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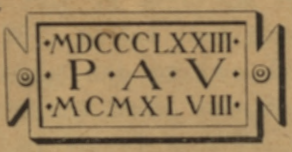

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O śmierci zarodka kurczęcia spowodowanej wysoką temperaturą. — On the thermal death of the chicken embryo.

Mémoire

de M. *H. SZARSKI*,

présenté le 10 Novembre par M. Z. Grodziński m. c.

The influence of supranormal temperatures on the development of the chicken embryo has been investigated several times (Bucciante 1929, Andersen 1931, Bělehrádek 1935). Among recent studies, the result of Ancel and Lallemand (1941), and also those of Rondinini (1942) should be mentioned here. Ancel and Lallemand stated that chicken embryos which were kept for forty-eight hours in temperatures of $+39^{\circ}$ C — $+42^{\circ}$ C showed an increase in the number of teratological specimens. According to Rondinini the development of chicken embryos in a temperature of $+40^{\circ}$ C — $+42^{\circ}$ C causes a depression of the growth rate of embryos. In contrast to these statements Mikawa (1937) writes that temperatures of $+45^{\circ}$ C — $+47^{\circ}$ C applied during one or two hours do not affect embryos. Some damage, but not death, was observed by Mikawa only after an embryo had stayed in a temperature of $+47^{\circ}$ C for more than two hours.

These and other similar discrepancies in results are due to differences in the method of heating. The specific heat of the egg is considerable, accordingly the temperature of the contents of the egg, transferred from a temperature of $+38^{\circ}$ C to a temperature of $+45^{\circ}$ C, rises slowly, and the rapidity of the rise depends on several factors, such as the dimensions of the incubator, the temperature of the air-chamber and of the water-mantle of the incubator, etc. Experiments conducted under varying conditions can therefore be compared only with caution. We can however state that the normal development of the chicken embryo

in temperatures exceeding + 43° C is impossible, and that such high temperatures cause the death of the embryo.

We know from other sources however that the isolated chicken embryo tissues can live in such temperatures, and die only when the temperature exceeds + 47° C (Lambert and Hanes 1913, Kemp and Juul 1931, Pincus and Fischer 1931, M. R. Lewis 1933, H. Szarski 1939).

The present paper presents an attempt to analyse the process of the death of chicken embryos in supranormal temperatures, which are yet not lethal for separate tissues. The methods used were similar to those used in the analysis of the survival of tissues after the death of the organism (Bucciante 1931, 1933, Grodziński 1932, Wilburg 1937).

Material and Methods

Before the experiments the eggs were incubated for ten days in a temperature of + 38° C. In the first series of experiments (exp. nos. 1—48) the eggs of White Leghorns were used; in the second series (exp. nos. 49—73), the eggs of the Polish greenleg breed (zielononóżki). The embryos of both breeds showed a similar resistance to heat.

Two plans of experiment were followed. In the first type, the intact egg was transferred directly from an incubator with a temperature of + 38° C to an incubator with a temperature of + 45.5° C. After an appropriate time the egg was removed, opened, and cultures of the tissues from various organs were prepared. In the second type of experiment, after the removal of the egg from the temperature of 38° C, a small hole was made in the round end of the egg. Trough this hole the egg membrane was removed from the air-chamber, then with the aid of small scissors the umbilical cord was cut, causing the exsanguination of the embryo (Grodziński 1932). The hole in the shell was then closed with a piece of tissue paper soaked in paraffin, and the egg put in an incubator with a temperature of + 45.5° C. After some time in the incubator the egg was removed and cultures prepared from the various organs.

The supranormal temperatures were obtained in an electric incubator made by Messrs. E. Leitz (fig. 1). The air-chamber

of this incubator is small, so that only one egg can be put in it at a time. The distance between the egg-shell and the wall of the air-chamber measures about 2 cm. The temperature of the

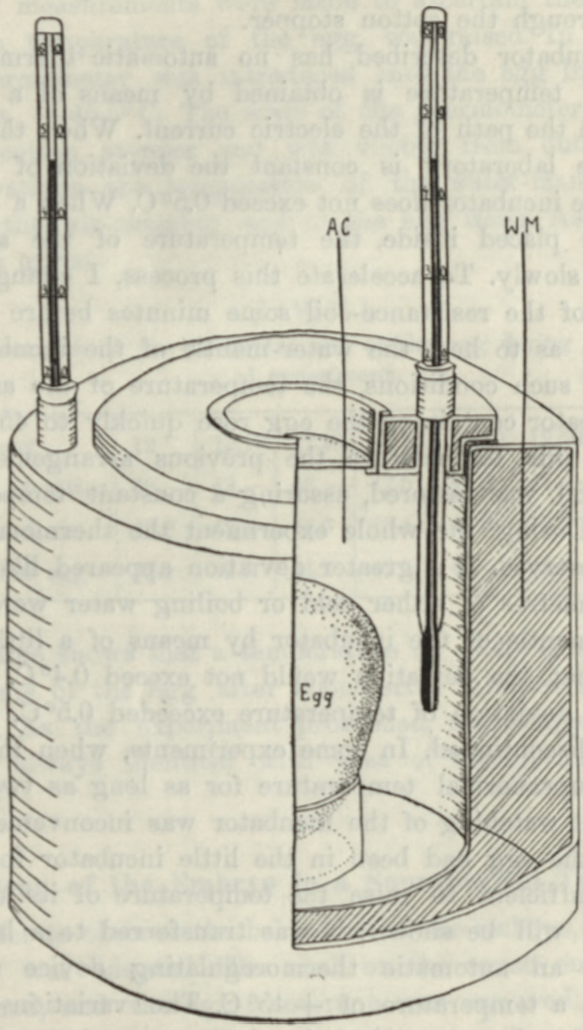


Fig. 1. Plan of the incubator of E. Leitz, which was used for the experiments. A. C. = air-chamber, Egg = egg, W. M. = watermantle.

egg-content therefore rises very quickly. There is a window, closed by a round piece of glass, in the cover of the incubator. This arrangement permits the observation of the contents without opening the air-chamber. The piece of glass can be removed and

the window closed by a cotton stopper. By such an arrangement, direct measurement of the contents of the egg can be carried out. The thermometer is inserted trough a small hole in the egg, and the scale of the thermometer passes out of the incubator trough the cotton stopper.

The incubator described has no automatic thermoregulator; the desired temperature is obtained by means of a resistance-coil fixed in the path of the electric current. When the temperature of the laboratory is constant the deviation of the temperature of the incubator does not exceed 0.5° C. When a cooler egg however, is placed inside, the temperature of the air-chamber rises very slowly. To accelerate this process, I changed the arrangement of the resistance-coil some minutes before putting in the egg, so as to heat the water-mantle of the incubator above + 48° C. In such conditions, the temperature of the air-chamber of the incubator containing the egg rose quickly to 45° C. When it reached this temperature, the previous arrangement of the resistance-coil was restored, assuring a constant temperature of + 45.5° C. During the whole experiment the thermometers were carefully observed. If a greater deviation appeared likely, several cubic centimetres of either cold or boiling water were added to the water-mantle of the incubator by means of a little glass pipette, so that the deviation would not exceed 0.4° C. If for any reason the deviation of temperature exceeded 0.5° C, the experiment was discontinued. In some experiments, when the egg was kept in a supranormal temperature for as long as twelve hours, this constant watching of the incubator was inconvenient. Therefore after the egg had been in the little incubator for an hour, which is sufficient to raise the temperature of its contents to + 45° C, as will be shown; it was transferred to a larger incubator with an automatic thermoregulating device which was adjusted to a temperature of + 45° C. The variations of temperature in this last-mentioned incubator ranged from + 45.0° C to + 45.9° C, and were rhythmical. One variation took about 25 minutes.

Methods of tissue culture were similar to those commonly used (Parker 1938). The cultures were mounted in hanging drops. The medium for the cultures was always formed by a mixture of identical drops of chicken plasma and chick embryonic extract

(pure tissue juice dissolved with three times its volume of Tyrode's solution).

Raising the Temperature of the Egg

Special measurements were made to ascertain the speed with which the temperature of the egg was raised. In order to do this, a thermometer was introduced into the egg inside the incubator at + 45.5° C. The scale of the thermometer was passed trough a cotton stopper and was visible from outside. During all observations the temperature of the water-mantle exceeded those of the air-chamber and of the egg itself. As an example Table I is given.

TABLE I

The temperatures of the incubator and of the egg during the first hours of experiment

Degrees in Centigrade	Hour	12	12.10	12.20	12.30	12.40	12.50	13	14
	T. of water	49.—	49.—	48.—	47.5	47.8	47.—	46.5	46.7
	T. of air	43.2	45.—	45.6	45.4	45.8	45.2	45.5	45.6
	T. of egg	38.9	39.9	41.2	42.5	43.—	44.8	45.2	45.6

The table shows that a temperature of + 45° C is reached by the contents of the egg after about sixty minutes in the heated incubator. As the experiment proceeded, the temperature of the egg was always identical with that of the air-chamber of the incubator.

Behaviour of the Embryo in a Supranormal Temperature

In order to observe the behaviour of the embryo, the following technique was adopted. The shell on the round end of the egg was opened, and the egg-membrane was removed, showing the embryonic membranes. The preparation was then put in the incubator, and the embryo was observed trough the glass window in the cover.

As in the experiments of Andersen (1931), the heart-beat was accelerated as the temperature rose. About the end of the first hour of the experiment, or during the second hour, the

heart ceases to beat. The temperature of the embryo must reach about 45° C at this moment. After the stopping of the heart, the blood vessels in the embryonic membranes gradually contract. The contraction reaches its height in thirty to sixty minutes after the stopping of the heart-beat, *i. e.* about two hours from the beginning of the experiment.

During the first ninety minutes of the experiment the embryo moves violently in the amniotic sac. About the end of the second hour its activity is considerably diminished. Small spontaneous movements were noticed even in the fifth hour of the experiment, but they were separated by longer and longer periods of rest. When disturbed by a touch, the embryo moves more visibly. The movement can be provoked by touching even during the seventh hour of experiment. About the end of the seventh hour, the movements cease completely. During the eigth hour even the crushing of the spinal cord does not induce any movement.

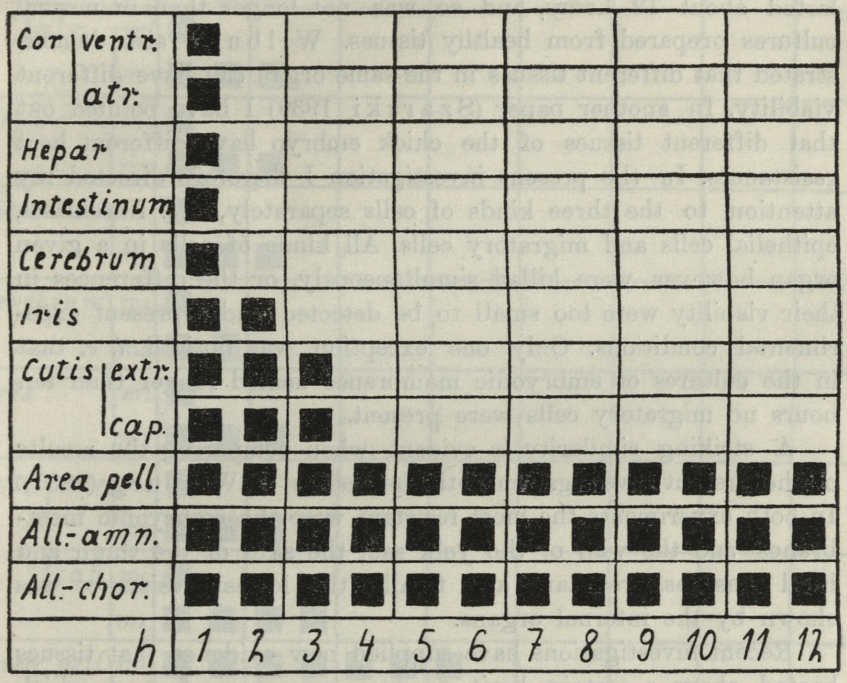
The Survival of Tissues

The survival potency of the following tissues was investigated:

The ventricle of the heart, the auricle of the heart, the intestine, the brain, the iris, the skin of the leg (taken from the outside surface of the thigh), the skin from the parietal region of the head, the area pellucida (a portion of the wall of the vitelline sac from the vicinity of the umbilical cord), the allantoamnion (a fragment taken from the portion covering the embryo when the egg is stood upright on its sharp end), and allantochorion (a piece of the tissue lying directly under the egg membrane in the air-chamber of the egg).

The results of these experiments are shown in Graphs I and II. In Graph I we see the results of supranormal temperature on the embryo killed by exsanguination. The results of the experiments were almost uniform. After the first hour of the experiments the following tissues lose their regenerative capacity: the ventricle and auricle of the heart, the liver, the intestine, and the brain. The iris lives a little longer, till the end of the second hour of the experiment. The skin of the thigh and of the head are not killed after three hours without circulation in

the high temperature. The highest resistance is shown by the embryonic membranes and the wall of the yolk sac, which can grow in the tissue culture even after twelve hours of the experiment. We must however emphasize here a circumstance not shown in the graph.



Graph I. Viability of tissues of the chick embryo, heated to 45.5C° after exsanguination. Black squares show that the tissue is able to grow in culture.

The cultures of easily-killed organs usually give very uniform results, but embryonic membranes and the wall of the yolk sac sometimes show considerable discrepancies. So for instance these organs regenerated in cultures every time when the experiment lasted ten hours. Once they were killed after eleven hours, once they were killed after twelve hours, but twice they regenerated after an experiment lasting twelve hours. In experiments which were extended over twelve hours the tissues were always killed.

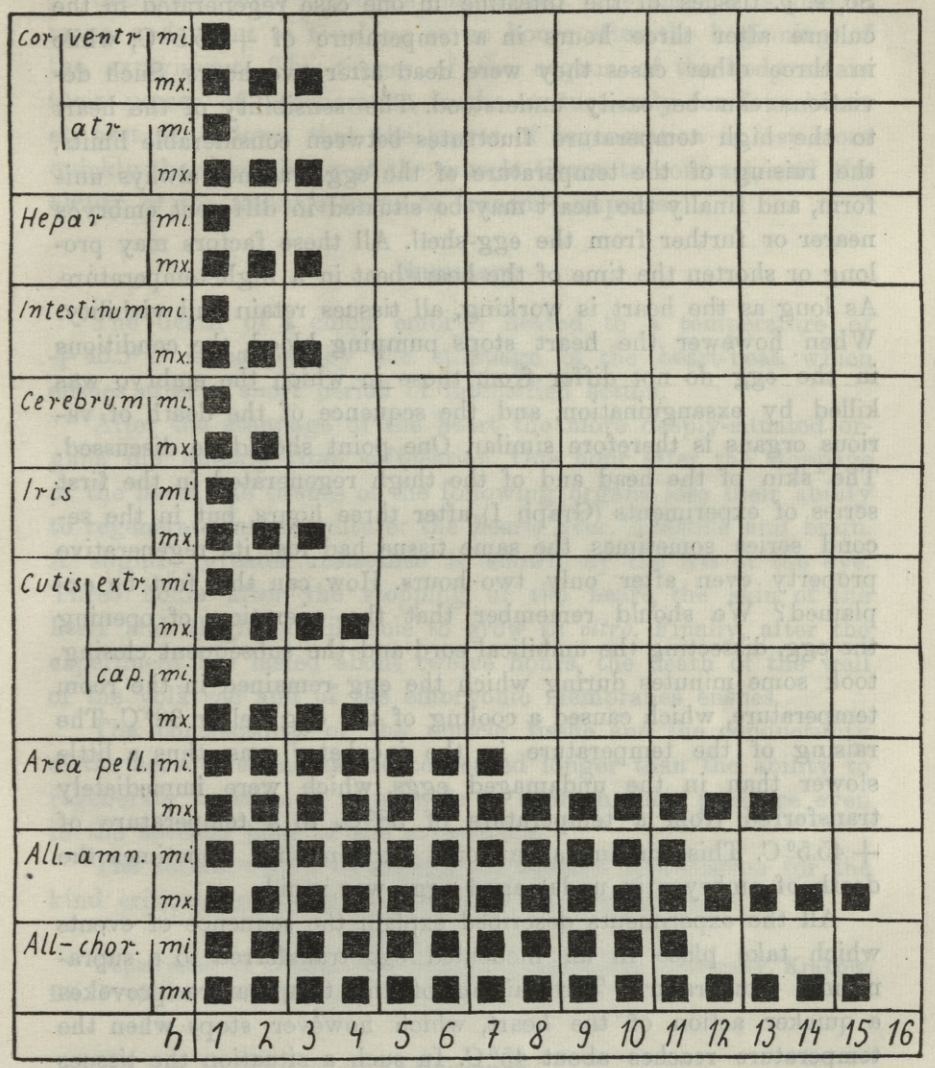
Wilburg (1937), analysing the viability of organs of a chick which was kept in a temperature of + 38° C after exsanguination,

noticed an interesting fact; *i. e.* the time which separates the beginning of the wandering of cells in the culture from the moment of the preparation of the culture was prolonged in the more seriously affected tissues. The duration of this period reached 72 hours. In my experiments the latent period usually lasted about 12 hours, and so was not longer than in normal cultures prepared from healthy tissues. Wilburg also demonstrated that different tissues in the same organ can have different viability. In another paper (Szarski 1939) I have pointed out that different tissues of the chick embryo have different heat resistances. In the present investigation I therefore directed my attention to the three kinds of cells separately, *i. e.* fibroblasts, epithelial cells and migratory cells. All kinds of cells in a given organ however were killed simultaneously, or the differences in their viability were too small to be detected under present experimental conditions. Only one exception was noticed, *i. e.* that in the cultures of embryonic membranes heated longer than ten hours no migratory cells were present.

A striking similarity is evident when comparing the results of the present investigation with the results of Wilburg (1937). In both experiments the most resistant were the embryonic membranes and the wall of the yolk sac; the skin of the thigh and head was less resistant, and finally the lowest resistance was shown by the internal organs.

Recent investigations have supplied new evidence that tissues heated above a certain limit produce some toxic factors, which circulate in the blood and can provoke the death of the organism (Heilbrunn et all. 1946). According to Moritz and Henriques (1945) the principal factor causing death after the burn is the hyperpotassemia, which is traced to liberation of potassium from the red blood cells. The results of my experiments can be explained without assuming the presence of such factors. It is probable that a temperature of $+45.5^{\circ}$ C, which is not lethal for tissues in cultures, does not cause the production of the toxic factors in the chick embryo. To understand the results of my experiments, it is sufficient to assume that the cause of the death of the tissues lies in the accumulation of the products of metabolism and in the lack of oxygen. The organs situated deeper and having a greater metabolism die sooner, the organs

situated nearer the surface, and having therefore an easier access to oxygen, live longer.



Graph II. Viability of tissues of the chick embryo heated to 45.5° C in an undamaged condition. Mi — lowest viability observed, Mx — highest viability observed.

Graph II shows the results of experiments in which an undamaged egg was put in a temperature of 45.5° C. As the results

were not so uniform as in the previous series, it was necessary to show in the graph both the highest and the lowest results. So, *e. g.* tissues of the intestine in one case regenerated in the culture after three hours in a temperature of + 45.5° C, while in three other cases they were dead after two hours. Such deviations can be easily understood. The sensibility of the heart to the high temperature fluctuates between considerable limits, the raising of the temperature of the egg was not always uniform, and finally the heart may be situated in different embryos nearer or further from the egg-shell. All these factors may prolong or shorten the time of the heart-beat in a high temperature. As long as the heart is working, all tissues retain full viability. When howewer the heart stops pumping blood, the conditions in the egg do not differ from those in which the embryo was killed by exsanguination, and the sequence of the death of various organs is therefore similar. One point should be discussed. The skin of the head and of the thigh regenerated in the first series of experiments (Graph I) after three hours, but in the second series sometimes the same tissue had lost its regenerative property even after only two hours. How can this fact be explained? We should remember that the operation of opening the egg, dissecting the umbilical cord and the subsequent closing, took some minutes during which the egg remained in the room temperature, which caused a cooling of the egg below 38° C. The raising of the temperature in the incubator was thus a little slower than in the undamaged eggs, which were immediately transferred from a temperature of 38° C. to a temperature of + 45.5° C. This circumstance could explain that sometimes the death of embryos in undamaged eggs was rapid.

All the experiments described explain the sequence of events which take place in an incubated egg transferred to a supranormal temperature. The raising of the temperature provokes a quicker action of the heart, which however stops when the temperature reaches about 45° C. In such a situation the tissues are quickly overloaded with the products of cell metabolism and die from suffocation. The embryonic membranes exhibit the longest resistance, as they have the greatest general resistance to external factors (Wilburg 1937, Szarski 1939) and have the easiest access to oxygen. We can assume that the death of

these structures is provoked in the first place by the accumulation of the nongaseous products of metabolism.

One observation should be emphasized. The embryo is able to move and react to touching seven hours after the beginning of the experiment. The tissues of the organs of the body retain their power of regeneration in the culture only for four hours at best. It follows that the power of regeneration is lost more quickly than the ability of the muscle tissue to contract, and the ability of the nervous tissue to transmit impulses.

Summary

The death of a chick embryo heated to a temperature of + 45.5° C is caused by the stoppage of the heart-beat, which ensues after a short period of intensified action.

After the stoppage of the heart the more deeply-situated organs die quickly from suffocation. One hour after the stoppage of the heart, the tissues of the following organs lose their ability to regenerate in the culture: the heart, liver, intestine and brain. A slightly greater resistance is shown by the iris of the eye. Three hours after the stopping of the heart, the skin of the head and thigh is still able to grow *in vitro*. Finally, after the experiment has lasted about twelve hours, the death of the wall of the yolk sac and of the embryonic membranes ensues.

The contractility of the muscle tissue and the conductivity of the nervous elements are conserved longer than the ability to regenerate *in vitro*. It is possible to confirm their presence even in the seventh hour of the experiment.

The author wishes to express his sincere appreciation for the kind criticism received from prof dr. Z. Grodziński.

Department of Comparative Anatomy. Jagellonian University. Kraków. Dir. Prof. dr. Z. Grodziński.

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System krwionośny Salientia. — On the blood-vascular system of the Salientia.

Mémoire

de M. *H. SZARSKI,*

présenté le 10 Novembre 1947 par M. Z. Grodziński m. c.

Contents:

1. Introduction

The knowledge of the vascular system of the *Salientia* is usually considered extensive. This opinion is supported by the fact that after many early works (Burow 1834, Gruby 1842, Rusconi 1845, Virchow 1880, Boas 1882, 1883 etc.), Gaupp gave, in the second volume of his anatomy of the edible frog (1899), a detailed account of the blood vessels of this species. No other author working on the anatomy of the *Salientia* has approached his accuracy.

There are also many descriptions of the blood-vascular system of other *Salientia* (Goette 1875, Klinckowström 1894, Crawshay 1906, Marriner 1906, Gillies 1914, Grobbelaar 1924

Bhaduri 1930, 1931 etc.). All the above mentioned authors do not however attempt a broader comparison of different forms, but notice only the chief points of difference between *R. esculenta* L. and the animals described.

The edible frog is not however a typical form of *Salientia*. The *Ranidae* are a large group and have numerous representatives in Europe and North America, but according to the present state of knowledge (Noble 1931) form a class apart together with the families *Brevicipitidae* and *Polypedatidae*, forming the suborder *Diplasiocoela*.

»*Rana*, which has been considered the typical salientian in most morphological works, is the most specialized in regard to the insertions of the posterior thigh muscles, just as it is the most specialized in many other ways« (Noble 1922, p. 37).

In consequence, the attempts to connect the various known facts into a harmonious whole on the basis of Gaupp's descriptions have failed, and in spite of many publications dealing with the blood-vascular system of *Salientia* only the description of Gaupp is quoted in textbooks, even in those attempting to give an extensive comparison of the assembled knowledge (Nierstrasz 1927, Hafferl 1933, Van Gelderen 1933). Therefore, some details of the structure, characteristic probably only of the family *Ranidae*, or of the related sub-orders *Procoela* and *Diplasiocoela*, are stated as the property of all *Salientia e. g.* the absence of the caudal artery and vein, the absence of the ischiadic vein, the prolongation of the facial vein into *v. cutanea magna* etc.

Hence I considered that an account of the blood-vascular system of some *Salientia* might be of value. As I had at my disposal a large material of injected specimens of the European spade-foot toad, *Pelobates fuscus* Laur., a member of the sub-order *Anomocoela* and the blood vessels of the animals belonging to this group are completely unknown, I decided to describe the blood-vascular system of the above-mentioned amphibian, and to compare the results with the systems of *R. esculenta* L., *Bombina bombina* L. and *Bufo bufo* L.

To avoid confusion I use always when possible the nomenclature of Gaupp. The introduction of names used by others authors, or of new names, is always underlined. This is omitted

only when the old names of Gaupp have to be modernized in consequence of the new anatomical nomenclature (I. N. A.) adopted in the year 1935 (Stieve 1936, Kopsch 1937, 1939).

2. Material and methods

I was working on the animals belonging to the following species: *Pelobates fuscus* Laur., *Bombina bombina* L., *Bufo bufo* L., *Rana esculenta* L. All specimens were caught in the vinicity of Kraków in the years 1937—1945 mainly during the spring. The blood vessels of the animals anesthetised with ether were injected with Prussian blue or with Indian ink from the *truncus arteriosus*, then the specimens fixed in toto in 10% formalin. The sections were performed under a low power binocular microscope.

The descriptions of the blood-vascular system of *P. fuscus*, *Bombina bombina* and *B. bufo* are the results of the afore-mentioned sections. The descriptions of the anatomy of *R. esculenta* L. are only partly original and are mainly based on the work of Gaupp.

As a consequence of injecting the ink through the *tr. arteriosus* the close vicinity of the heart and the heart itself are seriously damaged. I do not therefore describe the heart and the arteries and veins supplying the *bulbus cordis*.

3. Main arteries of the trunk

a) ***Pelobates fuscus*** Laur. The arterial arches are given off from the *truncus arteriosus impar*. This trunk divides into two vessels *(truncus arteriosus dexter et sinister)* in the anterior part of the pericardium, on its ventral side. Each of them is again divided by longitudinal partitions into three parallel trunks: *canalis caroticus*, *c. aorticus* and *c. pulmo-cutaneus*. From the *tr. arteriosus dexter* arises a small artery, supplying the *bulbus cordis*, named *a. bulbi cordis*. Each arterial trunk passes laterad through the pericardium and divides into three arterial arches: carotid, systemic and pulmo-cutaneous.

A. carotis communis, the carotid arch, runs dorsad through *m. m. petrohyoidei* and divides into the internal and external carotid arteries. At the point of division a swelling is found: the caro-

tid labyrinth, *glomus caroticum*. The carotid arteries are described together with the vessels of the head.

The systemic arch runs together with the carotid arch through *m. m. petrohyoidei* and sends off the laryngeal artery to the larynx. It then bends round the digestive tract, runs dorsad and on the dorsal side of the oesophagus gives off a short and very broad vessel directed craniad. This vessel is the common origin of the subclavian, occipito-vertebral and cranial oesophageal arteries (fig. 1).

From this point the thoracic aortae run caudad along the ventral side of the vertebral column. The left and right trunks approach each other and join under the sixth vertebra, forming the abdominal aorta. In the middle of the length of the thoracic aortae, the caudal oesophageal artery is given off from the left or right branch.

A. laryngea arises from the systemic arch at the place where the last-named passes through *m. m. petrohyoidei*. The laryngeal artery runs caudad for a very short distance, bends mediad and supplies the wall of the oesophagus, as also in the further course the larynx and its muscles.

A. subclavia (fig. 1, *A. sub.*) arises from the systemic arch by means of the common trunk with *a. occipito-vertebralis (A. occ. vert.)* and *a. oesophagica cranialis (A. oe. cr.)*. This trunk runs craniad for a short distance giving off *a. occipito-vertebralis* and *a. oesophagica cranialis* craniomesiad and *a. subclavia* laterad. At the point of its origin, the subclavian artery gives off *a. thoracica superior (a. th. sup.)*. In some animals the last-named artery does not arise from *a. subclavia*, but from the common arterial trunk. The further course of the subclavian artery is described with the vessels of the thoracic limb.

A. oesophagica cranialis (Gaupp's *a. oesophagea*) *(A. oe. cr.)* arises from the systemic arch together with the subclavian and the occipito-vertebral arteries. After a short course *a. oesophagica cranialis* divides into two vessels which supply the dorsal wall of the oesophagus.

A. occipito-vertebralis (A. occ. vert.) arises from the systemic arch together with the above-mentioned vessels. From the point of division the occipito-vertebral artery runs dorso-craniad, passes under the transverse processes of the second and third verte-

brae and penetrates the muscles of the trunk. Immediately under the transverse process of the second vertebra, the occipito-vertebral artery divides into two branches: *a. vertebralis dorsi* and *a. occipitalis.*

A. occipitalis is described with the vessels of the head.

A. vertebralis dorsi runs caudad, lateral to the transverse processes of the vertebrae *(proc. obliqui)* in the muscles of the trunk. It gives off a branch entering the vertebral canal anastomosing with *a. spinalis ventralis*, and several others to the muscles. The vertebral artery is a small vessel and can be followed only to the vicinity of the *sacrum*, where it ends.

