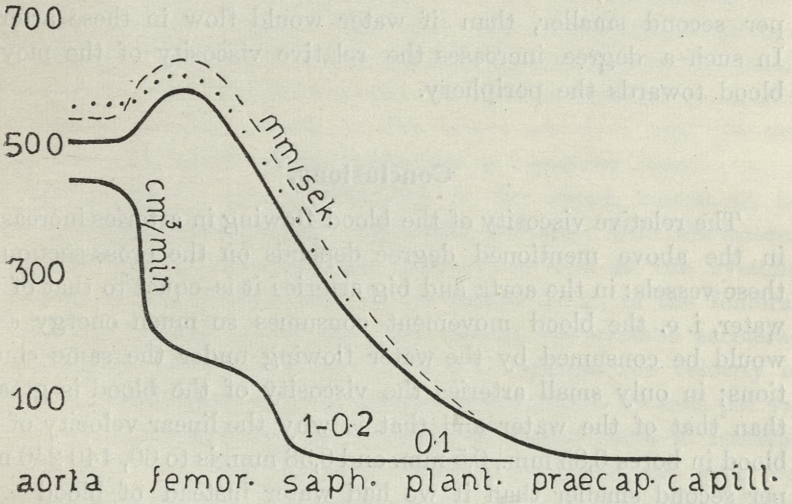

Fig. 4. In the upper tracing: the diastolic velocity (mm. p. sec.) is marked by a continuous line, the systolic acceleratiou by the dashed line, and the dicrotic acceleration by the dotted line. The lower continuous tracing represents the corresponding amounts of the blood in c. c. per minute.

The respiratory waving in the peripheral vessels is in the same connection to respiratory-movements of the chest and respiratory blood pressure waves as those in the aorta.

The III-order oscillatory waving reaches evidently to the arteries of 0,5 mm. bore, in smaller bores I couldn't specify them up to the present time.

The results of these experiments are shown schematically on the Fig. 4 (p. 49).

The viscosity of the blood flowing in arteries 0,85 mm. bore, consumes so much energy, that the velocity is 60 mm. per second smaller; in the arteries 0,5 mm. bore, the velocity is 140 mm. per second smaller, and in the arteries 0,38 mm. bore it is 240 mm. per second smaller, than if water would flow in these arteries. In such a degree increases the relative viscosity of the moving blood towards the periphery.

Conclusions.

The relative viscosity of the blood flowing in arteries increasing in the above mentioned degree depends on the cross-section of these vessels: in the aorta and big arteries it is equal to that of the water, i. e. the blood movement consumes so much energy as it would be consumed by the water flowing under the same conditions; in only small arteries the viscosity of the blood is greater than that of the water and that is why the linear velocity of the blood in bores 0,85 mm., 0,5 mm. and 0,38 mm. is to 60, 140 240 mm. per second smaller than if we had water instead of blood.

In spite of such an increase of the viscosity and progressive growth of the total cross-section of the arteries, the linear velocity of the blood is very great.

In the femoral and carotid artery of a dog the velocity is 600 mm. per second (509 - 664), the systolic acceleration 50, the dicrotic acceleration 55—60, but often the latter does not exceed the former or is smaller. The respiratory waves are changing the movement for 20—70, and the third-order waves for 100 mm. per second.

In the lower part of the femoral artery the velocity is 450 mm. per second (270—500), like that in the aorta, the systolic acceleration is 48; the dicrotic acceleration is here rarely greater than the systolic (10 mm.), usally smaller. The respiratory changes of the blood movement are 50 mm. per second (10—45) and third-order waves 30 mm. per second.

In the arteria saphena (a ramus of the femoral artery) of 0,5—1,2 mm. bore, the velocity amounts to 250 mm. per second (107—410), the systolic acceleration 24 mm. per second (3—70) and the dicrotic acceleration in the vessels of these diameters never surpasses the systolic. The respiratory waves in the arteria saphena are of 20 mm. per second (10—45) and third-order waves 30—70 mm. per second.

In the ramus plantaris arteriae saphenae of 0,38—0,2 mm. bore, the velocity is 135 mm. per second (47—270), if this vessel possesses a greater diameter (0,85 mm.) the movement is quicker (407 mm. per second). The systolic acceleration is here very small (0,5 - 3 mm.), and the blood-stream is often uniform as in capillaries. The respiratory waves in this artery are 4—7 mm. per second; the third-order waves could not be observed there.

With regard to the relationship of the blood movement in some arteries simultaneously registered, we meet with the interesting fact that in an artery the velocity as well as the systolic acceleration are smaller than in its ramus (e. g., in the femoral artery the velocity is 270 mm. per second, the systolic acceleration 38 mm. per second and in the a. saphena the velocity is 300 mm. per second and the systolic acceleration 70 mm. per second). Also in the aorta the velocity is smaller than in femoral or carotid artery. But this fact depends evidently not only on the smaller sum of the cross-sections of the branches of the aorta, because the same relationship is to be seen in quite peripheral rami, the sum of the cross-sections of which is much greater than that of their arteries. Such a relationship of the movement in various arteries is due to the pulsation of arteries.

O ruchu i ciśnieniu krwi w tętnicach. — On the blood flow and the blood pressure in arteries.

V. Ciśnienie krwi w tętniących naczyniach krwionośnych. — The blood pressure in pulsating arteries.

Mémoire

de M. ***A. J. KLISIECKI***,

présenté dans la séance du 13. Janvier 1930, par M. A. Beck m. c.

What is the cause of such a characteristic picture of the blood stream? The influence of the peripheral reflexion of the pulse waves, is not to be seen in the motion of the blood. Also the smaller resistance in the rami than in their arteries is not sufficient in order to explain all these phenomena. It remains, then, to look for the explanation of the aspect of such blood-movement, in the influence of the pulsation of arteries. I was induced to this view-point by the experiments in which the velocity was simultaneously registered with pressure in one or two given points.

Owing to the facility of using, I employed for pressure measurements glass-tubes, placed before the photo-camera together with the tubes of the differential-manometer. The lower end of the manometer was connected with the two right-angle cannula. It was filled up with Ringer-fluid to some level (zero of pressure) and then its upper end was closed. The period of vitration of this manometer is 25—45/sec. The comparison (Fig. 1) of the activity of such an air-manometer with those of the manometer with lever plate system Broemser, shows that the pulse-pressure changes in both instruments are synchronic, and have quite the same appearance. Only in the pulse-pressure of the aorta, there are absent the anacrotic secondary elevations in the air-manometer.

But certainly, these oscillations don't exert an influence on the motion of the blood, because of their shortness and weakness.

We can calculate the pressure in the air-manometer by comparison

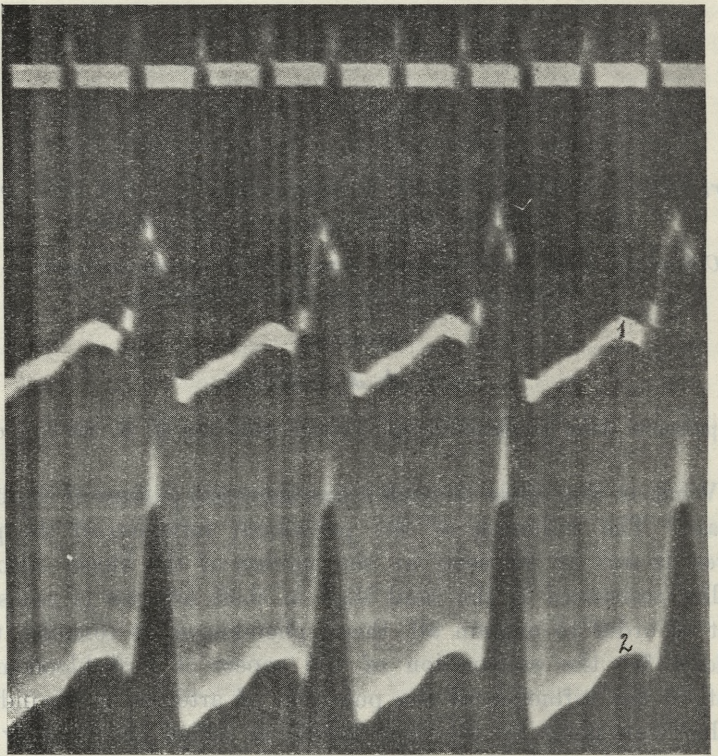

Fig. 1. Time in 0·2 sec. 1. pulse pressure in the aorta abdominalis of a dog, registered by the manometer with lever plate system Broemser. 2. the same pressure in the air-manometer. Both manometers were connected with the aorta by the Y-glass-tube.

with the Hg manometer or by means of the formula $p_1 = \left(\frac{p_1}{p} : \frac{V}{V_1}\right) \times \frac{PV}{V_1} = \sigma \frac{V_1}{V}$ (p barometer pressure, zero of pressure in the manometer, V volume of the air corresponding to zero of pressure, p_1 arterial pressure, V_1 volume corresponding to p_1, σ gradient of compressibility). The blood pressure measured in one end of the transversal tube of the two-right-angle cannula is higher than this in a vessel in natural condition (p_1 real), because of the angle resistance; p_1 real $= \sqrt{\frac{p_1^2}{2\cdot 1}}$.

The registration of pressure and motion by this method shows the following relation between pressure and motion.

9. V. 1928.

Femoral artery

velocity mm. p. sec.			pressure mm. Hg.		
systol.	dicrot.	diast.	systol.	diastol.	respiratory wave
505	505	485	100	64	
505	505	490	108	63	
537	**560**	**542**	**112**	63	
546	555	533	110	**64**	1
533	542	520	110	64	
520	520	495	104	62	
490	485	470	100	60	
475	480	464	99	59	
495	520	502	106	62	
542	**569**	**542**	**112**	63	
555	569	542	112	**64**	
551	560	533	112	64	2
533	528	500	112	62	
505	515	475	109	64	
495	495	475	109	64	
505	515	495	105	64	
533	551	533	110	64	
542	542	514	108	64	5
528	528	505	106	62	
505	490	475	100	64	
495	500	480	100	22	

after some minutes					the dicrot. pres.	The pressure in a. saphena; syst.	diast.
464	470	454	102	64	71	77	72
485	495	482	106	62	74	77	72
506	515	495	110	62	74	80	74
505	500	475	108	62	74	80	74
490	485	461	104	62	71	77	72
464	465	437	99	64	71	77	64
464	470	449	102	62	71	74	71
495	515	497	110	63	74	77	72
510	510	485	208	64	74	76	73
497	505	470	106	62	71	75	72
475	464	443	101	65	70	75	71
459	459	437	101	62	71	74	70

at the end of this experiment I measured the movement and pressure in the arteria saphena, and in the femoral artery only the pressure.

a. saphena					femoral artery	
velocity mm. p. sec.			pressure		pressure	
325	320	320	91	89	136	89
325	320	320	92	90	143	90
325	323	323	92	90	150	91
326	323	323	93	91	147	91
328	323	323	93	92	145	89
325	323	323	93	91	139	88
312	308	308	88	85	132	85
312	308	308	88	85	140	86
312	308	308	89	88	125	89
314	308	308	91	89	145	89
314	312	312	91	89	141	87
312	308	308	90	88	134	85
		etc.				

It is evident that in the heart's-waves there exists a complete harmony between the blood pressure and its movement. (See Fig. 3 b, IV). Here are neither the slightest traces of a sudden relaxation of the motion after the systole, nor oscillations, which should be shown by the reflexion of systolic waves. The size of the pulse pressure in the first part of this photogram is 36—50 mm. Hg.; it depends on respiration. The amplitude of the motion is 5 to 30 mm. p. sec.; in some heart's-periods the systolic movement is smaller than the diastolic one, e. g. in the 3rd period of the 1st respiratory wave (fat numbers of the exp. above) and in the 1st period of the 2nd respiratory wave. Such a relation of systolic acceleration to the diastolic velocity we met also in the aorta. This fact is caused by the diminishment of the resistance because of the distension of the arteries, and it is known that the respiratory pulse-pressure waves exert periodically such an influence upon the arteries. The systolic motion surpasses the diastolic one only in the middle or at the end of respiratory waves, i. e. in this time when the inspiratory output of the heart has distended enough the arteries. In the above experiment the maximum of the diastolic velocity is reached together, in the same heart's-period of a respiratory wave, with that of the systolic pressure; but the maximum of the systolic acceleration in movement of blood comes into view no sooner than only in the immediately following heart's-period, simultaneously with that of diastolic pressure of this respiratory wave. In the beginning of the 2nd respiratory wave the systolic pressure rises 7 mm. Hg., the diastolic only 3 mm. Hg.; the diastolic velocity increases 38 mm. p. sec., the systolic acceleration is only 25 mm. p. sec, greater than that in the former hearts'-period. It shows that the increase of pressure distending the arteries facilitates the ebb of the blood and that is why the diastolic velocity is greater in some periods of the respiratory waving than the systolic one. Such a relation of the diastolic movement to the systolic one is always evident when the peripheral resistance is diminishing. In the 2nd period of the 2nd respiratory wave the top of the diastolic respiratory-wave preceeds that of the systolic one and it appears simultaneously with the top of systolic respiratory wave; only in the 3rd heart's-period the maxima of the systolic acceleration and that of diastolic pressure come in view together. The dicrotic acceleration in this experiment generally exceeding the systolic acceleration, reaches its maximum in the same heart's-period as the diastolic velocity (see fat numbers).

This coincidence of the maximum of diastolic velocity and dicrotic acceleration with the top of the systolic pressure in respiratory waving, renders among others the origin of the dicrotic wave and dicrotic acceleration less occult, showing that they are (especially the acceleration) not produced by peripheral reflexion. The top of the respiratory pressure-wave reaching the respective arteries sooner than the maximum of the blood motion, exert evidently its influence in a given heart's period only on the aftersystolic motion i. e. the dicrotic and diastolic; the maximal influence of the increased pressure upon the systolic motion can appear only in the immediately following heart's-beat. The same is caused by systolic pressure in each heart's-beat, large spaces of arteries being extended, and that is why after each systole i. e. during the dicrotic and diastolic periods, blood movement is facilitated and accelerated although the heart doesn't work. But this influence of the systolic pressure on the motion in short heart's waves is rather difficult to be seen by this simple method, but is manifest in long respiratory pressure-waves, which, owing to the facilitation of dicrotic and diastolic movement, have the same importance for the blood motion in the arteries as the heart's waves. It is clear what a considerable part plays the depth of respiratory movements of the chest in the circulation of arterial blood. As the aorta and big arteries possess a great gradient of elasticity and a great amplitude of pressure in heart's- and respiration-periods, so the influence of the pulsation upon the dicrotic and diastolic velocity of blood should be greater in the aorta than in peripheral vessels. In fact it really takes place, because in the aorta as a rule during the dicrotic pressure-wave the velocity of blood is the greatest, also in big arteries when the pulsation is large; the diastolic velocity is influenced, too, by the pulsation produced by pressure changes, because it is so great as it would never be in a non-pulsating system.

The blood pressure in these two arteries in this experiment is somewhat curious; in the branch of femoral artery i. e. in the arteria saphena the systolic and diastolic pressure fall in the sphere of the femoral amplitude:

The average diastolic pressure in the a. femoralis is	64 mm. Hg.	(62—65)
dicrotic „ „	74 „	(72—75)
systolic „ „	107 „	(103—113)
diastolic pressure in the a. saphena	73 „	(72—75)
systolic „ „	78 „	(76—82)

In the final part of this experiment the blood pressure in both vessels increased: in the a. femoralis diastolic 91, systolic 144 mm. Hg.
a. saphena „ 91, „ 93 „

The experiment of 10. V. 1928 gives us an example of blood motion and its pressure in the arteria saphena and ramus plantaris: dog, 8 kg. weight, narcotized by veronal-natrium; in the central part of a. saphena the cannula 0·85 mm. bore, in the r. plantaris that of 0·38 mm. bore. Pulse-rate 172, respiration 24 p. minute.

in the a. saphena				in the r. plantaris	
velocity		pressure mm. Hg.		pressure mm. Hg.	
systol.	diastol.	systol.	diastol.	systol.	diastol.
231	216	93	85	79	79
253	231	101	87	59	79
266	245	103	89	83	83
271	241	103	89	84	84
266	242	101	85	85	83
238	216	93	82	83	82
231	206	93	82	79	77

after 15 minutes I measured the blood movement and pressure in r. plantaris, while in a. saphena only the pressure.

in the r. plantaris			in the a. saphena	
velocity		pressure:	pressure	
29	21	diastolic	124	107
27	23	117	127	109
36	27	slow	131	111
36	27	constant	131	110
36	27	increase to	128	109
34	21	121	126	109
		after some minutes		
59	57		127	113
59	57		135	115
61	57	122	135	116
61	57		134	111
57	53		130	109
55	51		128	111
55	51	„	134	114
55	51		134	115
55	51		125	113
53	49		131	110
51	49	125	128	110
49	47		133	114
47	45		134	116
43	43		135	114
43	41		133	110
41	39		131	113
41	39	„	134	114
		after some minutes (five)		
97	93	119	126	109
98	98		130	113
100	103	117	127	109
104	103		126	107
107	104	115		
		etc.		

The last column contains the numbers taken from different points of photogram; the two former columns show the subsequent changes in a given time period. Also in the ramus plantaris which is III-order branch of the aorta the diastolic pressure is higher than the central one:

the pressure in. a. saphena was formerly 88 diast. 99 systol. then
increased to 111 „ 130 „

the pressure in r. plantaris was 78 „ 81 „ „
increased to 120 „

In this experiment is expressed the relation of blood movement to the blood pressure in the arteries. In the 2nd column containing six subsequent heart's-periods the motion in the r. plantaris does not generally change, but the pressure rises from 117 to 121 mm. Hg.; similarly the pressure rises in a. saphena. In the 3rd column the pressure in r. plantaris is 1 mm. higher while the motion nearly twice quicker; afterwards the pressure rose to 125, while the motion was slower. The pressure in the a. saphena doesn't participate in those changes. In the last column the motion in the r. plantaris has reached 100 mm. p. sec. meanwhile the pressure diminished by 10 mm. Hg., as in the a. saphena but in a smaller degree. It is clear that for a longer time-period the relation of motion to the pressure is unaccountably variable: it is not constant owing to the various resistances in the peripheral vessels and consequently the different ebbings to the capillaries. The pressure and motion in an arterial vessel are greatly independent of those in the adjoining arteries or in the central ones; they can rise or fall without any influence upon the motion and pressure of other vessels.

The following experiments confirm also, that the diastolic blood-pressure rises towards periphery:

18. V. 1928. In the a. femoralis the diastolic pressure 57, systolic 96 mm. Hg.
a. saphena „ „ 75,

14. XII. 1928. Dog 8 kg. weight, narcotized by somnifen, urethan and magnesium-sulphat.

In the aorta caudalis diastolic pressure 22—31, systolic 58—81 mm. Hg.
a. femoralis „ „ 42—44, „ 79—97 „
a. plantaris „ „ 44. (Fig. 2).

18. XII. 1928. Dog 17·5 kg. weight, narcotized by somnifen as above.

In the aorta caudalis diast. pressure 60, dicrot. 86, systolic 170
a. femoralis „ „ 79, „ — „ 124
a. carotis „ „ 77 „ 116 „ 124

20. XII. 1928. Dog 23 kg. weight, narcotized as above.
In the aorta caudalis diast. pressure 121, dicrot. 140, systol. 200. (Fig. 3).
a. carotis dextra „ „ 102, „ 107 „ 125
a. maxillaris ext. „ „ 111 „ — „ 125 mm. Hg.

21. XII. 1928. I measured the pressure in the aorta abdominalis and in two places of a. femoralis, the tubes being inserted into a. femoris profunda and into the a. saphena. The dog 3 5 kg. weight, was very emaciated.

The diastolic pressure in the aorta	0,	systolic	65	mm. Hg
„ „ (upper part) a. femoralis	60	„	116	„
„ „ (lower part) a. femor	69	„	97	„

The diastolic pressure as we see in the aorta is zero, in the upper part of a. femoralis 60, and in the lower part sometimes 69 or 60.

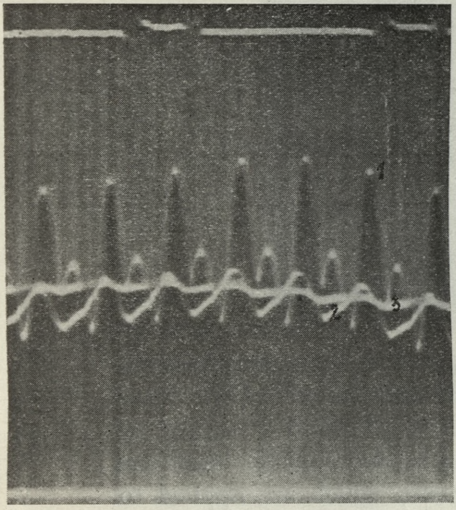

Fig. 2. Blood pressure: in the aorta caudalis 1—1, in the arteria femoralis 2, in the ramus plantaris 3.

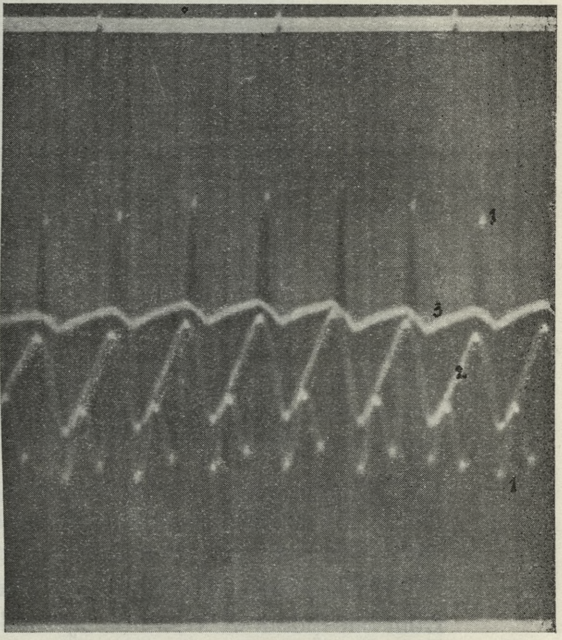

Fig. 3. Blood pressure: in the aorta caudalis 1—1, in the arteria carotis dextra 2, in the art. maxillaris externa 3.

The systolic pressure in the aorta (65) is lower than in the a. femoralis (116 and 97). After injection of adrenalin (1 cm. cub. 1/10000) in the aorta the diastolic pressure was 65, the systolic one 145; in the upper part of femoral artery the diastolic pressure was 121, the systolic one 209; in the lower part of this artery 111 in the diastole, 171 in the systole. The gradient of the fall of systolic pressure in the femoral artery increased from 19 to 38 mm. Hg., and the diastolic pressure after adrenalin injection didn't increase any more along the investigated length of femoral artery, but on the contrary showed a fall. Fig. 4 shows the pressures in this experiment after adrenalin.