A. oesophagica caudalis (A. oe. caud.) is an unpaired vessel arising from only one aorta, left or right. In some animals there was found a second symmetrical *a. oesophagica caudalis*, but then the arteries were of very different dimensions. *A. oesophagica caudalis* supplies the oesophagus. It was first described by Rau (1924) in *Ceratophrys* and by Bhaduri (1930) in *Bufo melanosticus* and *B. stomaticus* under the name *a. oesophagea.* Gaupp however had already used this name for *a. oesophagica cranialis*, called by Bhaduri *a. pharyngea.* To avoid confusion I call both vessels oesophageal arteries with adjectives added.

Aorta abdominalis. The right and left thoracic aortae join under the sixth vertebra in an unpaired vessel, the abdominal aorta. Immediately after the junction of the paired vessels into the unpaired *aorta abdominalis*, the coeliaco-mesenteric artery arises from the last named. The blood flows to the coeliaco-mesenteric artery mainly from the left thoracic aorta, the blood from the right being directed to the abdominal aorta. Between both vessels however a large spacious foramen is found.

The abdominal aorta runs caudad, giving off numerous branches called *a. a. lumbales* and *a. a. urogenitales.* Under the sacral vertebra arises in some specimens *a. mesenterica caudalis*, and further caudad begins *aorta caudalis* from the left side of the abdominal aorta. After the origin of the caudal aorta, the abdominal aorta continues caudad for a moderate distance and then divides into right and left *a. a. ilicae communes.*

A. coeliaco-mesenterica is described with the blood vessels of the digestive tract.

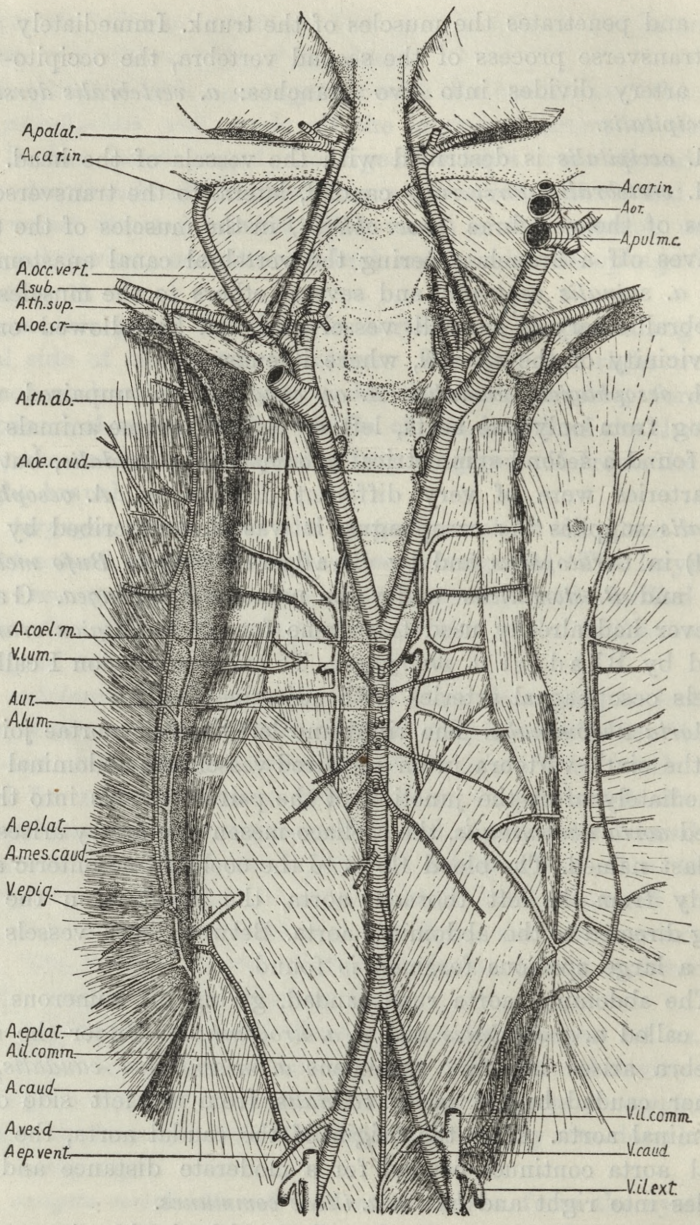

Fig. 1. Blood vessels of the trunk in a male spade-foot toad seen from the ventral side. The lungs, heart, alimentary canal with appendages, kidneys and nerves have been taken out. On the right side of the body (left

in the fig.) the pulmo-cutaneous arch and part of the systemic arch are also eliminated together with a portion of the abdominal muscles in order to show the anastomosis connecting the thoraco-abdominal artery with the lateral epigastric artery.

A. car. in.	: *a. carotis interna*	*A. oe. cr.*	: *a. oesophagica cranialis*
A. caud.	: *aorta caudalis*	*Aor.*	: *aorta thoracica*
A. coel. m.	: *a. coeliaco-mesenterica*	*A. palat.*	: *a. palatina*
A. ep. lat.	: *a. epigastrica lateralis*	*A. pulm. c.*	: *a. pulmo-cutanea*
A. ep. vent.	: *a. epigastrica ventralis*	*A. sub.*	: *a. subclavia*
A. il. comm.	: *a. ilica communis*	*A. th. ab.*	: *a. thoraco-abdominalis*
A. lum.	: *a. lumbalis*	*A. th. sup.*	: *a. thoracica superior*
A. mes. caud.	: *a. mesenterica caudalis*	*A. ur.*	: *a. urogenitalis*
A. occ. vert.	: *a. occipito-vertebralis*	*A. ves. d.*	: *a. vesicalis dorsalis*
A. oe. caud.	: *a. oesophagica caudalis*	*V. epig.*	: *v. epigastrica*
		V. lum.	: *v. lumbalis*

A. a. lumbales (A. lum.) are very variable. As an example I shall describe the relations in a male specimen: All arteries are paired. The first leaves the aorta immediately caudad to *a. coeliaco-mesenterica*, the second and third have roots in common with the urogenital arteries, the fourth and last leaves the aorta independently. In another animal all lumbar arteries had their origins in common with the urogenital arteries. On the one side of the body there were five, on the other four lumbar arteries. Still another case is drawn in fig. 1.

The anterior lumbar arteries run craniad along the vertebral column, and supply the muscles of the trunk. Their branches usually reach as far as the third vertebra. The medial arteries run dorso-laterad and supply the muscles of the trunk and the origins of the abdominal muscles. The posterior arteries run dorso-caudad and supply chiefly *m. coccygeo-ilicus*.

A. a. urogenitales (A. ur.) are also very variable. In most animals they are given off from the aorta together with the lumbar arteries, at more or less regular intervals. As an example I shall describe the relations in one specimen: There are seven urogenital arteries, two leave the aorta independently and five together with the lumbar arteries. From the above-mentioned seven vessels, two give off branches to both left and right sides of the body, five continue only to one side of the body. In another specimen, from the six urogenital arteries present, three were paired, three unpaired. Still another case is drawn on fig. 1.

The urogenital arteries run between the kidneys, bend laterad and continue on their ventral surface. The veins of the kidneys, which open into the *v. cava caudalis*, are situated ventrally to the arteries. On the lateral margin of the kidneys, the urogenital arteries send off branches, which run along the *mesorchium* or *mesovarium* and supply the genital glands. The pair of vessels situated nearest to the head supply the fat bodies.

In the breeding season the urogenital arteries are very large and conspicuous in the female. They give off branches supplying the middle part of the oviduct. It is worthy of mention that the anterior part of the oviduct is supplied in breeding females by branches of the thoraco-abdominal artery, the posterior *(»uterus«)* by the caudal mesenteric artery, or, when the last-named is lacking, by the urogenital arteries. Once a small branch of the pulmonary artery supplied the anterior part of the oviduct.

A. mesenterica caudalis (A. mes. caud.) was present in two females and in one male. One female and two males were deprived of this artery. The caudal mesenteric artery in males supplies the posterior part of the intestine, in females the majority of branches run to the posterior part of the oviduct. In one female all branches of the caudal mesenteric artery ran to the oviducts, and none supplied the intestine.

Aorta caudalis (A. sacralis media) (A. caud.) arises from the abdominal aorta, some millimeters craniad from the point of division of the abdominal aorta into the ilic arteries. The point of the branching off of the caudal aorta lies on the left, or in some animals, right surface of the aorta. To understand this point of anatomy we must consider the anatomical structure of that region in the tadpole (fig. 2). Here both the ilic arteries, right and left, have a common origin in the form of a vessel running caudoventrad from the abdominal aorta. During metamorphosis the pelvic arch moves dorsad, and the common ilic artery forms a prolongation of the abdominal aorta, pushing aside the rudimentary caudal aorta.

The caudal aorta in the adult animal extends above the parietal peritoneum caudad, under the heads of the muscles along the *os coccygis* (fig. 1). Above the anus it sends off branches to the neighbouring muscles and to the skin of the back.

A. epigastrico-vesicalis (figs. 1, 12, *A. ep. lat.*, *A. ep. vent.*, fig 2.

A. epig. ves.) is a branch of the ilic artery. A description is however given here, as it supplies the trunk. The epigastrico-vesical artery runs for a short distance laterad, between the muscles of the trunk and the peritoneum, passes across dorsad the lumbosacral neural plexus and divides into three branches: *a. vesicalis dorsalis* (fig. 1, *A. ves. d.*), *a. epigastrica lateralis (A. ep. lat.)* and *a. epigastrica ventralis (A. ep. vent.)*. In several animals however, *a. vesicalis dorsalis* was a separate branch of the abdominal aorta. The dorsal vesical artery passes along the side wall of the urinary bladder in which it ramifies.

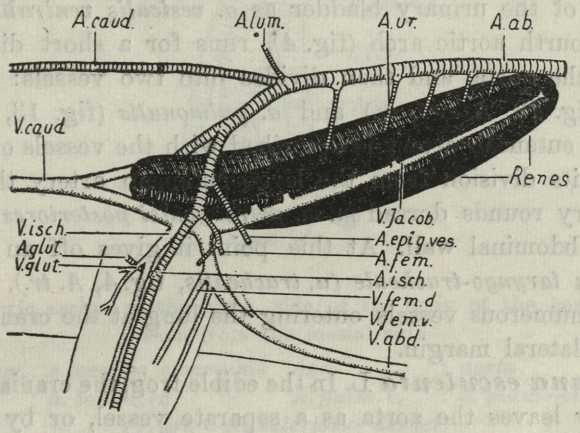

Fig. 2. Blood vessels in the region of the pelvic girdle in a tadpole of the spade-foot toad before metamorphosis (total length 95 mm, tail alone 55 mm, pelvic limb 30 mm). The kidneys are shifted a little ventrad.

A. caud.	: *aorta caudalis*	*A. ur.*	: *a. urogenitalis*
A. epig. ves.	: *a. epigastrico-vesicalis*	*V. abd.*	: *v. abdominalis*
A. fem.	: *a. femoralis*	*V. caud.*	: *v. caudalis*
A. glut.	: *a. glutaea*	*V. fem. d.*	: *v. femoralis dorsalis*
A. isch.	: *a. ischiadica*	*V. fem. v.*	: *v. femoralis ventralis*
A. lum.	: *a. lumbalis*	*V. glut.*	: *v. glutaea*
A. ab.	: *aorta abdominalis*	*V. isch.*	: *v. ischiadica*

V. Jacob. : *v. Jacobsoni*

The lateral epigastrical artery runs craniad on the ventral side of the muscles covering the *ilium*, bends laterally and dorsally and then reaches the ventral surface of the *fascia dorsalis*, along which it extends craniad to the anastomosis with the thoracoabdominal artery. Numerous branches are given off to the muscles of the abdomen.

The ventral epigastric artery (fig. 12, 13, *A. ep. vent.*) runs for a short distance caudad, bends laterad, and approaches the external ilic vein. Together with that vein it pierces the abdominal muscles, and runs to the abdominal branch of the femoral vein. Then it runs in the neighbourhood of that vein ventrad, between the muscles of the abdominal wall and muscles of the thigh. On the dorsal side of the insertion of *m. rectus abdominis* to the *pelvis*, the ventral epigastric artery bends craniad, gives off *a. cutanea abdominalis*, and extends along the lateral margin of that muscle ramifying in it. One small branch passes to the ventral wall of the urinary bladder as *a. vesicalis ventralis.*

The fourth aortic arch (fig. 4), runs for a short distance parallel to the aorta, and then divides into two vessels: *a. cutanea magna* (fig. 13, *A. cut. m.*) and *a. pulmonalis* (fig. 13, *A. pulm.*). The large cutanean artery is described with the vessels of the skin.

After its division from the large cutanean artery the pulmonary artery rounds dorsad *m. m. petrohyoidei posteriores* and pierces the abdominal wall. At this point it gives off an artery to the *cavum laryngo-tracheale (a. trachealis*, fig. 4, *A. tr.)*, and divides into numerous vessels entering the lung at the cranial end of its dorso-lateral margin.

b) ***Rana esculenta*** L. In the edible frog, the cranial oesophagic artery leaves the aorta as a separate vessel, or by means of a common origin with the occipito-vertebral artery. The subclavian is in all specimens a distinct vessel, never connected with the two above mentioned arteries. The caudal oesophagic artery is absent. According to Gaupp the main prolongation of the right thoracic aorta is the abdominal aorta, and the blood from the left thoraric passes mainly to the coeliaco-mesenteric artery. Both vessels are connected only »by a small aperture«. The caudal mesenteric artery is present. The caudal aorta is absent in adult animals.

c) ***Bombina bombina*** L. The laryngeal artery is in this species a very weak branch. The cranial oesophagic artery leaves the aorta together with the occipito-vertebral artery. It is however usually present only on one side of the body, right or left. The caudal oesophagic artery, present in some specimens, is developed also only on one side of the body. The subclavians are in all animals separate vessels. The mode of their branching from the

aorta is very characteristic. The first part of the subclavian is directed mediad, then the artery bends, making a semicircular curve dorsad and passes to the thoracic limb dorsad to the aorta.

The right and left thoracic aortae are connected in an abdominal aorta one millimeter craniad to the point of the coeliaco-mesenteric artery. The caudal mesenteric artery and the caudal aorta are both present.

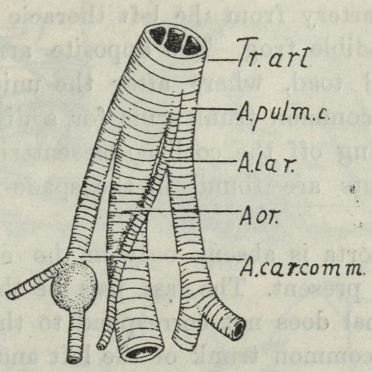

Fig. 3. Aortic arches of the right side of the body of the common toad, seen from the mesial side.

A. car. comm.: *a. carotis communis* *Aor.* : *aorta*
A. lar. : *a. laryngea* *A. pulm. c.* : *a. pulmo-cutanea*
Tr. art. : *tr. arteriosus dexter*

d) ***Bufo bufo*** L. The mode of branching of the laryngeal artery ought to be emphasized (fig. 3). The laryngeal artery is sent off from the posterior surface of the systemic arch, very close to the point where the last-named leaves the aortic trunk. Then it runs a short distance nearly parallel to the systemic arch, passes along its medial surface and supplies the wall of the larynx and of the oesophagus. It seems that such a mode of branching of the laryngeal artery points to the conclusion that the last-named is a rudiment of the absent third aortic arch. The cranial oesophagic artery is in all animals a branch of the occipito-vertebral artery, and the caudal oesophagic artery is present on the left side of the body. The subclavian leaves the thoracic aorta as a separate vessel. The connection between the right and the left aortae is spacious, but the direction of the branching of

the coeliaco-mesenteric artery indicates that the blood comes to this artery from the left aorta. The caudal mesenteric artery is absent, the caudal aorta present.

e) **General remarks.** The arrangement of vessels in the common toad points to the conclusion that the laryngeal artery is a remnant of the third aortic arch.

The origin of the blood going to the viscera through the coeliaco-mesenteric artery from the left thoracic aorta is most pronounced in the edible frog. The opposite arrangement is found in the fire-bellied toad, where after the union of the left and right aortae, the common trunk runs for a distance of one millimeter before giving off the coeliaco-mesenteric artery. Intermediary arrangements are found in the spade-foot toad and the common toad.

The caudal aorta is absent only in the edible frog. In all other forms it is present. The last part of the abdominal aorta of the adult animal does not correspond to the aorta of the tadpole, but to the common trunk of the left and right ilic arteries.

4. Veins in the vicinity of the heart

a) ***Pelobates fuscus*** Laur. The *sinus venosus* is situated on the dorsal side of the auricles. It is formed by the union of the caudal and cranial *venae cavae.*

The pulmonary veins immediately enter the left auricle.

V. v. cavae craniales (fig. 4, *V. cav. cr.*) are formed on both sides of the body by the union of the following vessels: ***v.*** *pericardiaca dorsalis (V. per. d.), v. jugularis externa (V. jug. ex.), v. anonyma* and *v. subclavia (V. subcl.).* All vessels unite at the same point on the ventral surface of the heart, lateral to the pericardial sac. The vein thus formed immediately pierces the pericardium and runs in the pericardial sac mediad, slightly dorsad and caudad. When it reaches the middle line of the body it is joined by the opposite vein and the caudal *vena cava*, forming the *sinus venosus (S. ven.).*

V. pericardiaca dorsalis (V. per. d.) collects the blood from the *m. hyoglossus* as an unpaired vessel running along the middle line of the body. This vein is joined by a small vessel coming from *corpus lymphaticum propericardiale* (Braunmühl 1926).

V. pericardiaca dorsalis runs caudad, and on the larynx divides into two branches, right and left. These branches extend on the dorsal wall of the pericardial sac bending laterally, and at the point of union of the large veins open into the cranial *venae cavae*. In many specimens only one branch, right or left, persists, as in fig. 4.

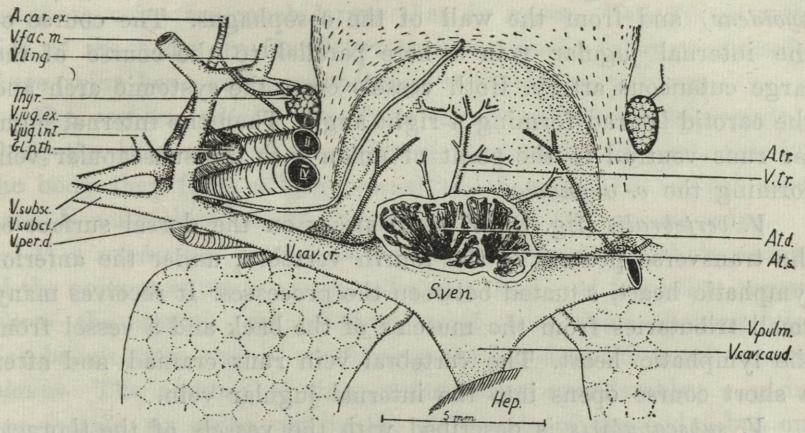

Fig. 4. The junction of the main venous trunks in the spade-foot toad seen from the ventral side. The heart, and also the blood vessels of the left side of the body have been taken out.

A. car. ex.	: *a. carotis externa*	*V. cav. caud.*	: *v. cava caudalis*
A. tr.	: *a. trachealis*	*V. cav. cr.*	: *v. cava cranialis*
At. d.	: *atrium dextrum*	*V. jug. ex.*	: *v. jugularis externa*
At. s.	: *atrium sinistrum*	*V. ling.*	: *v. lingualis*
Gl. p. th.	: *glandula parathyreoidea*	*V. jug. int.*	: *v. jugularis interna*
Hep.	: *hepar*	*V. per. d.*	: *v. pericardiaca dorsalis*
S. ven.	: *sinus venosus*	*V. pulm.*	: *v. pulmonalis*
Thyr.	: *glandula thyreoidea*	*V. subcl.*	: *v. subclavia*
V. fac. m.	: *v. faciomandibularis*	*V. subsc.*	: *v. subscapularis*
		V. tr.	: *v. trachealis*

V. jugularis externa (figs. 4, 6, *V. jug. ex.*) is formed in the vicinity of the thyroid gland by the union of *v. lingualis (V. ling.)* and *v. facio-mandibularis (V. fac. m.)*. It runs caudad along the pericardium crossing ventrad the arterial arches. It is joined by a small vein running from *gl. parathyreoideae (Gl. p. th.)*. The external jugular vein opens to the cranial *vena cava*.

V. anonyma is a short vessel formed by the union of the internal jugular vein (fig. 4, *V. jug. int.*) with the subscapular vein

(V. subsc.). It runs medio-ventrad and opens into the cranial *vena cava.*

V. jugularis interna (V. jug. int.) from the point of union with the vertebral vein (fig. 13, *V. vert.*) situated on the ventral surface of the transverse process of the third vertebra runs caudo-ventrad collecting small branches from the muscles *(v. v. petro-hyoideae)* and from the wall of the oesophagus. The course of the internal jugular vein is here parallel to the course of the large cutaneous artery. Both vessels cross the systemic arch and the carotid laterad forming a right angle. Then the internal jugular runs ventrad to the point of union with the subscapular vein forming the *v. anonyma.*

V. vertebralis (fig. 13, *V. vert.*) arises on the dorsal surface of the transverse process of the fourth vertebra, under the anterior lymphatic heart, situated between the processes. It receives many small tributaries from the muscles of the back and a vessel from the lymphatic heart. The vertebral vein runs craniad and after a short course opens into the internal jugular vein.

V. subscapularis is described with the vessels of the thoracic limb.

V. subclavia (figs. 4, 13, *V. subcl.*) is a short but broad vessel formed by the union of the large cutaneous vein (fig. 13, *V. cut. m.*) and the brachial vein (figs. 9, 13, *V. br.*). It arises on the ventral side of the body among the pectoral muscles, just caudad to the axillary joint. It receives a tributary from the pectoral muscles *(V. coraco-clavicularis)* anastomosing with the clavicular vein. The subclavian vein runs mediad, on the dorsal surface of the abdominal muscles of the pectoral girdle, and approaching the pericardium joins the cranial *vena cava.*

V. cava caudalis (figs. 4, 13, *V. cav. caud.*) is the largest tributary of the *sinus venosus.* This vein arises on the medial line of the body, from the union of the renal veins *(v. v. renales revehentes)*. The number of these veins varies, usually from two to five vessels arise from each kidney. From the union of these vessels a large unpaired vein arises, collecting also the genital veins, *v. v. corporis adiposi*, and in females *v. v. oviductus.* The caudal *vena cava* runs craniad, curves slightly ventrad and to the right, in the male it passes near the cranial border of the right testicle and enters the liver, namely the *processus descendens hepatis*,

which is pierced by it. The liver veins *(v. v. hepaticae revehentes)* open into the caudal *vena cava* on the cranial surface of the liver, then the caudal *vena cava* runs a short distance craniad and opens into the *sinus venosus*.

V. v. genitales leave the genital glands on their medial border and after a short course open into the caudal *vena cava*. In females these veins are much larger than in males. Usually on each side of the body are found two to five vessels. In some animals these veins have common openings with the renal veins.

V. v. corporis adiposi arise from the union of branches running along the long axes of the lobes of that body. On each side of the body they form a large vessel which enters the caudal *vena cava*. Usually this vein is joined by one of the genital veins.

V. v. oviductus. In female specimens along the whole course of the oviduct extends a vein collecting the blood from that organ. From the cranial part of this vessel arise veins opening into Jacobson's vein, and so conducting the blood to the renal venous plexus. The number of these veins varies considerably; *e. g.* in one female six veins ran on the right side of the body, but on the left only one vein joined Jacobson's vein. In the neighbourhood of the point where the oviducts enlarge, and form the so-called »*uterus*«, the longitudinal veins of the oviducts bend medially and are united on the ventral surface of the kidneys by a large anastomose. From this anastomose arises an unpaired wide vessel which runs craniad, and opens into the caudal *vena cava*. Thus a chain of anastomoses exists in the female, allowing the blood to pass from Jacobson's vein directly to the caudal *vena cava*, omitting the venous meshworks of the kidneys and liver. In the male such anastomosis is absent.

Only the pulmonary veins (figs. 4, 13, *V. pulm.*) open into the left auricle. They arise on the lung from a tangle of vessels, and run along the medio-ventral border of that organ. The endings of the pulmonary veins run on the dorsal wall of the *sinus venosus* and the right and left vessels unite on the level of *cavum laryngo-tracheale* forming a short trunk which runs craniad, bends ventrad, and opens into the left auricle. This trunk is joined by a tracheal vein.

V. trachealis (fig. 4, *V. tr.*) has not hitherto been described in *Salientia*. It arises on the ventral wall of *cavum laryngo-tracheale*

from numerous short branches. It opens into the pulmonary vein.

b) ***Rana esculenta*** L. The only distinct differences are the very weak *v. pericardiaca dorsalis* and the lack of *v. trachealis*.

c) ***Bombina bombina*** L. It is well known (Goette 1875) that in the adult fire-bellied toad both caudal cardinal veins persist. Owing to this, the veins in the region of the kidney appear as follows: the caudal *vena cava* runs along the medial line of the body, between the kidneys, and on the level of the cranial border of these organs divides into three branches. One, the central is a continuation of *v. cava caudalis*, the two lateral, *v. cardinales caudales*, extend along the dorsal wall of the stomach and oesophagus, parallel to the thoracic aortae. Under the *scapulae* they are joined by small tributaries from the alimentary canal, and open into the internal jugular veins.

V. trachealis is rather large in the fire-bellied toad.

d) ***Bufo bufo*** L. The veins in the vicinity of the heart of the common toad are very similar to those of the spade-foot toad, except that the *v. pericardiaca dorsalis* is absent.

5. Veins conducting the blood to the liver and kidneys

a) ***Pelobates fuscus*** Laur. The blood from the pelvic limbs, back, abdominal wall and the viscera passes in *Amphibia* through one of the venous meshworks, of the liver or of the kidneys before entering the heart. The veins conducting the blood to these plexuses are united by anastomoses.

The main vessel conducting the blood to the liver is *v. portae hepatis* (fig. 13, *V. por.*), this vein is described with the vessels of the viscera. This vessel is joined in the interior of the liver by *v. abdominalis* (figs. 5, 12, 13, *V. abd.*) which is formed on the ventral side of the *pelvis* by the union of the right and left *r. abdominalis v. femoralis* (figs. 5, 13, *R. ab. v. f.*, pelvic vein of Francis 1934). The abdominal vein runs craniad along the internal (dorsal) surface of the abdominal muscles, along the *linea alba*, as a very strong vessel. Several (usually three) veins from the wall of the urinary bladder *(v. v. vesicales ventrales)* open into the first part, then the abdominal vein is joined by segmental veins which run mediad across the *m. rectus abdominis (v. v. musculares)*. These veins collect the blood from the abdominal wall,

and along the lateral border of the rectus muscle are connected by anastomoses. The abdominal vein reaches the pericardial sac, receives *v. retrosternalis*, bends dorsad and slightly to the left, entering the liver on the dorsal wall of the pericardium. Here

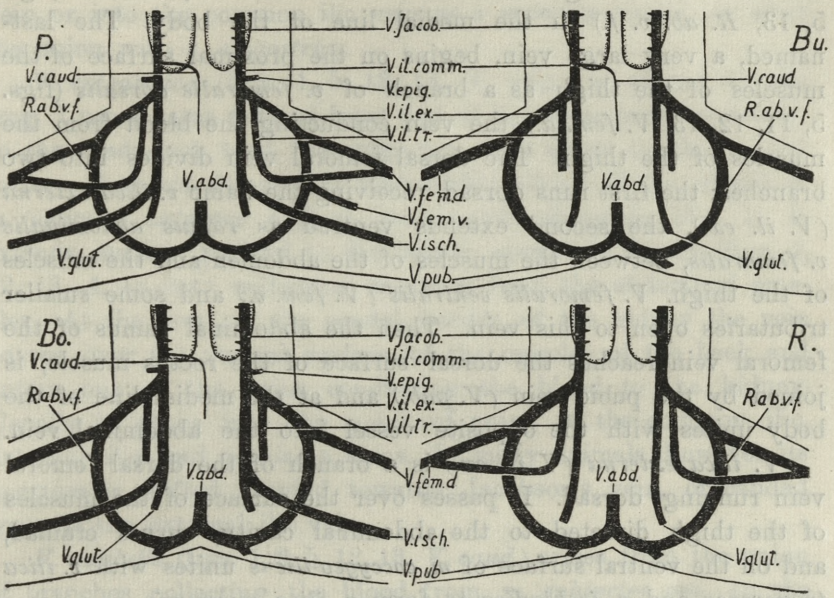

Fig. 5. Schemes showing the arrangements of veins in the region of the pelvic girdle.

P. : *Pelobates fuscus* Laur.	*Bu.*: *Bufo bufo* L.
Bo.: *Bombina bombina* L.	*R.* : *Rana esculenta* L.
R. ab. v. f.: *r. abdominalis v. femoralis*	*V. glut.* : *v. glutaea*
V. abd. : *v. abdominalis*	*V. il. comm.*: *v. ilica communis*
V. caud. : *v. caudalis*	*V. il. ex.* : *v. ilica externa*
V. epig. : *v. epigastrica*	*V. il. tr.* : *v. ilica transversa*
V. fem. d.: *v. femoralis dorsalis*	*V. isch.* : *v. ischiadica*
V. fem. v.: *v. femoralis ventralis*	*V. Jacob.* : *v. Jacobsoni*
V. pub. : *v. pubica*	

the vein from the gall bladder *(v. vesicae felleae)* opens into the abdominal vein, and after the abdominal vein and portal hepatic have united, they branch within the liver.

V. retrosternalis is a small paired vessel, which arises on both sides of the body on the dorsal surface of *m. rectus*, in the cranial part of that muscle, lateral to the pericardium. It runs me-

dially, bends caudad, then dorso-mediad and opens into the abdominal vein. In some specimens the right and left retrosternal veins unite in an unpaired vessel before entering the abdominal vein.

As was already been mentioned the abdominal vein arises from the union of the right and left *r. abdominalis v. femoralis* (figs. 5, 13, *R. ab. v. f.*) in the medial line of the body. The last-named, a very large vein, begins on the proximal surface of the muscles of the thigh as a branch of *v. femoralis dorsalis* (figs. 5, 11, 12, 13, *V. fem. d.*), the vein conducting the blood from the muscles of the thigh. The dorsal femoral vein divides into two branches; the first runs dorsad, receiving the name *v. ilica externa (V. il. ex.)*, the second extends ventrad as *ramus abdominalis v. femoralis*, between the muscles of the abdomen and the muscles of the thigh. *V. femoralis ventralis (V. fem. v.)* and some smaller tributaries open to this vein. Then the abdominal ramus of the femoral vein reaches the dorsal surface of the rectus muscle, is joined by the pubic vein *(V. pub.)* and at the medial line of the body unites with the opposite vessel into the abdominal vein.

V. ilica externa (V. il. ex.) is a branch of the dorsal femoral vein running dorsad. It passes over the surface of the muscles of the thigh directed to the abdominal cavity, curves craniad, and on the ventral surface of *m. coccygeo-ilicus* unites with *v. ilica transversa* and *v. ischiadica* to form *v. ilica communis*.

V. ilica communis (V. il. comm.) runs dorsad for a very short distance, and passes over the dorso-lateral surface of the kidney, where it receives the name *v. Jacobsoni (V. Jacob.)*. The common ilic vein is joined by *v. vesicalis dorsalis* and *v. epigastrica*. To one of the common ilic veins, right or left, opens *v. caudalis (V. caud.)*.

V. Jacobsoni (V. Jacob.) extends along the dorso-lateral margin of the kidney, supplying this organ with blood. It receives *v. v. dorsolumbales* and *v. v. oviductus*.

V. femoralis dorsalis, *v. femoralis ventralis*, *v. ilica transversa* and *v. ischiadica* are described with the vessels of the pelvic limb.

V. pubica (fig. 5, *V. pub.*) was not described by Gaupp, I must therefore use a new name. It corresponds to the *v. cutanea femoris anterior medialis* of the frog. In the spade-foot toad it is a short, but large vessel. It arises on the ventral surface of the *m. pectineus*, near the skin, from the union of the muscular and cutaneous branches. It runs craniad, passes under the insertion

of *m. rectus abdominis*, and enters the abdominal ramus of the femoral vein just before the formation of the abdominal vein.

V. vesicalis dorsalis is a small vein collecting blood from the lateral and dorsal wall of the urinary bladder. It runs dorsad, parallel to *a. vesicalis dorsalis* and opens into the external ilic vein or into the common ilic vein as a separate vessel, or after the union with *v. epigastrica.*

V. epigastrica (figs. 1, 5, 12, 13, *V. epig.*) is absent in the frog. I use a name formed from that of the corresponding artery. In the spade-foot toad the epigastric vein arises on the ventral surface of *fascia dorsalis*, in the neighbourhood of the origins of *m. obliquus externus* and *m. transversus abdominis* (fig. 1). It extends caudad, parallel to the lateral epigastric artery (figs. 1, 12, 13, *A. ep. lat.*) collecting branches from the abdominal muscles. At the level of the caudal border of the kidney the vein passes over the ventral surface of the muscles of the back and enters one of the veins conducting the blood to the kidney. Usually it opens into the point of union of the common ilic, external ilic and ischiadic veins. In many animals however its aperture is shifted craniad towards Jacobson's vein, or caudad towards the external ilic vein.

V. caudalis (figs. 1, 2, 5, 12, 13, *V. caud.*) arises from the union of branches collecting the blood from *m. sphincter ani*, on the dorsal side of the cloaca. It runs craniad along the middle line of the body, over the ventral surface of *m. coccygeo-sacralis*, reaches the caudal margin of the kidneys, bends laterad and joins one of the common ilic veins. In three animals the caudal vein opened into the left common ilic veins and in one to the right.

V. v. dorsolumbales (figs. 1, 13, *V. lum.*) collecting the blood from the muscles of the back are very variable. Most often the following arrangement is found: the most cranial vessel *(v. dorsolumbalis cranialis)* extends along the vertebral column, caudad, along the ventral surface of the spinal muscles. It collects the blood from the muscles and from the spinal cord, beginning from the neighbourhood of the third vertebra. When this vein reaches the level of the cranial border of the kidney, it curves ventrad and enters Jacobson's vein. Besides this vein other dorsolumbar veins occur, opening into Jacobson's vein separately or

connected by a shorter or longer common trunk. This trunk is in some specimens also connected with the cranial dorsolumbar vein. The dorsolumbar veins collect the blood from the muscles of the back in the neighbourhood of the sacrum. Their number varies. For instance in toad nr. 1, there were two veins on one side of the body and three on the other. In toads nrs. 2 and 3 there were two veins on one side and one on the other. Still another arrangement is shown in fig. 1: on both sides of the body *v. dorsolumbalis cranialis* is connected with other dorsolumbar veins, but on the right side of the body (left of the figure) an accessory vessel is present which opens into epigastric vein.

V. oviductus is described with the branches of caudal *v. cava* on the p. 159.

b) ***Rana esculenta*** L. The arrangement of the veins of the pelvic region in the edible frog is characterized by an extreme simplicity, resulting from the reduction of several vessels (fig. 5, *R.*). In the frog *v. femoralis ventralis*, *v. epigastrica*, *v. ischiadica* and *v. caudalis* are absent, and *v. pubica* collects the blood only from the skin (*V. cutanea femoris anterior medialis* Gaupp).

c) ***Bombina bombina*** L. In the fire-bellied toad occur all vessels described in the spade-foot toad (fig. 5, *Bo*). Only *v. femoralis ventralis* is absent.

d) ***Bufo bufo*** L. The common toad, like the frog, lacks three veins: *v. epigastrica*, *v. ischiadica* and *f. femoralis ventralis* (fig. 5, *Bu*). The caudal vein is however present even in adult specimens.

e) **General remarks.** The spade-foot toad has the most primitive arrangement of the veins of the pelvic region. Next to it comes the fire-bellied toad. The common toad and the frog differ considerably owing to the absence of several veins. In the female specimens of all the species investigated, during the breeding season a spacious chain of anastomoses extends between the caudal *vena cava* and the veins of the hind limbs. Owing to this short circuit the blood can avoid the venous plexuses of the kidneys and liver. In males such a short circuit is absent. It is worth to mention, that the presence of a similar connection was stated by Mignon (1938) in the alpine salamander. The anastomoses ran however in this amphibian in the immediate vicinity of the

kidney, or in the kidney itself, and were present in 80% of the animals investigated. Unfortunately Mignon does not mention the sex of the specimens dissected. It is however probable that the presence of anastomoses in *Salientia* has some connection with the increased circulation in the oviducts during the breeding season, and in the alpine salamander it can possibly be explained by the intensive circulation during the internal development of the embryos.

Three salientians described above retain in the adult condition the caudal vein (*P. fuscus* Laur., *B. bombina* L. and *B. bufo* L.), in *R. esculenta* L. only this vessel is absent. It was not however hitherto been described in any adult salientian. In connection with this fact it is worth mentioning that Bhaduri (1938) found the caudal vein in a specimen of *Rana catesbeiana*, but lacking the comparative material was unable to interpret this fact correctly.

6. Blood vessels of the digestive tract and its glands

a) ***Pelobates fuscus*** Laur. *A. coeliaco-mesenterica* (fig. 13, *A. coel. m.*) after a course of about 1 mm, divides into *a. coeliaca* and *a. mesenterica cranialis.*

A. coeliaca reaches the pancreas and on the right edge of that gland divides into two branches running in opposite directions, namely: *a. gastrica sinistra* and *a. gastrica dextra.*

A. gastrica sinistra extends craniad along the border of the pancreas. It branches extensively into many small vessels which convey the blood to the pancreas and to the left (dorsal) wall of the stomach. These arterioles reach the stomach along the insertion of the *mesogastrium.*

A. gastrica dextra runs for a short distance caudad, along the margin of the pancreas, curves and passes over the ventral surface of the gland where it gives off the hepatic artery. Often in this region the arteries are embedded in the gland. The right gastric artery breaks into numerous small vessels which pass over the ventral (left) wall of the stomach.

A. hepatica extends along the hepatic process of the pancreas, parallel to the hepatic portal vein and to the bile duct. After reaching the liver it gives off numerous vessels, one of which supplies the gall bladder.

A. mesenterica cranialis runs from *a. coeliaca* for a distance of about 1 mm, and then dichotomizes intensively. Its branches extend into the mesentery and reach the intestine. One of those arterioles supplies the spleen, the caudal runs to the rectum, and in some animals anastomoses with the caudal mesenteric artery.

V. portae hepatis (fig. 13, *V. por.*) arises from four distinct vessels joining in the pacreas: *v. gastrica dextra, v. gastrica sinistra, v. duodenalis* and *v. intestinalis.* These veins unite in the hepatic process of the pancreas forming a strong vessel running to the liver. In the last gland the portal vein anastomoses with the abdominal vein and divides into branches supplying the liver.

V. gastrica dextra and *v. gastrica sinistra* accompany the arteries of the same names.

The veins collecting the blood from the intestine open into a vessel which runs along the coils of the alimentary canal. From this vessel numerous veins run over the mesentery to the centrum of coils where they form *v. intestinalis.*

The vessels from the rectum open into this vein *(v. v. rectales)*, one of the last-named is joined by a splenic vein *(v. lienalis).*

V. intestinalis enters the pancreas, and through that gland runs craniad to the hepatic process.

The longitudinal vein extending along nearly the whole of the alimentary canal begins at the duodenum. Running between the duodenum and the pancreas it gives off some branches which run to the portal vein. The largest of those vessels, which extends along the bile duct has the name *v. duodenalis.*

b) **Other species.** The above description applies also to the other amphibians investigated. In the blood vessels of the alimentary canal no great differences occur. The variations of the caudal mesenteric artery are mentioned elsewhere (p. 152).

7. Blood vessels of the head

a) ***Pelobates fuscus*** Laur. The blood going to the head in *Salientia* may derive from three aortic arches: from the common carotid arch, from the systemic arch, or from the pulmocutaneous arch. The spade foot toad lacks an anastomosis between the large cutaneous artery and the temporal artery, so the blood of the head region is derived only from the first and second aortic arch.

A. carotis communis on arrival at the carotid gland divides into two trunks: *a. carotis externa* and *a. carotis interna.*

A. carotis externa (figs. 4, 6, 13, *A. car. ex.*) leaves the carotid gland ventro-mediad and almost immediately bends craniad. Its

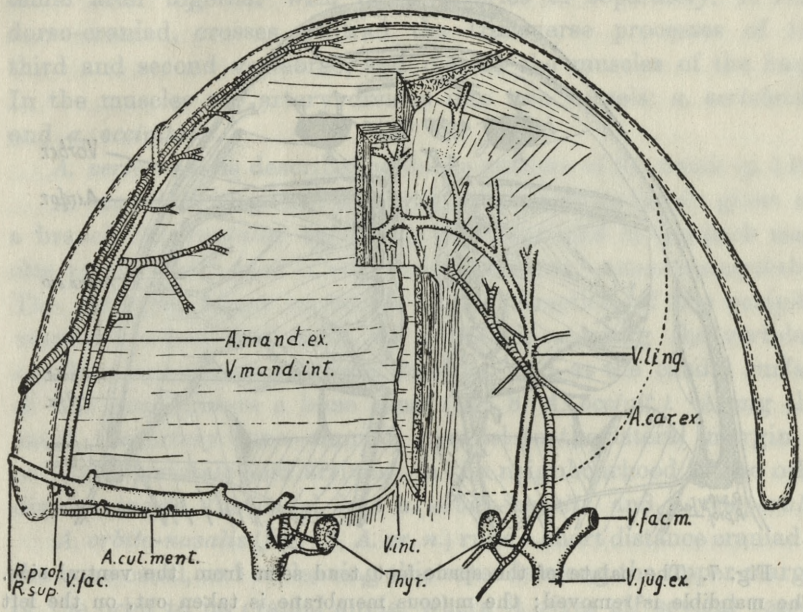

Fig. 6. *Pelobates fuscus* Laur. The blood vessels in the floor of the mouth and in the mandible seen from the ventral side. On the left side of the body (right in the figure), the muscles have been dissected, showing vessels running immediately under the mucous membrane of the mouth cavity.

A. car. ex.	: *a. carotis externa*	*Thyr.*	: *glandulae thyreoideae*
A. cut. ment.	: *a. cutanea mentalis*	*V. fac. m.*	: *v. faciomandibularis*
A. mand. ex.	: *a. mandibularis externa*	*V. int.*	: *v. intermuscularis*
R. prof. v. fac.	: *r. profundus venae facialis*	*V. jug. ex.*	: *v. jugularis externa*
		V. ling.	: *v. lingualis*
R. sup. v. fac.	: *r. superficialis venae facialis*	*V. mand. int.*	: *v. mandibularis interna*

first branch goes to the parathyroid gland *(r. glandularis).* It is sometimes given off together with the *r. thyreoideus.* The external carotid does not curve, but runs straight craniad, parallel to the lingual vein (fig. 6) on the floor of the mouth between the muscles and the mucous membrane. It sends off a branch to the

thyroid gland, the hyoglossus muscle and *»corpus lyphaticum propericardiale«* (Braunmühl) *(r. thyreoideus)* and several minute vessels to the mucous membrane of the mouth. Finally it reaches the base of the tongue where it ramifies forming *r. r. linguales.*

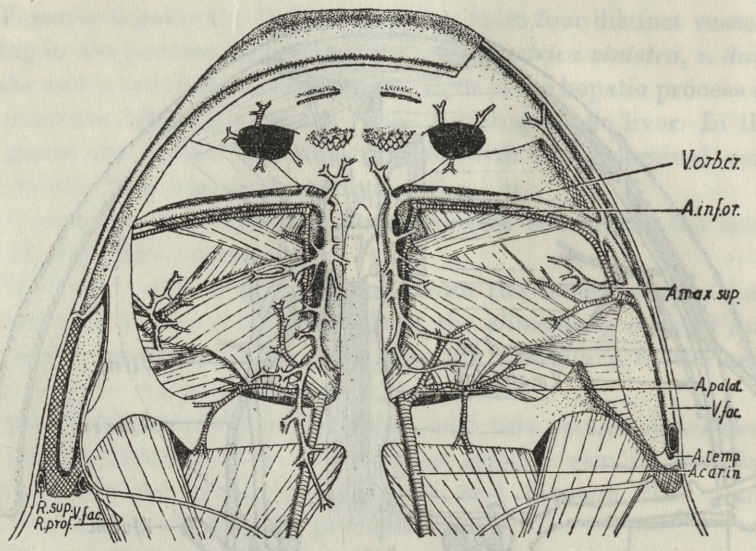

Fig. 7. The palate of the spade-foot toad seen from the ventral side. The mandible is removed; the mucous membrane is taken out, on the left side of the body (right in the fig.), the maxillary bone is also dissected.

A. car. in. : *a. carotis interna* — *R. prof. v. fac.*: *r. profundus venae facialis*
A. inf. or. : *a. infraorbitalis* — *R. sup. v. fac.* : *r. superficialis venae facialis*
A. max. sup.: *a. maxillaris superior* — *V. fac.* : *v. facialis*
A. palat. : *a. palatina* — *V. orb. cr.*: *v. orbitalis cranialis*
A. temp. : *a. temporalis*

A. carotis interna (figs. 1, 7, 13, *A. car. in.*) runs from the carotid gland parallel to the systemic arch. Both vessels pass on the dorsal side of the oesophagus, where the internal carotid bends craniad. It runs immediately under the mucous membrane of the oesophagus and pharynx, crosses the sphenoideum and divides into *a. palatina* and *a. encephalica.*

A. palatina (figs. 1, 7, *A. palat.*) runs to the mucous membrane of the palate, where it ramifies.

A. encephalica (*a. carotis cerebralis* Gaupp) enters the cavity of the skull, under the insertions of the optic muscles, and gives off a strong branch *(a. ophthalmica)* running to the optic bulb along the optic nerve. Finally it reaches the brain.

A. occipito-vertebralis (figs. 1, 13, *A. occ. vert.*) leaves the systemic arch together with other arteries or separately. It runs dorso-craniad, crosses ventrad the transverse processes of the third and second vertebrae, and pierces the muscles of the back. In the muscles the artery divides into two vessels: *a. vertebralis* and *a. occipitalis.*

A. vertebralis is described with the muscles of the trunk (p. 149).

A. occipitalis (fig. 13, *A. occipit.*) almost immediately gives off a branch *(r. cranialis)* supplying the insertions of the back muscles to the skull, and a cutaneous vessel *(a. cutanea occipitalis).* The occipital artery continues in the direction of the occipito-vertebral artery and sends off a branch entering the vertebral canal *(r. anastomoticus cum a. basialis)* and at the caudal surface of the skull enters a bone canal (fig. 8. *A. occipit.).* Along this canal the artery runs craniad, parallel to the lateral margin of os fronto-parietale and arriving in the neighbourhood of the orbit divides inside the canal into *a. orbito-nasalis* and *a. temporalis.*

A. orbito-nasalis (fig. 13, *A. or. n.*) runs a short distance craniad in the bone canal, and on leaving this extends along the upper margin of the orbit to its cranial angle, where it gives off several vessels namely:

1. *R. medialis narium*, running along the medio-dorsal wall of the nasal chamber. Sends off branches entering the skull along the olfactory nerve.

2. *R. lateralis narium*, running laterad on the anterior margin of the orbit, bends craniad and ramifies in the lateral wall of the nasal chamber.

3. *R. r. frontales* running to Harder's gland and the skin.

4. *R. descendens* running ventrad and reaching the palate where it anastomoses with the infraorbital artery (a branch of the temporal artery) and finally ramifies in the palate.

A. temporalis (fig. 13, *A. temp.*) runs inside the bone canal ventrad and after leaving the canal extends near the posterior margin of the orbit in a caudo-ventral direction. It reaches the ventral margin of the orbit, passes under the maxillary bone and gives off craniad *a. maxillaris superior.* Then the temporal artery

runs caudad, along the fenestra formed by the maxillary and tympanicum bones, parallel to the facial vein, immediately under the skin. On the posterior margin of the fenestra it gives ventrad *a. mandibularis externa* and caudad *a. thymica* and *a. cutanea mentalis.*

A. maxillaris superior (figs. 7, 13, *A. max. sup.*) runs from the temporal artery on the proximal surface of the ventral border of the orbit. From this artery is given off a small branch to the mucous membrane of the palate, which runs mediad. The superior maxillar artery runs then craniad, reaches the cranial margin of the orbit, curves mediad, runs over the palate under the name of *a. infraorbitalis* (*a. inf. or.*), and finally anastomoses with *r. descendens a. orbito-nasalis.*

A. mandibularis externa (fig. 6, *A. mand. ex.*) runs from the temporal artery under the maxillary bone ventrad. It emerges from the maxillary under the skin, surrounds laterally the mandible and reaches the medial surface of that bone where it runs craniad, on the ventral side of the insertions of the muscles. It gives off several branches to the muscles of the floor of the mouth cavity, one of which runs caudad in the direction of the mandibular joint, but does not however anastomose (as in the frog) with the internal mandibular artery, which is absent.

A. thymica runs from the temporal artery dorsad, along the caudal margin of the tympanic bone, giving off branches to the surrounding muscles, skin and thymus (Szarski H., 1937).

A. cutanea mentalis (a new name) (fig. 6, *A. cut. ment.*) is a distinct vessel which runs from the temporal artery caudad between the tympanic bone and *m. depressor mandibulae*, curves ventrad, extends mediad immediately under the skin, parallel to the facio-mandibular vein and supplies the skin of the ventral surface of the head and of the sternal region.

The principal vessels collecting the blood from the head in *Salientia* are the external jugular, internal jugular and eventually the large cutaneous vein.

V. jugularis externa (figs. 4, 6, 13, *V. jug. ex.*) arises near the thyroid gland on the ventral side of the body from the union of the lingual and facio-mandibular veins.

V. lingualis (figs. 4, 6, 13, *V. ling.*) begins in the tangle of vessels at the radix of the tongue. This venous plexus is also

connected with the internal mandibular vein (fig. 6, *V. mand. int.*). From the veins of the tongue arises a vessel perpendicular to the long axis of that structure which on the lateral borders bends caudad giving origin on each side of the body to the lingual vein. This vein runs caudad immediately under the mucous membrane of the floor of the mouth, parallel to the external carotid artery. It collects minute vessels from the floor of the mouth and from the region of the larynx. Finally it bends latero-ventrad and after receiving a small tributary from the thyroid gland enters the external jugular vein.

V. faciomandibularis (name of Bhaduri, 1933, 1938) (figs. 4, 6, 13, *V. fac. m.*) arises under the mandibular joint from the union of the following vessels: the internal mandibular vein *(V. mand. int.)*, the profound *(R. prof.)* and superficial *(R. sup.)* branches of the facial vein *(V. fac.)*. Immediately after the union of these vessels the faciomandibular vein is joined by a cutaneous vessel, then it runs from the mandibular joint medially along the caudal border of *m. submaxillaris*, collecting small tributaries from that muscle. Midway between the mandibular joint and the medial line of the body, into the faciomandibular the clavicular and intermuscular veins open, and the faciomandibular vein bends sharply caudad and unites with the lingual vein forming the external jugular vein (fig. 6).

V. clavicularis (a new name, the vessel was described by Gaupp but without name) arises on the ventral surface of the clavicle and coracoid under the pectoral muscles, from branches conducting the blood from the bones and from the muscles. It runs craniad, curves dorsad and joins the faciomandibular vein just near the opening of the intermuscular vein.

V. intermuscularis (fig. 6, *V. int.*) (a new name) arises at the median line of the body as an unpaired vessel in the intermuscular tendinous band which divides the *m. submaxillaris* into right and left portions. It runs caudad along the band. In some animals two parallel vessels are found, the one lying superficially, the other embedded in the muscle. On the caudal border of the submaxillar muscle, the intermuscular vein divides into right and left branches which run laterad and open to the faciomandibular veins. In one specimen the right branch of the intermuscular vein was absent.

V. mandibularis interna (figs. 6, 13, *V. mand. int.*) is formed by branches collecting the blood from the *m. submentalis* and from the anterior part of the mandible. These branches anastomose with the lingual vein. The internal mandibular vein runs close to the medial surface of the mandible. Halfway along course it is joined by a vessel conducting the blood from the skin on the lateral surface of the mandible, and finally unites with the branches of the facial vein forming the faciomandibular vein.

The first part of *v. facialis* has the name *v. orbitalis cranialis* (fig. 7, *V. orb. cr.*). This vein arises on the palate in the mediocranial angle of the orbit, by the union of branches running from Harder's gland, from the skin covering the dorsal surface of the skull and from the nasal cavity. By the union of these vessels a large trunk arises, which runs over the dorsal surface of the palate laterad, along the caudal margin of the palatine bone, curves caudad, and on the medial surface of the maxillary bone receives the name *v. facialis.*

The facial vein (figs. 7, 13, *V. fac.*) is joined almost at once by a tributary returning the blood from the anterior part of the palate. It runs caudad along the medial surface of the maxillary bone, reaches the caudal border of the orbit and here receives two vessels: one, *v. temporalis*, runs ventrad under the tympanic bone collecting the blood from the neighbouring muscles; the other, *v. orbitalis caudalis* (fig. 13, *V. orb. cd.*) returns the blood from the palate and from the orbital muscles. It begins at the insertions of the orbital muscles to the skull with anastomoses coming from the palatine vessels and the internal jugular vein. It receives a vein from the eye *(v. ophthalmica).* The caudal orbital vein runs laterad embedded in the muscles. Owing to this it is not visible in the fig. 7.

In its further course the facial vein runs on the medial side of the union of the maxillary with the tympanic and emerges under the skin in the fenestra formed by the two bones named. Along this fenestra it extends caudad, bending gradually ventrad. At the level of the mandibular joint the facial vein receives the infratympanic vein and divides into two branches: the superficial *(r. superficialis)* and the deep *(r. profundus)* (figs. 6, 7, *R. sup. R. prof. v. fac.*). The superficial branch runs ventrad, immediately under the skin, surrounding the quadratomaxillare and mandibu-

lar bones laterad. The deep branch disappears under *m. depressor mandibulae*, bends ventrad and surrounds the mandibular joint from the medial side. On the ventral side of the joint the branches unite, receive the internal mandibular vein and form the faciomandibular vein. The veins in the vicinity of the mandibular joint are very variable; several animals lack the superficial branch, in one specimen the facial vein was already divided into two vessels at the level of the fenestra.

V. infratympanica (*v. tympanica* Bhaduri) arises above the mandibular joint from veins conducting the blood from the sur-

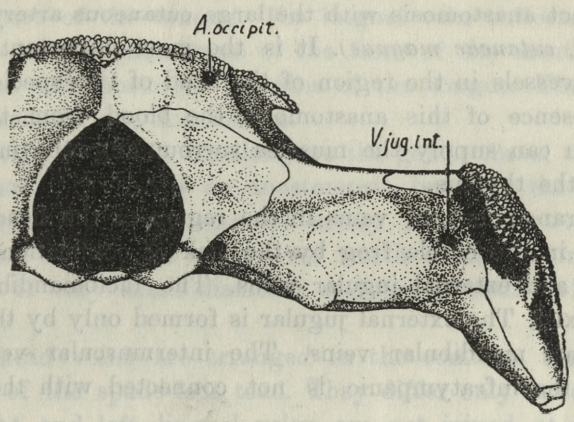

Fig. 8. The skull of the spade-foot toad seen from the back. The channels for the occipital artery *(a. occipit.)* and for the internal jugular vein *(v. jug. int.)* are visible.

rounding muscles and the skin. One of these branches, lying dorsad, is usually connected with the internal jugular vein. It is however a very slender vessel, like the whole infratympanic vein.

V. jugularis interna (fig. 13, *V. jug. int.*) arises in the angle of the skull formed by *os prooticum* and the wall of the cerebral bony box, near the foramen of the optic nerve, from the following veins: *v. cerebralis media*, *v. ophthalmica* and *v. orbitalis inferior*. The internal jugular vein runs laterad in a bony groove opened to the orbit and formed by the tympanic bone on the anterior wall of the ear capsule: it then bends caudad and passes between the bones on the posterior wall of the skull (fig. 8, *V. jug. int.*). Here it receives two small tributaries, one conducts the blood from the skin of the back *(v. cutanea occipitalis)*, the

other, very slender, anastomoses with the infratympanic vein. The internal jugular runs from here caudo-ventrad, between the back muscles to the point of union with the vertebral vein.

In the spade-foot toad the large cutaneous vein returns no blood from the head region.

b) **Rana esculenta** L. Among the branches of the carotid arch the presence of a large anastomosis between the palatine and maxillary arteries should be emphasised.

The arteries deriving from the aorta run here similarly to those described in *P. fuscus*. Only the thymic artery is connected by a distinct anastomosis with the large cutaneous artery *(r. auricularis art. cutaneae magnae)*. It is the most important detail of the blood vessels in the region of the head of this species. Owing to the presence of this anastomosis the blood from the fourth aortic arch can supply the muscles surrounding the mandibular joint and the thymus.

The arrangement of veins in the region of the head is characterised in the edible frog by the lack of connection between the facial and external jugular veins. The faciomandibular vein does not exist. The external jugular is formed only by the lingual and internal mandibular veins. The intermuscular vein is absent and the infratympanic is not connected with the internal jugular.

The facial vein in the edible frog opens into the large cutaneous vein, hence conducting a large part of the blood from the region of the head. The course of the internal jugular is in *Rana* very like that described in *Pelobates*. Differences occur only in the tributaries from the eye-ball.

c) ***Bombina bombina*** L. The arteries in the region of the head of the fire-bellied toad are on the whole very like those described in the spade-foot toad. It is worthy of mention only that the external carotid anastomoses at the base of the tongue with the external mandibular artery. The connecting vessel is quite large. Again as in the spade-foot toad, the large cutaneous artery is not connected with the temporal artery.

The system of veins in the head of the fire-bellied toad is also very similar to that described in the spade-foot toad. On account of the small dimensions of the animal the formation of the facial vein is simplified. Along the medial surface of the

maxillary runs a rather slender vessel, which only after union with a strong vein returning the blood from the eye and the palate *(v. orbitalis caudalis)*, gains considerable diameter. The facial vein passes the mandibular joint mediad and joins with the internal mandibular vein to form the faciomandibular vein.