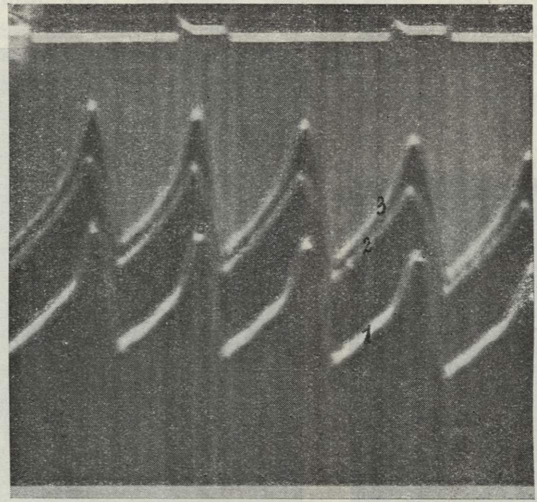

Fig. 4. Blood pressure: in the aorta abdominalis 1, in the upper part of the femoral artery 3, in the lower part of this artery 2.

We are accustomed to consider the haemodynamic questions from the point of view of hydraulic laws, which are applied to the motion of liquids in non-pulsating tubes. But evidently in the arteries the motion and pressure of the blood are not in agreement with these laws. That is why we coud not present in full the question of the blood motion, as the motion in elastic vessels has its own peculiarities being subjected to its own principles. In the arterial system not only the linear motion is at variance with the laws of the flow in stiff tubes, but the behaviour of pressure as well. Fick, for example, stated that sometimes the pressure in small arteries lies in the sphere of the aortic pressure. Frank affirms that in some cases the amplitude of peripheral pressure exceeds that in the aorta (69 and 38). These facts, however, were not properly explained but they were considered among others as the proofs for the peripheral reflexion of heart's-waves and peripheral origin of the dicrotic waves. As to the reflecting of pulse waves, the blood-movement does not show any disturbances which could testify it. The hypothesis of peripheral reflexion of pulse-pressure waves is based chiefly 1) on observations of Lortet confirmed later by other investigators, and 2) on the different character of the pulse in the aorta than that of the arteria cubitalis, radialis etc.

Ad 1) The Lortet's diagrams of blood movement and pressure show that the maximum of motion comes in view earlier than that of pressure, which is probably due to the friction of the blood; after the maximum of motion there is a decrease in it even below the diastolic minimum while the pressure shows a slight increase; afterwards there is a parallelism between the motion and pressure. Such a behaviour of pressure and motion were confirmed by Fick, v. Kries, Abele, Frank, Broemser. Briefly, after the systolic acceleration and just before the dicrotic elevation, when the heart is yet contracted, there is a sudden, brisk, stop of blood-movement. What cause could produce such a diminution of motion? Such a process could take place if the central pressure moving the blood in this moment suddenly decreased. We know that it is not so. Such a stoppage of movement could also arise if any impetus directed against the heart weakened in this short moment the movement of blood. Of course it ought to be a very strong force, greater than that produced by the heart, in order to be able to inhibit the rush of the blood flowing with a velocity about 500 mm. p. sec. under the pressure of more than 100 mm. Hg. The hypothetical reflected waves are too weak for this purpose. If the peripheral reflection could exert its influence upon such a high pressure, of course, it should be seen also in the blood-movement, which would be turbulent under such conditions; this would require a great loss of energy in the arterial system in which all ought to be arranged for the greatest economy of heart's-work. It is rather difficult to imagine such a disturbance of blood-flow, the more so that it would contradict the principles of the flow even in a net-work of elastic rubber-tubes the pulsation of which is much inferior to that of arteries. My experiments prove that in the arteries there are no traces of such disturbances in the blood motion, and in the moment after the systole the blood-movement is even more accelerated than during the systole, and directed towards periphery.

2) The different aspect of pulse-pressure waves of the aorta and other big arteries doesn't confirm the influence of the reflected waves upon the pressure and motion. It is evident that the aorta, for example, shows a pulse different from any other artery e. g. arteria cubitalis because the former is nearer the heart, more extensible, while the elasticity of the latter is smaller and the blood escapes more easily out of it towards the capillaries, as the flow of the blood is much shorter and the cross-section sum continually increases. The pulsation of aorta possesses a particular importance for the general blood motion and pressure. The motion and pressure in the aorta could be governed only by the heart and conditions of peripheral resistance; because the contraction or dilatation of the small vessels renders more difficult or facilitates the ebb of the blood for a longer or shorter time; accordingly they change also the picture of pulse pressure-waves.

The differences in the pulse-pressure of the a. cubitalis and radialis have the same cause. The sharpness of the radialis pulse proves that the blood escapes in an easy and quick way from the examined point of this artery; the lack of this sharpness in the cubitalis pulse shows that the blood ebbs with more difficulty owing to the longer distance from the capillaries or because of the greater output coming to this artery than to the radialis.

The changes of pulse character after medicaments altering the tonic state of small vessels give no evidence that the conditions of peripheral reflexion also change. The contraction of vessels causes a resistance, consequently renders the arteries less distensible; therefore the amplitude of pulse-waves is smaller, the rise of systolic pressure is steeper and the dicrotic wave is drawn nearer to the top of systolic pressure, since in the time of its appearance the usual amount of blood — because of contraction of vessels — cannot entirely escape from the examined point. The position of the dicrotic waves on pulse-tracings depends only on this amount of the heart's-output which remains in the time of the dicrotic wave in the examined point of artery; if the total output escapes before the dicrotic period, the dicrotic wave lies then on the base line of pulse pressure; in the case of a great dilatation of vessels the amplitude of pulse-pressure is small and the dicrotic wave disappears. After the injection of amyl nitrate or application of heat the aspect of pulse-pressure alters, not owing to the disappearance of reflected waves as states v. Kries but because of the facilitation of the blood-ebbing according to Hoorweg, rendering the pulsation of arteries worse or extinct, and it is well known that the dicrotic wave is connected with most perfect pulsation. The dicrotic acceleration of blood possesses a similar behaviour to the dicrotic pulse-pressure wave; it becomes smaller till total extinction during the dilatation of vessels, it increases up to certain limits by improving the pulsation when the pressure rises.

The statements of Fick and Frank do not confirm the influence of peripheral reflexion upon the pressure, being only particular signs of pressure in a pulsating system of tubes. The uniform outflow from such system is connected with special pressure. The pressure of the blood in arteries according to the above investigations is as follows: the diastolic pressure in the arterial ramifications is higher than that in their main-arteries, it rises towards periphery more and more. The systolic pressure diminishes in the same manner. Hence the amplitude of pressure in the pulsating ramifications is smaller than that in main-arteries and lies in the sphere of the central amplitude. In small arteries below 0·3—0·2 mm. bore all waving of pressure as well as that of movement is extinct, owing to the great cross-section sum and very great viscosity of the flowing blood. In bigger vessels, however, it may occur that the systolic pressure in a ramification (e. g. femoral artery) be higher than that in its artery (aorta) or that the diastolic pressure may be lower in a peripheral artery; but this fall of diastolic pressure is not a habitual state because in the same experiment it rises or falls for a given time, especially in smaller arteries, in connection with the local change of the tonic state of precapillaries.

The scheme of blood pressure in pulsating arteries is shown by the big lines on the Fig. 5; thin lines represent the pressure in some experiments. The pressure in small vessels is levelled by the rising of diastolic pressure and the diminishing of the systolic one. A very great part of heart's energy, which is not taking part in the blood-motion, is transported before the capillary system, and is at the disposal of the blood flow in the tissues. The rising of diastolic pressure is caused evidently by the I-order pressure- and motion-waves, which are aided also by II- and III-order waves. All this waving disappearing in the bores of 0·3—0·2 mm. produces before the capillaries a steady pressure, equal to the mean central pressure, as well as relatively very quick uniform linear motion.

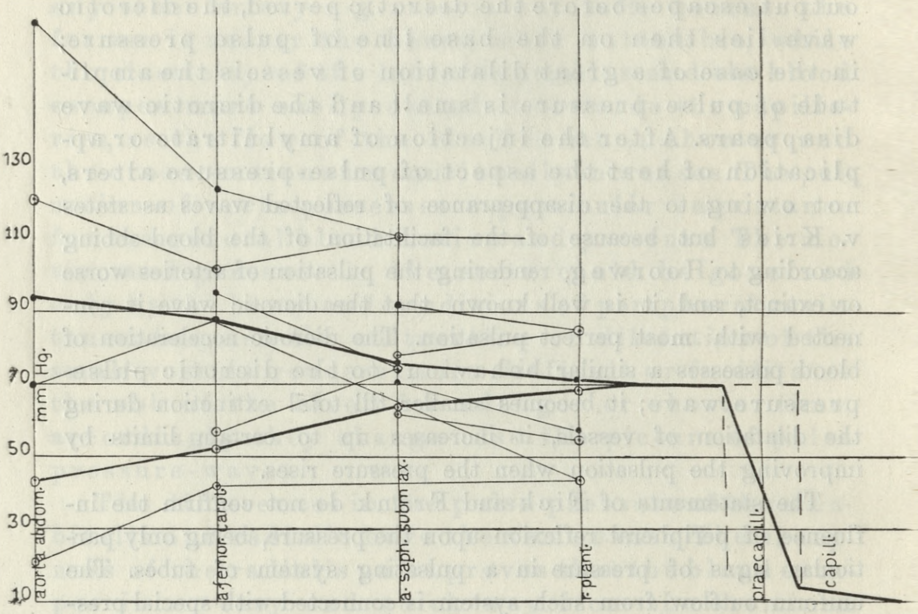

Fig. 5.

What is the cause of such a behaviour of pressure and motion? The supposed peripheral reflexion of systolic waves, the energy of which ought to deteriorate the pressure as directed towards the heart, evidently can't be taken into account in the explanation of this phenomenon. We shall find the cause in pulsation of the arteries according to the experiments with a rubber-tubes system.

Experiments.

Pressing 6·5 cm. cub. of the water periodically into a lead-tube with a rate of 66 per minute, we get such a pressure at the commencement (manometer M_0) and at the end of this tube (manometer M_1):

		min.	max.	amplit. mm. Hg.
1.	M_0	0	434	434
	M_1	0	197	197
2.	M_0	156	297	141
	M_1	68	99	31

After introduction of a flask of 70 cm. cub., filled up with water to the half of its volum, the bottom of which is upwards turned (air chamber), the outflow of the water becomes uninterrupted, it is appearent a positive minimum of pressure, and a smaller amplitude (2).

In a rubber-tube 0·55 cm. of bore, 5 m. long the pressure is such:

		min.	max.	amplit. mm. Hg.
3.	M_0	176	372	196
	M_1	146	331	185

The fall of pressure is not so steep, there is a small difference in the size of central and peripheral amplitude (3).

		min.	max.	amplit. mm. Hg.
4.	M_0	203	297	94
	M_1	146	272	126

After including of the air chamber minimal pressure in M_0 increased, while in M_1 didn't change. The maximal pressure fell in both manometers. The peripheral amplitude is larger than the central one (94, 126).

		min.	max.	amplit. mm. Hg.
5.	M_0	248	378	130
	M_1	219	337	118

The acceleration of the pulse-rate to 84 p. min. causes a rise of pressure. The peripheral minimum increased more than the central one (73 and 45), while the rise of the peripheral maximum, on the contrary, was smaller than that of the central one (65 and 81). 5).

The augmentation of the water output from 9 to 12·5 cm. cub. causes a further rise of minimum and maximum of pressure; but in the periphery (M_1) however the growth is greater, and that is why the fall of pressure along this rubber-tube 5 m. long, amounts only to 15 mm. Hg.

It were important, for the explanation of the blood-pressure course in arteries, to make the peripheral minimum and maximum higher than the central ones. In these conditions as above, I could not do it, but it is easy to attain in a bifurcated rubber-tube system as in Fig. 6. The output of 9·2 cm. cub. with a rate 72 p. min. dislocates the pressures as shows exp. 6.

6.	M_0	146	372	226
	M_1	33	122	89
	M_2	29	108	79
	M_3	29	108	79
	M_4	17	50	33

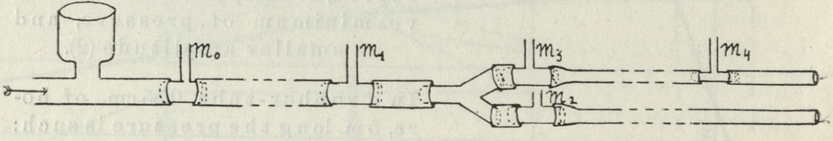

Fig. 6.

After having made narrower the end of the tube with manometer M_4, they rose minimum and maximum, but the latter in a greater degree. The amplitude was also larger excepting M_0. (7).

7.	M_0	214	434	220
	M_1	103	208	105
	M_2	94	192	98
	M_3	94	192	98
	M_4	42	79	37

Rendering the outflow yet more difficult by straitening the end of the other tube with manometer M_2, effects a rise of minimum towards periphery (310, 317, 337, 344), that of the maximum as well (419, 434, 446). The amplitude is also larger, and we meet with the peripheral amplitude being greater than the central one (97 and 102) (8). Similarly in the pulsating arteries the minimum of blood-pressure don't fall peripherwards but it raises, also the maximum of pressure is higher in the ramifications

8.	M_0	456	652	196
	M_1	310	419	109
	M_2	317	434	117
	M_3	337	434	97
	M_4	344	446	102

than in their arterial trunks (femoral, saphena art.). It depends on the pulsation connected with a suitable ebbing of the liquid. If the ebbing is difficult, then the minimum and maximum in a ramus lie higher than these in main-arteries.

9.	M_0	477	702	225
	M_1	456	534	78
	M_2	424	554	100
	M_3	424	524	100
	M_4	424	524	100

A change of the output of the pump from 9·2 to 11 cm. cub. dislocates the pressures another. In the commencement of the tube there is a slight rise of minim. ad maxim. (21 and 50) (9). Just before the bifurcation minim. increases 146, maxim. 115 mm. Hg.; beyond it minim. and maxim. present a horizontal line. The amplitude of pressure in the manometer M_0 is larger 30, before the bifurcation in M_1 is smaller 30 mm. Hg. than in the exp. 8; in the M_2, M_3, M_4 it is some smaller than it was formerly, although the output was greater.

10.	M_0	236	424	188
	M_1	94	181	87
	M_2	71	146	75
	M_3	89	181	92
	M_4	89	181	92

The opening of the end of the tube with manometer M_2 causes a general fall of pressures and their amplitudes (10). The lowest pressure and the smallest amplitude is in the open tube. In the partially closed tube (M_3, M_4) the pressures are equal, and their amplitudes are greater (92) than in the main-tube M_1 (87); it is appearent a slight fall of diastolic pressure on the length M_1—M_3, while the systolic pressure is the same (181).

11.	M_0	181	392	211
	M_1	42	111	69
	M_2	33	71	38
	M_3	42	89	47
	M_4	17	42	25

Making free the end of the branch with manometer M_4, lowers very the general pressure. It appears the fall of maximum of pressure, the minimum in M_1 and M_3 is levelled, in M_2 and M_4 it is lower owing to the easier ebbing of the water. The minimal pressure and the maximal as well in a branch are independent on the pressures in other places of a pulsating system, In this rubber-tubes system so primitive in comparison with the arterial-system, one can ad libitum raise the diastolic peripheral pressure above that of the central one, by a suitable choice of output and rate of pressing; one can change the maximum of pressure and influence the amplitude of peripheral pressure either by facilitating the liquid's outflow or by rendering it more difficult. In short, one can reproduce all these signs of pressure which we meet in the arterial system. It is evident that such a picture of blood pressure, as we described above, is due to the pulsation of vessels.

The pulsation of the aorta causes, that not the whole work of the heart's systole changes into kinetic energy in the form of systolic acceleration, but that its greater part accumulates potentially as dilatation of aorta and elastic arteries, and in the further kinetic form becomes apparent only later at the diastole as the dicrotic acceleration. That latter kinetic part has even a greater effect than the former (i. e. systolic), as the dicrotic acceleration in the aorta is as a rule greater than the systolic one. The motion of blood in the aorta and arteries consumes only a very small part of heart's energy, and we have then to find an explanation for the rest of its energy, for the statical one. According to my calculations about 30% of the work of a heart's-period amounting e. g. to 0·123 kgm. is used for the blood motion; i. e. the systolic acceleration (50 mm. p. sec.) consumes 2·5%, the maintenance of the diastolic motion (500 mm. p. sec.) 25%, and the dicrotic acceleration (70 mm. p. sec.) 3·5%. The remaining 69% according to present view-points are used in overcoming resistance; they perish without any use or taking part in circulation. If we consider the proper course of arterial pressure, we find this 69% near the tissues in statical form as a mean pressure, between the minimum and maximum of that in the aorta. On the way to small arteries the waving of pressure is levelled as in Fig. 5 by the increase of the minimum and decrease of the maximum. The fall of the maximum is caused by the increase of the sum of cross-sections and consumption of energy spent for pulsation and overcoming the viscosity of blood in small vessels. The rise of minimum is due to pulsation. In case of non-existence of pulsation the pressure even in the aorta and big arteries would have another aspect, and there would be a fall of minimum simultaneously with a normal fall of maximum.

The haemodynamic of the circulatory system will become more comprehensible if looked at from other view-point.

The blood-pressure line (Fig. 5) shows that the way of the arterial blood must be physiologically divided into three parts, possessing different degrees of importance for the moving blood. All pulsating arteries represent a reservoir at the end of which is a high and steady pressure. From this reservoir the blood flows out through the non-pulsating, tonically contracted channels. This second part acts as a dam with a network of sluices trough which the blood escapes to the third part of the arterial route — to the capillaries. On one side of this dam there is constant, levelled, high arterial blood-pressure, on the other side nearly 10 times lower capillar-pressure. How is it with the pressure in this second middle system? It is apt to vary. In the case of contraction of an investigated arteriole when the blood scarcely flows, the pressure in it is low; if the vessel is, on the contrary dilated and blood-flow is strong, the pressure is high, and then we may meet with a precapillar-pulse. It is clear that in a system arranged only in such a manner, a little dilatation of such sluices — precapillaries — is able to augment greatly (up to many times) the capillary flow just in that moment when the working tissues require it. In this second part of arterial route the pressure and motion are subject to the known hydraulics laws: they depend both on the length of non-pulsating vessels, their cross-section and viscosity of blood. The dilatation of a part of these sluices if great enough can lower the pressure in one or some arteries, can change the pulse-pressure, diastolic pressure-line etc. This second section, unfortunately, anatomically and physiologically is not yet fully explored.

Agreeing to such a division one cannot consider the differences of pressure in big arteries (aorta, carotis) in comparison with that of non-pulsating vessels as a loss of energy owing to friction. According to the views of Bohomolec and others 90% of the heart's work has to be consumed in overcoming resistances on the way from aorta to arteria auricularis media of a rabbit. But we see that such is not the case, as the heart's energy is transferred by the pulsation of vessels just before the capillar circulation in the form of a static energy of the pressure of blood. The heart and all pulsating arteries are the first functional unit. In this first unit normally we cannot speak about blood-pressure fall. Already Th. Young[1] (1809) had a similar conception when stating the pressure in arteries, somewhat thicker than human hair, 90% of that in central arteries. Poisseuille also couldn't find any pressure fall in the whole pulsating system. His opinion was shared by E. H. Weber. Afterwards Donders, Rollet, Fick suggested that the pressure was not decreasing in the arteries, only in the capillaries or small veins. Other investigators, on the other hand, approved the views of Volkmann (1850) about the consumption of a great part of pressure in arteries. Campbell formulated Volkmann's view so, that the fall of pressure in big arteries is comparatively speaking not great, being quick in small arteries; that opinion is to-day generally accepted. It is not difficult to find an explanation of the causes of these two different view-points when basing on my experiments upon dogs and rubber-tubes system. Young, Poisseuille, Donders, Fick were examining the pressure only in pulsating arteries, i. e. in the first part of the arterial blood section, and that is why they have not found the fall of pressure. Volkmann, Campbell and others compared the pressure in the pulsating system with that in a non-pulsating one. In short, they compared the pressure in the main-irrigating collector with that in a blood-escape channel. Some fall of pressure sometimes occurring in my experiments is not a habitual state but temporary and local, in consequence of the facilitation of the blood ebbing when the precapillaries are dilated. It is a local phenomenon without any influence on the pressure in adjoining vessels. Hence a fall of pressure can be observed in a healthy organism if measured in a temporarily dilated peripheral pulsating vessel or in a non-pulsating one. That is, I suppose, the cause of conflicting opinions of the former class of authorities.

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[1] Hand. d. norm. u. pathol. Physiol. 1927, XVII/2, 905.

The third section of arterial blood route is represented by the capillaries served by the first and second sections. The capillaries directly dispose with the function of precapillaries, they cause the contraction or dilatation of these vessels-sluices in the way of axonreflex. In the case of dilatation of a great part of capillaries, the danger of an extreme lowering of pressure at the end of the collector, i. e. before the capillaries, involves into action the heart, which by the acceleration of pulse-rate and increase of the output is able to some extent to maintain the pressure at such a height, which is required to satisfy a greatly increased capillar blood-motion. But if the heart is not able to transport by pulsation of arteries so much energy in static form near the capillaries at it is required, briefly, if there is apparent a fall of pressure during the work, then there appears the failure of the circulatory system, inability for further work. In some diseases accompanied with a poorer pulsation of arteries (e. g. sclerosis) or with a heart weakness, the course of the pressure cannot be typical, there must be a certain fall of diastolic pressure and the blood motion differs from that in a perfectly pulsating system and begins to be similar to the motion in stiff tubes.

Some individuals notwithstanding a healthy circulatory system may have in section I or II *locus minoris resistentiae.* A weak heart which meets the requirements of the work with an accelerated pulse-rate, doesn't produce such an efficient pulsation as a healthy heart, because the quicker the pulse-rate, the smaller is its amplitude. The failure of the I section is caused only in the arteries themselves if changed pathologically. As to the 2nd section there can arise too great a lability of its tonic state and consequently there follows inability for physical exertion. At any rate the matter is whether the heart and pulsation of arteries are able under different conditions to hold the pressure before the capillaries on a required height: on the other hand the matter is whether the precapillaries, regulating the pressure and motion, can supply the working organs with blood without a harmful lowering of pressure in the pulsating collector. On the contrary individuals hardened in work present a striking antithesis. Their first section is marked by distinctly slow pulse-rate, a low minimum, hence a great amplitude of pressure, in short, by a perfect pulsation, which transports so great a part of heart's-energy in the static form before the organs, and owing to the dicrotic acceleration facilitates the heart work in such a high degree. It follows that in physiological classification it is not so much the state of the heart which is decisive as the course of pressure in the pulsating section of arteries, the transferred sum of the heart's energy before the tissues. The suitability of these views regarding man will be properly demonstrated by further investigations; since possessing the criterion of a regular pressure-course in arteries, the lack of which is often felt, it will be easier te tell about the condition of the circulatory organ, and draw a strict and definite line between healthy and diseased individuals.