The infratympanic vein connecting the facial with the internal jugular is a very large vessel. The internal mandibular vein is not connected with the veins of the tongue. The intermuscular vein is connected only with one external jugular, right or left; the former is a rather large vessel also returning the blood from a large part of the tongue. The lingual vein collects the blood from the mucous membrane of the floor of the mouth and from the lateral and posterior margins of the tongue. The right and left linguals do not anastomose.

d) ***Bufo bufo*** L. Similarly to the genus *Rana*, the majority of common toads have an anastomosis between the large cutaneous artery and the temporal artery formed by *r. auricularis a. cutaneae magnae.* It is however worth of mentioning that this vessel is of very small diameter, and two animals lacked it completely.

The head veins are arranged in the common toad similarly to those of the spade-foot toad. They differ only in some details. The right and left lingual veins are not joined at the base of the tongue. The right and left mandibular veins are joined in the forepart of the mandible. The anastomosis runs along the caudal margin of *m. submentalis.*

The facial vein arises on the lateral side of the head, under the skin, between the orbit and the nasal cavity, from the branches running from the nares, palate and skin. *V. orbitalis caudalis* is absent, and thus the internal jugular and facial veins are not connected in the region of the orbit. A strong anastomosis however joins these vessels in the region of the ear as the infratympanic vein. The facial vein passes the mandibular joint mediad.

e) **General remarks.** Important modifications in the arterial system of the head occur in *Salientia* in the neighbourhood of the mandibular joint. In the genera *Rana* and *Bufo* an anastomosis is present between the large cutaneous and the temporal

arteries. In animals belonging to the genera *Pelobates* and *Bombina* such connection is absent.

In all the species investigated the mucous membrane of the mouth cavity is supplied by the branches of the first arch *(a. carotis communis)*, and accordingly receives blood of the same composition as does the brain, notwithstanding its stated respiratory activity.

The arrangement of the veins differs in every species. It is important that only in the genus *Rana* the facial vein continues as the large cutaneous vein, in all other animals the facial vein unites with the internal mandibular vein to form the faciomandibular vein, a tributary of the external jugular vein.

A characteristic feature of the spade-foot toad is a very robust skull framework. The connective tissue of the skin is partly ossified and the blood vessels of the head run inside bony canals. This peculiarity does not however apparently influence the course of the vessels.

8. Blood vessels of the thoracic limb

a) ***Pelobates fuscus*** Laur. The main vessel conducting the blood to the fore limb is the subclavian artery (fig. 1, *A. sub.*). The mode of its origin from the aorta is described elsewhere (p. 148). After turning laterad the subclavian runs without curves, adhering to the *n. brachialis*, in the direction of the shoulder-joint. The first branch of the subclavian given off on the part running craniad is *a. thoracica superior*. The next branch, *a. thoraco-abdominalis* arises from the straight segment running in the direction of the shoulder-joint. In the region of the shoulder-joint the subclavian gives off several arteries, namely the principal vessels of the leg: *a. brachialis* and *a. profunda brachii*, and some smaller branches: *a. coraco-clavicularis*, *a. dorsalis scapulae* and *a. pectoralis superior*.

A. thoracica superior (fig. 1, *A. th. sup.*) is very variable. It is a branch of the subclavian or, in some specimens, of the aorta. It gives off branches to the muscles of the back and to *n. spinalis III.*

A. thoraco-abdominalis (fig. 1, *A. th. ab.*) runs from the subclavian caudad, enters the dorsal insertions of the abdominal muscles to the dorsal fascia and extends in the muscles over their

internal surface further caudad. It gives off numerous vessels to the abdominal muscles. Halfway along the length of the body thethoraco-abdominal artery anastomoses with *a. epigastrica lateralis.* In female specimens, during the breeding period, one of the cranial branches of the thoraco-abdominal artery supplies the oviduct.

A. coraco-clavicularis leaves the subclavian in the region of the shoulder-joint, runs cranio-ventrad, reaches the dorsal surface of the clavicle and coracoid, passes between these bones on the ventral body side and supplies the muscles surrounding the shoulder girdle.

A. pectoralis superior is given off from the subclavian close to the origin of the coraco-clavicular artery. It runs caudad, then bends ventrad and reaches the pectoral muscle.

A. dorsalis scapulae leaves the subclavian, encircles the shoulder-joint caudad, arrives on the lateral side of the latter and runs cranio-dorsad, supplying the muscles covering the scapula from the lateral side.

A. brachialis (figs. 9, 13, *A. br.*) arises from the subclavian on the caudal side of the shoulder-joint, enters between the muscles and passes among them on the proximal side of the humerus, giving off branches to the bone and muscles. Along the whole course on the upper arm the brachial artery lies close to the *n. brachialis longus inferior.* Together with it, it passes on the flexor side of the elbow-joint and here gives off branches to the bone, muscles and a slender artery, *a. radiomarginalis* (fig. 9, *A. rad. m.*), finally changing its name to *a. interossea.*

Nomenclatoric remarks: The majority of investigators endeavour to form the names for the six parallel vessels running on the fore arm from those of the neighbouring bones. In this way the names *a.* and *v. radialis, a.* and *v. ulnaris, a.* and *v. interossea* have been formed. Gaupp however following in his nomenclature of vessels his nomenclature of nerves cannot use such names, as vessels called by him »*radiales*« run on the ulnar side of the arm. The above vessels run along the *n. radialis* of Gaupp. Gaupp based his name for the nerve on the fact that it supplies the extensor muscles of the fore-arm, and in the mammalian anatomy *n. radialis* is distributed to all the extensors of the fore-arm. The correspondence of the mammalian radial nerve, to the *n. radialis* of the frog has however not been proved, a point which Gaupp himself emphasises. The details cannot be described here. In his anatomy of the salamander, Francis (1934) does not use the mammalian nomenclature of nerves, but following Siegel-

baur calls the nerves on the lateral side of the fore-arm *n. n. extensorii*. Therefore, as the nomenclature of Gaupp is questionable, and disagrees not only with the nomenclature of bones but also with the names used by the majority of investigators working on the anatomy of other vertebrates (Grodziński 1933, Hafferl 1933, Francis 1934), I do not use it but in my description of the vessels of the fore-arm I use the nomenclature of Grodziński.

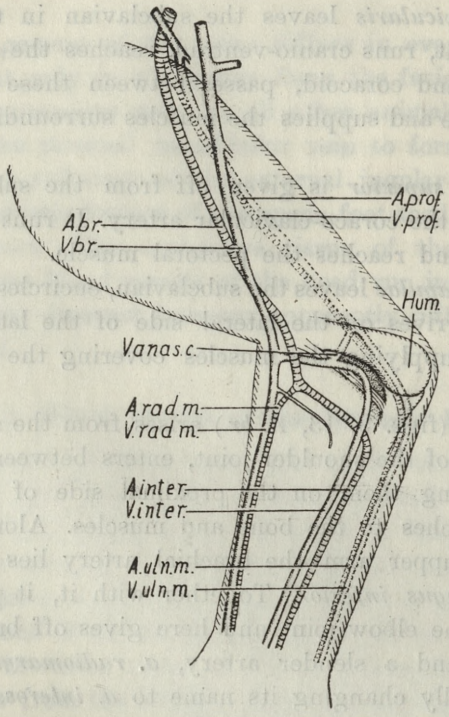

Fig. 9. *Pelobates fuscus* Laur. Outlines of the blood vessels on the right thoracic limb seen from the mesial side.

A. br.	: *a. brachialis*	*V. anas. c.*	: *v. anastomotica cubitalis*
A. inter.	: *a. interossea*	*V. br.*	: *v. brachialis*
A. prof.	: *a. profunda brachii*	*V. inter.*	: *v. interossea*
A. rad. m.	: *a. radiomarginalis*	*V. prof.*	: *v. profunda brachii*
A. uln. m.	: *a. ulnomarginalis*	*V. rad. m.*	: *v. radiomarginalis*
Hum.	: *humerus*	*V. uln. m.*	: *v. ulnomarginalis*

A. radiomarginalis (figs. 9, 13, *A. rad. m.*) is absent in the frog. In the spade-foot toad it is a slender vessel. It leaves the brachial artery in the neighbourhood of the elbow-joint and runs along the radial margin of the fore-arm parallel to *v. radiomar-*

ginalis and to the nerve called by Gaupp *r. cutaneus antebrachii et manus lateralis.* In the region of the wrist it anastomoses with *a. interossea.*

A. interossea (A. inter.) is the main continuation of the brachial artery on the fore-arm. It runs between the muscles and the antebrachial bone, along *n. brachialis longus inferior*, gives off branches to the bone and to the muscles, and proximad to the wrist-joint, gives off a larger branch running on the lateral surface of the arm, supplying the skin and the muscles and anastomosing with the ulnomarginal artery to form the *arcus arteriosus dorsalis manus.*

Arcus arteriosus dorsalis manus arises mainly from the interosseous artery. It runs from the lateral side of the arm in the direction of the thumb on the dorsum of the hand and gives origin to the digital and cutaneous arteries.

A. profunda brachii (figs. 9, 13, *A. prof.*) is given off from the subclavian on the dorso-caudal side of the shoulder-joint and runs on the lateral side of the upper arm among the muscles along *n. brachialis longus superior* and *v. profunda brachii.* It gives off branches to the muscles of the lateral side of the upper arm. In the vicinity of the elbow-joint *a. profunda brachii* sends off some small branches to the skin, muscles of the fore-limb and joint, then changes the name to *a. ulnomarginalis.*

A. ulnomarginalis (*a. radialis* Gaupp) *(A. uln. m.)* is a continuation of the profound brachial artery on the fore-arm. It runs under the superficial layer of the muscles, parallel to *n. radialis* (Gaupp, *n. extensorius* Siegelbaur) and to *v. ulnomarginalis.* In the region of the wrist it emerges under the skin, gives off muscular and cutaneous branches and unites with the interosseous artery in the formation of *arcus arteriosus dorsalis manus.*

The veins returning the blood from the digits of the arm enter a strong perpendicular vein, running across the dorsum of the hand. This vein is called »*arcus venosus dorsalis manus*«. On the ulnar side this vein opens into the ulnomarginal vein, on the radial it anastomoses with the radiomarginal vein; and gives off a branch surrounding the wrist and beginning the interosseous vein.

V. ulnomarginalis (*v. radialis* Gaupp) *(V. uln. m.)* arises on the ulnar side of the hand in the vicinity of the fourth digit. It

runs along the fore-arm parallel to the ulnomarginal artery, collecting tributaries from the muscles. In the neighbourhood of the elbow-joint it is joined by a vein from the skin and is united with a perpendicular strong vessel, passing on the flexor side of the elbow. This vessel is an anastomosis uniting the ulnomarginal vein with the interosseous *(V. anastomotica cubitalis, V. anas. c.)*. From the elbow-joint the vein continues under the name of *v. profunda brachii.*

V. profunda brachii runs on the lateral side of the upper arm parallel to *a. profunda brachii*, collecting small vessels from the muscles of the upper arm. On the dorso-caudal side of the shoulder-joint it unites with *v. dorsalis scapulae* to form *v. subscapularis.*

V. dorsalis scapulae collects the blood from the lateral side of the scapula, and from the *dorsalis scapulae* muscle. It runs ventrad, and in the vicinity of the shoulder-joint bends caudad and enters the subscapular vein.

V. subscapularis (figs. 4, 13, *V. subsc.*) is a continuation of *v. profunda brachii.* It surrounds *n. brachialis* and the shoulder-joint caudad, enters under the scapula and runs cranio-mediad. It unites with the internal jugular vein thus forming the brachiocephalic vein.

V. interossea (figs. 9, 13, *V. inter.*) begins on the palmar side of the wrist, among the muscles, of a branch running from *arcus venosus dorsalis manus*, surrounding the wrist on the radial side. This branch on the palmar side of the wrist is joined by the vein from the muscles *(m. m. volares)*, receives the name *v. interossea* and enters the muscles between which it runs parallel to the interosseous artery. In the vicinity of the elbow-joint it receives a vessel anastomosing with *v. profunda brachii (v. anastomotica cubitalis).* Proximad to the joint it approaches the skin and unites with the radiomarginal vein to form *v. brachialis.*

V. radiomarginalis (*V. superficialis antebrachii* Gaupp) *(V. rad. m.)* begins on the radial side of the wrist as a branch of *arcus venosus dorsalis manus.* The radiomarginal vein runs immediately under the skin on the radial side of the fore-arm parallel to *a. radiomarginalis.* In the vicinity of the elbow-joint it unites with the interosseous vein to form the brachial vein.

V. brachialis (V. br.) runs on the upper arm, immediately under the skin, parallel to the brachial artery and to *n. brachialis*

longus inferior on the medial side of the arm. About half-way along the upper arm the artery and the nerve pierce the muscle, and pass on to the lateral side of the limb, the vein leaving them and remainig on the medial side. It receives tributaries from the muscles and from the bone, and finally passes among the *m. m. pec-*

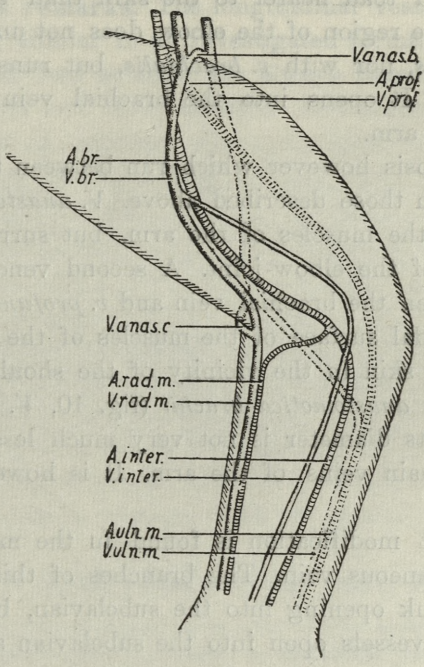

Fig. 10. *Bombina bombina* L. Outlines of the blood vessels on the right thoracic limb seen from the mesial side. Abbreviations as in fig. 9. *V. anas. b.*: *v. anastomotica brachii.*

torales, where it unites with the large cutaneous vein to form *v. subclavia.*

b) ***Rana esculenta*** L. The arrangement of vessels on the shoulder girdle and thoracic limb does not differ form the arrangement found in the spade-foot toad. Only the radiomarginal artery is absent.

c) ***Bombina bombina*** L. Only slight differences are found between the arteries on the shoulder and limb of the spade-foot toad and of the fire-bellied toad (fig. 10). *A. thoracica superior* leaves the subclavian in the middle of the segment running from

the aorta to the shoulder-joint. The thoraco-abdominal artery is given off in the immediate vicinity of the superior thoracic.

The longitudinal veins in *Bombina* can be easily compared with those described in *Pelobates*. The only important difference is seen in the course of the interosseous vein. This vessel runs in the fire-bellied toad nearer to the skin than the interosseous artery, and in the region of the elbow does not unite with *v. anastomotica cubitalis*, nor with *v. brachialis*, but runs on the medial side of the arm. It opens into the brachial vein only half-way along the upper arm.

The anastomosis however which run between the longitudinal veins differ from those described above. *V. anastomotica cubitalis* does not pierce the muscles of the arm, but surrounds them on the flexor side of the elbow-joint. A second venous anastomosis is present between the brachial vein and *v. profunda brachii*, running on the caudal surface of the muscles of the upper arm, directly under the skin in the vicinity of the shoulder-joint. This vein is named *v. anastomotica brachii* (fig. 10, *V. anas. b.*). It is a large vessel, its diameter is not very much less than the diameters of the main veins of the arm. It is however lacking in some specimens.

An important modification is found in the mode of opening of the large cutaneous vein. The branches of this vessel do not unite in one trunk opening into the subclavian, but in the form of two separate vessels open into the subclavian and subscapular veins.

d) ***Bufo bufo*** L. The arteries of the thoracic limb of the common toad do not differ from those of the spade-foot toad. Two branches of the subclavian however are absent: *a. thoracica superior* and *a. thoraco-abdominalis*. The first branches of the subclavian are given off in the vicinity of the shoulder-joint. One branch of *a. coraco-clavicularis* runs to the muscles of the abdomen, thus corresponding functionally with the absent *a. thoraco-abdominalis*. One branch of *a. coraco-clavicularis* supplies the parathyroids.

The longitudinal vessels on the thoracic limb run like those of *Bombina*. Two venous anastomoses are present. Their course is peculiar. *V. anastomotica cubitalis* pierces the muscles, distad to the elbow-joint, near the antebrachial bone. *V. anastomotica*

brachii is a small vessel, which surrounds the muscles caudad, running in the groove of the *m. anconeus.*

The cutaneous veins join to form the large cutaneous vein. The last-named opens into the subclavian vein as in *Rana* and *Pelobates.*

e) **General remarks.** The longitudinal vessels of the thoracic limb are very similar in all investigated forms. In the upper arm two veins and two arteries are always found, and in the forearm three veins and three arteries. The radiomarginal artery is lacking only in *R. esculenta.* The transversal veins however vary. In the spade-foot toad the longitudinal veins are connected twice: in the region of the wrist, and in the region of the elbow-joint. In the fire-bellied toad and in the common toad the longitudinal vessels are connected three times: in the neighbourhood of the wrist, the elbow-joint and the shoulder-joint. The anastomosing veins take various directions: piercing the muscles *(Pelobates, Rana, Bufo)* or surrounding the muscles under the skin *(Bombina).*

The variability of the transversal veins is probably caused by the differences in the development of the muscles of the limb, possibly in connection with the mode of life of species investigated. This question however deserves special study.

9. Blood vessels of the pelvic limb

To avoid misunderstanding note that in the description of the blood vessels of the pelvic limb the names of directions (lateral, dorsal etc.) are used as if the pelvic limbs were distended caudad, parallel to each other. Only the feet are described as if based on a surface.

a) ***Pelobates fuscus*** Laur. The blood to the pelvic limb comes through *a. ilica communis.* This vessel arises from the division of the abdominal aorta into two branches: right and left *a. a. ilicae communes* (figs. 1, 12, *A. il. comm.*). The common ilic artery sends off laterad as a first branch *a. epigastrico-vesicalis*, then it bends slightly dorsad and enters the musculature where it runs on the medial surface of the ilium giving off ventrad *a. femoralis.* The common ilic artery continues under the skin on the dorsal side of the hip-joint, passes on the ventral side of the lymphatic hearts (figs. 12, 13, *C. l.*) and receives the name *a. ischiadica.* Along the whole course described the common ilic artery closely follows *n. ischiadicus.*

A. ischiadica in the neighbourhood of the lymphatic hearts gives off *a. glutaea* and continues along *n. ischiadicus* in the furrow between *m. ileofibularis* and *m. semimembranosus*. Half-way along the thigh it sends off two vessels: on the lateral side of the thigh *a. profunda femoris arterior*, and on the medial *a. profunda femoris posterior*. In the vicinity of the knee-joint *a. ischiadica* divides on the flexor side into the following vessels: *a. peronea anterior superior*, *a. poplitea* and some lesser branches running to the muscles of the thigh.

A. femoralis (fig. 12, *A. fem.*) leaves the common ilic artery in the place where the last-named vessel passes on the medial side of the ilium. The femoral artery is a small vessel, which runs ventrad and passes over the surface of the muscles of the thigh directed to the body cavity and here gives off arterioles to the insertions of the muscles to the pelvis and to the skin of the thigh.

A. glutaea leaves the ischiadic artery on the ventral side of the caudal lymph hearts. It runs caudad, passes on the ventral side of the ischiadic vein and divides into branches running to the insertions of the muscles to the pelvis and supplying the neighbourhood of the anus. In fig. 12 *a. glutaea* is invisible.

A. profunda femoris anterior supplies the extensor muscles of the shank.

A. profunda femoris posterior divides into two branches. One supplies the femur and the deep flexor muscles, the other runs to the superficial flexors.

A. peronea anterior superior (fig. 13, *A. t. a. sup.*) leaves the ischiadic artery proximad to the knee-joint. It runs along *n. peroneus* on the lateral side of the joint, and where this nerve gives off a cutaneous branch it also sends a branch to the skin. It continues in the lower leg along *n. peroneus*, under *m. m. antici* (to which it sends several branches) and opens into *a. tibialis anterior* (fig. 13, *A. t. ant.*) proximad to the articulation between the leg and the tarsus.

A. poplitea (fig. 13, *A. popl.*) leaves the ischiadic artery in the same place as *a. peronea anterior superior*. At the beginning, the popliteal artery gives off a branch running on the medial side of the knee-joint: *a. circumflexa genus medialis superior*, and continuing on the flexor side of the knee-joint near the skin along

n. tibialis, gives off at short intervals: a skin branch, *a. tibialis posterior (A. t. post.)* and *a. circumflexa genus medialis inferior*. All these branches divide off very near to each other and very often they are joined at their start. The popliteal artery continues under the insertions of the superficial flexors of the shank giving off small branches to the muscles, enters *m. tibialis posticus* and passes over the dorsal (posterior) surface of *os cruris*. Here it sends off a very small artery *(a. interossea posterior, A. i. post.)*, runs for a short distance on the surface of the bone and halfway along the lower leg it pierces the bone, emerging on its ventral surface, where it receives the name *a. tibialis anterior (A. t. ant.)*. This runs distad on the surface of the bone, in the vicinity of the expansions of the shaft into the head it is joined by *a. peronea anterior superior*, gives off a small branch to the muscles and changes its name to *a. dorsalis pedis (A. d. p.)*.

A. tibialis posterior is a third longitudinal artery of the lower leg. It leaves the popliteal artery under the knee and runs along the medial side of the leg, immediately under the skin, on the surface of *m. plantaris longus*. Proximal to the tarsus *a. tibialis posterior* surrounds medially *m. plantaris longus* and disappears under the tendon of Achilles. On the inner side of the tendon it runs to the tarsus where it anastomoses with *a. malleolaris medialis*. Along its course it gives off branches to the muscles and skin.

A. circumflexa genus medialis superior is a branch of *a. poplitea*. It divides into two branches. One supplies the insertions of the muscles to the femur, the other surrounds the knee-joint on the fibular side and ramifies in the skin.

A. circumflexa genus medialis inferior surrounds the knee-joint on the fibular side. It gives off branches to the skin and to the insertions of muscles on *os cruris*.

A. interossea posterior (fig. 13, *A. i. post.*) is a very slender branch of *a. poplitea* which it leaves on the posterior (dorsal) surface of the *os cruris*, under *m. tibialis posticus*. In the first segment it runs along *a. poplitea*, in the following along *r. posterior n. tibialis*. In the region of the cruro-tarsal joint it anastomoses with *a. malleolaris medialis*.

A. dorsalis pedis is a continuation of *a. tibialis anterior*. It runs on the *dorsum pedis*. In the region of the cruro-tarsal joint

it sends off two branches: *a. malleolaris medialis* and *a. malleolaris lateralis superior*, continues on the surface of the foot and gives two vessels laterad: *a. cutanea dorsi pedis lateralis* and *a. malleolaris lateralis inferior*. Further on *a. dorsalis pedis* disappears under the muscles, giving off small arterioles to the tarsus. One of these, a little bigger, than the others receives the name *a. perforans tarsi inferior*. Immediately proximad to the tarso-metatarsal articulation *a. dorsalis pedis* divides into two branches: *a. tarsea lateralis* and *a. tarsea medialis*.

A. malleolaris medialis leaves *a. dorsalis pedis* and runs mesiad along the groove of the joint, and after surrounding the bones reaches the ventral side of the foot. Here it anastomoses with *a. interossea posterior* and *a. tibialis posterior*. From the union of these arteries arises *a. plantaris superficialis*, which runs on the sole of the foot and gives off numerous vessels to the muscles.

A. malleolaris lateralis superior leaves *a. dorsalis pedis* in the same place as the vessel mentioned above. It runs in the groove of the joint surrounding the bones on the lateral side.

A. cutanea dorsi pedis lateralis gives off branches to the skin and muscles on the dorsum of the foot.

A. malleolaris lateralis inferior is a very small vessel.

A. perforans tarsi inferior pierces the tarsus, runs on the ventral side of the tibiale and divides in the muscles of the sole of the foot.

A. tarsea lateralis and *a. tarsea medialis* arise from the division of *a. dorsalis pedis*. After a short course they ramify into small vessels running along the metatarsal bones *(a. a. interstitiales dorsales)*.

The blood from the digits is collected by *v. v. interstitiales*, which open on the dorsal side of the foot to *v. tarsea medialis* and *v. tarsea lateralis* between the muscles extending the digits.

The above-mentioned vessels unite after a short course to form *v. dorsalis pedis* (fig. 13, *V. d. p.*). The last-named is joined by *v. circumflexa tarsi* and *v. tarsi dorsalis profunda* and then passes on to the surface of the muscles extending the foot. It runs directly under the skin, nearer the lateral than the medial margin of the foot. From the skin it receives *v. cutanea dorsi vedis lateralis*. In the vicinity of the cruro-tarsal joint *v. dorsalis pedis* is joined from the medial side by *v. malleolaris lateralis*.

In the same region smaller branches from the muscles and the skin also open to the *v. dorsalis pedis*. The continuation of *v. dorsalis pedis* on the lower leg is called *v. peronea* (fig. 13, *V. peron*).

V. circumflexa tarsi begins on the sole of the foot, and after collecting the blood, circles the foot on the fibular side, and opens into *v. dorsalis pedis*.

V. tarsi dorsalis profunda begins in the muscles of the sole of the foot. It penetrates the tarsus between the tibiale and fibulare, and opens into *v. dorsalis pedis*.

V. malleolaris medialis begins on the sole of the foot by the union of branches connected with *v. tibialis posterior*, surrounds the cruro-tarsal joint on the medial side, and collects the blood from the muscles of the lower leg. Some of its tributaries begin as far away as the vicinity of the knee-joint. *V. malleolaris medialis* is itself a large tributary of *v. dorsalis pedis*.

V. malleolaris lateralis is a small vessel returning the blood from the lateral side of the cruro-tarsal joint to *v. dorsalis pedis*.

V. peronea (V. peron.) is a continuation of *v. dorsalis pedis* in the lower leg. Near the cruro-tarsal articulation it receives branches from the *os cruris* and the muscles. It runs along the *os cruris* on its lateral side and in the neighbourhood of the knee-joint is joined by a big vessel, *v. circumflexa genus lateralis inferior*. *V. peronea* then passes on the flexor side of the joint, accompanies *a. poplitea*, and receives the name *v. poplitea*.

V. tibialis posterior (V. t. post.) arises on the sole of the foot from muscular branches which anastomose with *v. malleolaris medialis*, and runs along the lower leg parallel to *a. tibialis posterior*. Near the knee-joint it opens into *v. poplitea*.

V. circumflexa genus lateralis inferior is a large vein, draining the blood from the neighbourhood of the knee-joint into *v. povlitea*.

V. poplitea is a further continuation of the main vein of the pelvic limb. It runs on the flexor side of the knee-joint, collecting numerous veins from the muscles, skin and bone *(v. v. circumflexae genus)*. It is also joined by *v. tibialis posterior*. *V. poplitea* passes on the posterior (dorsal) side of the thigh, where it receives the name *v. ischiadica*.

V. ischiadica (figs. 12, 13, *V. isch.*) is the main vein of the thigh. Near the knee-joint this vein receives small tributaries

anastomosing with *v. femoralis dorsalis* and *v. femoralis ventralis*. *V. ischiadica* closely follows the ischiadic artery and nerve. Over the whole course along the thigh *v. ischiadica* receives no tributaries. But further on in the neighbourhood of the hip-joint the *ischiadic* vein receives successively a vessel from the lymphatic hearts, *v. glutaea* and *v. v. pudendae*. Proximad of the openings of these vessels the ischiadic vein curves craniad and disappears among the muscles of the trunk passing mediad of the ilium. On the ventral side of *m. coccygeo-ilicus v. ilica externa* and its tributaries enter the ischiadic vein thus forming *v. ilica communis* (figs. 12, 13, *V. il. ex. V. il. comm.*).

V. glutaea (figs. 12, 13, *V. glut.*) was described in *R. esculenta* by Gaupp under an erroneous name, *v. ischiadica*. This vein begins on the medial side about the middle of the thigh from branches conducting blood from the flexors of the shank. It runs under *m. semimembranosus*, and in the vicinity of the posterior lymph hearts opens into the ischiadic vein.

V. v. pudendae return the blood from the muscles surrounding the anus to the ischiadic vein.

V. femoralis dorsalis (figs. 11, 12, 13, *V. fem. d.*) corresponds with the main vein of the thigh in the edible frog, described by Gaupp as *v. femoralis*. *V. femoralis dorsalis* arises directly proximad to the knee-joint from the union of small vessels anastomosing with *v. ischiadica* and *v. femoralis ventralis*. *V. femoralis dorsalis* runs on the thigh inside *m. triceps femoris*, namely between *m. cruralis* and *m. glutaeus magnus*. It receives several tributaries from the muscles. In the place where *m. cruralis* emerges under the skin *v. femoralis dorsalis* gives off *v. ilica transversa* (figs. 12, 13, *V. il. tr.*), curves ventrad, and arrives on the surface of the thigh muscles directed to the body cavity. Here it divides into *v. ilica externa* and *r. abdominalis v. femoralis*.