Conclusions.

The experiments in which I investigated blood movement simultaneously with blood-pressure in the same vessel show that there exists a complete harmony between velocity and pressure.

In the heart's waves the systolic acceleration appears at the same moment as the systolic pressure, the diastolic velocity comes in view simultaneously with diastolic pressure. As to the size of pressure and velocity, they are both in some certain constant proportion, which is disturbed by respiratory waves or by changes of the ebb through the action of precapillaries.

The dicrotic acceleration is also concordant with the dicrotic pressure in small arteries. But in big vessels there is a disharmony, because in the aorta during the dicrotic pressure the blood movement is more accelerated than during the systolic pressure; in the upper part of the femoral and carotid arteries the dicrotic acceleration is mostly equal to the systolic one or a little smaller; in the lower part of the femoral artery the diastolic acceleration exceeds the systolic on the top of the respiratory waves, if the respiration is sufficiently deep. But this disharmony proves neither the existence of reflected waves nor their influence upon the blood motion, because after the systolic acceleration the blood movement does not show such a relaxation as in the former experiments of Lortet and in recent investigations of Ph. Broemser, but on the contrary it is quicker.

The respiratory waves of velocity and pressure show a general parallelism. The maximum of the systolic pressure of a respiratory wave synchronises in any given heart-period with the maximum of the dicrotic acceleration and with that of diastolic velocity; only in the next heart-period the maximum of diastolic pressure of this respiratory wave coincides with the maximum of the systolic acceleration. This proves that the rising pressure of the respiratory waves extending over the whole pulsating system diminishes the resistance and so facilitates the blood flow; since the peak of the pressure wave reaches each respective artery more quickly than does the maximum movement produced by the heart, therefore the maximum of systolic respiratory pressure causes at first the maximum of the dicrotic acceleration and of diastolic velocity. The same is caused by systolic pressure in the heart beat, large portions of the arteries being extended, and that is why after each systole, i. e., during the dicrotic and diastolic times, blood flow is facilitated. But this influence of the systolic pressure on the flow in short first-order waves is rather difficult to see by this simple method, but is is manifest in long respiratory waves which, from this point of view, could be regarded as long heart waves. The respiration plays a very important part also in the flow of arterial blood.

The relationship of third-order linear waves to those of pressure has not yet been investigated.

The measurement of pressure by the help of the air-manometer explains also the question of blood-pressure. The rule is that the amplitude of pressure-waves in the arterial branches is smaller than that in main arteries and lies in the sphere of central amplitude; the diastolic pressure rises towards the periphery more and more, the systolic pressure diminishes, and in small arteries below 0·3—0·2 mm. bore, all waves of pressure as well as of movement are extinguished. But it may occur that the systolic pressure in a ramus is higher than in the artery at a given time or, that the diastolic pressure is lower in a peripheral artery; but it is not an habitual state, because in the same experiment the diastolic and systolic pressures, especially in smaller arteries, rise or fall relatively to the action of precapillaries. The scheme of blood-pressure is shown by the heavy lines in Fig. 5. In this way the blood-pressure in small vessels is levelled, and a great part of the heart's energy, which is not taking part in the blood-movement before it is transported to the capillary system, is at the disposal of the blood-flow in the tissues.

In the course of the arterial-blood three segments can be discerned. All the pulsating arteries represent a cistern (reservoir), at the end of which the blood-pressure is high and steady; from it the blood flows out through the non-pulsating, tonic contracted channels just as the water in an irrigation-system runs through the sluices in a dam. This is the second segment. The third is represented by the irrigating-channels, the capillaries. In the first segment there is a high blood-pressure, in the third segment it is one tenth as high. The pressure in the second segment depends on the contraction or dilatation of the respective vessel; if there is a contraction before the capillaries the pressure is high, if on the contrary the non-pulsating vessel is dilated there is apparent a lower pressure than in the pulsating system. From this point of view a difference of pressure in a big and a small artery can not be regarded as an argument for the regular arterial pressure fall, because the pressure in peripheral vessels is changing. This is concordant with the statement of Th. Young and Poisseuille.

The behaviour of blood-flow and pressure in the arteries is characterised by particular signs, such as dicrotic acceleration of the movement, the smaller linear velocity and smaller systolic acceleration of the blood in the arteries than in their rami, as well as by quicker linear movement in the peripheral vessels not proportional to the sum of their cross-sections; farther the lack of pressure-fall in the pulsating vessels, the lower systolic pressure in the arteries (e. g., femoral, carotid artery) than in their rami, which sometimes occurs. We have no proofs for the influence of the reflexion of the heart's wave in the periphery as the cause of these characteristic signs. The only reason is the pulsation of arteries. In fact we find the same phenomena of movement and pressure in a ramified system of rubber-tubes, when their pulsation is distinct and strong.

Wzrost ontogenetyczny a regeneracyjny u axolotla. — La croissance ontogénétique et la croissance régénérative chez l'Axolotl[1]).

Note préliminaire

de M. ***E. GODLEWSKI*** m. t. et de M^lle ***I. LATINIK,***

présentée dans la séance du 13 janvier 1930.

Introduction. Le problème à résoudre.

Les recherches sur la croissance des organismes sont appelées à jouer un rôle très important dans l'étude des phénomènes formatifs, d'autant plus que la croissance est une manifestation de la formation de la matière vivante. Ces recherches ont porté surtout sur la croissance ontogénétique; il ne faut cependant pas perdre de vue, que la régénération et les néoplasmes sont également des manifestations du pouvoir de proliferation et de croissance des organismes. Ces phénomènes méritent donc d'attirer notre attention.

Ce sont les botanistes qui les premiers ont étudié le problème de la croissance. Ils avaient à leur disposition un matériel plus approprié à ce genre d'investigations. En effet chez un grand nombre d'espèces végétales, la croissance est pour ainsi dire illimitée et dure toute la vie. D'autre part, les plantes n'étant pas dotées de motilité, les mensurations linéaires offrent moins de difficultés et peuvent être exécutées dans des conditions plus favorables. Les recherches que firent les botanistes pendant les premières années de la seconde moitié du siècle dernier, concernaient la croissance des différents

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[1]) Les recherches dont on trouvera les résultats résumés dans cettes études, ont été exécutées grâce à une subvention de la Fondation P. Tyszkowski.

secteurs de pousses ou de racines et tenaient compte de la part que prennent les parties de ces organes dans l'augmentation globale de la matière vivante nouvellement formée. Nous savons, grâce aux investigations des physiologistes, que la croissance des différents secteurs est très lente au début, qu'elle est ensuite bien plus intense pendant un certain temps, pour ralentir peu à peu enfin. Les physiologistes appellent »période de grande croissance«, le laps de temps pendant lequel la croissance est la plus intense.

On a étudié chez les animaux soit la croissance ontogénétique de l'organisme dans son ensemble, soit la croissance de ses différents organes. On a fait également des recherches en vue d'établir l'augmentation du volume et l'on a étudié l'accroissement de celui-ci pendant les phases successives du développement, en cherchant à se rendre compte aux depens de quelles substances s'élabore la matière vivante de l'embryon. On s'aperçut à cette occasion du rôle important que jouait l'eau absorbée par les oeufs, par les embryons en voie de segmentation et surtout par les embryons qui avaient atteint des stades de développement plus avancés. On chercha également à fixer une période de grande croissance chez les embryons considérés dans leur ensemble (non pour leurs différents secteurs), mais on vit qu'elle était différente de ce qu'elle est chez les plantes.

Dans la littérature scientifique consacrée à la croissance animale, nous ne trouvons jusqu'à présent pas de recherches systématiques exécutées au moyen de mensurations linéaires, intéressant les différents secteurs des organes axiaux pendant la période de croissance ontogénétique et durant la régénération. Au cours de nos recherches sur la greffe de la peau chez les axolotls, l'un de nous [1]) put observer qu'un morceau de peau provenant d'un axolotl noir, greffé sur un axolotl albinos, produisait une fois en régénération, des cellules noires, lesquelles s'étendaient le long de la queue vers l'extrémité distale de cette dernière. Cette observation nous encouragea à entreprendre des recherches systématiques en vue de déterminer l'intensité de la croissance en longueur et de la fixer aussi bien pendant l'ontogénèse que durant la régénération, pour différents secteurs délimités d'une façon particulière.

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[1]) E. Godlewski: L'hérédité dans les cellules végétatives au cours de la régénération chez l'axolotl. Bull. de l'Acad. Pol. des Sciences et des Lettres. Classe des Sc. Math. et Natur. Série B. Cracovie 1922.

Le problème que nous nous sommes proposé de résoudre au cours de nos recherches, était par conséquent le suivant: il s'agissait de déterminer pendant l'ontogénèse et pendant la régénération, la croissace de secteurs de la queue de l'axolotl, ces secteurs étant autant que possible égaux et placés les uns derrière les autres.

Matériel et méthodes.

Nous nous sommes servis dans nos recherches d'axolotls élevés à l'Institut de Biologie et d'Embryologie de l'Université des Jagellons à Cracovie. Les expériences ont été exécutées sur des animaux qui avaient moins d'un an au commencement des expériences, puis sur d'autres âgés de 18 mois, enfin sur des axolotls de deux ans et demi. Nous avons procédé aux mensurations sur des queues d'axolotls en voie de croissance. Comme l'axolotl ne dépasse jamais l'état larvaire, il ne cesse de croître durant toute la vie. Les déterminations du volume ont été exécutées par M. St. Hiller dans notre laboratoire. On trouvera dans son travail¹) les données concernant l'influence qu'exercent sur la croissance les conditions internes, la nutrition et particulièrement le jeûne.

Il fallait, avant d'exécuter les mensurations, indiquer les limites d'une série de secteurs situés les uns derrière les autres. Nous avons d'abord essayé de les marquer au moyen d'anneaux confectionnés avec du fil d'argent que nous fixions les uns après les autres. Ce procédé ne donna cependant pas de bons résultats, car on voyait se former des escarres par suite de la pression exercée sur les tissus par le fil d'argent, de sorte qu'une croissance normale était impossible dans ces conditions. Nous avons donc eu recours au tatouage, au moyen duquel nous marquions les limites des secteurs dans les expériences suivantes. Nous avons tracé des lignes perpendiculaires à l'axe de la queue depuis la base de celle-ci, en faisant une série de piqûres dans lesquelles nous introduisions de l'encre de Chine dans la peau d'un Axolotl albinotique. Nous nous sommes servis à cet effet d'une aiguille munie d'un manche, en la trempant dans l'encre de Chine avant de faire une piqûre. Les piqûres que nous faisions pour tatouer les lignes

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¹) S. Hiller, Wpływ głodu na regenerację u axolotla. Rozprawy Wydz. mat.-przyr. Polskiej Akad. Um. T. 67. B. 1928.

délimitant les secteurs, étaient exécutées à l'état de narcose. Lorsque l'animal est ainsi immobilisé et ne contracte pas les muscles de la queue, on réussit à exécuter les mensurations avec plus de précision. Nous nous servions d'une solution d'uréthane à 1% pour narcotiser les animaux.

Les lignes-limites tatouées étaient séparées par des intervalles plus ou moins égaux, dont la longueur mesurait le plus souvent 10 mm. Les intervalles, dont la longueur augmentait à mesure que croissaient les secteurs, étaient mesurés de temps en temps. En dehors des mensurations en rapport avec la croissance ontogénétique, nous avons appliqué la même méthode pour mesurer la croissance des différents secteurs de la partie régénérée. Nous coupions la queue d'un axolotl à proximité de la base, et nous stimulions ainsi la régénération. Une fois que la partie régénérée avait atteint une certaine longueur (2 cm environ), nous délimitions comme auparavant des secteurs placés les uns après les autres et nous les marquions par des lignes tatouées, s'étendant en sens transversal, après quoi nous mesurions l'augmentation de la longueur des intervalles. Lorsqu'à la suite d'une croissance plus prolongée ou plus intense, certaines lignes-limites s'étaient fortement éloignées les unes des autres, on divisait l'intervalle devenu trop long en deux ou en plusieurs secteurs, en traçant de nouvelles lignes transversales et l'on continuait à faire des mensurations. Les piqûres devenaient généralement indistinctes (d'habitude après plusieurs semaines), aussi fallait-il y introduire encore une fois de l'encre de Chine. Disons en passant que les piqûres disparaissaient le plus tôt dans les secteurs les plus jeunes de la partie régénérée. Lorsque plusieurs axolotls étaient placés dans le même aquarium, on voyait certains animaux ronger et mutiler les queues des autres, aussi dut-on les isoler et les mettre chacun dans un autre récipient. La durée d'une expérience s'étendait à plusieurs mois. La croissance de la queue n'était parfois pas symétrique à la suite d'une lésion unilatérale. Les animaux qui présentaient cette anomalie ne servaient pas aux expériences.

Les résultats des recherches sur la croissance ontogénétique.

Nous avons considéré comme mesure de la croissance ontogénétique, l'accroissement de la longueur de la queue chez un axolotl se développant normalement. On sait que lorsque la métamorphose n'a pas été déclanchée artificiellement chez cet animal, il est doté de tous les caractères d'un organisme larvaire et on pourrait croire que sa croissance peut se continuer indéfiniment. La queue de l'axolotl était divisée en secteurs au moyen de lignes tatouées, que nous tracions en procédant d'après la méthode indiquée dans le chapitre précédent, puis nous mesurions à des intervalles de plusieurs semaines, les distances séparant les lignes-limites. Lorsqu'on procède fréquemment aux mensurations et lorsque par conséquent les accroissements sont relativement insignifiants, les chances d'erreurs sont évidemment plus élevées, de sorte qu'elles peuvent compromettre la clarté des résultats. Dans les tableaux qu'on trouvera ci-dessous, nous avons indiqué par des chiffres romains les secteurs se suivant depuis la base de la queue jusqu'au bout de celle-ci. Dans chaque tableau, nous indiquons dans la partie A, les dimensions des secteurs mesurés, tandis que dans la partie B, nous donnons le pour-cent de l'accroissement, par rapport à la longueur du secteur, fixée par la première mensuration.

En examinant les chiffres des tableaux ci-dessous, nous devons faire abstraction d'abord de la dernière colonne à l'extrême droite (colonne V dans les tableaux 1 et 2; colonne VI dans les tableaux 3, 4, 5, 6; colonne VII dans les tableaux 7, 10; colonne VIII dans les tableaux 8 et 9). Si nous comparons les chiffres qui indiquent la longueur des secteurs dans la partie A et qui dans la partie B expriment le pour-cent de l'accroissement en longueur par rapport aux dimensions des secteurs fixées par la première mensuration, — nous ne tardons pas à nous apercevoir que la croissance est à peu près la même dans tous les secteurs, respectivement que les variations sont partout relativement peu fortes. La comparaison des chiffres exprimant l'accroissement, tels qu'on peut les noter pour tous les secteurs, à l'exception du secteur terminal, nous permettrait de conclure que la croissance en longueur est uniforme dans toute l'étendue de la queue. On s'en aperçoit en examinant les figures 1 et 2 (p. 89).

Notre analyse serait pourtant incomplète si nous ne tenions pas compte de la façon dont se comporte le secteur terminal. Nous observons de très fortes différences lorsque nous comparons les chiffres correspondant à l'acroissement de ce secteur dont la longueur est indiquée dans la dernière colonne à droite de nos ta-

TABLEAU 1 (expérience nº 44 e).

L'animal avait environs 9 mois au commencement des expériences.

A)

Durée de la période de croissance	Longueur des secteurs délimités (en mm.)				
	I	II	III	IV	V
Longueur initiale	9·5	10	10	10	10
3 mois et demi	14·5	15	15	15·5	16·5
7 mois	16·5	17·5	17	17·5	19

B)

Durée de la période de croissance	Pour-cent de l'accroissement des secteurs				
3 mois et demi	50	50	50	55	65
7 mois	70	75	70	75	90

TABLEAU 2 (expérience nº 44 a).

L'animal avait environ 9 mois au commencement des expériences.

A)

Durée de la période de croissance	Longueur des secteurs délimités (en mm.)				
	I	II	III	IV	V
Longueur initiale	9·5	9·5	9·5	8·5	9·5
2 mois	13	13	13·5	13	15
4 mois et demi	15·5	15·5	16·5	15·5	21·5

B)

Durée de la période de croissance	Pour-cent de l'accroissement des secteurs				
2 mois	35	35	40	50	60
4 mois et demi	60	60	70	80	125

TABLEAU 3 (expérience n⁰ 44 f).

L'animal avait environ 9 mois au commencement des expériences.

A)

Durée de la période de croissance	Longueur des secteurs délimités (en mm.)					
	I	II	III	IV	V	VI
Longueur initiale	10	10	10	10	10	10
3 mois et demi	15·5	15	15	15	14·5	13
7 mois	17	17	17	17	17	15·5

B)

Durée de la période de croissance	Pour-cent de l'accroissement des secteurs					
3 mois et demi	55	50	50	50	45	30
7 mois	70	70	70	70	70	55

TABLEAU 4 (expérience n⁰ 44 b).

L'animal avait environ 9 mois au commencement des expériences.

A)

Durée de la période de croissance	Longueur des secteurs délimités (en mm.)					
	I	II	III	IV	V	VI
Longueur initiale	10	10	10	10	10	10·5
2 mois	12·5	13	13	13	12·5	11
4 mois et demi	14·5	14·5	15·5	15	14·5	13

B)

Durée de la période de croissance	Pour-cent de l'accroissement des secteurs					
2 mois	25	30	30	30	25	5
4 mois et demi	45	45	55	50	45	25

TABLEAU 5 (expérience nº 44 d).

L'animal avait environ 9 mois au commencement des expériences.

A)

Durée de la période de croissance	Longueur des secteurs délimités (en mm.)					
	I	II	III	IV	V	VI
Longueur initiale	9·5	9·5	10	10	10	10
2 mois	12	11·5	12	12	12	12
4 mois	14	13	14	14	14·5	14

B)

Durée de la période de croissance	Pour-cent de l'accroissement des secteurs					
2 mois	25	20	20	20	20	20
4 mois	50	40	40	40	45	40

TABLEAU 6 (expérience nº 44 c).

L'animal avait environ 9 mois au commencement des expériences.

A)

Durée de la période de croissance	Longueur des secteurs délimités (en mm.)					
	I	II	III	IV	V	VI
Longueur initiale	10	10	10	10	10	9
2 mois	12·5	12·5	12·5	12	11·5	7·5
4 mois et demi	14	14·5	13·5	14	13	10
8 mois	14·5	15	14·5	14·5	13	9

B)

Durée de la période de croissance	Pour-cent de l'accroissement des secteurs					
2 mois	25	25	25	20	15	—16
4 mois et demi	40	45	35	40	30	11
8 mois	45	50	45	45	30	0

TABLEAU 7 (expérience nº 29).

L'animal avait environ 18 mois au commencement des expériences.

A)

Durée de la période de croissance	Longueur des secteurs délimités (en mm.)						
	I	II	III	IV	V	VI	VII
Longueur initiale	10·5	10	10	10	10	10	9
3 mois	11·5	10·5	11	11·5	11·5	11·5	16
6 mois et demi	12·5	11·5	12·5	12·5	12·5	12·5	19

B)

Durée de la période de croissance	Pour-cent de l'accroissement des secteurs						
3 mois	9	5	10	15	15	15	80
6 mois et demi	20	15	25	25	25	25	110

TABLEAU 8 (expérience nº 30).

L'animal avait environ 18 mois au commencement des expériences.

A)

Durée de la période de croissance	Longueur des secteurs délimités (en mm.)							
	I	II	III	IV	V	VI	VII	VIII
Longueur initiale	10	10	10	10	10	10	10	16
3 mois	11	11·5	11	11	11	11	11	15·5
6 mois et demi	12	12·5	13·5	12·5	12·5	13·5	13·5	19
9 mois et demi	13·5	13·5	14	13·5	13·5	15	15	22·5

B)

Durée de la période de croissance	Pour-cent de l'accroissement des secteurs							
3 mois	10	15	10	10	10	10	10	—3
6 mois et demi	20	25	35	25	25	35	35	20
9 mois et demi	35	35	40	35	35	50	50	40

TABLEAU 9 (expérience n⁰ 31).

L'animal avait environ 18 mois au commencement des expériences.

A)

Durée de la période de croissance	Longueur des secteurs délimités (en mm)							
	I	II	III	IV	V	VI	VII	VIII
Longueur initiale	10	10	10	10	10	10	10	5
3 mois	11·5	11·5	11·5	12	11	11	11	4·5
6 mois et demi	12	12	12·5	13	12	12	13	5

B)

Durée de la période de croissance	Pour-cent de l'accroissement des secteurs							
3 mois	15	15	15	20	10	10	10	—10
6 mois et demi	20	20	25	30	20	20	30	0

TABLEAU 10 (expérience n⁰ 33).

L'animal avait environ 18 mois au commencement des expériences.

A)

Durée de la période de croissance	Longueur des secteurs délimités (en mm)						
	I	II	III	IV	V	VI	VII
Longueur initiale	10·5	9·5	10	10	10	10·5	15
3 mois	12	10·5	12	12	11·5	12·5	15·5
6 mois et demi	13·5	12	14	14	14	16·5	19
9 mois et demi	14·5	13	14	14·5	15	17·5	22·5

B)

Durée de la période de croissance	Pour-cent de l'accroissement des secteurs						
3 mois	14	10	20	20	15	20	3
6 mois et demi	30	25	40	40	40	60	25
9 mois et demi	40	35	40	45	50	70	50

bleaux. En effet, dans certaines expériences (comp. les tableaux 1, 3, 5 et 10), ce secteur se comporte comme les autres. En effet dans environ 40°/₀ des cas le secteur terminal s'accroît comme les autres secteurs; dans d'autres expériences (comp. les tableaux 2 et 7), l'accroissement est beaucoup plus grand, tandis que dans d'autres encore il est bien plus petit. Enfin, dans certains cas (comp. le tabl. 8), on observe une modification de la marche de la croissance, en d'autres termes, celle-ci est d'abord bien plus lente pour devenir beaucoup plus rapide pendant les mois suivants.

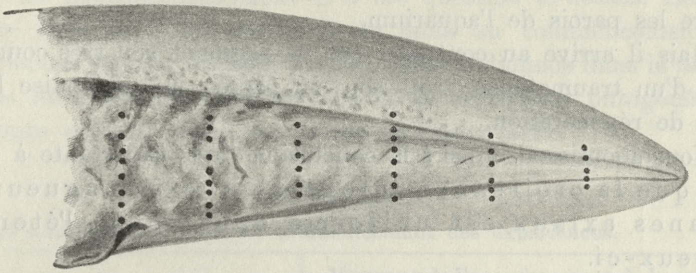

Fig. 1.