V. ilica transversa (figs. 12, 13, *V. il. tr.*) begins in the thigh as a branch of *V. femoralis dorsalis*. It surrounds *m. glutaeus magnus* and emerges from the muscles under the skin, near the hip-joint. Here it is joined by *v. cutanea caudalis* and by branches from the muscles of the trunk. The posterior lymph hearts open into it. In some animals a weak anastomosis with *v. ischiadica* was found in this region. *V. ilica transversa* runs

for a short distance mediad, directly under the skin, curves caudad, disappears under *m. coccygeo-ilicus* and joins *v. ilica externa.*

V. femoralis ventralis (figs. 11, 12, 13, *V. fem. v.*) begins proximad to the knee-joint on the medio-ventral side of the thigh. It runs over *m. pectineus*, covered on the side of the skin by *m. sartorius.* In the region of the insertions of the muscles to the pelvis the ventral femoral vein curves dorsad and opens into *r. abdominalis v. femoralis.*

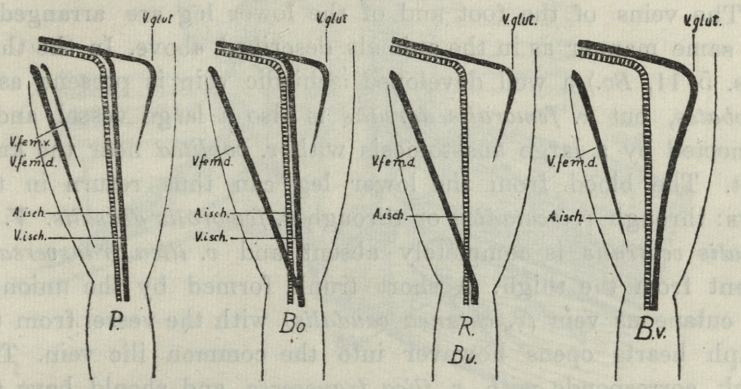

Fig. 11. Schemes of the arrangement of the principal blood vessels of the thigh.

P. : *Pelobates fuscus* Laur.
Bo.: *Bombina bombina* L,
Bu.: *Bufo bufo* L.
A. isch. : *a. ischiadica*
V. fem. d.: *v. femoralis dorsalis*
V. fem. v.: *v. femoralis ventralis*
B. v.: *Bufo bufo* L. abnormal specimen
R. : *Rana esculenta* L.
V. glut.: *v. glutaea*
V. isch.: *v. ischiadica*

b) ***Rana esculenta*** L. The arteries on the pelvic limb are developed in a very similar way to those of the spade-foot toad (figs. 5, 11, *R.*).

The arrangement of veins in the foot and in the lower leg is similar to that of the spade-foot toad. Great differences are however found in the thigh (fig. 11). The vein parallel to the artery and nerve *V. ischiadica* is absent. The vein described by Gaupp under this name does not follow the artery and nerve, but returns blood from the dorsal (posterior) muscles of the thigh and accompanies *a. glutaea.* I therefore give it the name *v. glutaea. V. femoralis ventralis* is absent. *V. femoralis dorsalis* named

by Gaupp more shortly *v. femoralis* is strongly developed. It is joined near the knee-joint by *v. poplitea* and thus returns nearly all the blood from the pelvic limb.

c) ***Bombina bombina*** L. The only difference between the fire-bellied toad and the forms already described in the course of the arteries of the pelvic limb is the weak development or complete absence of *a. femoralis*. This vessel is however also small in *Rana* and *Pelobates*.

The veins of the foot and of the lower leg are arranged in the same manner as in the animals described above. In the thigh (figs. 5, 11, *Bo.*) a well developed ischiadic vein is present, as in *Pelobates*, but *v. femoralis dorsalis* is also a large vessel and is connected by a large anastomosis with *v. poplitea* near the knee-joint. The blood from the lower leg can thus return in two ways: through *v. ischiadica* or through *v. femoralis dorsalis*. *V. femoralis ventralis* is completely absent and *v. ilica transversa* is absent from the thigh. A short trunk formed by the union of the cutaneous vein *(v. cutanea caudalis)* with the vessel from the lymph hearts opens however into the common ilic vein. This trunk corresponds with *v. ilica transversa* and should have the same name.

d) ***Bufo bufo*** L. The arteries of the pelvic limb, as also the veins on the foot and lower leg are arranged as in amphibians already described. The femoral artery is present.

The veins of the thigh are arranged similarly to those of *R. esculenta* (figs. 5, 11, *Bu.*): *v. ischiadica* is absent, as also *v. femoralis ventralis*. The main vessel of the thigh is the dorsal femoral vein. The transverse ilic vein is however developed as in the fire-bellied toad: only a short trunk formed by the cutaneous vein and the vessel from the lymph hearts is present.

An interesting abnormality was found in one animal (fig. 11, *B. v.*). In one limb the dorsal femoral vein was only a small vessel, beginning proximad to the knee-joint by the union of muscle branches, and the blood from the lower leg ran through a large vein which connected *v. poplitea* with *v. glutaea*. In this abnormal case, the main vessel of the thigh constituted *v. glutaea*. The other leg of the same individual was normal.

e) **General remarks.** In all species investigated the course of the veins and arteries in the foot and lower leg is similar. Va-

riability appears in the arrangement of the veins of the thigh. I consider the arrangement found in *Pelobates* to be the most primitive: an ischiadic vein and two femoral veins are present.

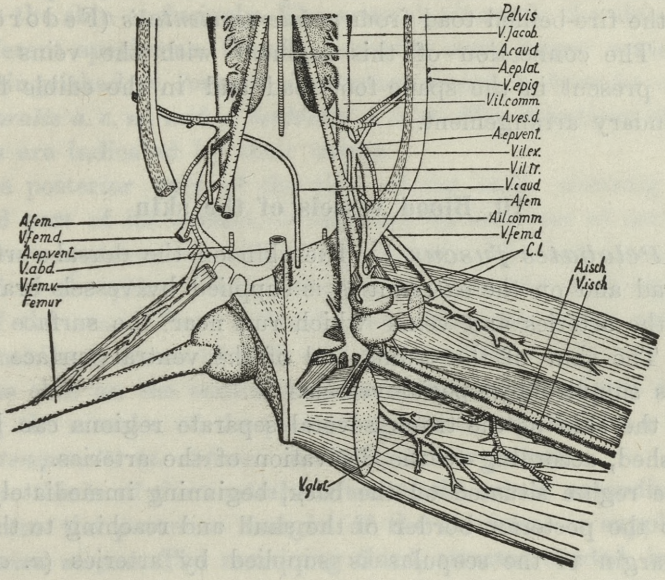

Fig. 12. The blood vessels of the pelvic region in the spade-foot toad (half-schematic) seen from the dorsal side. The majority of the muscles have been taken out, except those from the right thigh. From the left thigh only *m. sartorius* is left in place. A segment of the ilic bone has been removed.

A. caud.	: *aorta caudalis*	*V. epig.*	: *v. epigastrica*
A. ep. lat.	: *a. epigastrica lateralis*	*V. fem. d.*	: *v. femoralis dorsalis*
A. ep. vent.	: *a. epigastrica ventralis*	*V. fem. v.*	: *v. femoralis ventralis*
A. fem.	: *a. femoralis*	*V. glut.*	: *v. glutaea*
A. il. comm.	: *a. ilica communis*	*V. il. comm.*	: *v. ilica communis*
A. isch.	: *a. ischiadica*	*V. il. ex.*	: *v. ilica externa*
A. ves. d.	: *a. vesicalis dorsalis*	*V. il. tr.*	: *v. ilica transversa*
C. l.	: *cordes lymphatici*	*V. isch.*	: *v. ischiadica*
V. caud.	: *v. caudalis*	*V. Jacob.*	: *v. Jacobsoni*

In *Bombina* *v. femoralis ventralis* is absent, *v. femoralis dorsalis* is connected with *v. poplitea*, but *v. ischiadica* is also present. In *Bufo* and *Rana* the ischiadic vein is always absent, and the main vessel of the thigh is formed by *v. femoralis dorsalis*.

The short segment of *v. ilica transversa* situated between the posterior lymph hearts and the opening of the vein into the common ilic vein is homologous in all animals, as it is developed from *v. caudalis lateralis* of the tadpole in the majority of forms, or, in the fire-bellied toad from *v. intersegmentalis* (Fedorowicz 1914). The connection of this segment with the veins of the thigh, present in the spade-foot toad and in the edible frog, is a secondary arrangement.

10. Blood vessels of the skin

a) ***Pelobates fuscus*** L. The skin on the dorsal surface of the head and on the extremities is supplied by vessels branching from the arteries and veins which run near the surface of the body. The skin of the trunk and of the ventral surface of the head is supplied by special vessels.

In the skin of the trunk several separate regions can be distinguished, according to the derivation of the arteries.

The region situated on the back, beginning immediately caudad to the posterior border of the skull and reaching to the caudal margin of the scapulas is supplied by arteries (*a. cutanea occipitalis* — a new name) which are branches of *a. a. occipitales* emerging under the skin in the neighbourhood of the insertions of the muscles to the occipital bones. These vessels run caudad over the internal surface of the skin.

The largest territory is supplied by *a. cutanea magna*. This territory begins on the back, on the posterior margin of the scapulas, continues caudad over two-thirds of the length of the trunk and includes also the side and ventral surfaces of the trunk.

A. cutanea magna (fig. 13, *A. cut. m.*) is a branch of the fourth aortic arch. It leaves the pulmo-cutaneous artery on the ventral surface of *m. m. petrohyoidei* caudad and runs for a short distance latero-caudad, curves and assumes a cranio-dorsal direction which it follows over the lateral surface of *m. m. petrohyoidei*. It crosses the large arteries passing laterad to the aorta and *a. carotis communis* and mediad to the *a. subclavia* and *v. jugularis interna*. On the mesial surface of the scapula it bends into a curve, surrounding the scapula craniad, and reaches the skin.

Along the whole course, from the pulmo-cutaneous trunk to the skin it does not give off any branches.

A. cutanea magna runs caudad over the inner surface of the skin and immediately breaks into many branches. All its branches supply the skin exclusively. The arterial plexus in the skin varies in different specimens. Usually however some larger vessels can be distinguished; *r. dorsalis a. cutaneae magne*, *r. lateralis a. c. m.*, *r. pectoralis a. c. m.* and *r. ventralis a. c. m.* The directions of these vessels are indicated by their names.

The posterior part of the skin of the back, covering about a third part of its surface, is supplied by branches of *aortà caudalis* — *a. cutanea caudalis* (a new name). The last-named runs caudad to the place where the skin is connected with the muscles of the anus. Here it breaks into arterioles which enter the skin making a curve of 180° and run craniad.

The skin on the ventral surface of the mouth cavity and covering the muscles of the pectoral girdle is supplied by a branch of *a. temporalis* (*a. cutanea mentalis*, a new name).

Two-thirds of the ventral surface of the trunk, extending caudad from the posterior margin of the clavicles, is supplied by *a. cutanea magna*. The remaining third, situated caudad, is supplied by a branch of *a. epigastrica ventralis* (*a. cutanea abdominalis*, a new name).

The veins returning the blood from the skin lie nearer the outer surface of the skin than the arteries, and build a plexus of large vessels connected by numerous anastomoses. The venous plexus of the skin has several openings into the large veins. The majority of the blood flows to *v. cutanea magna*, which arises on the lateral surface of the trunk and runs craniad to the shoulder-joint, gradually leaving the skin, so that near the joint it runs deeper than the arterial plexus. In the vicinity of the joint the large cutaneous vein passes over the dorsal surface of *m. pectoralis*, from which it receives two veins *(v. v. musculares pectorales)* and unites which *v. brachialis* to form *v. subclavia*.

The second vein according to diameter, is *v. cutanea caudalis* (a new name), which opens into *v. ilica transversa*. Nearly as large is *v. cutanea occipitalis* (a new name), which opens near the occipital bone into the internal jugular vein. The smallest vessel is *v. hyoidea superficialis* (a new name) which returns the blood

from the skin on the ventral surface of the head to the facio-mandibular vein.

b) ***Rana esculenta*** L. The skin on the extremities is supplied by branches running near the surface of the body. The skin of the head is however to a large degree independent of local vessels and is supplied by special cutaneous vessels.

A. cutanea occipitalis is absent. The arteries of the skin on the back and on the dorsal surface of the head arise from *a. cutanea magna*, so the region supplied by this artery is much larger in the edible frog than in the spade-foot toad.

A. cutanea magna divides into following three vessels near the cranial border of the scapula: *r. lateralis a. c. m.* — which corresponds to the continuation of *a. cutanea magna* in other species, *r. auricularis a. c. m.* — which supplies the muscles of the mandibular joint and the mucous membrane of the palate and anastomoses by means of *a. temporalis* with the arteries derived from the systemic and carotid arches, and lastly *r. dorsalis a. c. m.* — which runs dorsad and supplies the skin of the back and on the dorsal surface of the head, between the sense organs.

The posterior part of the skin on the dorsal surface of the trunk is not supplied with branches of the large cutaneous artery. The arterioles reaching this region do not however rise from *aorta caudalis*, which is absent in the frog, but are given off by *a. ischiadica*.

The skin on the ventral surface of the body is almost completely supplied by branches of *a. cutanea magna*. Only in the immediate vicinity of the mandible *a. mandibularis interna* gives off several cutaneous vessels, and the posterior region on the belly is, as in the spade-foot toad, supplied by *a. cutanea abdominalis*.

A striking difference between the arrangement of the blood vessels of the edible frog and that of the other salientians is the presence of cranial branch of *v. cutanea magna*. This returns the blood from the skin of the head and from the nasal chamber. It arises in the cranio-ventral angle of the orbit by the union of *v. nasalis externa* with *v. orbitalis anterior*. It runs immediately under the skin caudad, under the name of *v. facialis*, passes dorsad of the mandibular and shoulder joints, as a large cutaneous vein, bends in a large curve mesiad and runs craniad collecting

vessels from the skin of the trunk, finally unites with *v. brachialis* to form *v. subclavia.* The cranial branch of the large cutaneous vein, called by Gaupp shortly »*v. cutanea magna*« is a very important vessel in the edible frog, returning more blood than all the other branches of the large cutaneous vein together.

The remaining cutaneous veins develop in the frog similarly to those of the spade-foot toad.

c) ***Bombina bombina*** L. *A. cutanea occipitalis* is absent The skin on the back and on the dorsal surface of the head is supplied by branches of *a. cutanea magna.* The large cutaneous artery however runs undivided from the pulmo-cutaneous trunk as far as the skin, where it divides. The cutaneous territory supplied by the large cutaneous artery is very large, extending from the eyelids to the neighbourhood of the posterior limbs and also covering the ventral surface of the body. The skin on the posterior part of the back is supplied by two little arteries, branches of *a. ischiadica* in spite of the presence of *a. caudalis.*

The skin on the ventral surface of the head and on the pectoral muscles is supplied by a branch of *a. coraco-clavicularis.* The blood passes through a branch of *a. epigastrica* to the posterior part of the skin on the belly.

The venous plexus of the skin in the fire-bellied toad forms a different pattern from that in other salientians. The principal vein of the skin is *v. cutanea magna.* This vein arises on the ventral surface of the body, near the mandibular joint as a large vessel connected with the faciomandibular vein. It runs under the skin dorso-laterally, surrounds the fore-limb dorsad and opens into the subscapular vein. Besides this vessel the blood from the skin is returned by the following vessels: *v. cutanea caudalis*, *v. cutanea occipitalis* and *v. hyoidea superficialis*, which run similarly to the same vessels in the spade-foot toad, and a second branch of *v. cutanea magna* which opens into *v. subclavia.* This second branch however is much smaller than the main trunk which opens into the subscapular vein.

d) ***Bufo bufo*** L. The skin of the dorsal surface of the head and trunk, and also that on the sides of the trunk and on the belly, is supplied by *a. cutanea magna.* It is worth mentioning that in this species *r. auricularis a. cutaneae magnae* is present. The course of this vessel is similar to that in the edible frog.

In two specimens however it was not possible to find *r. auricularis a. c. m.*, the large cutaneous artery thus conducting the blood only to the skin, as in *Pelobates* and *Bombina*. Other details of the arteries of the skin do not differ from the description given of those of the edible frog.

In spite of a similarity to *Rana* in the pattern of the skin arteries, the common toad differs from that genus in the arrangement of the veins, which follows closely that in *Pelobates*.

e) **General remarks.** The peculiarity of the *Salientia* lies in the arrangement of the blood vessels of the skin, which corresponds to the well developed ability of these animals to use cutaneous respiration. The main part of the skin is in all species supplied by *a. cutanea magna*, a branch of the fourth arterial arch, thus conducting a blood poor in oxygen. In animals from the genera *Rana, Bombina* and *Bufo* the cutaneous region supplied by this artery is very similar. In genus *Pelobates* the large cutaneous artery supplies a smaller region. It is difficult to explain the presence of *r. auricularis a. c. m.* in *Rana* and *Bufo*, a branch of *a. cutanea magna* driving the blood to the muscles of the mandibular joint. The presence of this vessel probably points to the fact that the blood from the fourth arterial arch carries enough oxygen so supply the muscles more rarely used. One of the main causes of the mixing of the two categories of blood is just the presence of cutaneous respiration, as the oxygenated blood from the skin is conveyed not to the left, but to the right auricle.

In *Bombina* and *Pelobates* the large cutaneous artery supplies the skin only.

The respiratory function of the skin modified the cutaneous arteries to a greater degree than the cutaneous veins. In all species investigated, a distinct cutaneous vein from the trunk is present *(v. cutanea magna)* which collects the bulk of the blood from the skin. This vein however never opens into the left auricle, which would ensure the separation of the two kinds of blood within the heart, as in the fire-bellied toad it opens into the subscapular vein and in other forms investigated into the subclavian vein.

The region from which the large cutaneous vein returns the blood is largest in the edible frog, as here it also embraces the

cutaneous veins of the head. In the common and spade-foot toads the large cutaneous vein collects the blood only from the skin of the trunk, and in the fire-bellied toad it reaches the faciomandibular vein with a strong branch thus attaining the possibility of conducting part of the blood from the skin of the head.

It is safe to assume that the skin on the limbs has also a respiratory function, and the blood from it is returned in the same vessels which conduct the blood from the muscles, another circumstance which causes the presence of oxygenated blood in the right ventricle.

11. Discussion of results

In Salientians, the arteries supplying the head, brain, and mucous membrane of mouth cavity arise from the first arterial arch *(a. carotis communis)*. Such an arrangement must be discussed. As is well known (Noble 1931), the mucous membrane of the mouth cavity takes an active part in the gaseous exchange, but in spite of this fact receives blood identical in its properties to that which passes to the brain. This circumstance raises the question whether the mechanism in the ventricle of the heart separating arterial from venous blood and described by various investigators (Sabatier 1873, Gaupp, etc.) is really present.

Some authors try to explain the above-mentioned relations by emphasising the importance of the anastomoses which connect the arteries of the palate with *a. cutanea magna* through *r. auricularis a. c. m.*, *a. temporalis* and *a. maxillaris superior*. These anastomoses however are only present in the edible frog and partly in the common toad. In other species they are absent. But even in forms where they are present they appear as small, narrow vessels difficult to find, so they cannot conduct great quantities of blood or play great part in supplying the palate with blood. The whole problem corresponds with the question raised by cutaneous respiration; we shall come back to it later.

In the arteries derived from the systemic arch the following details are important. The way the laryngeal artery branches from the aorta in the toad suggests that this artery is a rudiment of the third arch. To determine this point an investigation of freshly metamorphosed specimens would be necessary, as according to

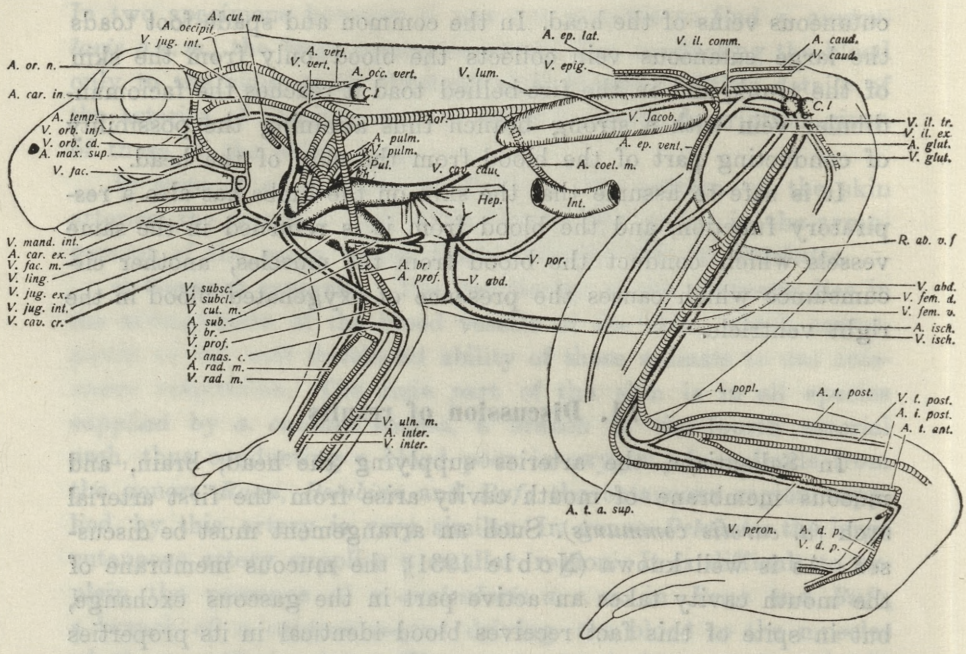

Fig. 13. Scheme showing the principal arteries and veins in the spade-foot toad.

A. br.	: *a. brachialis*	*A. rad. m.*	: *a. radiomarginalis*
A. car. ex.	: *a. carotis externa*	*A. sub.*	: *a. subclavia*
A. car. in.	: *a. carotis interna*	*A. t. ant.*	: *a. tibialis anterior*
A. caud.	: *aorta caudalis*	*A. t. a. sup.*	: *a. peronea anterior superior*
A. coel. m.	: *a. coeliaco-mesenterica*		
A. cut. m.	: *a. cutanea magna*	*A. temp.*	: *a. temporalis*
A. d. p.	: *a. dorsalis pedis*	*A. t. post.*	: *a. tibialis posterior*
A. ep. lat.	: *a. epigastrica lateralis*	*A. uln. m.*	: *a. ulnomarginalis*
A. ep. vent.	: *a. epigastrica ventralis*	*A. vert.*	: *a. vertebralis*
A. glut.	: *a. glutaea*	*C. l.*	: *cordes lymphatici*
A. inter.	: *a. interossea*	*Hep.*	: *hepar*
A. i. post.	: *a. interossea posterior*	*Int.*	: *intestinum*
A. isch.	: *a. ischiadica*	*Pul.*	: *pulmones*
A. max. sup.	: *a. maxillaris superior*	*R. ab. v. f.*	: *r. abdominalis v. femoralis*
A. occipit.	: *a. occipitalis*		
A. occ. vert.	: *a. occipito-vertebralis*	*V. abd.*	: *v. abdominalis*
Aor.	: *aorta thoracica*	*V. anas. c.*	: *v. anastomotica cubitalis*
A. or. n.	: *a. orbito-nasalis*	*V. br.*	: *v. brachialis*
A. popl.	: *a. poplitea*	*V. cav. caud.*	: *v. cava caudalis*
A. prof.	: *a. profunda brachii*	*V. cav. cr.*	: *v. cava cranialis*
A. pulm.	: *a. pulmonalis*	*V. caud.*	: *v. caudalis*

V. cut. m.	: *v. cutanea magna*	*V. ling.*	: *v. lingualis*
V. d. p.	: *v. dorsalis pedis*	*V. lum.*	: *v. lumbalis*
V. epig.	: *v. epigastrica*	*V. mand. int.*	: *v. mandibularis interna*
V. fac.	: *v. facialis*		
V. fac. m.	: *v. faciomandibularis*	*V. orb. cd.*	: *v. orbitalis caudalis*
V. fem. d.	: *v. femoralis dorsalis*	*V. orb. inf.*	: *v. orbitalis inferior*
V. fem. v.	: *v. femoralis ventralis*	*V. peron.*	: *v. peronea*
V. glut.	: *v. glutaea*	*V. por.*	: *v. portae hepatis*
V. il. com.	: *v. ilica communis*	*V. prof.*	: *v. profunda brachii*
V. il. ex.	: *v. ilica externa*	*V. pulm.*	: *v. pulmonalis*
V. il. tr.	: *v. ilica transversa*	*V. rad. m.*	: *v. radiomarginalis*
V. inter.	: *v. interossea*	*V. subcl.*	: *v. subclavia*
V. isch.	: *v. ischiadica*	*V. subsc.*	: *v. subscapularis*
V. Jacob.	: *v. Jacobsoni*	*V. t. post.*	: *v. tibialis posterior*
V. jug. ex.	: *v. jugularis externa*	*V. uln. m.*	: *v. ulnomarginalis*
V. jug. int.	: *v. jugularis interna*	*V. vert.*	: *v. vertebralis*

Marshall and Bles (1893) the third arch only disappears some months after the metamorphosis.

In the *Caudata* both systemic arches, right and left, are equivalent, receive identical blood, and give origin to similar arteries. Reptiles differ sharply in this point. The right arch conducts better oxygenated blood to the head and muscles, the left one receives blood poorer in oxygen and conducts it to the internal organs of the body. In *Salientia* asymmetry is sometimes present, but never pronounced. As its symptoms should be noted in the frog the incomplete communication between the right and left aortae in the place of origin of *a. coeliaco-mesenterica*, and in the toad the prolongation of the left arch into this artery. Similar relations were described in several exotic forms: *R. tigrina*, *R. clamata*, *B. mauritanicus*, *B. melanosticus* etc. (Crawshay 1906, Bhaduri 1931). The opening connecting the right and left arches at the basis of *a. coeliaco-mesenterica* is however also large in *Bufo bufo* L. (Hafferl 1933) and in the spade-foot toad. In the fire-bellied toad the arrangement is peculiar, as both arches unite completely before the rise of *a. coeliaco-mesenterica* and *a. oesophagica caudalis* with *a. oesophagica cranialis* are asymmetrical vessels on the right or the left side of the body.

The differences in the mode of origin of *a. subclavia*, *a. occipito-vertebralis* and *a. oesophagica cranialis* have probably small comparative value, being only a result of slight differences in the body proportions of different species. The individual origin of

every vessel might be regarded as the more primitive *(Bombina)*, and the common origin as secondary *(Pelobates)*, which is however present also in *Pipa* (Klinckowström 1894). In the frog and the common toad the arrangement is intermediary.

The pattern of the branches of *a. subclavia* on the fore-arm is similar to that found in *Caudata* (Grodziński 1930, 1933, Francis 1934). Three parallel arteries: *a. radiomarginalis*, *a. interossea* and *a. ulnomarginalis* are present. Only the edible frog lacks the radiomarginal artery. Hafferl (1933) however, extends the ranid arrangement to all amphibians, which is obviously unjustifiable.

In all species investigated, except *Rana esculenta*, the caudal aorta is present in the form of a slender vessel. The presence of the caudal aorta in metamorphosed specimens is naturally a primitive feature. Among *Salientia* the caudal aorta is best developed in *Pipa americana* (Klinckowström 1894).

A characteristic point in the anatomy of *Salientia* is the presence of *a. cutanea magna* — an important branch of the fourth arch. No similar arrangement can be found among vertebrates. The large cutaneous artery drives to the skin a part of the same stream of blood which is directed to the lungs, and permits therefore a very intensive cutaneous respiration. As shown by Dolk and Postma (1927), cutaneous respiration in *Rana temporaria* L. plays a very important role. At low temperatures the pulmonary respiration is irregular, or completely inhibited, at higher temperatures more oxygen is taken through the lungs than through the skin, the output of carbon dioxide however is chiefly eliminated through the skin.

Cutaneous respiration is important also in some *Caudata* lacking lungs, *e. g. Spelerpes*, *Aneides*, *Pseudotriton* etc. The anatomical structure in these however is not so well adapted to physiological requirements, as no artery runs to the skin from the fourth arch and the skin is supplied by a branch of the subclavian artery. A similar arrangement has been found in *Pipa* (Klinckowström 1894). In this animal the pulmonary artery gives off only one branch which supplies the mucous membrane of the pharynx and larynx, while the skin on the back is supplied by a branch of the subclavian artery. In *Xenopus* (Grobbelaar 1924) the large cutaneous artery is present, but it does

not supply a wide region of the skin, as the main part of the skin receives blood through the branches of *a. subclavia*. In *Pelobates fuscus* Laur. and *Bombina bombina* L. the great cutaneous artery is very well developed and supplies the greater part of the skin on the trunk, but does not anastomose with other vessels. Finally in *Bufo bufo* L. and *Rana esculenta* L. the great cutaneous artery supplies the skin with blood and anastomoses through *r. auricularis a. c. m.* with arteries derived from the aorta. The explanation of the functionary significance of this anastomosis is difficult. Owing to its presence the blood from the fourth aortic arch passes to the muscles of the mandibular joint and to the thymus (Szarski 1937). I imagine that this arrangement of vessels points to the fact that the blood in the great cutaneous artery is in some degree oxygenated.

The ventricle of the heart of a salientian receives varying quantities of blood from the right and left auricles. A smaller quantity (according to Acolat (1938) about one-third of the whole amount) of oxygenated blood from the lung comes from the left auricle. The greater part of the blood (according to Acolat about two-thirds) comes from the right auricle. The blood from the right auricle carries however a quantity of oxygenated blood coming from the skin of the body. In the cold season, when the pulmonary respiration is reduced or inhibited, the greater part or even the whole of the oxygenated blood is derived from the skin, and passes to the ventricle through the right auricle.

It has been postulated for a long time that the two streams of blood, from the left and right auricles, do not mix in the ventricle (Brücke 1851, Sabatier 1873 etc.). More recently this fact was confirmed by Noble (1925) during experiments which consisted in injections of Indian ink into the pulmonary vein. Acolat however emphasises (1935, 1938) that two-thirds of the whole blood of the ventricle is received from the right auricle, and the pulmo-cutaneous arches can take in only half of that amount. The second half of the blood from the right auricle and one-third of the total contents of the ventricle must return to the body. Finally, the oxygenated blood from the left auricle which amounts to one-third of the volume of the ventricle, is forced into the systemic and carotid arches. The preceding cir-

cumstances were demonstrated by Acolat with the aid of convincing experiments[1]).

Owing to such functioning of the heart, some quantity of venous blood is received by *a. carotis communis* as well as by the systemic arch, which enables the mucous membrane of the mouth cavity to perform a respiratory function. On the other side owing to the cutaneous respiration and the mixture of the blood from the skin with the blood from the internal organs of the body in the right auricle, a quantity of oxygenated blood is received by the pulmo-cutaneous artery.

All the circumstances described above suggest an explanation of the functional activity of the anastomoses of *r. auricularis a. cutaneae magnae* in *Rana* and *Bufo*. The arteries, deriving from *auricularis a. c. m.*, supply the muscles of the mandibular joint and the thymus. These organs have not an active metabolism and the quantity of oxygen which is present in the great cutaneous artery is sufficient for their needs. Only at the moment of the taking in of food, and especially when the living prey must be firmly held, the mandibular muscles perform a great amount of work and have temporarily a high metabolic rate. Then the flow of blood can take an opposite course, owing to the presence of anastomoses, thus supplying the muscles with a better oxygenated blood from the systemic arch.

The main venous trunks in all species investigated are constructed in a similar manner. Attention is attracted by the variability in the development of *v. pericardiaca dorsalis*. This is very conspicous in the tadpole (*v. laryngea*, Fedorow 1913), where it collects the blood which has no respiratory function from the gill arches. It is present, and easily visible, in *Pelobates* and *Bombina*, very slender in *Bufo* and absent in *Rana*. Another important fact is the presence in *Bombina* of *v. v. cardinales caudales*.

V. jugularis interna has a similar course in all species investigated. The transverse anastomoses, however, which connect this vein with the facial vein vary. In *Pelobates* a large anastomosis runs in the orbital region. It is formed by *v. orbitalis posterior*. The second anastomosis, in the otic region, is slender *(v. infra-*

[1]) Recently Foxon and Walls (1947) stated that there is a considerable mixture of blood in the ventricle of the frog. Even if their conclusions are right they will not disturb the course of following reasoning.

tympanica). In *Rana* only the orbital anastomosis is present. In *Bombina* both anastomoses, orbital and otic are conspicous, in *Bufo* only the otic anastomosis exists, and *v. orbitalis posterior* is absent.

V. jugularis externa is constructed in a similar manner in all *Salientia* except *Rana*. In the majority of forms the external jugular vein is formed by the union of the lingual and faciomandibular veins, the last is formed by *v. mandibularis interna* and *v. facialis*. This pattern can be regarded as primitive as it is found in *Caudata* (Francis 1934) and in tadpoles of all *Salientia* (Goette 1875, Marshall and Bles 1890). From this arrangement *Bombina* diverges in which form a large anastomosis named *v. cutanea magna* runs from the faciomandibular vein to *v. subscapularis*. In *Rana esculenta* L., *R. temporaria* L. and *R. terrestris* Andrz. the facial vein does not open into the external jugular vein but continues caudad as *v. cutanea magna*. Finally in several other species of *Rana*: *R. catesbeiana*, *tigrina*, *cyanophlyctis*, *limnocharis*, *hexadactyla*, *crassa*, *afghana* (Bhaduri 1933, 1938) an intermediary arrangement is found: *v. facialis* continues caudad as *v. cutanea magna*, the primitive connection of this vein with the faciomandibular is however also present in adult specimens.

A small vein in the floor of the mouth *(v. intermuscularis)* is *Pelobates*, *Bombina* and *Bufo*, is remarkable as this vein forms an anastomosis between the right and left external jugular veins, and O'Donoghue (1934) described several cases of abnormalities in *R. temporaria* L. (examples 7—15) consisting in the presence of an identical anastomosis, but was not able to name any species or developmental stage characterized by a regular presence of such anastomosis.

Gaupp first omitted the anastomosis which connects the veins in the region of the elbow-joint in the frog. Later on he noticed his fault and on p. 539 in »*Zusätze und Berichtigungen*« he completed the description, but his correction was usually omitted by readers. Owing to this it is commonly stated that *Salientia* lack the ulnar anastomosis (Van Gelderen 1933). We see that this is not true. In *Salientia*, as in *Caudata* (Francis 1934) and *Reptilia* (Grodziński 1934) the veins of the fore-arm are connected in the ulnar region. In every species investigated however the course of *v. anastomotica cubitalis* is different.

The arrangement of the cutaneous veins varies greatly in different species. *V. cutanea magna* in the fire-bellied toad differs completely from that in other species, as it opens not into *v. subclavia*, but into *v. subscapularis*. In the spade-foot toad and in the common toad, the large cutaneous vein collects the blood only from the skin of the trunk. In the European species of *Rana* the large cutaneous vein begins in the head as facial vein, runs a long distance caudad, bends in a curve, and after a craniad course enters the subclavian vein. So on the under surface of the skin the characteristic loop is formed, which in American and Asiatic species is connected with the faciomandibular vein.

The explanation of the functional significance of the large cutaneous vein is difficult. Seemingly its strong development corresponds to the cutaneous respiration. Often such opinions are found in the literature. But it ought to be remembered that the large cutaneous vein enters the vein which returns the blood from the thoracic limb, and therefore the blood from the skin, in spite of the presence of the large cutaneous vein immediately gets mixed with the poorly oxygenated blood. I suggest therefore, that the reason for the development of the large cutaneous vein is to be seen in the presence of extensive lymphatic sinuses underlying the skin, which are penetrated by vessels in only a few places.

According to the arrangement of the blood vessels in *Caudata* (Francis 1934) the primitive condition of the veins on the thigh is characterised by the presence of *v. ischiadica* as well as *v. femoralis*. In mammals and birds the ischiadic vein is always absent. In reptiles sometimes both veins are present, sometimes only *v. femoralis* is found. Similar arrangements are found in *Salientia*, where the ischiadic vein is present in the fire-bellied and spade-foot toads, and is absent in the frog and common toad.

Salientia form a comparatively homogenous group and therefore the discussion of their mutual relations was very difficult, especially as our knowledge of the anatomical structure of the various forms was very incomplete. Finally Noble (1922) after a thorough study of the structure of the vertebral column and of the musculature of the thigh, was able to build up a classification founded on a sound base. Further anatomical investigations of *Salientia* may accumulate new evidence for the correctness of Noble's views, or raise doubts.

Recently the skull of *Salientia* has especially attracted the attention of anatomists. The results of recent investigations (Wagner 1934, de Viliers 1935/6, Ramaswami 1936) are in accordance with the classification of Noble. My studies were extended over too small a number of species to have any immediate value for a systematist. It can only be stated that the examination of four species, belonging to four suborders of *Salientia* (the suborder *Amphicoela* was not studied), showed great differences between one species and another in the arrangement of veins in the thoracic limb, in the thigh and in the skin. It is impossible to state now whether these differences are characteristic of whole suborders, or are only features of the species investigated.

12. Summary

Thee blood-vascular system of the edible frog (*R. esculenta* L.) which is usually considered an example of a salientian in reality differs considerably from the structures found in the majority of these animals.

The principal points in which the blood vessels of *R. esculenta* differ from those of the other forms are as follows:

Unequivalency of the right and left systemic arches.

The absence of *a. radiomarginalis.*

The absence of *aorta caudalis.*

The presence of *r. auricularis a. cutaneae magnae.*

The strong development and peculiar course of *v. cutanea magna.*

The absence of *v. ischiadica.*

The absence of *v. caudalis.*

The absence of *v. epigastrica.*

The arrangement of some veins differs between one species and another. The differences are most prominent in the cutaneous veins, in the anastomoses in the region of the elbow-joint and in the veins of the thigh.

In conclusion I have great pleasure in expressing my deep gratitude to Prof. Dr. Z. Grodziński whose kind advice and criticism assisted me in the carrying out of above work. I am also greatly indebted to my friend Dr. W. Juszczyk, who provided the greater part of the animals investigated.

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Badania nad fauną i florą denną Zatoki Gdańskiej dokonane przy użyciu hełmu nurkowego. — Część II. Investigations of the bottom fauna and flora in the Golf of Gdańsk made by using a diving helmet. — Part II.

Mémoire

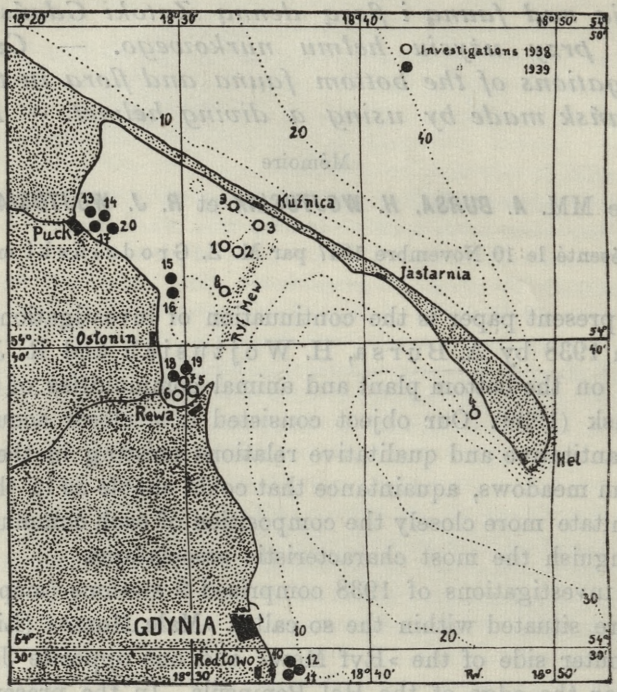
de MM. **A. BURSA, H. WOJTUSIAK** et **R. J. WOJTUSIAK,**

présenté le 10 Novembre 1947 par M. Z. Grodziński m. c.

The present paper is the continuation of investigations undertaken in 1938 by A. Bursa, H. Wojtusiak and R. J. Wojtusiak on the bottom plant and animal communities of the Golf of Gdańsk (1939). Our object consisted in a closer acquaintance with quantitative and qualitative relations existing in the biotope of bottom meadows, aquaintance that could enable us in the future to delimitate more closely the composition of each community and to distinguish the most characteristic associations.

The investigations of 1938 comprised 9 stations (map 1) 8 of which are situated within the so called »Małe Morze« (Little Sea) on the outer side of the »Ryf Mew« and one opposite Jastarnia-Bór, near the edge of the Hel Peninsula. In the present paper we give the results of investigations referring to quantitative floral and faunistic composition of further 11 stations, chosen so as to fill the gabs left in our investigations of 1938. Out of these 11 stations three numbered 10, 11 and 12 are located in the outer part of the Bay, south-east of Gdynia, facing Redłowo, four other stations, numbers 13, 14, 17 and 20, were chosen within the Puck Bay opposite the village Puck and the mouth of the Putnica stream, 2 other stations no 18 and 19 are opposite Rewa, close to the stations 5, 6 and 7 and the two last no 15 and 16 are situated nearly at the half distance between Rewa and Puck. The stations 18 and 19 near Rewa were not unimportant for the comparison of results obtained in 1938 and 1939.

As was the case in former years the investigations were carried out with the aid of a diving helmet system Beebe (1926) which makes it possible to descent to the sea bottom and to collect the whole amount of plant and animal materials from a given area. We had at our disposal two of such helmets, one belonging to the Gdynia Marine Station and another which was our



Map. 1.

own property. In order to be able to work on days when the water was too cold we used a special rubber costume to be donned on our dressing.

The sampling areas were generally 50 cm² marked by a wire frame 50 cm square with coloured strips to make it more visible among the bottom vegetation. According to Gislen (1930) who undertook similar observations with the epibioses of the Gullmar Fjord, an area of 25 cm² accurately analysed is quite sufficient to obtain satisfactory results. The material collected was closed in a pail and brought to the surface. Flower plants and algae

growing on the bottom were then counted as well as sessile or creeping animals. Besides the flora and the fauna gathered from the surface of the sea bottom a sample 3 cm thick of the ground was cut and scrutinized as to its contents in animals. Together with the samples a certain amount of slow swimming animals such as *Isopoda*, *Amphipoda*, insect larvae found eventually their way into our tank and were counted as well. These individuals being only a part of those that entangled into the bottom vegetation were unable to escape, their numbers are given in brackets. Other details referring to our underwater work have been given in our former paper.

In our results, as done formerly the amount of plants and animals are counted for an area of 1 m^2. Plants were counted both in tufts and separate individuals. Counting was done in the same way as in 1938. Numbers referring to the amount of individuals are given in brackets. In numbering animals living in societies we considered groups presenting themselves as units disregarding their size. In *Mytilus edulis* the size was taken in consideration and the individuals divided into 3 groups: those smaller than 5 mm, specimens between 5—15 mm and those whose shell was longer than 15 cm. General quantitative relations of the fauna are illustrated by figures containing all the species of animals observed on the surface of 1 dm^2. Species present on the surface of 1 m^2 in less than 100 individuals are marked as one specimen.

Our last investigations similarly as those of 1938 are to be treated as materials for a final separation of ecological communities of the bottom of the Golf of Gdańsk as well as for general considerations. It is for this reason that throughout our work the term of community designing biotic relations in various stations was given preference to that of association which as an ecological unit may be differentiated only in the future. We had to put up this classification so much more that at the moment which this paper was written the most competent botanist Mr. A. Bursa who could say a great deal in the question of plant associations was absent from our circle.

The investigations necessarily had to limited to summer months and such days on which the sea water in the Golf of Gdańsk was transparent enough for submarine work. This is the case mostly with West and North winds (Demel 1938). The use of

a diving helmet was besides involving other technical difficulties, principally the necessity of a boat or a schooner and adequate personal staff. In this regard we had to reckon with the possibilities of the Marine Station at Gdynia. To prof. M. Bogucki, the director of the Station we are indebted for much aid and facilities. To Dr. K. Demel the vice-director of the Station and to Mr. B. Dixon we owe also much gratitude. To all these gentlemen and the whole personal staff of the Station we express here our heartfull thanks. The general atmosphere preceding the outbreak of the war was far from facilitating our task. The investigations were made possible by a subsidy received from the Ministry of Commerce and Industry by the mediation of the late prof. M. Siedlecki who took a particular interest in our work. It is to the memory of this great man of science and ardent sea-lover, who killed in 1940 in a german concentration camp at Sachsenhausen, did not live as long as to see the publications of work, that we play here our hommage and reverence.

Fig. 1.

This community is characterized by the predominance of *Fucus vesiculosus*, covering in large tufts the stones of the bottom. These brown algae are deprived of floating vesicles, and dominant over other species both by quantity and size with the only exception of *Ceramium diaphanum*. The covering of the bottom with this last species and the algae belonging to the genera *Ceramium, Cladophora*, *Furcellaria* and *Polysiphonia* is complete. The *Fucus* is over grow scarcely by the epiphytic tufts of *Elachista fuciola*. The distribution of the algae on the stones is clearly differentiated. The upper part is covered by *Fucus*, smallar algae, mostly *Furcellaria fastigiata*, occupying the sides immediately above the sea-bottom especially on larger stones (fig. 1).

Station No 10 (1)[1]) located opposite Redłowo. Distance from the shore about 25 m. Temperature 13° C.

Community of *Fucus vesiculosus*.

Material gathered from 0·25 m².

Date	Depth	Character of bottom	Species	Number of individuals per 1 m²
12. VII. 1939	4 m	Rocky	*Fucus vesiculosus* (tufts)	72
a. Plants		bottom	*Furcellaria fastigiata* (tufts)	16
			Cladophora sp.?	12
			Ceramium diaphanum	80
			„ *rubrum*	4
			Polysiphomia nigrescens	16
			General amount of individuals or tufts	200
b. Animals			*Membranipora pilosa* (colonies)	204
			Mytilus edulis length up to 5 mm	1340
			„ „ between 5—15 mm	372
			„ „ above 15 mm	92
			Neritina fluviatilis	204
			Hydrobia sp.?	292
			Planaria	24
			Polychaeta (Pygospio elegans)	64
			Balanus improvisus	52
			(Isopoda)	(968)
			(Amphipoda)	(664)
			General amount of individuals and colonies	2.644
			(Together with those swimming freely)	(4.276)

It is here also that appear the epiphytic rhodophytes. Places between the stones are sometimes covered by fine grained sand with debris. In some places arow scattered tufts of *Zostera nana* free from epiphytes.

Among the animals the mussel *(Mytilus edulis)* show absolute dominance. 1804 individuals appearing per 1 m² make nearly one half of all the noted animals. The greater portion of them 74%, are young individuals less than 5 mm long, the smallest number is made by specimens above 15 mm. Mussels of medium size,

[1]) The numbers of the stations are given in continuation with the year 1938. The running numbers from 1939 are put in brackets.

between 5 and 15 mm make 20.6% of the whole number. Colonies of *Membranipora pilosa*, motile *Neritina fluviatilis* and *Hydrobia* appear much less abundant than the mussels. Among sessile animals the barnacle *(Balanus improvisus)* are the least in number. Among swimming animals there is a great number of *Amphipoda* and *Isopoda*. Between the *Fucus* communities one could notice groups of small fishes which kept almost constantly over the sandy portions of the stony ground avoiding visibly the plant tufts.

Station No 11 (2) located opposite Redłowo.
Community of *Cladophora glaucescens*.
Material gathered from 0·25 m².

Date	Depth	Character of bottom	Species	Number of individuals per 1 m²
13. VII. 1939	0·60 m	Sandy bottom with rich detritus	*Cladophora glaucescens*	692
a. Plants			*Fucus vesiculosus*	4
			Ceramium	4
			General amount of individuals or tufts	700
b. Animals			*Mytilus edulis* length up to 5 mm	160
			„ „ „ between 5-15 mm	37
			„ „ „ above 15 mm	—
			Neritina fluviatilis	284
			Hydrobia sp.?	32
			Cardium edule (small specimens)	652
			Macoma baltica	8
			Polychaeta sedentaria	44
			Nereis diversicolor	64
			Other *Polychaeta*	8
			Planaria	48
			Nemertina	36
			Other *Vermes*	4
			(Isopoda)	(172)
			(Amphipoda)	(7405)
			Larvae of *Chironomidae*	(11206)
			Larvae of other insects	12
			General amount of individuals	1.377
			(Together with those swimming freely)	(20.368)

The shallow waters of this station made it possible to gather the material directly by dipping ones hands, without the use of

a diving helmet. The character of this community is semi-saline and rich in debris. Among plants there is a crushing predominance of green algae of the genus *Cladophora* and a quite unusual poverty of brown algae *(Fucus)* and the red ones *(Ceramium)*.

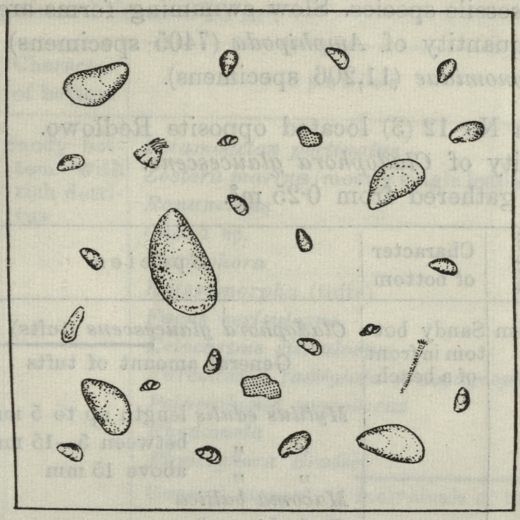


Fig. 2. Station No 10. Amount of bottom animals per 1 dm².

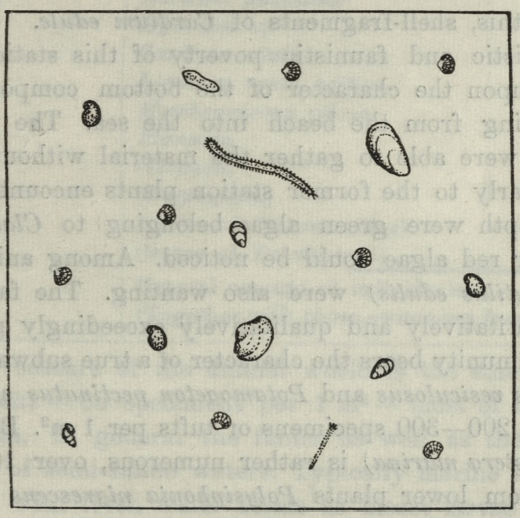


Fig. 3. Station No 11. Amount of bottom animals per 1 dm².

The fauna of this station is characterized by a noticeable poverty of the marine forms. Species such as *Mytilus edulis* and *Cardium*

edule do not grow to the size encountered elsewhere and appear only in small specimens. The lack of larger plants is reflected in the want of sessile species. Slow swimming forms are represented by a large quantity of *Amphipoda* (7405 specimens) and the larvae of *Chironomidae* (11,206 specimens).

Station No 12 (3) located opposite Redłowo.
Community of *Cladophora glaucescens.*
Material gathered from 0·25 m².

Date	Depth	Character of bottom	Species	Number of individuals per 1 m²
14. VII. 1939	0·60 m	Sandy bottom in front of a beach	*Cladophora glaucescens* (tufts)	32
a. Plants			General amount of tufts	32
b. Animals			*Mytilus edulis* length up to 5 mm	16
			„ „ between 5—15 mm	4
			„ „ above 15 mm	—
			Macoma baltica	4
			Hydrobia sp.?	60
			Polychaeta	4
			General amount of individuals	88

Besides this, shell-fragments of *Cardium edule.*

The floristic and faunistic poverty of this station is clearly dependant upon the character of the bottom composed of mere sand extending from the beach into the sea. The water being shallow we were able to gather the material without the diving outfit. Similarly to the former station plants encountered here at the same depth were green algae belonging to *Cladophora* but no brown or red algae could be noticed. Among animals, larger mussels *(Mytilus edulis)* were also wanting. The fauna is here besides quantitatively and qualitatively exceedingly poor.

This community bears the character of a true subwater meadow, where *Fucus vesiculosus* and *Potamogeton pectinatus* are dominant appearing in 200—300 specimens or tufts per 1 m². Besides these, eelgrass *(Zostera marina)* is rather numerous, over 100 tufts per 1 m², and from lower plants *Polysiphonia nigrescens* and *Furcellaria fastigiata.* Other species of algae appear in quantities below 50 tufts per 1 m². The presence of *Ranunculus* points to a semi-saline character of this station.

Station 13 (4) near Puck, past Beka.
Communities of *Fucus vesiculosus* and *Potamogeton pectinatus*.
Material gathered from 0·25 m².

Date	Depth	Character of bottom	Species	Number of individuals per 1 m²
19. VII. 1939	3 m	Sandy bottom with rich detritus	*Potamogeton pectinatus*	224
a. Plants			*Zostera marina* (mostly single leaflets)	160
			Ranunculus	4
			Chara sp.	12
			Cladophora	4
			Enteromorpha (tufts)	20
			Fucus vesiculosus	352
			Ectocarpus siliculosus	28
			Furcellaria fastigiata f. aegagrophila	108
			Polysiphonia nigrescens	128
			Rhodomela	8
			Phyllophora Brodiei	36
			General amount of individuals or tufts	1.084
b. Animals			*Mytilus edulis* length up to 5 mm	8
			„ „ between 5—15 mm	32
			„ „ above 15 mm	28
			Neritina fluviatilis	36
			Hydrobia sp.	436
			Cardium edule	28
			Limnaea ovata baltica	12
			Membranipora pilosa	264
			Planaria	44
			(Isopoda)	(68)
			(Amphipoda)	(148)
			(larvae of *Chironomidae*)	(80)
			(larvae of *Trichoptera*)	4
			General amount of individuals	892
			(Together with those swimming freely)	(1.188)

A striking feature of the animal world is the small quantity of *Mytilus edulis* — 68 specimens per 1 m² — most of them being of medium size. In general the fauna as well as the flora has the character of semi-saline waters. Typically marine species appear together with fresh water forms as insect larvae and especially *Chironomidae* and *Trichoptera*.

The floristic and faunistic composition of this station ressembles that of the former. The ressemblance is explained by the

small distance separating one from another and a similar character of the bottom. The differences lie rather in the quantitative

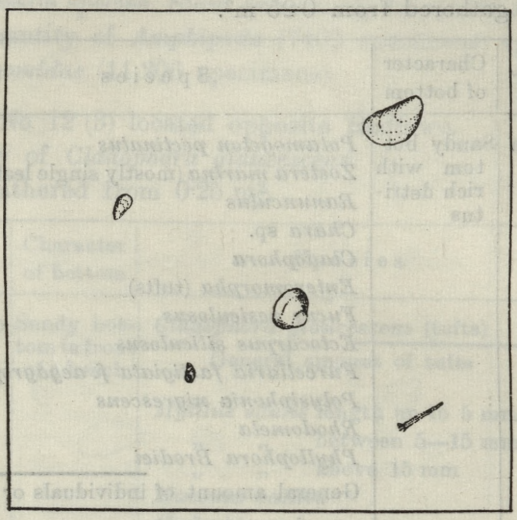


Fig. 4. Station No 12. Amount of bottom animals per 1 dm².

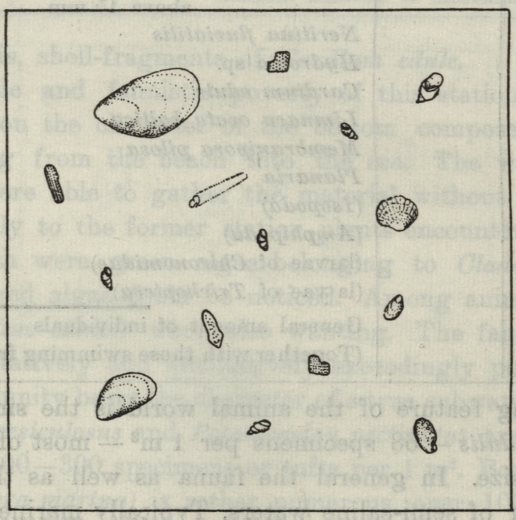


Fig. 5. Station No 13. Amount of bottom animals per 1 dm².

relations of the various species, though in general *Fucus vesiculosus* f. *baltica*, *Potamogeton pectinatus* and the genus *Furcellaria*

Station No 14 (5) near Puck, past Beka, near the station 13 (4).

Communities of *Zostera marina*, *Fucus vesiculosus* and *Potamogeton pectinatus*.

Material gathered from 0·25 m².

Date	Depth	Character of bottom	Species	Number of individuals per 1 m²
19. VII. 1939 a. Plants	3·50 m	Sandy bottom with humus	*Potamogeton pectinatus*	124
			Zostera marina	96
			Enteromorpha clathrata	72
			Fucus vesiculosus f. *baltica* (small specimens)	624
			Ectocarpus siliculosus	44
			Furcellaria fastigiata	333
			Polysiphonia nigrescens	4
			Phyllophora Brodiei	188
			General amount of individuals or tufts	1.485
b. Animals			*Mytilus edulis* length up to 5 mm	12
			„ „ between 5 – 15 mm	72
			„ „ above 15 mm	36
			Neritina fluviatilis	912
			Hydrobia sp.	488
			Cardium edule	92
			Membranipora pilosa	332
			Laomedea flexuosa	4
			Planaria	80
			(Isopoda)	(88)
			(Amphipoda)	(288)
			Polychaeta sedentaria	20
			(larvae of *Chironomidae)*	(100)
			General amount of individuals and colonies	2.048
			(Together with those swimming freely)	(2.524)

are also clearly dominant here and *Zostera marina* is also present. The vegetation is nearly by $^1/_3$ more dense than in the former station. The fauna also is quantitatively twice as rich as that of the former. The mussels are represented equally by specimens of medium size.

The submarine meadows of this station resemble by their general appearance those of the stations 13 and 14. This resemblance is expressed both in quantitative and qualitative flo-

Station No 15 (6) located opposite Osłonin.
Communities of *Fucus vesiculosus* and *Potamogeton pectinatus.*
Material gathered from 0·25 m².