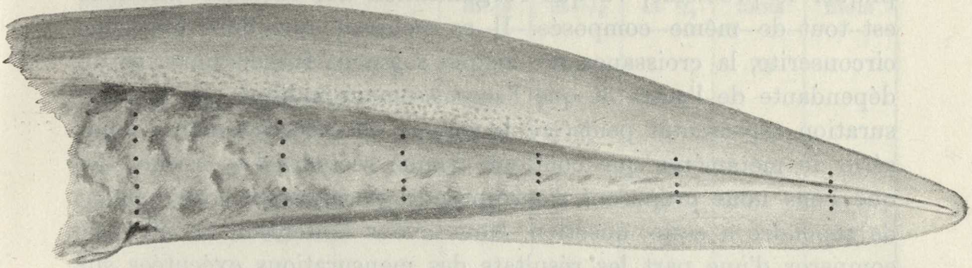

Fig. 2.

La fig. 1. représente la queue de l'axolotl de l'exp. 44 d, sur laquelle on voit des lignes tatouées. La fig. 2 fait voir le même organe après une période de 3 mois. On s'aperçoit que la croissance de tous les secteurs de la queue est uniforme.

Nous comprendrons plus facilement ces phénomènes, lorsque nous aurons étudié la croissance régénérative. Nous verrons alors qu'elle n'est pas aussi uniforme que pendant l'ontogénèse et que la croissance de la partie terminale de l'organe est la plus forte.

En effet, à la croissance ontogénétique se superpose la croissance par régénération, celle-ci étant due aux traumatismes auxquels l'extrémité distale de la queue est exposée par suite des frottements contre les parois de l'aquarium.

Mais il arrive au contraire que ce segment soit très court par suite d'un traumatisme trop souvent répété et qui épuise la faculté de régénération.

Nous aboutissons ainsi à la conclusion, très importante à notre avis, que la croissance ontogénétique en longueur des organes axiaux est uniforme dans toute l'étendue de ceux-ci.

Lorsqu'on examine de plus près la question, on doit se demander si la structure métamérique de l'organe ne vient pas compliquer le problème, vu que l'organisation des secteurs délimités est tout de même composée. Il se pourrait que dans une zone circonscrite, la croissance de chaque segment fut distincte et indépendante de l'autre et que l'accroissement indiqué par la mensuration représentât peut-être la somme des accroissements d'une série de métamères que contient chaque secteur. Les recherches que nous nous proposons d'entreprendre permettront certainement de répondre à cette question. Nous avons l'intention en effet de comparer d'une part les résultats des mensurations exécutées sur des organes axiaux dont la structure est métamérique et de l'autre sur des organes dont l'organisation est plus homogène.

Une autre question que nous devons examiner, est celle de savoir si la croissance des secteurs marqués sur la peau correspond réellement à la croissance de tout l'organe. L'un de nous [1]) a déjà attiré l'attention sur ce problème en étudiant le phénomène de la greffe chez l'Axolotl. Un morceau de peau noire qu'on avait greffée sur un axolotl albinos et qui était situé à la limite de la partie régénérée, commençait à s'éloigner de la naissance de la queue. A présent, que nous avons fait les recherches que nous venons de résumer, nous croyons pouvoir affirmer qu'il s'agit là d'une conséquence de la croissance du secteur situé entre la base de la queue et l'emplacement où avait été exécutée la greffe.

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[1]) E. Godlewski, loc. cit.

L'influence de l'âge sur la croissance de la partie régénérée.

Nous nous sommes servis de deux séries d'animaux pour exécuter les mensurations dont il a été question ci-dessus. Les uns étaient âgés de 9, les autres de 18 mois au commencement des expériences (comp. les tabl. 7—10). Nous indiquons dans le tableau 11 les résultats des mensurations de la croissance ontogénétique, exprimés en pour-cent, pour l'une et l'autre série.

TABLEAU 11.

A) Axolotls de 9 mois au commencement des expériences.

Nr. de l'exp.	Longueur de l'axolotl au commencement des recherches	Moyenne de l'accroissement de la queue, exprimée en $^0/_0$, après une période de				
		2 mois	3 mois et $^1/_2$	4 mois et $^1/_2$	7 mois	8 mois
44 e	102 mm		50		75	
44 a	113 mm	40		70		
44 f	120 mm		50		70	
44 b	140 mm	30		50		
44 d	140 mm	20		40		
44 c	152 mm	25		40		45

B) Axolotls de 18 mois au commencement des expériences.

Nr. de l'exp.	Moyenne de l'accroissement de la queue, exprimée en $^0/_0$, après une période de		
	3 mois	6 mois et $^1/_2$	9 mois et $^1/_2$
29	11	25	—
30	10	30	40
31	15	25	—
33	16	37	47

En comparant les chiffres de la partie A du tableau avec les chiffres de la partie B, on constate que les axolotls plus jeunes

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[1] Nous savons fort bien que ce tableau est incomplet, toutefois cette question ne s'est posée qu'après que nous ayons exécuté nos expériences. Nous comptons faire de nouvelles recherches en vue de l'élucider.

croissent beaucoup plus vite que les animaux plus âgés. Nous voyons ainsi que chez cet animal qui ne depasse jamais le stade larvaire, la croissance diminue, plus l'âge est avancé. Nous n'avons cependant pas pu nous rendre compte si elle s'arrête complètement chez les animaux âgés.

Les résultats des recherches sur la croissance régénérative.

Les données relatives à la croissance ontogénétique de la queue de l'Axolotl que nous avons indiquées dans le chapitre précédent, nous autorisent à nous demander, si l'intensité de la croissance régénérative de cet organe axial est uniforme. La queue d'un axolotl de 18 mois, puis celle d'un animal de 30 mois faisant partie d'un autre lot, était amputée de façon à ce qu'il reste un moignon de 20 à 40 mm. dépassant la base de cet organe. Après avoir attendu que la partie régénérée eut atteint une longueur d'environ 20 mm., nous tracions une série de lignes tatouées pour délimiter aussi bien sur le moignon que sur la partie régénérée, des secteurs s'étendant les uns après les autres. Nous avons mesuré ensuite à des intervalles de quelques semaines, les distances entre les lignes-limites, et nous fixions ainsi les accroissements des différents secteurs. Une fois que le secteur terminal avait considérablement poussé, nous le subdivisions à nouveaux, pour pouvoir observer sur chacun d'eux les acroissements de l'organe.

Pendant que nous étions en train de faire ces recherches et après avoir déjà exécuté une partie des expériences, nous prîmes connaissance du travail tout récemment paru de Kołodziejski[1]) qui est pour ainsi dire une continuation de la note préliminaire (1923) publiée par l'un de nous, que nous avons citée ci-dessus. L'auteur a consacré dans ce travail quelques réflexions à la croissance régénérative qu'il avait observée sur des secteurs délimités par des lignes tatouées dont il avait mesuré la distance. Il aboutit à la conclusion que »Das Wachstum des jungen Regenerats erfolgt dabei wahrscheinlich am raschesten in seinen distalen Partien«. Nous verrons dans la suite que cette conclusion considérée comme probable, a été confirmée par nos expériences. On trou-

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[1]) Kołodziejski Z., Untersuchungen über die Beteiligung der transplantierten Haut an der Regeneration. Bull. de l'Acad. Pol. des Sciences et des Lettres. Classe des Sciences math. et natur. Série B. Cracovie 1928.

TABLEAU 12 (expérience nº 25).

L'animal avait un an et demi au commencement des expériences.

A)

Durée de la période de régénération	Temps écoulé depuis l'exécution des premières mensurations	Longueur des secteurs (en mm.)							
		du moignon				de la partie régénérée			
2 mois et demi		10	10	10	7·5	5·5	5	4·5	6
5 mois et demi	3 mois	10·5	10	10	8	6	6·5	7	$\overbrace{6{\cdot}5\quad 6{\cdot}5\quad 7{\cdot}5}^{20{\cdot}5}$
8 mois	5 mois et demi	10·5	10·5	10·5	8	7	7·5	8	$\overbrace{7{\cdot}75\quad 8\quad 8{\cdot}5}^{24{\cdot}25}$
11 mois et demi	9 mois	11·5	11·5	11·5	8·5	7	7·5	8·5	$\overbrace{8{\cdot}5\quad 8{\cdot}75\quad 8{\cdot}5}^{25{\cdot}75}$
15 mois	12 mois et demi	12	11·5	11·5	8·5	7·5	8	9	$\overbrace{9\quad 10\quad 8}^{27}$

B)

Durée de la période de régénération	Temps écoulé depuis l'exécution des premières mensurations	Pour-cent de l'accroissement des secteurs par rapport à leur longueur initiale							
5 mois et demi	3 mois	5	0	0	7	9	30	35	215
8 mois	5 mois et demi	5	5	5	7	30	50	75	270
11 mois et demi	9 mois	15	15	15	13	30	50	90	300
15 mois	12 mois et demi	20	15	15	13	40	60	100	315

C)

Période comprise entre	Durée de la période	Pour-cent de l'accroissement des secteurs dans une période donnée							
2 m. $\frac{1}{2}$ et 5 m. $\frac{1}{2}$	3 mois	5	0	0	7	9	30	55	215
5 m. $\frac{1}{2}$ et 8 m.	2 mois et demi	0	5	5	0	17	15	14	$\overbrace{19\quad 23\quad 13}^{18}$
8 m. et 11 m. $\frac{1}{2}$	3 mois et demi	9	9	9	6	0	0	6	$\overbrace{10\quad 9\quad 0}^{6}$
11 m. $\frac{1}{2}$ et 15 m.	3 mois et demi	4	0	0	0	7	7	6	$\overbrace{6\quad 14\quad -6}^{5}$

TABLEAU 13 (expérience nº 26).

L'animal avait un an et demi au commencement des expériences.

A)

Durée de la période de régénération	Temps écoulé depuis l'exécution des premières mensurations	Longueur des secteurs (en mm.)						
		du moignon			de la partie régénérée			
2 mois et demi		10	10·5	6	5	5·5	4·5	6·5
5 mois et demi	3 mois	10	10·5	6	6	7·5	9	$\overbrace{8 \quad 8 \quad 6{\cdot}5 \quad 7{\cdot}5}^{30}$
8 mois	5 mois et demi	10·5	11	6	6·5	8·5	10	$\overbrace{9{\cdot}5 \quad 9{\cdot}5 \quad 8{\cdot}5 \quad 11}^{38{\cdot}5}$
10 mois et demi	8 mois	11	11·5	6·5	6·5	9	10·5	$\overbrace{10{\cdot}5 \quad 10{\cdot}5 \quad 9{\cdot}5 \quad 14}^{44{\cdot}5}$
13 mois et demi	11 mois	12	12	6·5	6·5	9	11	$\overbrace{11 \quad 11 \quad 10{\cdot}5 \quad 16{\cdot}5}^{49}$

B)

Durée de la période de régénération	Temps écoulé depuis l'exécution des premières mensurations	Pour-cent de l'accroissement des secteurs par rapport à leur longueur initiale						
5 mois et demi	3 mois	0	0	0	20	35	100	360
8 mois	5 mois et demi	5	5	0	30	55	120	490
10 mois et demi	8 mois	10	10	8	30	65	130	580
13 mois et demi	11 mois	20	15	8	30	65	140	650

C)

Période comprise entre	Durée de la période	Pour-cent de l'accroissement des secteurs dans une période donnée						
2 m. ½ et 5m. ½	3 mois	0	0	0	20	35	100	360
5 m. ½ et 8 m.	2 mois et demi	5	5	0	8	13	11	$\overbrace{19 \quad 19 \quad 30 \quad 45}^{28}$
8 m. et 10 m. ½	2 mois et demi	5	5	8	0	6	5	$\overbrace{10 \quad 10 \quad 12 \quad 27}^{15}$
10 m. ½ et 13 m. ½	3 mois	9	4	0	0	0	5	$\overbrace{5 \quad 5 \quad 10 \quad 18}^{10}$

TABLEAU 14 (expérience n° 27.

L'animal avait 2 ans et demi au commencement des expériences.

A)

Durée de la période de régénération	Temps écoulé depuis l'exécution des premières mensurations	Longueur des secteurs (en mm.)					
		du moignon		de la partie régénérée			
2 mois et demi		11	8·5	5·5	6	4	6·5
5 mois et demi	3 mois	11	9	6·5	8·5	7·4	$\overbrace{7{\cdot}5\quad 6\quad 5{\cdot}5\quad 6\quad 7}^{32}$
8 mois	5 mois et demi	11	9	7	9	9	$\overbrace{9{\cdot}5\quad 7{\cdot}5\quad 7{\cdot}5\quad 8{\cdot}5\quad 10}^{43}$
10 mois et demi	8 mois	12	10	7	10	10	$\overbrace{10{\cdot}5\quad 8{\cdot}75\quad 8{\cdot}75\quad 10{\cdot}5\quad 16{\cdot}5}^{55}$
13 mois et demi	11 mois	12	10	7·5	10	10·5	$\overbrace{11\quad 9\quad 9\quad 11\quad 17{\cdot}5}^{57{\cdot}5}$

B)

Durée de la période de régénération	Temps écoulé depuis l'exécution des premières mensurations	Pour-cent de l'accroissement des secteurs par rapport à leur longueur initiale					
5 mois et demi	3 mois	0	6	18	40	90	390
8 mois	5 mois et demi	0	6	30	50	125	560
10 mois et demi	8 mois	10	18	30	65	150	750
13 mois et demi	11 mois	10	18	40	65	160	790

C)

Période comprise entre	Durée de la période	Pour-cent de l'accroissement des secteurs dans une période donnée					
2 m. ½ et 5 m. ½	3 mois	0	6	18	40	90	390
5 m. ½ et 8 m.	2 mois et demi	0	0	8	6	20	$\overbrace{27\quad 25\quad 36\quad 40\quad 40}^{35}$
8 m. et 10 m. ½	2 mois et demi	9	11	0	11	11	$\overbrace{10\quad 17\quad 17\quad 23\quad 65}^{28}$
10 m. ½ et 13 m. ½	3 mois	0	0	7	0	5	$\overbrace{5\quad 3\quad 3\quad 5\quad 6}^{5}$

TABLEAU 15 (expérience nº 28).

L'animal avait deux ans et demi au commencement des expériences.

A)

Durée de la période de régénération	Temps écoulé depuis l'exécution des premières mensurations	Longueur des secteurs (en mm.)					
		du moignon		de la partie régénérée			
2 mois et demi		10	10	5	5	5	4
5 mois	2 mois et demi	10	10	6·5	7·5	10	$\underbrace{28}_{5\ 5\ 5\ 5\ 5\ 3}$
7 mois et demi	5 mois	10·5	10	7	9	12·5	$\underbrace{43{\cdot}5}_{6{\cdot}5\ 6{\cdot}5\ 7\ 7{\cdot}75\ 8{\cdot}5\ 7{\cdot}75}$

B)

Durée de la période de régénération	Temps écoulé depuis l'exécution des premières mensurations	Pour-cent de l'accroissement des secteurs par rapport à leur longueur initiale					
5 mois	2 mois et demi	0	0	30	50	100	600
7 mois et demi	5 mois	5	0	40	80	150	990

C)

Période comprise entre	Durée de la période	Pour-cent de l'accroissement des secteurs dans une période donnée					
2 m. ½ et 5 m.	2 mois et demi	0	0	30	50	100	600
5 m. et 7 m. ½	2 mois et demi	5	0	8	20	25	$\underbrace{55}_{30\ 30\ 40\ 55\ 70\ 140}$

TABLEAU 16 (expérience nº 10).

L'animal avait deux ans et demi au commencement des expériences.

A)

Durée de la période de régénération	Temps écoulé depuis l'exécution des premières mensurations	Longueur des secteurs (en mm.)						
		du moignon		de la partie régénérée				
3 mois		9·5	8·5	6	4·5	6	7	8
6 mois	3 mois	10	9	7	6	8	10·5	28
								6·5 7 7 7·5
9 mois	6 mois	10	9	7·5	7	9	13	41
								8·5 9 10 13·5
11 mois et demi	8 mois et demi	10	9·5	8	7·5	10	14	46·5
								9·75 10·5 11·5 14·75

B)

Durée de la période de régénération	Temps écoulé depuis l'exécution des premières mensurations	Pour-cent de l'accroissement des secteurs par rapport à leur longueur initiale						
6 mois	3 mois	5	6	17	33	33	50	250
9 mois	6 mois	5	6	25	55	50	85	410
11 mois et demi	8 mois et demi	5	10	30	65	65	100	480

C)

Période comprise entre	Durée de la période	Pour-cent de l'accroissement des secteurs dans une période donnée						
3 mois et 6 mois	3 mois	5	6	17	33	33	50	250
6 mois et 9 mois	3 mois	0	0	7	17	12	24	46
								30 29 40 80
9 m. et 11 m. et ½	2 mois et demi	0	5	7	7	11	8	13
								15 17 15 9

vera dans les tableaux (p. 93—97), les chiffres en rapport avec la croissance de la partie régénérée. Les chiffres de la colonne à droite dans le tableau, indiquent la longueur du secteur terminal de cette partie, tandis que les chiffres au-dessous de l'accolade correspondent à la longueur des secteurs, marqués ultérieurement sur le secteur terminal.

Nous analyserons à présent les chiffres réunis dans les tableaux 12—16. Les chiffres dans les colonnes à gauche du tableau, indiquent la croissance du moignon. Il faut considérer cette croissance comme ontogénétique, aussi son intensité devrait-elle correspondre à la croissance indiquée dans les tableaux 1—10. Cependant, lorsqu'on compare les chiffres relatifs aux accroissements chez les animaux dont la queue n'est pas régénérée avec les chiffres qui correspondent aux animaux qui la reconstituent, on ne tarde pas à s'apercevoir que surtout pendant les premiers stades de la régénération, la croissance des secteurs rapprochés de la base de la queue qui ne se régénère pas, est plus intense que celle du moignon qui produit la partie régénérée. Nous nous apercevons en examinant les chiffres du tableau 12, qu'en 5 mois et demi l'accroissement correspond à 5—7% dans les secteurs du moignon, que ce pour-cent s'élève à 15 après 9 mois et qu'enfin il équivaut à 13—20 après 12 mois. Les animaux dont nous avons indiqué la longueur des secteurs dans les tableaux 13—16, se comportaient d'une façon analogue. Nous sommes par conséquent amenés à conclure que la croissance ontogénétique du moignon est ralentie par suite de la régénération de la queue. Les chiffres qui indiquent la croissance de la partie régénérée, s'accordent fort bien dans nos expériences. Nous avons représenté sur les fig. 3 et 4, la croissance des secteurs de la partie régénérée. Il suffit de jeter un coup d'oeil sur ces figures, pour s'apercevoir que la croissance des secteurs plus rapprochés de l'extrémité est de plus en plus intense. Les chiffres indiquant les accroissements des secteurs de la partie régénérée, qu'on trouve du côté droit des tableaux 12—16, nous apprennent: 1° que la croissance de ces secteurs est plus forte que celle des secteurs du moignon; 2° qu'elle est plus intense, plus le secteur est rapproché de la périphérie; 3° que l'intensité de la croissance augmente dans de très fortes proportions dans le dernier secteur qui est par conséquent le plus à la périphérie. C'est surtout lorsqu'on examine la partie B de nos tableaux où nous avons in-

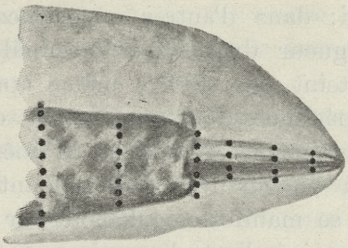

Fig. 3.

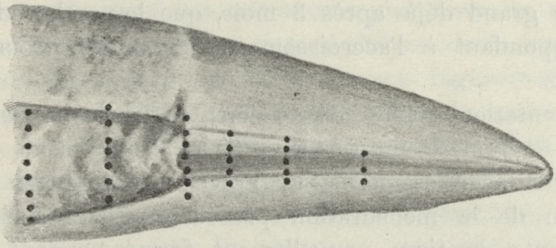

Fig. 4.

La fig. 3 représente la partie régénérée délimitée par des lignes tatouées, 2 mois et demi après le commencement de la régénération (expér. 28).

La fig. 4 fait voir la même partie régénérée 2 mois plus tard.

diqué l'accroissement exprimé en pour-cents des différents secteurs, qu'on s'aperçoit combien il est considérable dans les secteurs terminaux. On observe dans toutes les expériences cet accroissement très fort du dernier secteur par rapport aux secteurs plus rapprochés de la base de la queue. La zone de la plus forte croissance embrasse les quelques derniers milimètres de la partie régénérée. On s'en aperçoit clairement lorsqu'on compare les tableaux 12—15 [1]). En effet, dans les expériences où le secteur

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[1]) Pour permettre de se rendre compte des effets que produit un traumatisme, nous avons donné dans les tableaux ci-dessus les résultats de l'expérience 25 (tableau 12), où à la suite d'une lésion, la partie terminale ne croissait non seulement pas après un certain temps, mais où l'on voyait même sa longueur diminuer. Nous avons indiqué cette diminution par un chiffre négatif.

terminal était plus court, le pour-cent de l'accroissement de celui-ci était bien plus élevé. Ainsi dans l'expérience 28 (v. le tabl. 15), ce secteur mesure 4 mm et l'accroissement atteint 600% après deux mois et demi; dans d'autres expériences (comp. les tabl. 12 – 14), où la longueur du secteur terminal s'élève à 6·5 mm., l'accroissement n'atteint pas 400%, même après une période de 3 mois. Dans les expériences dont nous venons de comparer les résultats, les parties régénérées avaient le même âge. Cette plus forte croissance du secteur terminal pendant les premiers mois de la régénération, se manifeste également par le fait, que le nombre de millimètres qui indique l'accroissement du secteur terminal de la partie régénérée ayant 2 mois et demi, qu'on avait divisée en 4 secteurs à peu près de la même longueur — est environ 3 fois plus grand déjà après 3 mois, que le nombre de millimètres correspondant à l'accroissement des autres trois quarts de cette partie.

L'augmentation rapide des valeurs dans la partie C des tableaux 12—16, offre un grand intérêt. Nous avons indiqué le pour-cent des accroissements par rapport à la longueur déterminée à l'occasion de la mensuration précédente, par conséquent les accroissements de tissu nouvellement formé pendant la période de la régénération comprise p. ex. entre 2 mois et demi et 5 mois et demi, entre 5 mois et demi et 8 mois, entre 8 mois et 10 mois et demi, enfin entre 10 mois et demi et 13 mois et demi. Les chiffres correspondant à la croissance des différents secteurs de la partie régénérée, nous apprennent que l'intensité de la régénération subit une diminution à mesure que dure ce processus. On s'aperçoit par conséquent qu'à mesure que la partie régénérée s'allonge, la croissance des différents secteurs ralentit. Ce ralentissement est peut-être le plus prononcé dans le secteur terminal où la période de croissance très intense ne s'étend pas à plus de 5 ou 6 mois et où l'on voit cette croissance diminuer très rapidement pendant les mois suivants de la régénération. (Comp. le tableau 15 où la croissance du secteur terminal correspond à 600% pendant la période comprise entre 2 mois et demi et 5 mois; 2 mois et demi plus tard, le pour-cent de l'accroissement du secteur terminal nouvellement délimité, atteint 140. Nous voyons une baisse analogue dans le tableau 16; en effet, l'accroissement du secteur terminal qui s'élevait à 250% pendant les trois premiers mois après la délimitation, ne correspond plus qu'à 80%, après les trois mois suivants. Notons que les secteurs terminaux que nous venons de comparer, avaient à peu près la même longueur). Le ralentissement de la croissance est moins prononcé pour les secteurs plus rapprochés de la base de la queue, mais on l'observe dans tous.