Date	Depth	Character of bottom	Species	Number of individuals per 1 m²
28. VII. 1939	4 m	Sandy	*Potamogeton pectinalus*	40
a. Plants		bottom	*Cladophora* sp.	236
			Fucus vesiculosus f. *baltica* (small tufts)	724
			Pillayella littoralis	20
			Furcellaria fastigiata	316
			„ „ f. *aegagropila*	8
			Polysiphonia violacea	44
			Ahnfeltia plicata	8
			Phyllophora Brodiei	16
			General amount of individuals or tufts	1.412
Besides are to be noticed numerous debris of *Potamogeton* and *Zostera.*				
b. Animals			*Mytilus edulis* length up to 5 mm	20
			„ „ between 5—15 mm	156
			„ „ above 15 mm	56
			Neritina fluviatilis	1432
			Hydrobia sp.	492
			Cardium edule	116
			Macoma baltica	40
			Mebranipora pilosa	300
			Limnaea sp.	12
			Polychaeta sedentaria	92
			Other *Polychaeta*	64
			(Isopoda)	(116)
			(Amphipoda)	(276)
			Planaria	116
			(Hirudineae, Piscicola)	(16)
			(larvae of red *Chironomidae*)	(428)
			(larvae of other insects incusively other *Nematocera*)	(56)
			General amount of individuals and colonies	2.780
			(Together with those swimming freely)	(3.888)

ristic and faunistic composition. Some slight differences exist in the quantitative relations of the separate species. *Zostera marina* does not grow on the spot but must occur in the vicinity as can be inferred from debris found in the water.

The animal world is more diversified in forms and quantitatively richer. A striking feature may be found also in the rela-

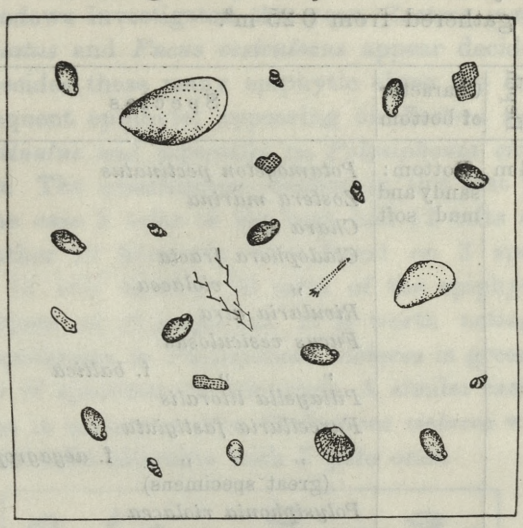


Fig. 6. Station No 14. Amount of bottom animals per 1 dm².

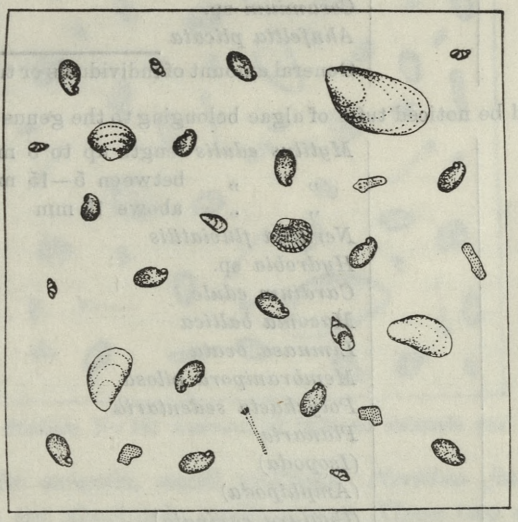


Fig. 7. Station No 15. Amount of bottom animals per 1 dm².

tively greater number of insect larvae especially those of gnats. Among mussels *(Mytilus edulis)* medium sized individuals are dominant.

Station No 16 (7) located opposite Osłonin.
Community of *Fucus—Potamogeton—Zostera.*
Material gathered from 0·25 m².

Date	Depth	Character of bottom	Species	Number of individuals per 1 m²
28. VII. 1939	4 m	Bottom: sandy and mud soft	*Potamogeton pectinatus*	300
a. Plants			*Zostera marina*	188
			Chara sp.	28
			Cladophora fracta	64
			„ *violacea*	48
			Rivularia atra	164
			Fucus vesiculosus	292
			„ „ f. *baltica*	152
			Pillayella litoralis	144
			Furcellaria fastigiata	68
			„ „ f. *aegagropila* (great specimens)	4
			Polysiphonia violacea	172
			„ *nigrescens*	124
			Phyllophora Brodiei	132
			Ceramium sp.	4
			Ahnfeltia plicata	36
			General amount of individuals or tufts	1.916
Besides could be noticed tufts of algae belonging to the genus *Spirogyra* sp.				
b. Animals			*Mytilus edulis* length up to 5 mm	—
			„ „ between 5—15 mm	62
			„ „ abowe 15 mm	100
			Neritina fluviatilis	1664
			Hydrobia sp.	1920
			Cardium edule	484
			Macoma baltica	32
			Limnaea ovata	12
			Membranipora pilosa	916
			Polychaeta sedentaria	80
			Planaria	48
			(Isopoda)	(40)
			(Amphipoda)	(268)
			(Cyatura carinata)	(12)
			(black cocons gen.? sp.?)	(44)
			General amount of individuals and colonies	5.362
			(Together with those swimming freely)	(5.682)

The submarine meadows of this station is floristically and faunistically both in quantitative and qualitative respect the richest of all the meadows investigated this year. *Zostera marina*, *Potamogeton pectinatus* and *Fucus vesiculosus* appear decidedly dominant here. Besides these many epiphytic algae are encountered. The most frequent epiphyte, appearing on *Zostera marina*, *Potamogeton pectinatus* and especially on *Polysiphonia violacea* — is *Rivularia atra*. The quantitative relation in this last plant is as follows: in one case 2 tufts of the host had 11 tufts of the epiphyte, in another 15 *Rivularia* were found on 3 specimens of *Polysiphonia*, in still another 20 tufts of the epiphyte covered 1 single specimen of *Polysiphonia*. It is worth noting that the majority of specimens in *Polysiphonia violacea* is green in colour, but a number of specimens is colourless. A similar case of colourless specimens is encountered in *Cladophora violacea* where 5 normally coloured tufts alternate with 7 pale ones.

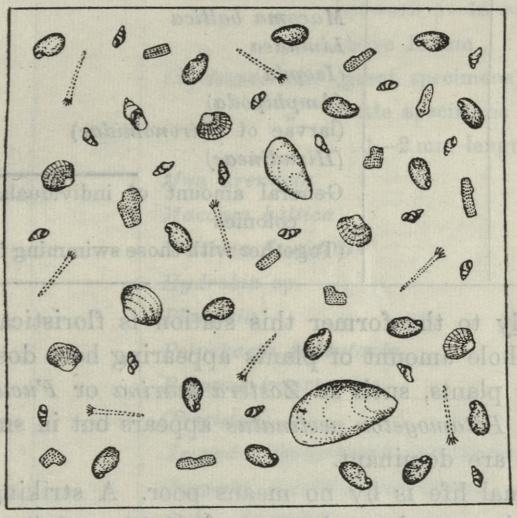


Fig. 8. Station No 16. Amount of bottom animals per 1 dm^2.

Among the animals, small molluscs: *Neritina fluviatilis* and *Hydrobia* sp. are absolutely predominant. These two species constitute the half of the whole amount of animal organisms found at this station. Mussels (*Mytilus edulis*) are present mostly in large specimens (above 15 mm). The young ones are competely wanting.

Station No 17 (8) near Puck.
Community of *Potamogeton pectinatus.*
Material gathered from 0·25 m².

Date	Depth	Character of bottom	Species	Number of individuals per 1 m²
28. VII. 1939	3 m	Botom: soft mud with very rich detritus	*Potamogeton pectinatus* (tufts)	52
a. Plants			*Cladophora fracta*	4
			Rivularia atra	56
			Sphacellaria cirrhosa	4
			Furcellaria fastigiata f. *aegagropila*	4
			Ceramium sp.	4
			General amount of individuals or tufts	124
b. Animals			*Membranipora pilosa*	188
			Hydrobia sp.	1484
			Neritina fluviatilis	304
			Cardium edule	500
			Macoma baltica	8
			Limnaea	28
			(Isopda)	(4)
			(Amphipoda)	(84)
			(larvae of *Chironomidae*)	(52)
			(Hirudineae)	(4)
			General amount of individuals and colonies	2.512
			(Together with those swimming freely)	(2.656)

Contrarily to the former this station is floristically the poorest. The whole amount of plants appearing here does not exceed 124. Larger plants, such as *Zostera marina* or *Fucus vesiculosus* are wanting. *Potamogeton pectinatus* appears but in small quantity. Small algae are dominant.

The animal life is by no means poor. A striking feature of the list is the complete absence of *Mytilus edulis.* Small sized molluscs have an absolute predominance. The branches of *Potamogeton pectinatus* are covered by *Membranipora pilosa.*

This station is located about 400 m from Rewa in the direction of Gdynia. The bottom is sandy, covered on the meadows with a brown »dust« of diatoms. Between the narrow stones covered with *Chara*, there are tufts of eelgrass *(Zostera marina).*

Station 18 (9) located opposite Rewa.

Community of *Zostera marina* and *Chara delicatula* f. *verrucosa*.

Material gathered from 0·25 m².

Date	Depth	Character of bottom	Species	Number of individuals per 1 m²
29. VII. 1939	3·20 m	Sandy	*Zostera marina*	472
a. Plants		bottom	*Chara delicatula* f. *verrucosa*	408
			Tolypella nidifica f. *condensata*	64
			Ceramium rubrum	± 24
			„ sp.	±176
			Polysiphonia violacea	± 20
			General amount of individuals or tufts	1.164
b. Animals				
			Membranipora pilosa	512
			Mytilus edulis length up to 5 mm	1364
			„ „ between 5—15 mm	4036
			„ „ above 15 mm	576
			Cardium edule (great specimens)	60
			„ „ (little specimens 1—2 mm length)	152
			Mya arenaria	68
			Macoma baltica	56
			Neritina fluviatilis	28
			Hydrobia sp.	116
			Planaria	8
			Polychaeta sedentaria	364
			Balanus improvisus	72
			(Piscicola)	(40)
			(Isopoda, Sphaeroma rugicauda)	(100)
			(Isopoda, Cyathura carinata)	(32)
			(Other *Isopoda*)	(132)
			(Amphipoda)	(356)
			(larvae of *Chironomidae*)	(124)
			(caterpillars of *Acentropus niveus*, *Lepid.*)	(4)
			General amount of individuals and colonies	7.404
			(Together with those swimming freely)	(8.200)

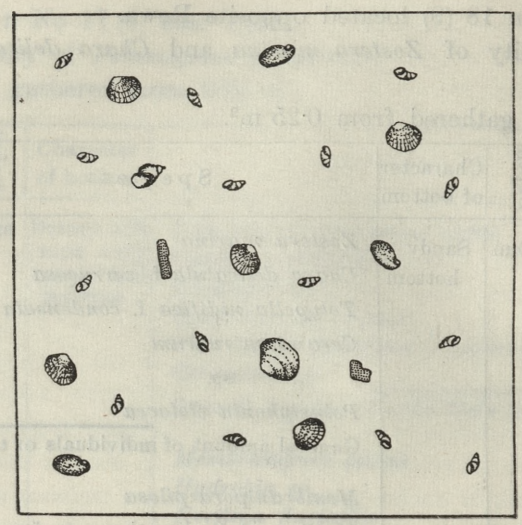


Fig. 9. Station No 17. Amount of bottom animals per 1 dm².

Outside the meadows the bottom is covered with light sand with *Mya arenaria*.

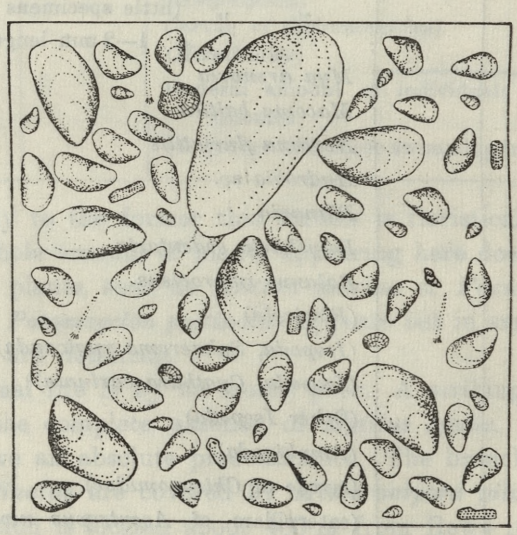


Fig. 10. Station No 18. Amount of bottom animals per 1 dm².

The characteristic components of these submarine meadows *Zostera marina* and *Chara delicatula* f. *verrucosa* are, absolutely

dominant over the algae mostly epiphytic. Quantitatively these meadows count among the rich ones within the »Little Sea«. The fauna of this community is rich both from the qualitative and quantitative point of view. Mussels *(Mytilus edulis)* are absolutely dominant with about 6.000 individuals upon the total of 7.404 animal forms connected with the ground. The semi-saline character of these parts is emphasized by the presence of insect larvae. Their number is however much smaller than is the case in some

Station No 19 (10) located opposite Rewa (close to station 9
Community of *Chara delicatula.*
Material gathered from 0·25 m².

Date	Depth	Character of bottom	Species	Number of individuals per 1 m²
29. VII. 1939	3·20 m	Sandy	*Chara delicatula* f. *verrucosa*	444
a. Plants		bottom	*Tolypella nidifica*	396
			Cladophora sp.	84
			Pilayella litoralis	8
			General amount of individuals or tufts	932
b. Animals			*Mytilus edulis* length up to 5 mm	32
			„ „ between 5—15 mm	24
			„ „ above 15 mm	8
			Cardium edule (very small specimens 1—2 mm length)	20476
			Macoma baltica	4
			Limnaea sp.	8
			Neritina fluviatilis	32
			Hydrobia sp.	56
			Mebranipora pilosa	56
			Balanus improvisus	8
			Polychaeta sedentaria	1196
			Nereis diversicolor	28
			Nemertina	4
			(Hirudineae, Piscicola)	(44)
			(Isopoda)	(116)
			(Amphipoda).	(172)
			(larvae of *Chironomidae*)	(648)
			General amount of individuals and colonies	21.932
			(Together with those swimming freely)	(22.912)

stations discussed above. A fact worth noting is the occurence of caterpillars *Acentropus niveus* Oliv. a butterfly belonging to the family *Pyralidae*. This species, as we had shown formerly (Wojtusiak 1931) lives as caterpillar among te leaves of *Zostera marina* and contrarily to the opinion emitted by Zerny and Bayer (1936) represents the only species of butterfly living in semi-saline marine waters (Remane 1940).

From the floristio point of view and quantitatively, this community located some 400 m from the shore, near the station 18 (9), is rather poor. The subaqueous meadow is characterized by

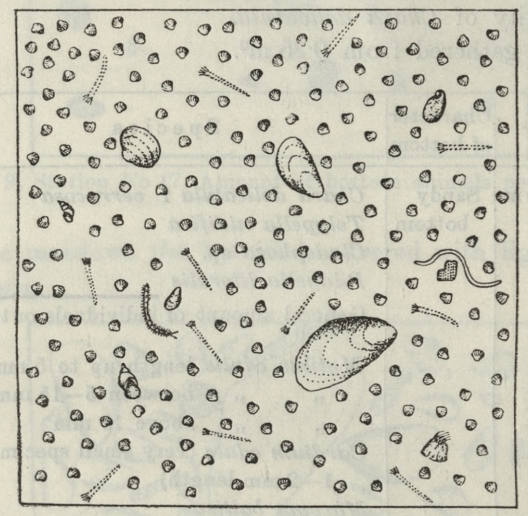


Fig. 11. Statiou No 19. Amount of bottom animals per 1 dm².

Chara delicatula f. *verrucosa* which is absolutely dominant. This last species is almost quantitatively equalled by *Tolypella nidifica*. Other algae appear in very scarce quantity.

The quantitative composition of the fauna in this community is pretty rich. Quantitatively the station shows a great superiority over other stations. The most striking feature is the unusual number of *Cardium edule*, ten times more abundant than all other animal forms taken together. The specimens of this species, it is true, are all very young 1—2 mm long sticking in masses to the branches of *Chara delicatula*. It looks as if *Chara* were the multiplying centre of the cochle. It seems highly probable that *Chara delicatula* has a special pover of attraction for the larvae of these

molluscs, which settle upon its branches, giving rise to little cardia, whose quantity given by us is rather too small than too high. The next place, what regards quantity is taken by *Polychaeta sedentaria* building the sandy tubes and belonging probably to the species *Pygospio elegans*. Other species of sessile or bottom dwelling animals appear nowhere in more than 56 spe-

Station 20 (11) near the mouth of the Putnica river.
Community of *Fucus vesiculosus*.
Material gathered from 0·25 m².

Date	Depth	Character of bottom	Species	Number of individuals per 1 m²
29. VII. 1939	3·80 m	Sandy	*Zanichellia palustris*	4
a. Plants		bottom	*Cladophora glomerata*	12
			Enteromorpha sp.	8
			Fucus vesiculosus f. *baltica*	80
			Pilayella litoralis	40
			General amount of individuals or tufts	144
Besides very numerous debris of *Potamogeton*.				
b. Animals			*Cardium edule*	808
			Macoma baltica (great specimens)	40
			Limnaea ovata	1272
			Hydrobia sp.	4196
			Neritina fluviatilis	1240
			Membranipora pilosa	180
			Polychaeta sedenteria	20
			(Isopoda)	(32)
			(Amphipoda)	(52)
			(larvae of *Chironomidae*)	(8)
			General amount of individuals and colonies	7.756
			(Together with those swimming freely)	(7.848)

cimens per 1 m². Only slow swimming animals, mostly crustaceans belonging to the group of *Amphipoda* and *Isopoda* and the larvae of *Nematocera* appear in more than 100 specimens.

The flora of this meadow is quantitatively and qualitatively poor. *Fucus vesiculosus* f. *baltica* is dominant. Other algae are much less abundant and because of their size easier to overlook. In the water, the great number of *Potamogeton* debris, brought

from the adjacent subaqueous meadows of another type is highly characteristic.

The fauna of this station qualitatively rather poor consists mostly of smaller snails *Hydrobia, Neritina fluviatilis* and *Limnaea*

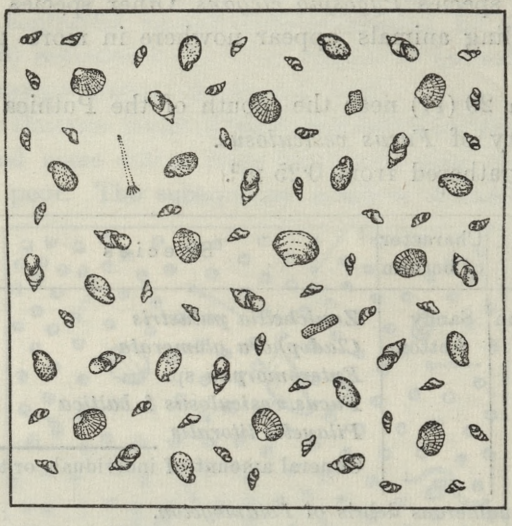


Fig. 12. Station No 20. Amount of bottom animals per 1 dm^2.

ovata which quantitatively put this meadow on a par with the rich communities of the former stations. *Mytilus edulis* is quite absent.

Summary of results

The materials of the foregoing studies complete the data referring to the qualitative and quantitative relations in the fauna and flora of the Golf of Gdańsk, gathered in 1938. In both of these investigations the diving helmet proved of high efficiency. Owing to this method of work, the sampling can be done directly from the most characteristic spots of the bottom. The material is collected with much more accuracy than it is possible by using of a dredge or bottom sampler. The lowest value for the animals connected strictly with the bottom, obtained in our last investigations was 88 specimens (station 12 (3)), the highest value being 21.932 specimens (station 19 (10)). In other stations the values obtained ranged between 1.768 specimens (station 18) and 38.116 specimens (station 13). These data, though far beyond the

record ciphers of 1938 are still much higher than the data obtained by Mulicki (1938) with the aid of a bottom sampler. In this authors paper the corresponding ciphers range between 16 and 12.868 specimens per 1 m^2.

The differences in quantitative relations presented above do not result only from a different method of work. These differences, besides, reflect also the biocoenic relations at different depths. Our investigations referred to a rather shallow zone from 60 cm — 4 m, Mulicki took samples from a depth of 5 m to 108 m. We may repeat here what we stated already in our former work that shallow well illuminated parts of the Golf of Gdańsk have a much richer flora and fauna than those situated at a greater depth where light conditions are less favourable. This is not only probable but can be even extended to optimal development of the flora in shallow and well illuminated waters. The fact was established formerly mostly for waters of the Puck Bay, west of the sand-bank Ryf Mew. As our research area comprised in 1939 also some parts of the Golf of Gdańsk situated east of this bank, the fact must be generalized for all submarine shallower waters going as deep as 4 m.

The efficiency of the diving helmet as opposed to the dredge and bottom sampler is still more apparent in the sampling of the flora. This question was discussed more accurately in our former paper and we won't repeat it here. The observations made in 1939 confirmed fully our former conjectures that sampling done directly by the investigator gives better results than can be expected from accidental tufts of less resisting vegetation brought up to the surface by a dredge or a bottom sampler.

Among more interesting discovering details must be mentioned the occurence of *Mya arenaria* in a place opposite Rewa (station 18). By the same our first observations indicating the distribution of this species in our sea as being much wider than accepted by Demel (1935), have been confirmed.

The investigations discussed above show better than it was done ever before, that the subaqueous meadows of our Baltic Sea are qualitatively very differentiated. In 1938 we distinguished following communities dependent from the dominant species of plants: *Fucus vesiculosus* (station 5), *Potamogeton-Zostera* (station 1), *Potamogeton-Ceramium* (station 3), *Ceramium diaphanum* (station 2),

Zostera-Zanichellia (station 4), *Chara-Potagometon* (station 8), *Chara crinita* (station 6 and 7), *Chara baltica* (station 9). Of all these communities that of *Zostera-Zanichellia* is the richest.

In our present studies several other communities have been distinguished, out of which only *Fucus vesiculosus* (station 10 and 20) bears some ressemblance with the *Fucus* community of our former studies. All other communities are different i. e. *Cladophora glaucescens* (stations 11 and 12) from a depth of 60 cm, *Fucus-Potamogeton-Zostera* (stations 13, 14 and 16), *Fucus-Potamogeton* (station 15), *Potamogeton-Rivularia* (station 17), *Zostera-Chara* (station 18), *Chara delicatula* (station 19). The diversity of communities results from the different quantitative appearance of the species. The same species dominant in one community appears less numerous in another or is quite absent. The qualitative floristic composition may be also different in each community.

The differences are easy to perceive when comparing the three communities of *Fucus vesiculosus* from the station 5 (1938) and the station 10 and 20 (1939). In all these three cases *Fucus vesiculosus* is the dominant species. Yet each of the three communities shows another set of accompanying species of plants. The greatest qualitative variety is met with in station 5 where *Fucus vesiculosus* is accompanied by no less than 11 other species of plants. In stations 10 and 20, the dominant species is accompanied only by 4 to 5 other species, none of which is common to both stations. These differences cannot be explained by bathymetric conditions, the samples of the three stations being taken at nearly the same depth, those of stations 5 and 10—4 m, samples of station 20 at 3·80 m. The character of the bottom may be of some consequence. In stations 5 and 20 the bottom was sand, in station 10 stony on a sandy ground. The only markable difference between the stations was the distance between them and their topographic situation. The station 20 is located inside the Puck Bay, at the mouth of the Putnica stream where the admixture of fresh water is rather considerable, station 10 is located south-east of Gdynia, not far from the shore yet its waters are more open sea waters, station 5 is situated in the mid-way between the two former stations. It is possible that we have to deal in these stations with various aspects of the same community.

As mentioned in the introduction we do not intend to undertake a close analysis of sociological and floristic relations existing in subaqueous meadows of the Polish Baltic Sea. The afore said diversity of communities requires further materials before any general conclusions can be drawn and the communities would be set apart with more precision. All we wanted was to try a general grouping of communities according to dominant species as we have done it with *Fucus vesiculosus*.

One of such groups may be *Cladophora glaucescens* shown in two stations 11 and 12 from a depth of 60 cm. In some specially favourable spots this dominant is accompanied by rare tufts of *Fucus vesiculosus* and *Ceramium*. In other more barren places *Cladophora* appears alone in scarce quantity.

Some communities with dominant *Potamogeton pectinatus*, *Zostera marina* and *Fucus vesiculosus*, met with in stations 3, 4, 13, 14 and 16 have probably the character of associations. These plants from rich submarine meadows in which however the quantitative relation of the components varies from one station to another, constituting a short of facies as understood by Shelford (1935). On one side we see clearly predominating *Potamogeton pectinatus*, *Zostera marina* in a lesser degree and *Fucus vesiculosus* as addition (station 3). Another extreme is the community with dominant *Fucus vesiculosus* while *Potamogeton* and *Zostera* remain on the second plan (stations 13, 14, 16). Occasionally one of the chief components may be wanting, as f. ex. *Zostera marina* in station 15. In this latter case we have a sort of passage between the meadow community with *Potamogeton* and *Zostera* (station 1) and the community with *Fucus vesiculosus* (station 17 and stations 5, 10 and 20, discussed above). A gradual disappearance of *Potamogeton* and *Fucus* leads to communities with predominating *Zostera marina*, which may be accompanied then by other species as f. i. *Chara* (station 18). *Potamogeton* forms also with *Chara* a separate community. Where the caracteristic species disappears a pure *Chara* community is formed, composed either of *Ch. delicatula* (station 19) or *Ch. baltica* (station 9). These four plant communities have been already separated by Demel (1926) in his study of the Benthic Fauna of the Polish Baltic and their distribution range drawn on map for the first time. As it appears now between these extremes exist a number

of passages and combinations whose closer analysis must be reserved for the future when a more abundant material will be available and the whole question taken up by a plant sociologist.

What regards the fauna, the investigations made so far establish a certain correlation between the quantitative and qualitative abundance of animal life and the plant communities. The richest fauna appears in communities in which *Zostera marina* and *Potamogeton pectinatus* are clearly dominant. The following stations may serve as instances: no 4 — *Zostera-Zanichellia* (38.116 specimens), no 3 — *Potamogeton-Ceramium* (17.716 specimens), no 8 — *Chara-Potamogeton* (9.627 specimens), no 18 — *Zostera-Chara* (7.404 specimens), no 16 — *Zostera marina* (5.362 specimens). The second place must be given to the community of *Fucus vesiculosus* from the station 19 (21.932 specimens). The first of them is, as mentioned above, an exception among other *Fucus vesiculosus* communities of which the one (station 10) has 2.644 specimens and another (station 5) 3.136 specimens. The seeming large quantity of specimens in the communities of *Chara delicatula* is to be explained by the presence of minute *Cardium edule*. Without these latter the quantity of all other species of animals would be reduced to 1.456 specimens.

In other communities in which various species of the genus *Chara* predominate the ciphers range between 1.768 (station no 9) and 3.276 (station no 7). The least abundant are the shallow water communities with predominance of *Cladophora* from the stations 11 and 12 (80 — 1.377 specimens). Places having a richer vegetation show a greater quantity and more variety in their fauna composition (station 12). This correlation between fauna and flora seems to be a general rule at our coast though it does not appear always so strongly marked as in the community *Cladophora*. The submarine meadows form at any rate the very base for the development of animal life similarly as is the case with vegetation on land.

The qualitative composition of the bottom fauna in the Golf of Gdańsk depends upon the degree of salinity of the water and the character of the ground. As it was emphasized while discussing the separate stations, a relatively large admixture of brackish and fresh water forms, especially the larvae of caddis-flies, *Chironomidae* and snails of the genus *Limnaea* are met with near the mouth of the rivers. These relations agree perfectly with the statements by

Demel (1935). The greatest abundance of forms is found in submarine meadows growing on a sandy bottom, eventually with a detritus admixture. On a muddy bottom where decomposition processes take place, the number of animal species is distinctly lower.

A detailed zoological characteristic of the communities was given above at each station. Other general conclusions must be postponed till the moment when further investigations will bring a more abundant material.

(From: The Polish Marine Biological Station in Gdynia, the Department of Psychology and Ethology of Animals, Jagellonian University and the Museum of Natural History of the Polish Academy of Sciences in Cracow).

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Naczynia krwionośne mięśni tułowiowych u pstrąga tęczowego (Salmo irideus Gibb.) — Les vaisseaux sanguins des muscles du tronc de la truite (Salmo irideus Gibb.)

Mémoire

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présenté le 10 Novembre 1947 par M. Z. Grodziński m. c.

Introduction

On peut distinguer chez les poissons les vaisseaux sanguins longitudinaux, qui conduisent le sang le long d'un axe longitudinal et les vaisseaux latéraux, qui partent des précédents et qui fournissent le sang à toutes les parties du corps en le conduisant de nouveaux aux vaisseaux longitudinaux (Grodziński). Les aortes et les veines principales *(vv. cardinales)* appartiennent au premier groupe et les vaisseaux segmentaires (les veines et les artères) au second groupe. L'aorte chez *Teleostei* passe au-dessous de la colonne vertébrale et se colle si étroitement aux vertèbres, qu'elle acquiert une forme ondulée. Elle porte le nom de la partie du corps qu'elle traverse, *Aorta dorsalis* et *A. caudalis.*

Les veines principales se divisent en veines principales antérieures *(vv. cardinales anteriores)* et les veines principales postérieures *(vv. cardinales posteriores).* Ces veines se rencontrent dans la région du coeur et elles forment ensemble le *Ductus Cuvieri,* par lequel elles se jettent dans le coeur. Les veines principales postérieures passent de deux côtes de l'aorte. Il est rare chez les poissons Téléostéens que ces deux veines aient la même grosseur; d'ordinaire la dimension de la veine droite surpasse celle de la gauche.