Nous voyons par conséquent que la forte croissance des secteurs terminaux ralentit très sensiblement avec le temps et qu'elle finit par être égale à la croissance des autres. C'est à ce moment que la croissance régénérative est terminée à notre avis, aussi peut-on considérer la croissance ultérieure comme ontogénétique, vu son uniformité dans tous les secteurs.

La diminution de l'intensité de la croissance de la partie régénérée, coïncide avec une croissance plus forte du moignon, en d'autres termes, la croissance ontogénétique de la queue devient plus intense, du moment où la croissance régénérative diminue. On la voit passer de 5 à 15 et 20% dans le tableau 12 B, elle monte de 5 et 0 à 10 et 20% dans le tableau 13 B, enfin de 0 et 6, elle atteint 10 et 18% dans le tableau 14. Nous voyons ainsi confirmé le fait déjà mentionné, que la régénération exerce une influence inhibitrice sur la croissance ontogénétique; en effet, à mesure que la régénération ralentit, la croissance ontogénétique de l'animal augmente.

Si nous examinons les chiffres des tableaux 1—10 et si nous les comparons avec les chiffes réunis dans les tableaux 12—16, nous ne tardons pas à nous apercevoir de la différence entre la marche de la croissance ontogénétique et la marche de la régénération. Nous avons vu que les mensurations des secteurs de la queue exécutées au cours de la croissance ontogénétique, permettent de constater des accroissements à peu près uniformes dans toute l'étendue de cet organe. Par contre, la croissance régénérative est loin d'être uniforme. Le secteur apical de la partie régénérée se distingue par la croissance la plus forte et les secteurs situés en arrière de celui-ci, croissent de plus en plus lentement, à mesure qu'on se rapproche de la base. Ce mode de croissance à dû se produire de la façon suivante: lorsqu'au début de la régénération, le bourgeon régénératif en voie de prolifération dont la croissance était rapide en ce moment, a atteint une longueur plus considérable et lorsqu'après un certain temps la période de grande croissance de la partie rapprochée de la base de ce bourgeon a été terminée, il est possible de distinguer dans celui-ci une série de zones, dont celles qui sont plus proches de la base de la partie régénérée croissent plus lentement, tandis que les zones voisines de l'extrémité terminale continuent à être dans la période de grande croissance. A mesure que ces zones s'éloignent de la partie apicale par suite de l'allongement, leur croissance devient plus lente. Nous sommes ainsi en présence de rapports que nous connaissons par les tableaux 12—16: les accroissements des secteurs qui se suivent sont d'autant plus grands que ceux-ci sont plus rapprochés de l'extrémité distale, de sorte que les accroissements atteignent le maximum dans le secteur apical.

Ces zones d'accroissement observées pendant la croissance régénérative, correspondent à la croissance en longueur des organes orthotropiques chez la plupart des plantes. Nous citons à titre d'exemple d'après Popovici[1]), les chiffres en rapport avec la croissance ontogénétique des secteurs disposés les uns après les autres de la racine du Haricot:

XII	XI	X	IX	VIII	VII	VI	V	IV	III	II	I
0	0·25	0·25	0·35	0·6	1·0	1·5	3	5	7	16	1

Ce n'est que la toute petite partie la plus distale qui ne croît presque pas du tout, mais la croissance du secteur périphérique suivant est très rapide, infiniment plus forte que celle du secteur qui vient immédiatement après et celle des autres secteurs plus rapprochés de la base. Si nous faisons abstraction de l'extrémité de la racine, nous voyons que le type de croissance ontogénétique de l'organe axial d'une plante, est identique au type de la croissance régénérative que nous avons observé sur l'organe axial d'un animal.

Croissance et régénération.

La littérature biologique a débattu la question du rapport entre la régénération et la croissance, en considérant le fait que pendant la formation de la matière vivante on voit se manifester le phénomène de la croissance, aussi bien lorsqu'on est en pré-

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[1]) Popovici, cité d'après Benecke-Jost, Pflanzenphysiologie, Jena 1923. T. II, page 24.

sence de la formation de cette matière au cours du développement ontogénétique, que lorsqu'on a affaire à la régénération. Le rapport en question est des plus étroits pour Przibram, qui dans une série d'études s'efforce de fournir des arguments à l'appui de la théorie, suivant laquelle la régénération ne serait qu'une croissance accélérée. Voici ce que nous lisons dans l'introduction d'un des principaux travaux[1]), que cet auteur a consacré à la question qui nous intéresse: »In allen meinen einschlägigen Schriften habe ich seit 1896 die Theorie zu begründen gesucht, dass die im Thierreiche gewöhnlichste Form der Restitution nicht auf dem Erwachen schlummernder Reservekeime, sondern auf einer Beschleunigung des ohnehin fortwährend vor sich gehenden Wachstumsersatzes beruhe«. Les mensurations que Przibram a exécutées sur les pattes de *Sphodromantis bioculata* pour se rendre compte de l'intensité de la croissance ontogénétique et de la croissance régénérative, ont montré que les accroissements étaient sensiblement plus forts pendant la régénération que pendant la croissance ontogénétique. Przibram considère l'inhibition caractéristique de la croissance au cours de la régénération et pendant le développement ontogénétique, comme un autre trait commun à l'un et à l'autre phénomène, aussi croit-il pouvoir appliquer à tout le règne animal, la théorie suivant laquelle la régénération ne serait qu'une croissance accélérée.

Les mensuration exécutées en vue de determiner la vitesse de la régénération chez *Tenebrio*, amènent Křizenecky[2]) à des conclusions analogues. Il existe, d'après lui, »un parallélisme entre la régénération et la croissance normale« (»...lässt sich eine Parallele zwischen der Regeneration und dem normalen Wachstum feststellen«).

L. v. Ubisch[3]) se place à un point de vue différent. Ce n'est pas la croissance, mais la différenciation qu'il considère comme le trait essentiel de la régénération. Dans une organisation polaire,

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[1]) Przibram H., Tierische Regeneration als Wachstumsbeschleunigung. Arch. f. Entw. Mech. 45, 1919.

[2]) Křizenecki J. Ein Versuch sur statistisch-graphischen Untersuchung und Analyse der zeitlichen Eigenschaften der Regenerationsvorgänge. Arch. f. Entw. Mech. Bd. 42, 1916, p. 639.

[3]) Ubisch L. von. Über die Aktivierung regenerativer Potenzen. Arch. f. Entw. Mech. Bd. 51. 1922.

la différenciation est la plus prononcée dans la partie antérieure de l'organisme et on la voit devenir moins nette plus on s'avance dans la direction opposée. Ce phénomène dénote une diminution de la vitesse de la différenciation. On observe un phénomène analogue suivant v. Ubisch, lorsqu'on étudie la différenciation régénérative, aussi après avoir soumis à l'analyse les résultats de ses recherches sur des Vers et des Batraciens, croit-il pouvoir tirer la conclusion suivante: »Das Vorhandensein eines Differenzierungsgefälles erscheint darnach als die Grundlage der Regeneration«.

Il résulte de ces différentes opinions sur la régénération que nous venons de passer brièvement en revue, que certains auteurs considèrent ce processus comme une croissance accélérée, tandis que pour d'autres, il s'explique par une diminution de l'intensité de la différenciation.

Nous ne saurions partager aucune de ces opinions. La croissance et la différenciation ne sont évidemment que des notions générales et complexes, par lesquelles on comprend l'ensemble des résultats produits par des agents très différents, dont la formation de la matière vivante (croissance) ou son organisation interne (différenciation morphologique et physiologique), sont la conséquence. Cependant, l'un comme l'autre phénomène sont au service de l'action formative de la matière vivante dont le développement ontogénétique et la régénération sont l'expression tangible. Dans le présent travail nous n'avons étudié que la croissance, cependant le domaine de nos recherches s'étendait aussi bien à la croissance ontogénétique qu'à la régénération. Or comme nous l'avons vu en étudiant le matériel à notre disposition, cette croissance se distingue par d'autres caractères pendant le développement ontogénétique et durant la régénération. Elle est uniforme sur toute la longueur et dans tous les secteurs pendant l'ontogenèse, tandis que pendant la régénération on voit en dehors d'une marche en général accélérée, son intensité répartie d'une façon particulière; en effet elle est plus forte dans les secteurs antérieurs que dans les secteurs postérieurs. Nous avons l'impression que d'autres facteurs encore interviennent pendant la régénération et qu'ils sont différents de ceux auxquels on a affaire pendant la croissance ontogénétique. En effet, on voit au cours de la régénération se produire une différenciation dans les secteurs proximaux du tissu récemment formé et la proximité du vieux tissu différencié peut agir sur le secteur le plus rapproché de la base de la partie régénérée; enfin le secteur dont la différenciation a commencé, peut exercer de l'influence sur le secteur suivant de la partie régénérée, par le fait d'exercer une action inhibitrice sur sa croissance et d'agir sur la différenciation ultérieure.

Les raisons mentionnées ci-dessus nous font croire que la théorie qui n'aperçoit dans la régénération qu'une accélération de la croissance, ne saurait rendre compte de l'ensemble de ce phénomène. Des facteurs qui règlent non seulement la croisance mais aussi la différenciation de l'organe en voie de formation, entrent ici certainement en jeu.

Przyczynek do kraniolologji współczesnych i wymarłych ludów Azji środkowej (Mongoło-Chałchasów, Burjatów, Urgińskich metysów i pogrzebanych w zrębach). — Contribution à la craniologie des peuples actuels ou disparus de l'Asie Centrale (Mongolo-Khalchases, Bouriates, métis d'Ourga et peuples ensevelis dans des caisses formées par un assemblage de pièces de bois[1]).

Mémoire

de M. **J. TALKO-HRYNCEWICZ** m. t.,

présenté dans la séance du 3 février 1930.

(Planches 1—4).

Les recherches anthropologiques que j'ai poursuivies pendant de longues années en Asie Centrale (1892—1908), intéressaient en dehors d'individus en vie, aussi bien les crânes des peuples actuels que les crânes de races depuis longtemps disparues. Je pouvais me procurer les crânes d'individus appartenant aux races actuels, à l'occasion des courses que je faisais en qualité de médecin au service de l'Etat. Je les trouvais au hasard le long des chemins, dans le champs, les forêts et les cimetières. Pendant les dernières années de mon séjour en Transbaïkalie, les règlements sanitaires défendaient aux Bouriates de jeter les cadavres comme proie aux bêtes fauves et leur enjoignaient de les enterrer dans des cercueils. Les bouddhistes considèrent cependant le fait d'avoir été dévorés par des bêtes féroces comme la sépulture la plus honorable. On tâchait donc de circonvenir les ordonnances de la police, en mettant les morts dans des caisses con-

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[1] La façon de construire ces caisses, rappelle la structure des chaumières habitées par les paysans russes.

struites avec des planches ou en les étendant sur une planche qu'on couvrait d'une mince couche de terre. J'ai pu collectionner des crânes sans me heurter à la moindre difficulté pendant plusieurs séjours que j'ai fait en Mongolie à Ourga, la ville sainte des bouddhistes. Sur la place du marché et dans les chemins, on pouvait voir des cadavres ou des membres épars rongés par des loups ou par des chiens vivant à l'état sauvage, que la population indigène appelle »ludojedy« (»mangeurs d'hommes«). Les fervents adeptes du lamaïsme regardaient ce spectacle d'un oeil indifférent. Les ossements que j'avais ramassé étaient soumis à la cuisson ou traité par des acides pour en détacher les parties charnues. Ils étaient ensuite exposés à l'action des rayons du soleil brûlant de Mongolie, ainsi qu'à l'action du vent pour les faire sécher.

On procédait autrement avec les os déterrés dans de vieux tombeaux. Les tombes où les morts étaient enterrés à une petite profondeur, avaient été le plus souvent pillées, aussi les os et les différents objets qu'elles contenaient ont-ils disparu. Les tombes où les morts étaient ensevelis dans des caisses formées par un assemblage de pièces de bois, étaient en général mieux conservées, vu qu'il était difficile de les reconnaître et qu'elles étaient très profondes, circonstance qui rendait leur accès difficile. Loin des villages et des artères de communication plus importantes, se trouve la localité dite Soudja, dont le nom provient de celui d'une petite rivière de montagnes. Celle-ci s'étend à 15 km. au Nord-Est du chef-lieu de district Troïckowsk, dans l'ancien territoire transbaïkalien et à 10 km. au sud du village d'Ust'Kiachta où se voit un ancien cimetière dont les Bouriates habitant plusieurs »yourtes«, prétendent qu'il renferme des trésors. On trouve le nom de Soudja chez les anciens auteurs et l'historien persan Rachid-Edin (Dżami-Ut-Tewarich) mentionne cette localité comme un terrain de luttes continuelles. La localité de Soudja dont je parle à présent, est située dans le territoire historique du triangle délimité par les sources de la Tola, du Keroulen et de l'Orchon, considéré comme le berceau des Mongols. Elle est éloignée de 400 km. de Karakoroum, l'ancienne nécropole des khans de Mongolie. La petite rivière appelée Soudja, s'étend sur une longueur de plus de dix kilomètres pour se jetter dans la Sawa. Les rives en sont abruptes et le lit desséché ne se remplit d'eau qu'à l'époque où il pleut plus fort. Comme tous les torrents, elle est formée par de nombreux ruisseaux qui se rejoignent. Les bords de la Soudja sont couverts de bouleaux, de mélèzes et surtout d'ormes. On y voit également des buissons et des arbustes, au milieu desquels se trouvent trois grands cimetières, dont l'un à proximité des sources, l'autre situé sur le cours moyen du torrent, enfin le troisième, au milieu de dunes, à son embouchure. De nombreuses tombes, p. ex. celles de Derestoujskij Koltouk, ont été détruites par les eaux. Les tombes sont séparées les unes des autres par une distance de quelques mètres. Il était difficile de reconnaître à première vue, les tombes couvertes d'herbe, car non seulement elles ne s'élèvent pas au-dessus du niveau du sol, mais elles présentent au milieu un renfoncement en forme d'entonnoir, autour duquel on aperçoit de petits blocs de pierres, disposés circulairement ou formant un quadrilatère. Un sentier large d'un demi-mètre, bordé également de pierres aboutit à chaque tombe du côté sud. Le sol dans lequel on trouve les tombes intactes, est en général sablonneux mais couvert d'une couche d'humus, produit de la décomposition des parties végétales. Les tombes ont 4—7 mètres de profondeur. A une distance de 25 cm. à deux mètres de la tombe, on voyait une forte poutre en bois de mélèze dont une extrémité avait été carbonisée, probablement avec une torche, pendant la cérémonie funéraire. Cette poutre était enfouie dans le sol en sens transversal. La tombe était parfois entourée de plaques de pierre et de plusieurs boules rouges ou jaunes en argile. Le cercueil qui avait la forme d'une grande caisse, était orienté du Nord au Sud. Les parois du cercueil étaient formées par trois pièces superposées de bois de mélèze, jointes au moyen d'un assemblage et fixées avec de long clous de fer. Les caisses avaient 2 m. à 3 m. 25 cm. de long sur 50 cm. ou 1 m. de large. La partie de la caisse qui correspondait à la tête du mort, était parfois plus large que celle où se trouvaient les pieds. Le fond de la caisse était en planches. Sur les planches, souvent défoncées et pourries, qui formaient la partie supérieure des caisses, nous trouvions une ou deux minces feuilles d'or, fixées à la planche du milieu au moyen d'un clou de fer. Une ou deux planches placées en travers de la caisse, divisaient celle-ci en deux ou plusieurs compartiments. Dans le compartiment plus grand, on voyait étendu un ou deux morts, parfois un adulte et un enfant. La tête regardait le Nord, les bras et les jambes étaient en extension. Du côté des pieds du mort, ou bien dans le compartiment regardant le Sud, on trouvait généralement des crânes d'animaux. C'étaient d'habitude des crânes d'une variété locale de taureaux (*Bos taurus*) ou des crânes de taureaux croisés avec l'yak (*Bos gruniens* L.). Très souvent, on trouvait des os de moutons (*Ovis aries*) ou de chèvres (*Capra hircus*), parfois on découvrait des os de cerfs (*Cervus maral*) ou de Djigetajs (*Equus hemionus* Pall. Ss.). On voyait à côté du mort, différents objets en métal, surtout des objets en fer, le métal le plus répandu. Il y avait là des clous, des agrafes, des pointes de flèches, des couteaux etc. Certains objets avaient perdu leur forme primitive, de sorte qu'ils représentaient une masse informe, pour ainsi dire scorifiée et mêlée à des bouts de cuir, à des morceaux de bois où à des parcelles d'or, p. ex. sur les poignées des épées. On trouvait également des miroirs polis de bronze, coupés en deux et portant des inscriptions qui indiquaient les manufactures chinoises où on les avait fabriqués; il y avait aussi de fines feuilles en métal, décorées d'ornements repoussés, des lamelles de cuivre doré qui représentaient des dragons et d'autres animaux, des lamelles dorées et ajourées en cuivre fondu avec des images d'oiseaux et d'animaux mythologiques, qu'on fixait à la paroi intérieure des caisses. Les objets en os étaient très nombreux dans certaines tombes; on y voyait de petits couteaux, des agrafes, des lamelles allongées dont la forme rappelait celle d'un poisson, de petites cuillères, des parties de l'arc, des trompettes sur lesquelles on apercevait un dessin représentant un dragon, etc. On découvrait très souvent de la poterie, en général insuffisamment cuite et brisée en morceaux. La couleur de ces vases variait du gris clair au gris foncé et était parfois rouge. Quant à leurs formes et leurs dimensions, elles offraient une grande variété. Il y en avait de tout petits et de grands pouvant contenir plusieurs litres de liquide. C'étaient en général des pots très primitifs, décorés de stries s'étendant en longueur. Dans certaines tombes, on trouvait des rangées de perles en verre, de différentes formes et couleurs, puis, quoique moins souvent, des parties de harnais décorées de plaques de bronze. On découvrait également parfois des lambeaux d'une étoffe fine ou épaisse de soie et il était possible d'y distinguer des fils tressés comme dans les nattes. D'autres morceaux d'étoffe étaient noir à bandes rouges, enfin il y en avait de fins comme du papier qui se déchiraient dès qu'on les touchait et ne permettaient pas de reconnaître les fils. Parmi les objets les plus précieux que renfermaient certaines tombes, il nous faut mentionner des monnaies chinoises en cuivre, avec une ouverture carrée au milieu, qu'on trouvait du côté des pieds du mort. C'étaient des monnaies dites »czochi«, remontant à la dynastie des Khans. D'après les recherches de Markow, on les appelait »Wu-czu«. Elles avaient été frappées en 118 av. J. C. et circulaient jusqu'à l'an 518 de notre ère, au temps de la dynastie Sin.

La façon dont les morts étaient ensevelis dans les caisses, éveilla un vif intérêt en Russie. Elle permit d'établir que le célèbre naturaliste et érudit, Simon Pierre Pallas avait décrit un rite funéraire analogue à l'occasion des voyages qu'il fit en Russie dans le courant de la seconde moitié du XVIII^e^ s. et qu'il avait emprunté sa description au récit des pilleurs de tombes qui les ravageaient en Sibérie occidentale, notamment dans la région dite de Minusińsk. C'est précisément de ces pilleurs que Pallas acheta de nombreux objets en or, réunis actuellement dans la belle collection sibérienne de Pierre le Grand, qu'on trouve au Musée de l'Ermitage à Léningrad. Le caractère et la forme de ces objets rappellent de très près les objets que j'ai découverts à Soudja. On sait qu'on ouvrait très fréquemment les anciennes tombes au XVIII^e^ siècle en Sibérie et que les objets déterrés circulaient dans le commerce. Beaucoup d'objets furent ainsi perdus, d'autres étaient achetés par des commerçants ou des fonctionnaires, pour en faire des collections archéologiques, dont la mode était alors très répandue en Sibérie; encore d'autres étaient détruits. Les objets en or étaient fondus ou expédiés à différentes destinations, tandis que ceux qui n'avaient pas de valeur aux yeux des acheteurs sibériens, étaient vendus à vil prix ou gaspillés. Comme j'avais appris que les tombes sur l'Orchon et sur l'Onon rappellent beaucoup celles que j'avais étudiées à Soudja, je voulus y entreprendre des recherches. En effet, le Comité International pour les recherches en Asie Centrale et en Asie Orientale me proposa en 1907 de faire des études dans cette région, néanmoins je ne pus mettre mes projets en exécution pour des raisons indépendantes de ma volonté.

Lorsque après mon départ, les recherches ne furent plus continuées en Sibérie, on réussit en 1914 à faire des trouvailles importantes sur les confins de l'Asie Centrale. En effet, l'archéologue Aurélien Stein décrivit dans les tombes du bassin du Tarym (partie orientale du Turkestan), des objets de néphrite (espèce de jaspe) et de bronze, des étoffes de soie, puis des feutres, couverts de dessins remontant à l'époque de la dynastie des Khans. Le genre du matériel employé à confectionner tous ces objets, leur exécution, enfin les ornements dont ils étaient couverts, rappelaient de très près les objets mis à jour par les fouilles qu'on avait faites en Sibérie occidentale et dans le bassin de la Selenga dans l'Est de la Sibérie.

Grâce à un heureux concours de circonstances, l'expédition de P. K. Kozłow put faire des trouvailles importantes à Noïn-Uła, localité située à 100 km. au Nord d'Ourga et à 150 km. au Sud de Soudja. Elles ont été décrites par MM. G. J. Borowski et S. A. Tiepłoouchow que l'Académie des Sciences de Léningrad avait envoyés pour les étudier sur les lieux. La brève communication provisoire que l'Académie des Sciences a publiée sur ce sujet, insiste sur la grande importance de ces trouvailles pour l'histoire de la civilisation en Asie. Elle constate ensuite que les rites funéraires en usage à Noïn-Ouła où les morts étaient enterrés dans des caisses, sont non seulement identiques avec le mode d'inhumation qu'on retrouve dans le vieux cimetière de Soudja, mais qu'ils sont les mêmes dans tout le Sud de la Sibérie et en Turkestan. On put se rendre compte en effet que les morts étaient partout enterrés dans des caisses enfouies à une grande profondeur; dans tous ces cimetières on put trouver des plaques d'or ou de bronze doré ainsi que des plaques de bronze à jour avec des dragons, des taureaux ailés, des lions, des oiseaux, ou avec la représentation d'un combat entre un élan et un griffon. Tous ces objets avaient certains traits caractéristiques communs. On découvrit de plus dans ces tombes de belles houppelandes de soie avec des bordures en fourrure, des étoffes et des tapis sur lesquels on distinguait des dessins scytho-grecs ou chinois, autant de preuves que ces objets dataient de l'époque où régnait la dynastie des Khans. En été 1929, l'Académie de Léningrad envoya une commission présidée par M^r G. P. Sosnowski qui a ouvert près de 50 tombes du cimetière de Soudja, où j'avais fait des recherches autrefois. Parmi les objets qu'on trouvait fréquemment dans les tombes, il faut noter la présence d'étoffes de soie décorées de dessins, puis celle de petits vases en bois verni.

Il résulte des dernières recherches que les tombes à caisses où les morts sont enterrés suivant un rite qui relie le cérémonial funéraire gréco-scythique aux rites sino-sibériens, sont disséminées dans toute l'Asie Centrale où vivait un peuple qui connaissait cette coutume pendant le règne des dynasties des Khans et des Sins. Ce peuple n'était autre que les Huns. La majorité des auteurs admet qu'ils étaient d'origine mongolique, d'autres supposent qu'ils appartenaient à la race finnoise, voire même à la race slave. Personne n'a toutefois fait de recherches anthropologiques sur les crânes d'individus ayant appartenu à ce peuple. J'ai le premier fait des recherches craniologiques sur 44 crânes (♂ 25, ♀ 19) et les ai comparés avec des crânes provenant de la Mongolie Orientale que j'avais étudiés. J'ai également fait des études comparées sur les premiers crânes puis sur 49 crânes de Khalchases (♂ 19, ♀ 21), sur 19 crânes bouriates (♂ 14, ♀ 5) et sur 9 crânes de métis d'Ourga (♂ 4, ♀ 5), qui sont le produit d'un croisement entre Chinois et femmes mongoles. Pour pouvoir établir des comparaisons avec le matériel dont je disposais, j'ai tenu compte des recherches d'A. Iwanowski sur les crânes de Kalmouks habitant l'Ouest de la Mongolie, puis des crânes provenant de la province Szan-Si dans le Nord de la Chine, que j'avais étudiés moi-même.

Nous avons conclu d'après les mensurations et les rapports entre les différentes dimensions, que le crânes des individus ensevelis dans des caisses, sont les plus grands en ce qui concerne la circonférence horizontale (523 mm.) et la circonférence sagittale (357). Ils sont plus développés en longueur (184 mm.) qu'en largeur (143 mm.) et en hauteur (124 mm.), de sorte qu'ils se rapprochent des crânes subdolichocéphales (indice 77·94, rapport entre la hauteur et la longuer = 68·17). Ce sont des crânes aplatis latéralement, au front étroit (indice exprimant le rapport entre la longueur et la hauteur = 55·11), à l'occiput large (indice exprimant le rapport entre la hauteur et la largeur = 41·32). La figure est étroite et allongée (119 mm.), les orbites sont développées dans le sens de la hauteur (89·94 mm.), le nez moyen (49·60), le palais plutôt étroit et allongé (77·92).

Les crânes provenant de la Mongolie Orientale (ceux des Khalchases et des Bouriates, ainsi qu'en partie les crânes des métis d'Ourga), sont également de fortes dimensions, cependant leur circonférence horizontale (512—516 mm.) et verticale (351—361 mm.). sont un peu plus petites. Ils sont plus courts (176—181 mm.), plus développés en largeur et se distinguent par des tempes bombées, phénomène en rapport avec l'extrême brachycéphalie qui les caractérise (84·40—84·79; chez le métis, seulement 77·30). Ce sont des crânes assez bas, au front plutôt large (57·7—60·15) et à l'occiput étroit (60·55—64·34). Contrairement à ce qu'on observe sur les crânes précédents, la figure est très large (128 – 134 mm.; indice = 55.79—59·86). Les orbites sont développées en largeur (92·61—93·51), le nez est petit (48·94—49·96), le palais large et fort (79·67—83·38).

Les crânes provenant de la Mongolie occidentale (Kalmouks), sont également assez grands (521 et 358 mm.) et l'indice brachycéphale les rapproche de la mésocéphalie (82·07). Ils sont plus hauts (127 mm., indice = 71·49), se distinguent par un front (53·49) et par un occiput étroit (63·14). La figure est très large (13·6 mm., indice = 53·01), les orbites fortement développées en largeur (90·21), le nez est petit et large (48·98), le palais très large (81·90).

Les crânes provenant du Nord de la Chine, se distinguent par une circonférence horizontale relativement petite (515 mm.) et par une forte circonférence sagittale (360 mm.), néanmoins ils sont plus allongés (178 mm.), étroits, mésocéphales et plus hauts que d'autres (74·11). Le front (58·62) et l'occiput (62·19) sont plus larges, la figure est développée en largeur (135 mm.) mais plus longue (55·85), les orbites élargies en sens transversal (91·91), le palais large (81·90).

Les crânes mentionnés ci-dessus correspondent à deux types fondamentaux. On trouve d'abord des crânes représentant le type asiatique, dans lequel je range les crânes provenant de la Mongolie Orientale (Khalchases et Bouriates), plus développés en largeur qu'en longueur et en hauteur. Ce sont des crânes nettement brachycéphales au contours arrondis, au front large, à l'occiput applati, au nez petit, aux orbites développées en sens horizontal, au palais large et fort. Tous ces traits sont propres à la race mongole.

Les crânes trouvés dans les tombeaux à caisses ont une forme tout à fait différente de celle des crânes mongols. Leurs dimensions sont plus fortes que celles de tous les autres crânes étudiés et ils sont plus développés en longueur qu'en largeur. L'indice subdolichocéphale les rapproche des crânes mésocéphales; ils sont plutôt développés en longueur, le front est plus étroit, l'occiput plus large. La figure est plus large et plus allongée, les orbites sont développées en hauteur et leurs bords sont arrondis, tandis que dans les crânes mongols les bords des orbites sont saillants, le nez est étroit, l'arête nasale plus marquée, le palais étroit et allongé. Si les recherches anthropologiques ultérieures qu'on entreprendra sur d'autres crânes trouvés dans les tombes à caisses, confirment les résultats déjà obtenus, on apprendra peut-être que ce type probablement turc, disparu aujourd'hui en Asie Centrale que nous appellerons euro-asiatique, était bien celui des Huns.

Les crânes provenant de la Mongolie de l'Ouest (familles kalmouks), occupent en ce qui concerne les dimensions, une place intermédiaire entre les crânes de l'Est de la Mongolie et les crânes trouvés dans les tombes à caisses. Plus développés en largeur qu'en longueur, ils sont d'une hauteur moyenne et brachycéphales avec une tendance à la mésocéphalie. Le front est plus étroit, l'occiput plus large, la figure basse s'étend en largeur, les orbites sont larges, le nez petit, le palais large et épais.

Les crânes de fortes dimensions du Nord de la Chine sont peu développés en largeur, plus allongés et étroits. Ils sont mésocéphales avec une tendance à la dolichocéphalie et se distinguent par leur développement en hauteur. La figure est plus allongée, les orbites sont développées en hauteur, le palais est large. On peut en dire autant des crânes des métis d'Ourga qui occupent une place intermédiaire entre les crânes de la Chine du Nord et les crânes mongols.

Il résulte de cette étude anthropologique comparée que nous sommes en présence de deux types principaux. Le premier type, mongol et contemporain, comprend deux variétés dont l'une orientale (Khalchases relativement purs et Bouriates représentant le produit d'un croisement), l'autre occidentale, mélangée peut-être avec des Turcs. Le second type représenté par une race turque peut-être pure, est aujourd'hui disparu et on en retrouve les restes dans les tombes à caisses. Cette race que nous appelons euro-asiatique qui s'est mélangée avec d'autres p. ex. avec les Mongols, était autrefois plus nombreuse et comprenait divers rameaux. C'est elle qui a atteint les confins nord-est de l'Asie Centrale et a emprunté sa civilisation aux Chinois, pour construire des routes carossables, des canaux d'irrigation et des instruments d'agriculture. C'est encore elle qui laissa des traces de son passage dans les inscriptions turques rappelant des runes, qu'on déchiffre sur les pierres tombales des Khans à Karakoroum. Les Huns appartenaient-ils à cette race? On pourrait le croire en jugeant d'après la description des crânes et d'après la puissante charpente des squelettes dont les os longs sont pourvus de fortes apophyses et d'aspérités. Comme nous ne disposons que de renseignements incertains et peu nombreux sur les Huns, sur leur genre de vie et leur structure physique, je n'hésite pas, en m'appuyant sur les données anthropologiques, à les ranger plutôt parmi les Turcs, qu'à les considérer comme des Finno-Mongols, voire même comme des Slaves, ainsi que le voudraient certains auteurs. Les Huns et leur civilisation ont été anéantis dans la suite par l'invasion des hordes mongoles sauvages venant du Sud. Il est possible de retrouver leurs traces en étudiant les crânes des Kalmouks.

Explication des figures des planches 1—4.

Pl. 1. *Norma verticalis.* Fig. 1 et 2. Cimetière de Soudja, crânes trouvés dans les tombeaux à caisses. Fig. 3. Mongolo-Khalchase. Fig. 4. Mongolo-Bouriate.

Pl. 2. *Norma lateralis.* Fig. 1 et 2. Cimetière de Soudja, crânes trouvés dans les tombeaux à caisses. Fig. 3. Mongolo-Khalchase. Fig. 4. Mongolo-Bouriate.

Pl. 3. *Norma facialis.* Fig. 1 et 2. Cimetière de Soudja, crânes trouvés dans les tombeaux à caisses. Fig. 3. Mongolo-Khalchase. Fig. 4. Mongolo-Bouriate.

Pl. 4. *Norma occipitalis.* Fig. 1 et 2. Cimetière de Soudja, crânes trouvés dans les tombeaux à caisses. Fig. 3. Mongolo-Khalchase. Fig. 4. Mongolo-Bouriate.

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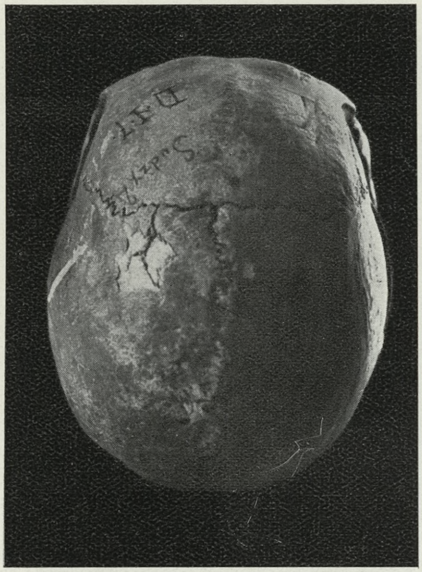

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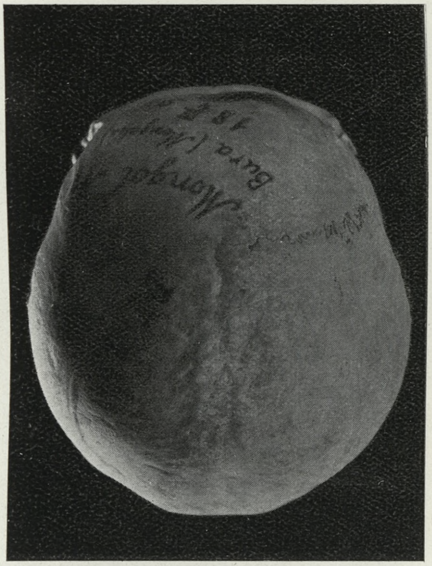

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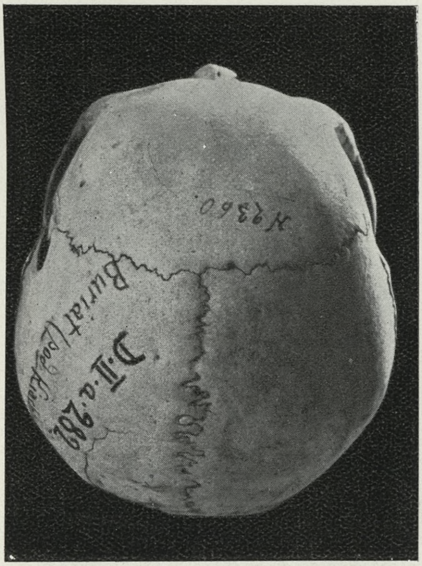

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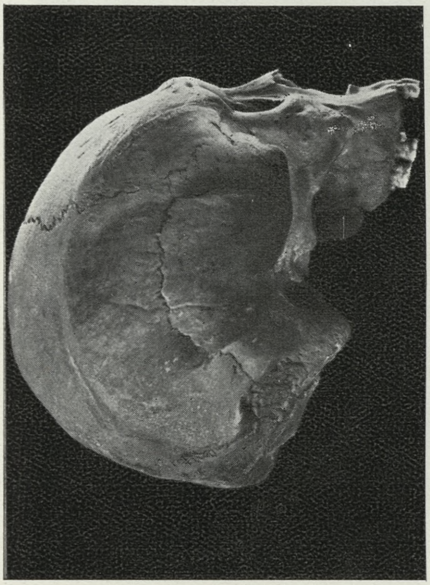
J. Talko-Hryncewicz.



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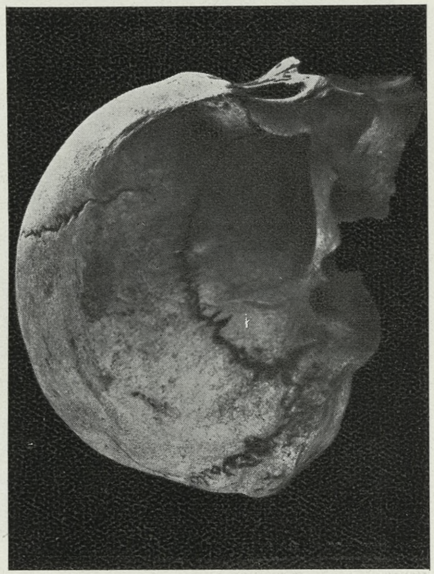

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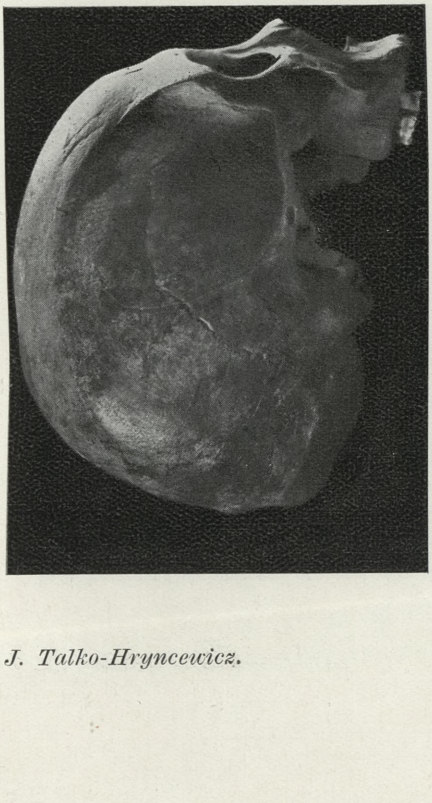

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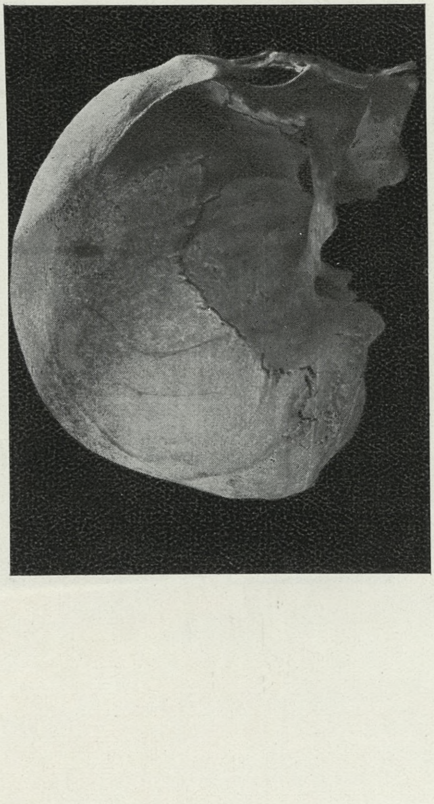

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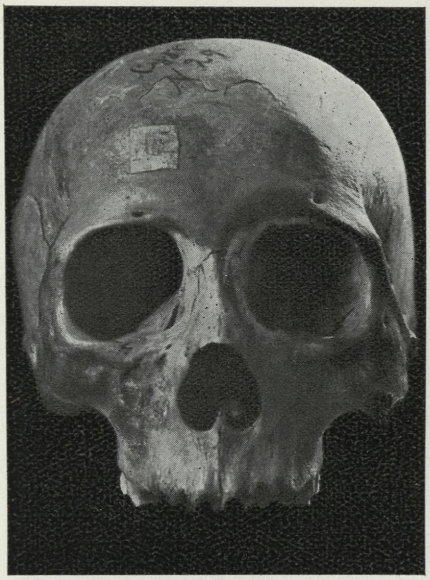

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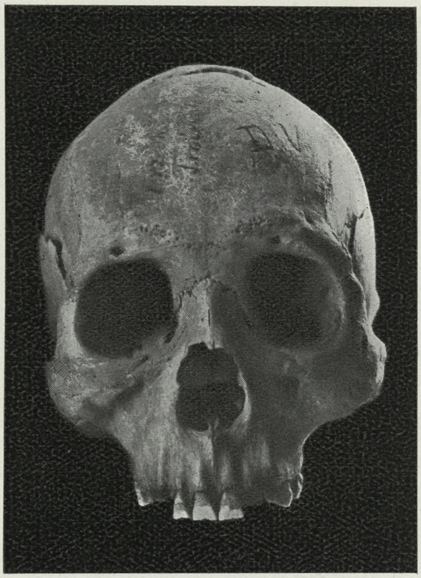

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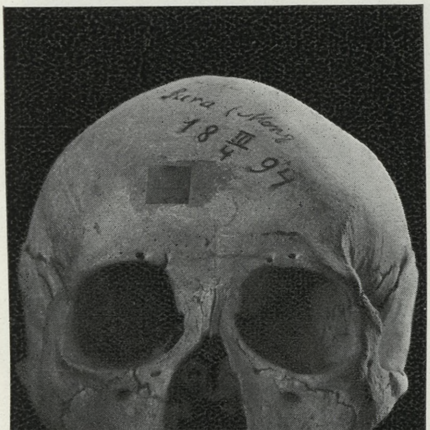

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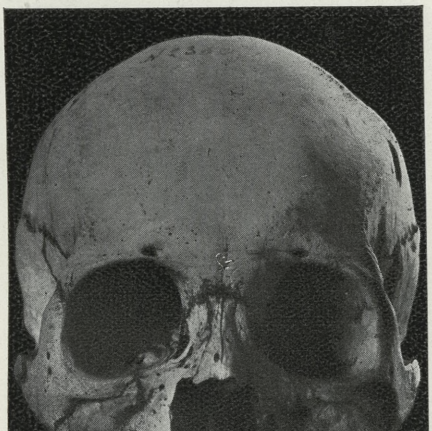

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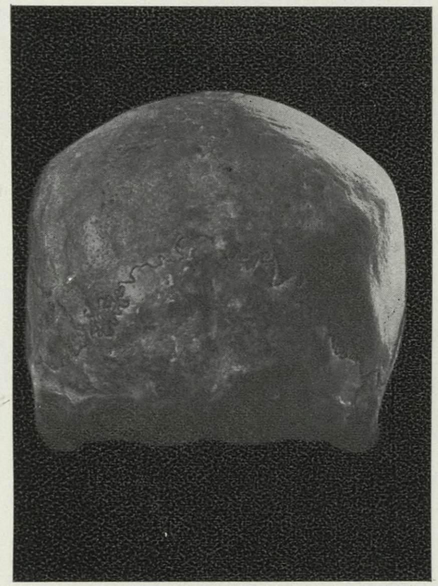

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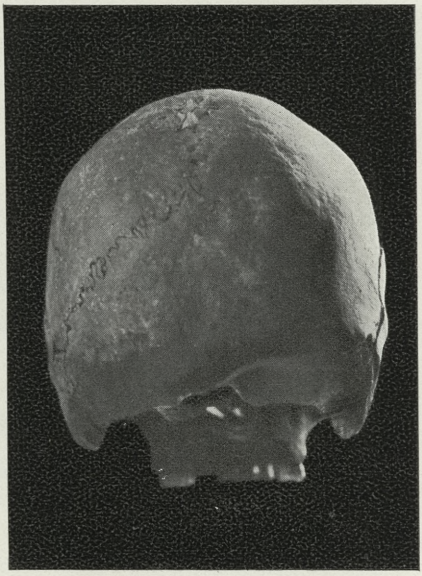

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J. Talko-Hryncewicz.

Studja genetyczne nad psem domowym. — Genetic studies on the domestic Dog.

Mémoire

de M. ***T. MARCHLEWSKI,***

présenté dans la séance du 10 Février 1930, par M. H. Hoyer m. t.

(Plance 5)

Contents:

1. Introduction.

The genetics of the domesticated dog, abstracting from a number of studies, concerning colour inheritance and bearing the stamp of pure studbook work, have been a comparatively little investigated field although the dog, from a number of reasons presents and interesting and important object.

The reasons for this state of things are numerous and obvious. The high costs and difficulties of maintaining a larger kennel of dogs for purely experimental reasons surpass most frequently the financial possibilities of even well endowed Institutions, further the arrangments necessary for an adequate study of the most interesting features of the subject now under discussion, i. e. psychical and mental traits involving adequate training and upbringing commodities, cause still greater methodical troubles.

On the other hand, mere observations of the results of practical breeders, of operations conducted within the limits of the so called pure breed, are in so far not complete, that in almost every litter born, part of the young is destroyed soon after birth and from the remaining a goodly number is disposed of early in life, so that only in exceptional cases, can a representative sample of any given litter can be observed latter in adult life.

Thus owing to the situation outlined above, with the exception of the genetics of coat colour and hair length and type, both characters, that may be pretty well defined in a pedigree study, our knowledge of the genetics of the dog, is but fragmentary, and for a great part accidental.

In the present writers opinion, it is rather important to gain a certain amount of well founded information concernig at least one Carnivorous species and its genetics.

Both, purely comparative reasons and certain phylogenetic considerations require such kind of knowledge. The circumstances point again to the domestic dog as to the most suitable, and in a way, critical object.

The present study is to a large extent, the outcome of certain efforts to preserve a strain of dogs under rather adverse conditions, from the breeders point of view. In consequence the very mode of the presentations of our evidence, must necessarily be more colloqulal, and to a degree circumstantial, than it is customary in publications dealing with genetic results.

On the other hand however, certain matings we carried out so extensively, that they may safely be regarded as cases of carefully planned diallell matings, one of the most accurate methods of genetic analysis. This instance, and above all the fact, that rather extensive data have been collected offers in the writers opinion reasons, for publishing the hitherto gained results.

The material dealt with in my observations, consisted mostly, of dogs belonging to the breed designed as the English Pointer.

This breed may in its origin, be regarded as an instance of the result, of a carefully planned Mendelian experiment, conducted on a grand scale, in which a number of characteristics of the modern Foxhound, and the now extinct Spanish Pointer have been blended, and which represents a breed homozygous for its most important features.

Certain crosses have been resorted to, and these as well as observations made upon a few accidental matings do furnish the material for the present study.

It is proposed to discuss in the following the results of observations of the characteristic behaviour of the different body structures and mental characteristics separately.

2. The mode of inheritance of two distinct types of skull formation.

One of the most characteristic features of the modern Poniter is the type of the animals head, which though moderately long, is rather wide in the facial part or the so called »snout« and shows a marked depression just above the eyes on the border between the cranium and the facial portion of the skull, the so called »stop» of sportsmen.

The upper profile line is frequently somewhat concave, giving the face a so called dished expression which is regarded as one of the most characteristic features of the breed.

Photo Nr. 1. may serve as a typical example of the typical kind of head formation in the discussed breed.

The actual material upon which the reported observations have been made consisted of a pair of pure bred dogs, the bitch »Norma of Kutti« with a very typical head, and the dog »Royal Shot« which was a very well built animal and an excellent perfomer in the field but had a somewhat lightly moulded head, though lying closely within the limits of the standard type.

The pedigrees of the observed material are presented in the Appendix. The above pair was used extensively for breeding purposes, and yielded progeny which showed practically no serious departures from the acknowledged type of their breed.

The first departure was observed in the progeny of the original sire and his daughter the bitch »Fit Kujavia« (cfr & Pedigree Nr. 3).

The last named bitch resembled her father in so far, as her profile line was straight rather than concave. and that the circumference of her mouth was rather small giving the impression of so called snipeness, a feature regarded as faulty by breeders of all varieties of so called Gundogs.

As a result of the mentioned mating the dog »Shot II« (cfr. ped. Nr. 4) was produced. This animal though in all other respects exhibiting the typical features of the Pointer, was noticeable by an extremely narrow and pointed snout, which gave the animal much similarity to the Greyhound.

As no photograph of this specimen is available, the photo of a very narrow headed dog is given in the following, as well as a Photograph of a pure Greyhound.

The above photographs as well as historical data test beyond any doubt, that the Greyhound as well as the Foxhound have played an important role in the moulding, of recent breeds of British Sporting dogs i. e. the Pointer and most varieties of Setters.

Undoubtedly, within the mentioned breeds dogs with very long snipy heads and other peculiarities of the Greyhound have been quite common about a century ago.

In the face of the above facts, it is interesting to trace the behaviour of the progeny of the Greyhound like dog »Shot II«.

Mated with his mother »Fit Kujavia« he produced two bitches one of which served for breeding purposes.

This bitch was very »greyhoundlike« like her father. The other though also somewhat »snipy« did not show resemblance to a Greyhound, at least not in such a strongly pronounced manner, than the afore mentioned specimen.

The first bitch »Norma« (cfr. pedigree Nr. 5) was mated with a so called »German« Pointer. This breed differs from the British variety in so far, that the frame of the animal is much heavier, the head broad and heavy, the profile convex rather than concave.

In short, the characteristic features of this breed resemble closely the now extinct »Spanish Pointer«, one of the ancestors of the modern English breed.

The litter resulting from mating the mentioned pair consisted of five offspring, which without exception showed the typical »greyhoundlike« head of their mother, and the same time, comparatively light and agile bodies.

One of these halfbred dogs »Verdun« backcrossed with his mother produced similarly »greyhoundlike« offspring (cfr. pedigree Nr. 6).

All the above evidence would seemingly point to the conclusion, that the elongated narrow head of the Greyhound as well as the light, agile body structure behaves in crosses as a decidedly dominant feature.

A further instance of dominance of narrowheadness of a similar, though distinct type, of two accidental crosses of Pointer bitches with a so called »Alsatian« Wolfdog. In both cases, the progeny resembled in head type, the «Sheep dog« much closer, than the Wolfdog (cfr. Phot. Nr. 9).

Converse evidence concerning the recessive nature of the broad and dished Pointer type of head may be summarised as follows:

The snipy headed bitch »Fit Kujavia« was mated with the dog «King« breed by Mr. Christiani nr. Rzeszów. This animal was of a extremely broad and dished faced appearence.

About half of the resulting offspring in a litter of six inherited their fathers type of head formation.

One of the young the bitch »Fit II« Phot. Nr. 6 pedigree Nr. 6 was selected by the writer for breeding purposes. As she was very extensively tested her breeding record is summarised on table I.

It should be noted, that the produce of this bitch with a dog, showing a similarly typical head conformation, the whole litter did exhibit the characteristically dished type of head development.

In employing the first and second cross progeny of the »greyhoundlike« bitch »Norma II« it was found, that half of the offspring was broadheaded, whilst the other was directly »greyhoundlike« or at least »snipy«.

Thus, the above evidence points to the conclusion, that both, the extremely light and narrow type of head and skull formation as well as the narrow type of head met in various sheepdogs, a type denominated by students of the origin of domesticated dogs as the type of *Canis Optimae matris,* behave as distinctly dominat features in relation to the more broad face, typical to hounds and gundogs which owing to certain similarities with some subfossil findings is often denominated as the *C. Intermedius* type.

The breeding records of the broad and dish faced bitch »Fit II« as table I shows, tend to the conclusion, that whenever the bitch was mated with a broad headed dog, the whole litter

TABLE I.

The Progeny of the Outcrossed Pointer bitch «Fit II» mated with different sires.

Year	Description of Mating of sire	Number of young born	Number of young reared	Type of head		Coat colour				
				grey-hound	dish	self	black	liver	yellow	roan
1920	Dish faced liver & white Pointer	5	5	0	5	0	0	4	1	0
1921	»Verdun« cfr. pedigree roan greyhound like head	7	6	5	2	0	0	5	2	2
1922	«Ram« liver self colour, dish faced half bred dog showing roaning on breast	8	3	0	3	5[1]	0	8	0	1
1923	»Titan« liver white roan dish faced Pointer Dog	8	3	0	3	0	0	6	2	2
1924	Alsatian wolf grey dog (accidental mating)	8	4	4	0	8[2]	8	0	0	0
1926	»Brillant cfr. pedigree. Liver & white greyhoundlike	3	3	3	2	0	0	0	3	0
1928	»Brillant« as above	1	1	0	1	0	0	0	1	0
	Totals	40	25	5	16	13	8	23	9	5

resembled the parents in head development. On the other hand, when the mentioned animal was mated with the a »greyhound-like« dog as in the case of the half breed dog »Verdun« or the three parts breed »Brillant« respectively which by their breeding are necessarily heterozygous for the »broad« type of head for-

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[1] one liver and tan.

[2] four black and tan.

mation, the offspring consisted of both types of head formation in about equal proportions.

These findings clearly demonstrate that, firstly, the tendency to the Greyhoundlike type of head formation behaves in crosses as a decided dominant and secondly, that the genetic basis of the discussed features is relatively simple, and shows clearly cut segregation.

A further question, whether the distinct types of head formation discussed in the above, are caused by genetic forces forming a triple allelomorphic system, though rather probable, cannot as yet, be answered definitely.

One further important point, namely the question, of the first origin of the »greyhoundlike« type remains as yet unsettled.

It may perhaps be supposed, that the first appearence of the »greyhoundlike« dog »Shot II«, was due to a mutation arising in the germ cells of one of his immediate forebearers.

In the present writers opinion however, a different kind of interpretation seems more probable and in better accord, with facts established from early history of the breed under discussion.

As mentioned before, besides the Foxhound, the smooth coated English Greyhound played and important role in moulding the modern Pointer.

Thus, it seems fairly natural, that in order to conform to the demands of the Standard within strains carrying a fair proportion of Greyhound blood much selection was practisised in favour of the rather broad and dish faced individuals.

It is therefore possible, that individuals carrying the »greyhound gene« have been ultimately produced, which in spite of all, within certain limits did conform to the demands of the Standard head formation, and, expecially in the eyes of certain judges, were regarded as equally, valuable as dogs of different breeding and origin.

A certain laxity amongst breeders in the mentioned respect that was to be observed within recent times, caused that a great majority of snipy headed dogs were recently produced, and that numerous voices deploring the lack of type and quality in head formation amongst the leading breeds of Gundogs, are to be found in the columns of sporting press.

Within the last few years a certain improvement in head type can be observed from recently published paintings.

Still it may be safely stated that head conformation of the present day British Pointer deviates more seriously from the original type, than the material found in the Scandinavian countries, notably in Sweden.

On the other hand, the light type of head formation is at present decidedly in favour amongst American breeders.

Taking all the evidence concerning the matter in to account, it seems most probable that at least in some strains of Pointers and most likely other Gundogs also, a modified kind of the »greyhoundlike« headed dog ist most common i. e. a type carrying the »greyhoundlike« factor or factors, but at the same time owing to the action of continuous selection, approaching more or less the broadheaded standard type of animals.

It would seem therefore, that our foundation dog »Royal Shot« belonged to the last named type, and was heterozygous for the modifying agences in question.

Inbred to his own daughter, which evidently was also heterozygous for the modifier in question, a »greyhoundlike« modifier free individual could and was in fact produced in the dog »Shot II«.

This individual, being free from the disturbing modifying agences did produce heterozygous »greyhoundlike« offspring resembling their sire in appearence.

In the face of all above evidence, the recessive nature of the wide concave and the dominance of the »greyhoundlike« and sheep dog type of head formation as well as the existance of specyfic modifying factors seems to be well established.

The results quoted by »Stonhenge« of crosses of Greyhounds and Bulldogs in the last century and quite recent results of the late Dr. Wriedt which showed that the broad concave »pekingese« type of head conformation behaves like a recessive with somewhat intermediate heterozygous form lead to the conclusion, that the Bulldog and eventually the »Pug« type of skull formation are decidedly recessive in relation the the more elongated types.

The uniform behaviour of the studied types offers certain probability that multiple allelomorphism lies at the basis of the distinct types of head formation in the dog. Further studies are needed however, to exhaust this problem entirely.

It should be further noted that in man and cattle, brachycephalism, seems in most cases to behave as a dominant character.

Certain cases, as the classical case of the »Niata« breed recently studied by Staffe, and certain subletal features met amongs Scandinavian breeds, do suggest, that also in other mammals the inheritance of cranial characters may follow a similar course like in the dog.

3. Observations concerning the mode of inheritance of certain structural peculiarities, including certain abnormal conditions.

Taking in to consideration the most important points of structural formation typical to the English Pointer one finds, that in accord with the animals vocation this dog, like the Foxhound is built for speed and endurance.

The body is comparatively light but strongly moulded, with a comparatively very deep and only moderately wide chest basket a medium long very muscular neck, short and well muscled lumbar region. The legs especially the fore ones, are straight and strong, the paws compact and rounded (cat like). The above characterisation applies with a very moderate range of variability to all most all well bred individuals of the race.

The greyhound headed individuals described in the preceding section, were still somewhat lighter than the average of their race. The lumbar region narrower and the general conformation somewhat less compact than in typical specimens.

Our breeding experiments, as stated above relate to crosses of the English breed with the German variety.

This breed as shown by the photograph Nr. 5, is widely different in conformation from the described above.

The frame is much heavier than in the English variety, the chest rather wide than deep. The fore legs often poorly covered with flesh and bended sideways, the lumbar region rather long, the feet elongated and open »hare like«.

As a characteristic feature of the breed we may mention the so called dewlap or the presence of loose folds of skin on the underside of the neck. The English Pointer as well as the Greyhound and Foxhound are entirely free from these apandages.

A fairly reliable measure of the relative development of the respective breeds, is the relative value of the girth in relation to the height at the withers. For about twenty English Pointer males this ratio is like 60 : 62 whilst an analogous measure for the German variety is like 58 : 61.

The observations of practical breeders tend to the conclusion, that the first crossbred generation between the English and German variety is decidely lighter in build, than the German dog.

This observation was confirmed in the cross of the pure bred Pointer bitch »Nora« with an extremely heavy German dog.

The whole resulting litter whilst showing the typical »Greyhoundlike« head formation described previously, was at the same time very lightly built lying well within the limits of the pure English variety. In fact these dogs were more »windy« than typical Pointers.

The chest basket was however less developped in debth showing a rather intermediate development.

It should be further mentioned, that the so called dewlap was present in every specimen of the F_1 generation.

Of further interest may be the results of mating the pure bred English Pointer bitch »Fit II« with the three parts bred dog »Brillant« (cfr. Table I). In two litters four young were born. Two of them like the specimen depicted on Photo Nr. 7, showed the extremely heavy forms of the German variety, whilst one of them save the undeveloped chest basket show the typical traits of the English breed.

The fourth specimen, a bitch, which unfortunately was lost before her photograph was taken, showed extreme Greyhoundlike proportions associated with a marked development of the dewlap.

The above evidence shows, that the lighter type of body build in the dog behaves as a dominant feature in relation to opposite qualities.

Additional information was gained in a cross within the German variety when a selected lightly built bitch was mated with an extremely lightly statured dog. In the resulting litter of five two extremely heavy uncouth animals were found.

The findings would to a certain degree find its analogy in the case of the sheep, where according to Wriedt, the recessivness of the heavy blocky type of the Soutdown in crosses with Merinos has been ascertained.

Segregation of the types encountered here is apparent and striking.

Thus the general type of light, or »English« conformation seems to be dominant in our case. The development of the chest basket bowever seems to follow a rather intermediate mode of inheritance.

Further, there seems to be a certain amount of independence between the different proportions. Thus the heavily framed dog Photo Nr. 7. shows a deep English Pointer like development of the chest basket whilst structurally typical Pointer of a brother of the above shows a rather poorly developed, »German« like chest basket. The dewlap seems to be a typically dominant feature.

Besides these peculiarities, certain features which lie on the border of structural deformities may be mentioned here. Thus it was found, that the dog »Skogis Pampas« imported from Sweden showed an abnormally short, protruding sternal bone causing abnormal development of the chest as a whole.

In the first generation produced with different normal bitches a number of young showing the anomality was found. It seems therefore, that we are dealing here with a dominant feature. Lastly two distinct structural features should be mentioned here.

As mentioned above, two distinct types of foot structure were encountered in our work. i. e. the compact »cat like« foot of the Pointer and the elongated outspread »hare like» of the German variety.

The first crossbred generation showed an intermediate structure with a certain preponderance of the »cat like« type.

The matter was however, not studied further so as to give a clue to the exact mode of inheritance of the feature under discussion. Lastly the differences in the form of the ear need some comment. The ear of the English Pointer is of a triangular »vinegar leaf like shape«. The somewhat larger ear lobe of the German variety is rounded in its contour and ends in a semicircular curvature. The first crossbred generation shows without exception the »triangular« type supporting the formely expressed opinion of practical breeders of its dominants nature.

In the Pointer-Alsatian crosses, where the pendulous gundog ear was crossed versus the erect ear of the wolfdog, resembling the primitive condition of the wild type, small but hanging ears resulted showing some similarity to the type found in certain pastoral breeds and in the Mastiff.

This last result show, that the hanging type of ear dominates the primitive erect condition, and that the small sized organ similarly behaves as a dominant in relation to the larger type.

It must be admitted that the hitherto gained information is rather scanty, it does on the other hand, undoubtedly show the general tendences of the studied feature and demonstrates the undisputable fact of distinct segregation of structural characters.

4. Remarks concerning the mode of inheritance of certain characteristic mental traits.

Genetic investigations concerning mental and psychical characters are, as yet only very scanty and fragmentary.

It is obvious that the dog, in which certain peculiarities of the nervous system have been moulded in to typical breed characteristics would lend itself especially well, for the study of the characters in question.

The results gained in our material pertain to the most typical mental characteristics of pointing gundogs, and may be summarised as follows:

a. The pointing instinct (steadiness). The very typical, and from a shooters point of view most valuable feature of a Pointer or Setter, is the falling in a very typical attitude, after perceiving the existence of game. This peculiarity of falling into the pointing attitude is developed very early in life in well bred dogs, and is perhaps comparable to certain nervous anomalies, found in Rodents like in the »dancing« rat or mouse, or to certain anomalies of the equilibrium system found in some varieties of pigeons.

The pointing instinct was most strongly developed in the now extinct Spanish Pointer, which was reported to remain »on point« often for a period of six hours, or more.

In the present English dog, the discussed capacity, though less pronounced than in the Spanish variety is comparatively stronger pronounced than in other breeds. The most common stimulus evoking the pointing »reflex« are olfactory sensations, connected with the presence of game. Other impressions, especially the sight of another dog in the «pointing« attitude do also evoke the attitude in well bred dogs (so called backing). The foundation stock of our material, showed typical development of the features in question and still more in the inbred specimems the »greyhoundlike« dog »Shot II» and his daughter »Nora« in which the tendency was developed in so far as to impair the usefulness of the respective animals in the field.

It may be interesting to note, that the outcrossed bitch »Fit II« whose both parents showed, a very strongly developed »backing« instinct. though her pointing properties were normal, showed no tendency to back whatever.

Observations concerning crossbred dogs, show that in crosses with the German variety a certain improvement of the pointing capacity as compared with the average German dog was noticeable.

These dogs, were however not as steady as good specimens of the English breed and especially poorly developed were their backing properties.

A somewhat more detailed account of the behaviour of the mentioned tendences in latter generations, was made hy the observation of the backcross generation gained between the three parts bred dog «Brillant« and the Pointer bitch »Fit II« (cfr. Table I).

It was found, that amongst three offspring reared, one the very greyhoundlike »Nora«, exhibited very strong pointing and backing properties comparatively very early in life. The very heavily framed dog »Shot« phot Nr. 7. showed only very rudimentary tendences in the mentioned direction for in his second year or life, this dog would point a covey of partridges for not longer than a few minutes, under most favourable scenting conditions. The third litter mate, observed here, the dog »Mars« which was taken in training rather late in life, showed again intermediate development of the feature in question, being steady enough for practical shooting, but required a considerable amount of training, before the feature was developed. (His backing properties were again very moderate). The above observations lead to the following results:

The pointing instinct, seems to be inherited rather indepedently from other features, especially features of body structure. The higher grades of the tendency seem to be imperfectly dominant over the lower ones (the English versus German variety).

It seems that the backing instinct, in the grade of its expression, is dependent upon specyfic genes, which may be different in nature in different strains, and in consequence in crosses of different strains may give an atavistic loss of the ability to back.

Further and more valid deductions should be expected in crosses of pointing and not pointing breeds, and these crosses would obviously be of importance in the ascertaining of the exact mode of inheritance of the character in question.

b. High versus low style of hunting and loud and silent hunting.

Our observations lead to the suggestion, that the low style of hunting i. e. the question of foot scent typical to hounds and certain gundogs (e. g. part of the German varietes of Pointers) behaves as a recessive feature in relation to the capacity to hunt with the head held high up and the ability to utilise the scent emanated by the body of the game in to the atmosphere, typical to high class Pointers.

Lastly the property of young gundogs to hunt their prey uttering yielping sounds, to the mode of hounds, found in the German breeds of Pointers seems to be a recessive feature in relation to the silent manner of hunting typical to the Pointer.

The above results, are of course only suggestive and require further confirmation from more extensive, and carefully planned crossing experiments.

5. Colour genetics, facts and considerations.

The inheritance of coat colour in the dog is unquestionably one of the most thoroughly investigated field, of work concerning this animal.

Most of the corresponding information has been gained by pedigree work though a certain amount of experimental study, has also been performed.

Nevertheless, there is a certain amount of interesting data that have been collected in our study, which may serve to elucidate certain obscure or uncertain points of earlier investigations.

These facts and certain general considerations. I propose to present in the following sections:

a. dominant and recessive black.

According to the opinion of most writers black in the dog is dominant to other colours. There are, however instances, in which black is reported to behave as a recessive in relation to red or to yellow,

Castle supposes, that the grey colour typical to most primitive breeds, like for instance the North American, or rather Canadian »husky« is dominant over black, found in the more refined domestic varieties.

In relation to this question, the writer is able to produce the following facts:

In two litters by a wolfgrey Alsatian sheepdog and brown or »liver« coloured Pointer bitches, 16 young were born, which were uniformly black in colour.

Little has found, that in a cross of yellow and liver coloured Pointers, black young are often produced in F_1, giving a dyhibridal ration in F_2.

The yellows mentioned in the quoted work, are however yellow dogs with a black nose and lips, and a certain amount of black on their ears. The eyes are dark brown, the nails likewise pigmented.

Two dogs of this description may produce, liver offspring, but they do not produce black. This kind of yellow is termed by Little »dominant« yellow.

Dominant yellow crossed with black gives black, as the writer could ascertain in matings between a black nosed yellow dog and the self coloured black bitch »Champion Blackfield Fate«.

It seems therefore, that black is a decided dominant.

The results reported above are in good accord with the findings of Little & Jones, based chiefly on pedigree studies on Great Danes.

Here black is also found to behave as a dominant, over brindle, yellow and red which seem to form links in a chain of a multiple allelomorph system, to which probably the »wild grey colour« of the Eskimo, Alsatian etc. regarded by Castle as probably dominant over black may be added.

All the above evidence pertaining to results gained in the study of Pointers Setters and Great Danes as well as Spaniels are totally uniform and confirm the above conclusion, that black is a distinctly dominant feature.

On the other hand, the writer has gathered certain facts, which seem to lead to a totally different interpretation of the genetic rank of black colour in dogs.

In a number of litters of a wolfcoloured Alsatian bitch by a black and tan dog of the same breed. a number (three) totally black pupies were born, under condition were no question of paternity could arise. To the writers knowledge came further a number of reports, in which the occurence of black puppies from two wolgrey parents was positively stated. This occurence must be somewhat frequent in certain strains of wolfdogs, as special enquiries concerning the phenomenon were made in the Polish Press devoted to the breeding of smaller animals (Polski Drób 1929).

Further evidence, of black behaving similarly to the black of the Alsatian was gained in the observation of the »white« sheepdog of the higher Carpathian and »Tatra« mountains, the so called »Liptak«. This breed resembling iu body structure the St. Bernard is of an entirely white colour with a certain amount of pale yellow markings. The nose, lips and eyes of these animals, are black, or of a very dark, brownish hue.

The discussed breed does therefore give the impression of carrying the so called »dominant yellow« colour, which is found to to be recessive in relation to dominant black.

A study of these dogs was maintained for a number of years by Dr. H. Wilczyński in Zakopane, who liberally enabled the writer, all desired access to his notes and his breeding stock.

It was soon found, that amongst the offspring of typically coloured dogs occassionally black and whites were born amongst their yellow litter mates.

These black pups were as a rule discarded, and at any rate never bred from. Still, the occasional occurence of a black pup was a quite usual happening within the discussed Kennel, as well as amongst the breed as a whole.

It should be mentioned lastly, that black young are reported to arise in litters of Irish Setters. Castle, when discussing the relation between black and red, basing evidently on the results, of Ankers work on the Dachshund states further: »in Dachshunds red is not uniformly recessive; it apparently may be dominant«.

All the above evidence, proves in the writers opinion, that in the Dog two genetically absolutely distinct black colours are to be met with.

One, recessive, comparable to that of the rat and rabbit hypostatic to dominant yellow but epistatic over »brown« (chocolate) and recessive yellow, and of course absolutely recessive, to the »wild« or wolfgrey of colour.

The other, comparable the dominant black of the rabbit, and probably like in the latter species, belonging to the allelomorph series of the extension factor epistatic to all other types of colour and pigment formation.

Te results of raising two backcross litters from black halfbred Pointer Alsatian bitches heterozygous for brown, by a wolfgrey Alsatian dog, known to produce black, yielded 14 black and 3 wolf grey pups, what clearly indicates the existence of two kinds of black in the above stock and at the same time the relation of recessive black to brown (liver, chocolate).

It the light of the above facts, the existence of two kinds of black within the domestic dog, seems to be well established.

In connection with the above, it is interesting to note, that the distribution of both dominant and recessive black as well as of both kinds of yellow seems to be different in distinct breeds, or rather groups of breeds.

Thus dominant yellow, and its allelomorph brindle, seems to be very common if not uniformly met with, in the Great Dane, and most likely in the Bulldog and Mastiff, where yellow with a »black mask«, is a very frequent colouring.

In gundogs, taking into consideration the results of Barrows & Phillips, as well as those of Little, besides our observations, dominant black seems to be typical to that group.

Both kinds of yellow seems to be present in the Pointer. The first mention of this colour in the discussed breed was made by Little, who based his studies on American material. According to the writers observations this colour is very rarely met with in England, and was not present in our experimental stock.

It seems however to be quite common in the Scandinavian countries, where, as in Danemark a distinct dominant yellow variety, the so called »Hertha Pointer« breed is kept.

The perusal of records of dogs of Russian and French origin, which I owe to the kind courtesy of Mr. St. Czerski of Warsaw show, that dominant yellow was practically absent from that material.

It seems that the factor will be disseminated in the Polish strains of Pointers through the recent importation of the »dominant» yellow dog »Skogis Pampas«.

In sheep and pastoral dogs, the conditions are in so far reversed, that dominant yellow and recessive black seem to be the most characteristic colour of the group.

In terriers the black tipped dominant yellow, in certain breeds attaining the hue of a bright red is the most commonly met type of yellow.

The black of this group may at least in certain cases be also of the dominant type.

Al least the black of the Foxterrier seems to be of the dominant kind.

In Dachshund, there seems to be little doubt, that anything else but dominant yellow and recessive black, are typical of the breed and its subvarieties.

This breed, showing a certain kind of intermediate character between the Terrier group and the hounds, which on the whole, are nearly related to Gundogs show a rather distinct behaviour, as far as the frequence of the two most frequently met with colours are concerned.

Amongst Setters, which according to historical traditions have as a group, a certain infusion of sheepdog blood, the existence of recessive black seems to be rather frequent.

It would remain to be ascertained whether the black of the English Setter, a breed in which yellow of the recessive kind is frequent, behaves as the dominant kind or otherwise. In the Irish Setter, dominant yellow and recessive black, just like in the case of primitive sheepdogs, seems to be most prevalent.

The above mentioned differences in colour distribution, which may be at present somewhat obscured owing to recent intermingling of types, may have some bearing on the early differentiation of breeds and breedgroups of the domestic dog.

Whether this differentiation has been indicated prior to domestication and is a direct argument in favour of a polyphyletic origin of the domesticated dog, cannot with certainty be settled at present. Anyhow regarded under the above point of view, colour formation and distinct types of genetic factors present in various groups of breeds, to a certain extent may be of value in a study concerned with the origin and evolution of the domestic breeds of dogs.

b. Inheritance of certain other colours and the genetics of roaning.

The inheritance of certain other colours, such a brown, as far as our material is concerned lies closely in accord with the findings of other writers.

The foundation stock of English Pointers described in the present paper carried recessive yellow characterised by a fleshy nose and light eyes. It was found, in crosses with the German breed or English dogs of other strains, that liver is decidedly dominant to this kind of yellow, and gives a 3:1 ratio in F_2 (cfr. Table I).

As shown on the above Table, the extensively tested bitch »Fit II« was heterozygous for tan, the only colour, which is seriously selected against in the Pointer, and which owing to its recessive nature, is as its occasional appearence testifies, bv no means eradicated from the breed as such.

The second characteristic feature, dealt with in our material is the so called roaning.

This feature is chiefly met with in the German varieties. It consists of the appearence of a certain amount of dark hairs amongst the white ares of the spotted or piebald dog. The quantity of these dark hairs, which arise when the animal is a few weeks old increases usually in so far, that the animal makes the impression of a silvery grey dog, and from a certain distance of a uniformly coloured, dark being.

Eyckman describes a similar feature in a number of varieties of American hounds, which he calls »ticking«. Judging from the photographs of this writer, »ticking« consists of a much lighter number of dark hairs present in the otherwise white areas of the coat, as compared with true roaning. In fact, a piebald dog especially a Pointer or Setter, is rarely free from dark ticks, which occasionally may form quite a fair amount of »ticking«.

Such ticking is very characteristic in the piebald English Setter, the »blue« (black or yellow, orange) belton. In all these cases the amount of pigmented ticks does not approach the number of pigmented areas of the roan »German Pointer« or »Cocker Spaniel«.

Roaning in dogs, does offer one fundamental difference, as compared with roaning in horses, cattle, or the Silver Rabbit. In the last named species, the colour in question is brought about by a number of white hairs, that are scattered on the othewise dark pigmented areas. In dogs a directly opposite process does take place. Consequently and uniformly coloured or »self coloured« dog cannot show any traces of roaning even, if he is roan genetically. If however, such an animal does posses some traces of white i. e. on the toes or chest, the roaning tendences are at once manifested, for the mentioned markings assume a very characteristic silvery hue, which is a sure indication of the roaning complex.

The results of mating roan (German) with ordinary piebald, in part presented on Table I. are 10 roan: 8 non roan i. e. an approximate 1:1 ratio) which shows the dominance of the roan factor.

In this respect roaning resembles closely »ticking« for which dominance was ascertained by Eyckman.

The relation of both these factors is at yet uncertain. There is certain possibility, that both these factors are allelomorphic, but is not ascertained as yet.

As far as our somewhat incidental observations go, the heavier grades of ticking are dominant over the lighter grades. This again suggests that a whole allelomorphic chain is involved here, or eventually, that distinct and independently transmitted modifiers are at play.

At any rate, it is a certain fact, that the amount of ticking of a given individual, often excedes that of it parents. That would suggest that modifiers of an additive type are at play here, but needs still more carefull study.

Ticking would lend itself for such a study much better than instances of true roanig, where the animal is of an uniform roan colour with only a very limited range of variability.

c. Spotting and peculiarities of pattern.

In this respect the dog, like the rabbit seems to represent a less specialised form than horses or cattle, where we have only one kind of spotting, dominant in the former and recessive in the latter.

Besides typical recessive spotting, of the Gundog, sheepdogs and hounds we find typically dominant spotting, comparable to that of the horse, or the English Rabbit, in te Dalmatian Dog and the Harlequine Great Dane.

Besides the spotted or piebald condition white markings on otherwise uniformly coloured animals i. e. on the chest, toes etc. are often found.

In the present writers opinion these markings are as well as in cattle recessive, and behave differently than in the horse, where according to Munckell, these markings are inherited in a dominant manner. The extension of pigmented areas of bicoloured (piebald) dogs is subject to a great deal of variation. Some dogs and breeds have greatly extended pigmented areas, whilst in others, as in most Pointers pigmented areas are often reduced th head markings a small spott above the tail and one or two small spots on the body.

The results of crossing heavier pigmented grades of piebald dogs with lighter ones, suggests a dominant tendency of the »heavier« i. e. more pigmented grades. On the other hand, it does occasionally happen, that on mating non related dogs with reduced pigmentation the progeny showes a marked increase of the pigmented areas.

The results do of course suggest the action of some non allelomorphic modifier, acting in both the crossed types in similar direction. Two further peculiarities of pigment distribution may be mentionod yet in the following. One of them consisted of the appearence of white spots on the ear which is usually pigmented in piebald dogs.

This tendency quite common in Foxterriers and English Setters, was first found in the bitch »Fit Kujavia« and likewise existed in her maternal grandmother. Further behaviour of this feature proved that we are dealing here with a recessive character, which in the heterozygote manifests itself by the appearence of a few white hairs scattered amongst the pigmented areas. The second feature, very widely distributed amongst piebald Pointers consist of a pigmented point located on the top of the head in a white area usually dividing the pigmented auricular regions,

This feature behaves as a typical dominant. It was found for instance in the majority of offspring of the foundation pair, where both parents possessed the feature, though occassionally a spot free individual was met within the progeny. Similar results were observed in matings where the feature in question was brought only by one parent in a given mating. These results are quoted in order to show, that insignificant and apparently trivial features. are nevertheless inherited in a true Mendelian fashion, just as certain minute details of pigmentation found in the horse and related by Wriedt.

d. General considerations.

The facts reported above do in the writers opinion offer a certain possibility of comparison of the most important features met in coat colour of mammals.

The hitherto studies Carnivora in relation to Rodents on the one hand, and on the other with domesticated Herbi- and Omnivora may be of considerable importance and evolutionary significance.

A survey of this kind is attempted on Table II, given below.

On the above Table, the most striking features of our domestic animals are brought together. Characters. which do appear in more than one allelomorphic form are mentioned with a single »+« for brevities sake. Certain features though superficially similar, may of course be totally different even in allied Genera and Species.

On the whole however, it is believed that the above Table may give a fair account of the genetic situation typical to the most important kinds of hitherto studied mammals.

Certain general impressions regarding the occurrence of different colour mutations may be summarised as follows: As far as the extension series is concerned, we find dominant extension, the so called »dominant black« was found in the rabbit, rat pig. sheep and dog. In the mouse dominant extension is represented by the well known yellow colour and its lethal effect. Intermediate extension corresponding to the colour of the Japanese rabbit is found in the Guinea pig, the dog and possible in cattle.

Dilution is seemingly present in all the studied species of Mammals as well as the recessive »chocolate« or »brown«.

White spotting in both its form recessive and dominant, is found in the rabbit the mouse (dominant spotting with lethal effect) and the dog.

TABLE II.

A comparison of known mutant characters in various Genera of Mammals.

Name of Species	Family	Normal	a. Series ef extension factor allelomorphs.		
			Dominant	Intermediate	Recessive
Rabbit	Lagomorpha	+	+	+	+
Guinea Pig	Caviidae	+	+——	+	+
Rat	Muridae	+	+	——	+
Mouse	Muridae	+	———	——	+
Pig	Suidae	+	+	——	?
Horse	Equide	+	——	——	+
Cattle	Bovidae	+	——	———	+
Sheep	Ovinae	+	+	——	+
Cat	Felidae	+	+	——	+
Dog	Canidae	+	+	+	+

Name of Species	Family	b. spotting, dominant recessive, brown dilution and albinism						
		Spotting		Periferal Spott.		Dilution	Brown	Alb
		Dom.	Rec.	Dom.	Reces.			
Rabbit	Lagomorpha	+	—	—	+	+	+	+
Guinea Pig	Cavidae	+	+	?	?	+	+	+
Rat	Muridae	+	+	?	?	+	+	+
Mouse	Muridae	+	+	?	?	+	+	+
Pig	Equidae	+	+	—+	——	+	+	+
Horse	Suidae	——	+	+	+	+	+	+
Cattle	Bovidae		+		+	+	+	+
Cat	Eelidae		+		+	+	+	+
Dog	Canidae	+	+		+	+	+	+

In the horse seemingly only one form of white spotting, the dominant one is to be found, whilst in the pig, the sheep and cattle the recessive kind seems to be solely present.

An interesting remnant of dominant white spotting met in cattle forms the white head of the Hereford and certain other breeds. A white blaze of a decidedly recessive type is to be found however, in this species as well. Thus we may come to the conclussion, that as far as the extension and spotting series is concerned Rodents, Carnivora (i. e. cats and dogs), and to a certain extent the pig represent the less differentiated and more primitive forms, whilst in herbivore forms a greater degree of specialisation does exist. True dominant extension has not been found as yet in horses or Cattle. It does however, exist in the sheep. Dominant spotting seems to be the only one met in the horse, whilst its recessive form seems to be common in cattle, sheep and swine. Rodents and Carnivora would as far at least as the spotting and extension series are concerned seem to form the less specialised forms in which more diverse kinds of characters, expresed by a simmilar phenotype are present. The horse and cattle where the actual position of »extension« black and ordinary black are by no means settled above doubt, present the in a sense, more specialised forms as far as coat colour is concerned.

Albinism though known to occur in almost every species of mammals seems to be especially frequent in Rodents. In Carnivora it is reperesented by the albinistic tendeny found in the Syamese cat. In cattle true, red eyed dilution seems to occur. In the other form discussed here the condition does not appear in the extreme form as stated above. Non albinotic white born horse, is a comparativelly insufficiently studied feature, so that no general conclusions can be drawn as yet.

It is obvious, that a comparative study of colour genetics in Mammals can make but little progress in the present state of exact knowledge concerning the genetics of most the higher Mammalian Genera.

There is however little doubt, that a study on the above lines is bound to offer much valuable information concerning the development of Mammals and secondly, yielding knowledge concerning the different rate of mutation in analogous genes in different loci, may form a rich source of basic and higly important information.

Even the hitherto gained knowledge, meagre as it is, may in comparison to general results of comparative anatomy of a earlier date show certain points in common. For taking for instance the fact into consideration that recessive spotting and both kinds of extension are found in the pig, we seem to confirm the old rule, that though a certain amount of progressive development may be observed in allied forms, in singular features these related species behave independently, forming a transgressive rather, than continous chain.

The above deductions are presented here in order to draw attention to the possibilities inherent in the comparative study of coat colour in Mammals.

The material on which the facts related here have been collected, was raised for the most part during the Great War under in every respect, very adverse conditions.

It is therefore only fair, to acknowledge that the possibility to raise and maintain the experimental stock of our material was almost solely due to the high skill and excellent husbandry of the late Mr. Suder laboratory Attendant, the whom the writer feels deeply intebted for keen and zealous help in the technical part of his task.

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Appendix — Pedigrees.

PEDIGREE Nr. 1.

Pedigree of the Foundation Dog »Royal Shot«.

Royal Shot	Champ. Melksham Lemon 1427	Ch. Lunsedale Wagg. K. C. I. 295 F.	Ch. Woolton Druid K. C. S. B. 36082
			Druidess K C. C. 651. A.
		Ch. Coronation K. C. S. B. 32 G.	Ch. Lurgan Royalty K. C. B. 651. A
			Ch. Princess May
	Royal Belle. — K. C. 1. 1607	Field Robur K. C. I. 993	Rochet of Meshes K. C. B. 155.
			Field Jenny K. C. I.
		Aida de Laval L. S. O. H. 4621.	Brodick Castle Sandy K. C. St. B. 42. 355.
			Ch. Archiduchesse K. C. St. B. 364 B.

PEDIGREE Nr. 2.

Pedigree of the Foundation bitch »Norma of Kutti.

Norma of Kutti	Lord of Jéke O. H. St. B. XX. III.	Rex of Hanva 365	York 414
			Seicken Mask 845
		Luff of Nyiregyhaza 528	Pajtas of Hanva
			Knico 507
	Fitful of Hanva O. H. St. Bd. XXIII	Aldin Fluke 31035	Fluke 1375
			Belle
		Seabreeze 624 E	Brodick Castle Sandy 40.35
			Mermaid

PEDIGREE Nr. 3.

Pedigree of The bitch «Fit of Kujavia«.

- Fit Kujavia
  - Royal Shot
    - Ch. Melksham Lemon 407
      - Ch. Lunesdale Wagg K. C. I. 295
      - Ch. Coronation K. C. St. B. 32 G.
    - Royal Belle K. C. I. 1908
      - Rex of Hanva 365
      - Aida de Laval L. S. O. H. 4621
  - Norma of Kutti
    - Lord of Jéke O. H. St Bd. XXIII.
      - Rex of Hanvaa 365
      - Luff Nyiregiháza 528
    - Fitful of Hanva O. H. St. Bd. XXIII.
      - Aldin Fluke 31035
      - Seabreeze

PEDIGREE Nr. 4.

Pedigree of the inbred dog »Shot II«.

- Shot II
  - Royal Shot ■
    - Ch. Melksham Lemon 1407.
      - Ch. Woolton Druid K. C. S. B. XXIII.
      - Druides K. C. St. XXIII.
    - Royal Belle K. C. I. 1908.
      - Field Robur K. C. I. 293.
      - Aida de Laval L. S. O. H. 4621.
  - Fit Kujavia
    - Royal Shot ■
      - Ch. Melksham Lemon 1407.
      - Royal Belle 1908.
    - Norma of Kutti
      - Lord of Jeke
      - Fitul of Hanva

PEDIGREE Nr. 5.

Pedigree of the inbred bitch »Norma II«.

- Norma II
  - Shot II ◡
    - Royal Shot ■
      - Ch. Melksham Lemon K. C. I. 1407.
      - Royal Belle K. C. I. 1908.
    - Fit Kujavia ▲
      - Royal Shot ■
      - Norma of Kutti
  - Fit Kujavia ▲
    - Royal Shot ■
      - Ch. Melksham Lemon 1407.
      - Royal Belle K. C. I. 1908.
    - Norma of Kutti
      - Lord of Jéke O. H. St. XXIII.
      - Fitful of Hanva O. H. St. XXIII.

PEDIGREE Nr. 6.

Pedigree of the outcrossed bitch »Fit II«.

Fit II	»King«	Landsnor	
		Isle de France	
	Fit of Kujavia ▲	Royal Shot ■	Ch. Melksham Lemon 1407.
			Royal Belle 1907.
		Norma of Kutti	Lord of Jéke XXIII.
			Fitful of Hanva XXIII.

PEDIGREE Nr 7.

Pedigree of the halfbred German Pointar Dog »Verdun«.

Verdun	Tref German Pointer heavy strain		
	Norma II	Shot II ◡	Royal Shot ■
			▲ Fit Kujavia
		▲ Fit Kujavia	Royal Shot ■
			Norma of Kutti

PEDIGREE Nr. 8.

Pedigree of the »threeparts bred« Pointer »Brillant«.

Brillant	Verdun	Treff	
		• Norma II	Shot II ◡
			▲ Fit Kujavia
	Brillant	Shot II ◡	Royal Shot ■
			▲ Fit Kujavia
		▲ Fit Kujavia	Royal Shot ■
			Norma of Kutti

PEDIGREE Nr. 9.

Pedigree of the »7/8« litters presented on Table I.

X. X.	Brillant	Verdun	Treff
			• Norma II.
		• Norma II	Shot II
			▲ Fit Kujavia
	Fit II.	King	Lansnor
			Isle de France
		▲ Fit Kujavia	Royal Shot ■
			Norma of Kutti

Explanation of photographs.

Nr. 1. The ideal type of an English Pointers Head.

Nr. 2. The type of head met in the Alsatian Wolfdog.

Nr. 3. The type of head found in the Greyhound.

Nr. 4. Greyhoundlike headed bitch »Hetka«. Table I. litter 1921.

Nr. 5. Photograph of a German Pointer.

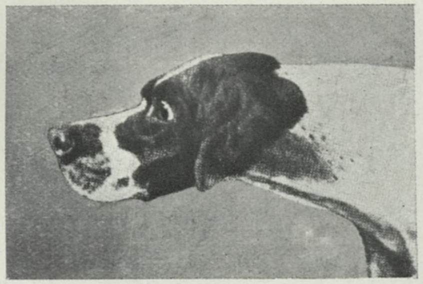
Nr. 6. Photograph of the dish faced bitch »Fit II».

Nr. 7. Photograph of a heavy specimen from the Third Pointer German Pointer backcross generation.

Nr. 8. The type of Pointer bred at Present in England. The winnig dog »His Majesty« (courtesy Mr. H. Lonsdale, Carlisle, England).

Nr. 9. a F_1 German Pointer Alsatian Wolfdog cross.

Nr. 10. A profile Photo of a head of a Pointer showing recessive white on ear.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7


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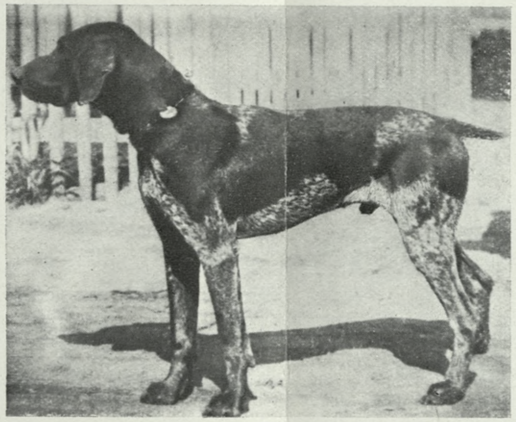
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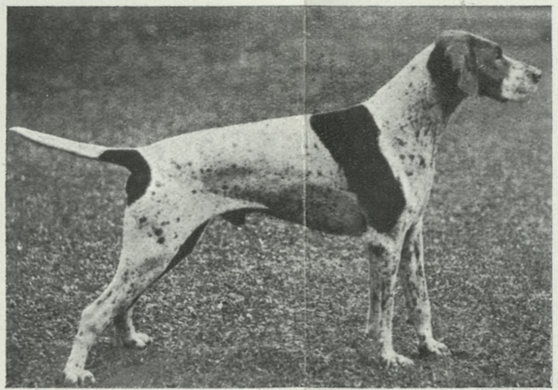
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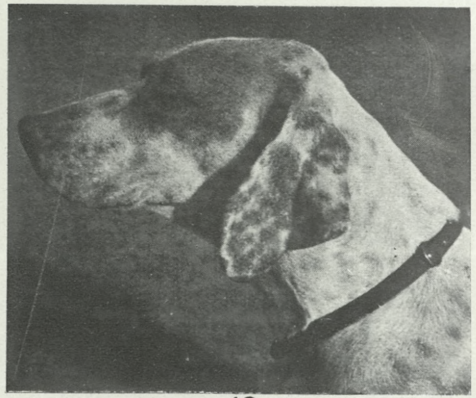
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