Le système des vaisseaux segmentaires chez *Teleostei* comme chez les autres poissons correspond à une construction métamérique du corps. Ces vaisseaux passent par les myoseptes, qui divisent les muscles en myotomes. On peut distinguer trois grou-

pes de vaisseaux segmentaires, à savoir latéraux, dorsaux et ventraux. Les vaisseaux segmentaires partent des vaisseaux principaux longitudinaux (l'aorte et *vv. cardinales*). Les vaisseaux segmentaires latéraux passent par le myosepte horizontal, qui sépare les muscles latéro-dorsaux des muscles latéro-ventraux. Les vaisseaux segmentaires dorsaux se dirigent vers le haut en longeant le myosepte primaire, qui divise les myomères et ils touchent en son milieu le squelette axial. Les vaisseaux segmentaires ventraux gagnent les viscères par la voie la plus courte. Les capillaires sanguins chez les poissons ont été peu étudiés jusqu'à présent.

Le but de ce travail est de décrire les principaux vaisseaux sanguins des muscles du tronc de la truite (*Salmo irideus* Gibb.), de montrer comment les capillaires sanguins se ramifient dans les muscles et de les énumérer.

Les truites qui ont été examinées provenaient d'un élevage de Ojców. On a choisi les truites du sexe masculin, de 20 à 25 cm de longueur. On a injecté dans les vaisseaux sanguins soit de l'encre de Chine soit une solution aqueuse de bleu de Prusse et de gomme laque rouge. Après une fixation au formol et un éclaircissement à la glycérine on a préparé les fragments choisis du corps des poissons sous la loupe binoculaire. On a fait des sections transversales des muscles aussi sur le microtome, de 18 microns d'épaisseur. Ces coupes étaient colorées par la méthode van Gieson et elles ont servi ensuite à des recherches microscopiques sur les rapports entre les faisceaux de muscles du squelette et les capillaires sanguins.

Le système musculaire

La distribution des vaisseaux sanguins et capillaires dépend en majorité de la configuration des muscles et du squelette.

On voit chez la truite (*Salmo irideus* Gibb.) sous la peau, en trois endroits, des muscles superficiels plats. La continuité de leurs fibres n'est rompue par aucun myosepte (Fig. 1 Ms). Le plus important de ces muscles est le muscle latéral droit (*Musculus rectus lateralis*, Fig. 1, 3 Ml), qui se trouve au milieu du flanc du tronc, dans un creux correspondant au myosepte horizontal (Fig. 1 Sh). La ligne médiane du dos est parcourue par le muscle dorsal droit (*Musculus rectus dorsalis*, Fig. 1 Md), séparé longitudinalement par un myosepte sagittal en un muscle droit et un

muscle gauche. Le milieu du ventre est occupé par le muscle ventral droit (*Musculus rectus ventralis*, Fig. 1 Mv).

Après l'écartement des muscles superficiels on voit les muscles proprement axiaux (Fig. 1 Msb, Msp). Le myosepte horizontal les divise en muscles latéro-dorsaux et latéro-ventraux. Un certain nombre de myoseptes transversaux divisent les muscles axiaux en myomères. Le bord extérieur des myoseptes transversaux passe en zigzag à travers les muscles, en formant une lettre »W«, ayant ses branches latérales largement ouvertes vers la tête (Fig. 1). Les faisceaux de fibres musculaires striées passent dans les myomères parallèlement à l'axe longitudinal du corps, et ce n'est que dans la partie abdominale qu'ils passent obliquement de la tête à la partie inférieure de la queue. En se basant sur ce parcours des fibres musculaires striées on peut distinguer le muscle parietal (*Musculus parietalis*) et le muscle oblique (*Musculus obliquus*).

Les muscles du tronc possèdent deux sortes de faisceaux de fibres striées, les uns sont épais (la surface de leur coupe transversale a de 3200 à 7000 μ carrés), les autres sont plus minces (la surface d'une coupe transversale a de 314 jusqu' aux 706 μ carrés). On voit très nettement cette différence sur leurs coupes microscopiques. Le nombre moyen des faisceaux épais (moyenne de 5 coupes) vus sur une superficie de 1 mm^2 est 182 et celui des faisceaux minces de 584.

Les fibres striées groupées dans les faisceaux minces forment le muscle superficiel latéral droit. Le muscle superficiel dorsal droit se compose de faisceaux un peu plus épais, mais leur mesure n'atteint pas celle des faisceaux des autres muscles axiaux. Ce n'est que dans les muscles moteurs du globe de l'oeil que les faisceaux minces se trouvent près de faisceaux épais.

Le système des troncs vasculaires de la Truite

A. Les vaisseaux longitudinaux

L'aorte (Fig. 1 Am) et la veine cardinale postérieure (*V. cardinalis posterior*, Fig. 1 Vcp) appartiennent aux vaisseaux longidinaux principaux du tronc. Elles ont été déja plusieurs fois décrites chez la Truite et d'autres poissons Téléostéens.

Outre ces vaissaux il y a encore dans la paroi du tronc de vaisseaux longitudinaux secondaires, à savoir une grande veine

abdominale (*Vena abdominalis*, Fig. 1, 2 et 3 Vab) passant dans la ligne médiane du ventre, très près de la peau et *A.* et V. *epigastricae* (Fig. 1, 2 et 3 AVe) situées latéralement très près et au-dessous du péritoine.

L'aorte du tronc est un vaisseau impair. Elle est située entre la colonne vertébrale et la surface dorsale du rein. Dans la partie caudale elle se prolonge en une artère caudale (*A. caudalis*). La veine caudale dans la queue accompagne l'artère du même nom. A l'entrée de la cavité abdominale elle pénètre le rein droit et atteint le coeur comme *V. cardinalis posterior dextra.* De la veine principale postérieure gauche ne reste qu'une trace sous la forme d'un segment cardial de cette veine.

Aa. et *Vv. epigastricae* unissent la région de la ceinture pectorale à la région pelvienne. Elles longent les deux côtés du tronc, entre le péritoine (Fig. 1, 3 AVe) et les muscles du bord dorsal du *Musculus rectus abdominalis.* Leurs parois se touchent en de nombreux points. Leur parcours, aussi bien des artères que des veines est onduleux. *V. epigastrica* dans son trajet est plus grosse que l'artère du même nom. Chez quelques individus cette différence est très nette. Les deux vaisseaux s'éloignent dans la région de la ceinture pectorale de la ligne médiane du ventre en se dirigeant vers les nageoires pectorales où ils s'unissent à leur base à l'*A.* et *V. subclavia* (Fig. 3). Les segments postérieurs de ces vaisseaux ont leurs branches dans les muscles de la ceinture pelvienne. *Vv. epigastricae* s'unissent, aussi par des branches transversales à l'axe du corps, avec *V. abdominalis.* Les plus nettes anastomoses sont visibles dans la région des nageoires ventrales et dans le milieu du tronc. *Aa.* et *Vv. epigastricae* s'unissent aussi directement avec *Aa.* et *Vv. intercostables* et aux *Aa.* et *Vv. intersegmentales ventrales*, au moyen de capilaires sanguins.

V. abdominalis (Fig. 1, 2 et 3 Vab) se place dans la ligne médiane du ventre entre le bord interne des deux muscles droits, en touchant étroitement la peau. Elle se comporte comme un vaisseau impair. Dans la région des nageoires pectorales tout près de leur base ainsi qu'au milieu de la longueur du tronc, entre la ceinture pectorale et pelvienne, elle s'approche nettement du péritoine et là s'unissent à elle les branches des *Vv. epigastricae* (Fig. 3). Dans la région postérieure du ventre *V. abdominalis* s'unit chez quelques individus à *V. ilica* (Swienty) et, chez tou-

tes les truites aux veines intestinales (Fig. 3). Chez la Truite se trouve ici le mésentère ventral (*mesenterium ventrale*), qui unit la moitié postérieure de l'intestin spiral avec la paroi médiane du ventre. Dans la bifurcation ventrale de ce mésentère se trouve aussi *V. abdominalis*, qui envoie par le mésentère ventral 7 veines courtes à l'intestin. Ces veines passent obliquement en avant et s'ouvrent sur la paroi ventrale de l'intestin dans *V. subintestinalis*. On ne voit pas cette union chez les embryons d'une longueur de 14 mm (Grodziński). Il est probable qu'elle a lieu ensuite, à mesure de l'élargissement de la cavité abdominale et de la naissance du mésentère ventral. En tout cas cela prouve que ce sont là des rapports primitifs, qui n'ont pas encore été étudiés chez les vertébrés. On voit derrière l'anus, jusqu'à la nageoire anale tout près de la peau des vaisseaux impairs déja plus petits, qu'on peut considérer comme un prolongement postérieur de la *V. abdominalis*.

On peut identifier les vaisseaux secondaires longitudinaux (*Aa.* et *Vv. epigastricae* et *V. abdominalis*) dont on a parlé se basant sur les rapports topographiques et ceux du développement, avec les vaisseaux du même nom chez les Elasmobranches et chez les Urodèles, mais ils sont moins gros. La veine abdominale de la truite s'unit aux vaisseaux intestinaux, cependant chez les Elasmobranches et chez les Urodèles il n'y en a pas. Chez les *Spheroides*, Poissons Téléostéens, Rosen a décrit probablemeut *Vv. epigastricae* en les comparant à tort avec *V. cutanea lateralis* des Elasmobranches. Celle-ci passe tout près de la peau à la hauteur de la ligne latérale du corps, tandis que la veine décrite par Rosen se trouve entre le péritoine et les muscles abdominaux, donc dans la position des *Vv. epigastricae* de la Truite. Outre cela on ne sait rien de plus sur les vaisseaux longitudinaux de la paroi du tronc. Il est donc difficile de décider s'ils constituent un de plusieurs caractères anatomiques des *Salmonidae*, ce qui montrerait leur place très primitive entre *Teleostei*, ou s'ils ont un trait commun à tous les représentants de ce groupe systématique.

Grodziński mentionne à propos du développement des *Aa.* et *Vv. epigastricae* chez la Truite, qu'il a vu chez les embryons de 18 mm de longueur un réseau vasculaire étroit entre *Musculus rectus abdominalis* et *Musculus parietalis*. Ce réseau est formé par l'union des segments terminaux des *Aa.* et *Vv. intercostales*. Grodziński émet l'hypothèse, qu'à partir de ce réseau lâche artério-veineux se

forment chez les embryons adultes les vaisseaux correspondant aux unions des *Aa.* et *Vv. epigastricae* des Urodèles. On n'a pas examiné jusqu'ici le développement de *V. abdominalis* chez la Truite.

Tous les vaisseaux nommés ci-dessus existent déjà chez les jeunes poissons de 25 mm de longueur, c'est-à-dire chez ceux qui n'ont plus de vitellus, mais il leur manque encore beaucoup pour être comme les adultes. Dans le muscle abdominal droit se trouve chez eux le réseau vasculaire lâche et irrégulier, qui s'unit au réseau vasculaire décrit par Grodziński chez les embryons de 18 mm de longueur. Au milieu de ce réseau on voit deux vaisseaux parallèles longitudinaux (*V. abdominalis*) qui voisinagent seulement sur le tiers de leur longueur avec le coeur. Dans la partie médiane et postérieure du réseau on ne remarque encore aucun canal. Les deux canaux mentionnés ci-dessus s'unissent dans la région de la ceinture pectorale en un seul vaisseau, qui passe ensuite du côté gauche du corps. Ils se dirigent sous le péritoine vers la base de la nageoire pectorale, puis ils entrent dans la *V. subclavia* gauche tout près de la nageoire. Le réseau vasculaire dans la région du muscle abdominal droit chez le poisson peu âgé (26 mm) se simplifie considérablement et il disparaît partiellement, mais on voit cependant deux veines dans la ligne médiane du ventre. Dans la partie voisine de l'anus les deux canaux s'unissent à un seul gros vaisseau impair, allant jusque derrière la ceinture pelvienne. Les canaux décrits ci-dessus sont des rudiments de *V. abdominalis*, qui ne se transforment en un seul canal impair que chez les poissons plus agés, que je n'ai pas examinés. Le développement de ce vaissseau rappelle le développement de *V. abdominalis* chez la Salamandre (Hochstetter) et un peu chez le *Triton* (Grodziński). Le réseau vasculaire existe d'abord chez ces deux Urodèles, situé de la même façon au milieu de l'abdomen; à partir de ce réseau se forme chez le *Triton* la veine abdominale, tout de suite impaire, tandis que chez la Salamandre elle passe par la phase du développement où existent deux canaux paralèlles.

Chez les mêmes individus existent aussi des rudiments des canaux *Aa.* et *Vv. epigastricae.* Ces vaisseaux sont nets chez les poissons plus jeunes (25 mm) mais seulement dans le segment antérieur du tronc, tout près du coeur.. Ils sont déjà dans leur état définitif, dans lequel la veine a un diamètre beaucoup plus

supérieur à celui de l'artère qui l'accompagne. Ces deux vaisseaux, l'artère et la veine, se dirigent vers la base de la nageoire pectorale et vont à la rencontre des vaisseaux souclaviens (*A.* et *V. subclavia*). Chez le poisson plus âgé on voit déjà plus nettement et dans tout son trajet *V. epigastrica*. L'artère est moins nette. Ces vaisseaux ne se développent que très tard, lorsque le vitellus a tout à fait disparu et dans la paroi de l'abdomen commencent à se montrer distinctement les muscles.

B. Les vaisseaux segmentaires

Les vaisseaux segmentaires sont en union étroite avec les vaisseaux principaux (les artères et les veines), et ils forment trois groupes: les vaisseaux segmentaires dorsaux, latéraux et ventraux (*Aa.* et *Vv. segmentales dorsales, laterales* et *ventrales*). Les derniers vaisseaux vascularisent les intestins et n'arrivent pas aux muscles du tronc, c'est pourquoi nous n'en parlerons plus.

Aa. segmentales dorsales (Fig. 1, 2 Asd) quittent l'aorte immédiatement à la base du corps d'une vertèbre et en la longeant latéralement elles se dirigent verticalement vers le haut. Au-dessus de la partie annulaire elles s'infléchissent en arrière, puis elles accompagnent latéralement les apophyses épineuses (Fig. 1 W) de ces vertèbres, arrivent enfin à la surface de la peau sur la ligne dorsale. Ces artères apparaissent comme des vaisseaux pairs, c'est-à-dire qu'il y en a deux dans chaque segment, une droite et une gauche. Ces deux artères sont également très développées, en quoi elles diffèrent un peu des vaisseaux d'autres Téléostéens, chez lesquels l'un de ces vaisseaux, particulièrement celui de la queue est moins volumineux que l'autre (chez *Lopholatilus*—Silvester). On voit surtout très nettement cette différence chez *Pleuronectes* (Biborski). *Aa. segmentales dorsales* s'unissent immédiatement sous *Musculus rectus dorsalis*, à l'aide d'un réseau de capillaires sanguins avec *Aa. intersegmentales dorsales* (Fig. 1 Aisd) et vascularisent *Musculus rectus dorsalis*. Des vaisseaux segmentaux dorsaux propres sortent latéralement les branches et à travers les muscles elles vont presque perpendiculairement dans la direction de la peau. Ces vaisseaux, nommés artères musculaires (*Aa. musculares*, Fig. 2 Ams, Amt) quittent *Aa. segmentales dorsales* en différents endroits de leur trajet, de même que d'après

Biborski, chez la Sole. Puis *Aa. musculares primae* (Fig. 1 Asl) émergent des *Aa. segmentales dorsales* à la hauteur du bord inférieur des vertèbres et elles vont dans le myosepte horizontal de muscles axiaux. *Aa. musculares secundae* (Fig. 2 Ams) quittent *Aa. segmentales dorsales* perpendiculairement, au-dessus de la par-

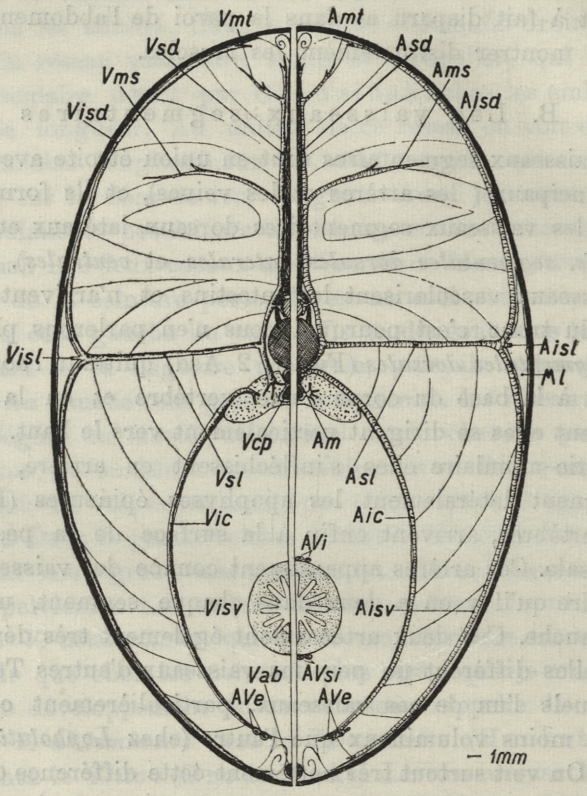

Fig. 2. Schéma de la distribution des vaisseaux du tronc chez la Truite, en projection sur la coupe idéale transversale du corps du poisson.

tie annulaire de la vertèbre. Ces artères sont courtes et se ramifient abondamment dans les muscles latéraux. La troisième branche sort tout près de la base de la nageoire dorsale; c'est la plus mince d'entre eux, et on la nomme *A. muscularis tertia* (Fig. 1 Amt). Elle envoie des branches dans les nageoires dorsales. Les artères dorsales percent les muscles voisins et en se ramifiant toujours de plus en plus, se terminent en capillaires sanguins,

qui forment avec des branches analogues de vaisseaux voisins un réseau serré. Entre les artères musculaires voisines existent outre cela les connexions au moyen des artères fines.

Le segment terminal de la première artère musculaire se comporte autrement que la seconde ou la troisième. La topographie de cette artère et son développement nous montrent qu'elle correspond aux artères segmentales latérales des Elasmobranches et des vertébrés terrestres. A cause de cela on la nommera ici *A. segmentalis lateralis* (Fig. 1 Asl). Ces artères sortent, comme on l'a déjà dit, presque perpendiculairement des artères segmentales dorsales à la hauteur du bord inférieur de la vertèbre et se dirigent vers le myosepte horizontal, lequel sépare les muscles latéro-dorsaux et latéro-ventraux. Elles arrivent ainsi au fond d'un creux où se trouve *Musculus rectus lateralis* et là elles se subdivisent en trois branches. Deux entre elles s'ouvrent d'en haut et d'en bas et parcourent la surface des muscles axiaux en gardant plus ou moins la direction du bord souscutané des myomères (*Aa. intersegmentales dorsales* et *ventrales*, Fig. 1, 2 Aisd, Aisv). Elles envoient tout le long de leur trajet des ramifications à la peau et aux muscles. Enfin elles se divisent en capillaires sanguins. La troisième branche *A. intersegmentalis lateralis* (Fig. 1, 2 Aisl), beaucoup moins grosse que les deux précédentes, passe dans l'axe du vaisseau principal et, en se divisant en petites branches, pénètre dans *Musculus rectus lateralis*.

Les artères intercostales (*Aa. intercostales* Fig. 1, 2 Aic) forment le dernier groupe d'artères dans le système segmental. *Aa. intercostales* s'éloignent directement de la paroi inférieure de l'aorte et se dirigent presque perpendiculairement aux côtes entre le péritoine et les muscles. Chemin faisant elles croisent les côtes (Fig. 1 C) en les omettant à l'intérieur. A la hauteur du tiers supérieur de la cavité viscerale elles se dirigent en arrière sous un angle plus ou moins aigu et elles continuent plus loin au voisinage des côtes. Les artères intercostales, par leurs divisions terminales s'anastomosent avec l'artère epigastrique (*A. epigastrica*). Sur toute leur longueur elles envoient des branches latérales qui vascularisent les muscles latéro-ventraux du tronc, le péritoine et les côtes. Ces branches pénètrent aussi *Musculus rectus ventralis*.

Les vaisseaux intercostaux sont, chez beaucoup d'autres vertébrés tels que les mammifères (Evans), les oiseaux (Neuge-

bauer), les serpents, les urodèles (Grodziński), les branches plus ventrales des *Aa. segmentales laterales*. Chez les Truites adultes elles s'unisent directement à l'aorte. Des recherches sur leur développement pourraient fournir quelques explications sur le sujet des différences dans les réunions des artères intercostales. Hélas, nous ne connaissons leur mode de formation que chez les Amniotes, chez lesquels *Aa. intercostales* sont dès le début des branches des *Aa. segmentales laterales*. D'abord elles sont petites mais bientôt dépassent en dimension le tronc originaire (Evans, Grodziński). C'est pourquoi chez l'homme on les nommait autrefois à tort vaisseaux principaux et qu'on considérait *Aa. segmentales laterales* comme des branches latérales de ces vaisseaux. Le diamètre d'une artère intercostale de la Truite n'égale jamais celui de l'artère segmentale latérale. On ne sait pas, si dans leur développement elles etaient liées. En tout cas leur parcours est homologue de celui des artères intercostales des animaux terrestres.

Le trajet et les ramifications des veines segmentales (*Vv. segmentales dorsales*, *laterales*, Fig. 1, 2 Vsd, Vsl) et des veines intercostales (*Vv. intercostales* Fig. 1, 2 Vic) ressemblent à ceux des artères correspondantes. Elles apparaissent en principe dans les segments qui n'ont pas d'artères et elles ont une disposition alternée: une artère, une veine. Quand les veines ou les artères occupent deux myoseptes voisins, cette disposition peut être exceptionnellement troublée.

Les différences les plus considérables entre le système segmental des artères et celui des veines reposent sur leur mode d'union avec les vaisseaux longitudinaux du corps. Les artères ont toujours leur plus grande base dans les aortes. Les extrémités de toutes les veines segmentales pénètrent dans le rein et là elles se divisent »en arbre« en vaisseaux de plus en plus minces. Le sang après son passage dans ces vaisseaux va par des vaisseaux de plus en plus grands dans une *V. cardinalis posterior*. Il existe chez la Truite comme chez tous les Poissons le système de la veine-porte du rein. Une autre différence consiste en ce que les branches terminales de *Vv. intercostales* s'unissent à une *V. epigastrica* correspondante, pendant que les artères entrent dans un tronc artériel du même nom.

Le système des vaisseaux veineux de la Truite (*Salmo irideus* Gibb.) est en comparaison avec celui des Elasmobranches plus ré-

duit; il n'a pas autant de troncs veineux longitudinaux. Il y a chez les Elasmobranches outre les veines nommées ci-dessus (*Vv. epigastricae*, *v. abdominalis*) deux grosses veines dont l'une passe sous la peau au bord d'un myosepte horizontal (*V. cutanea lateralis*)

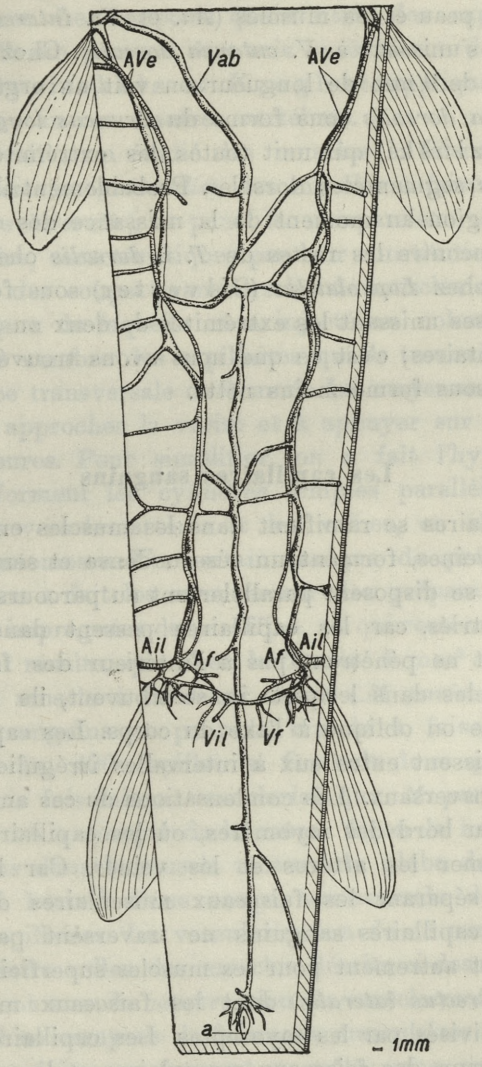

Fig. 3. *V. abdominalis* et *Aa.* et *Vv. epigastricae* de la Truite (d'un poisson adulte) situées dans la paroi abdominale, vues du côté du péritoine.

et l'autre parcourt la ligne médiane du dos (*V. cutanea dorsalis*). Les vaisseaux segmentaires s'unissent à ces veines longitudinales, ce que l'on ne rencontre pas chez *Teleostei*. Cette remarque concerne surtout les vaisseaux segmentaires latéraux, dont les extrémités s'unissent à *V. cutanea lateralis* et aussi les veines qui passent entre la peau et les muscles (*Aa.* et *Vv. intersegmentales dorsales*) et qui s'unissent à *V. cutanea dorsalis*. Chez les embryons de la Truite de 9 mm de longueur on voit un organe homologue de *V. cutanea dorsalis* sous forme du *Truncus longitudinalis dorsalis* (Grodziński) qui unit toutes les extrémités des artères et des veines segmentales dorsales. Probablement il s'est atrophié dans cette région au moment de la naissance des capillaires sanguins. On rencontre les restes de *T. l. dorsalis* chez la sole (Biborski) et chez *Lopholatilus* (Silvester) sous forme de courtes anastomoses unissant les extrémités de deux ou plusieurs vaisseaux segmentaires; c'est ce que nous avons trouvé aussi chez la Truite mais sous forme moins nette.

Les capillaires sanguins

Les capillaires se ramifient dans les muscles entre les artères fines et les veines, formant un réseau dense et serré. Les mailles de ce réseau se disposent parallèlement au parcours des faisceaux musculaires striés, car les capillaires passent dans leur couche conjonctive et ne pénètrent pas à l'intérieur des faisceaux. Suivant les muscles dans lesquels ils se trouvent, ils ont leur parcours parallèle ou oblique à l'axe du corps. Les capillaires longitudinaux s'unissent entre eux à intervalles irréguliers à l'aide de vaisseaux transversaux. Les condensations de ces anastomoses ont lieu surtout au bord des myomères, où les capillaires se réunissent pour former les artères et les veines. Car les myoseptes transversaux séparant les faisceaux musculaires des myomères voisins, leurs capillaires sanguins ne traversent pas cette frontière. Il en est autrement pour les muscles superficiels chez Truite (*Musculus rectus lateralis*) dont les faisceaux musculaires ne sont pas subdivisés par les myoseptes. Les capillaires longent ici toute la longueur des faisceaux musculaires et leurs anastomoses transversales, qui forment un réseau dense, sont plus ou moins réguliers dans le muscle tout entier.

Car les capillaires sanguins parcourent la couche conjonctive des faisceaux musculaires; ils sont donc plus denses dans les muscles superficiels du tronc (*M. rectus lateralis*) que dans les axiaux, puisque les premiers muscles contiennent dans 1 mm² de coupe tranversale presque trois fois plus de faisceaux musculaires que les autres. Les rapports quantitatifs des capillaires des muscles de la Truite peuvent être mis en évidence de la manière inventée par Spalteholz et Krogh et appliquée par plusieurs chercheurs au cas d'autres vertébrés.

Dans ce travail on a étudié des muscles à faisceaux musculaires épais (*Musculus parietalis*), des muscles à faisceaux minces (*Musculus rectus lateralis*), et pour la comparaison, des muscles du globe oculaire, caractéristiques par leur constitution. On a fait des calculs sur des coupes transversales de muscles de la Truite, dans les vaisseaux de laquelle on a injecté un colorant. D'abord on a compté le nombre des capillaires qui se trouvaient à la surface d'une coupe transversale de 1 mm². La moyenne de 5 coupes nous suffira à approcher la verité et à appuyer sur lui des déductions ultérieures. Pour simplifier, on a fait l'hypothèse que les capillaires forment les cylindres simples parallèles et ne se concentrent pas vers les artères et les veines, on n'a pas tenu compte des anastomoses. Un certain manque de précision vient aussi de ce qu'on a fait les mesures sur des préparations fixées, déshydratées et impregnées de paraffine, ce qui resserait les tissus.

De ce calcul résulte, que chez la Truite 1 mm² d'une coupe transversale du muscle à faisceaux épais (*M parietalis*) possède 123 capillaires sanguins et pour le muscle à faisceaux minces (*M. rectus lateralis*) 400 capillaires. On voit donc que *M. rectus lateralis* est trois fois mieux vascularisé que *M. parietalis*. Pour la comparaison on a compté de la même façon le nombre de capilaires sanguins dans le muscle moteur du globe de l'oeil et on a constaté, que 1 mm² d'une coupe transversale de ce muscle contient 276 capillaires. La vascularisation de ce muscle est donc intermédiaire entre celles des muscles décrits ci-dessus. Cela concorde étroitement avec la construction du muscle moteur du globe oculaire, car il se compose de faisceaux musculaires épais et minces, en quoi ces faisceaux peuvent se mêler sans ordre, les uns avec les autres, ou ils peuvent former dans un seul muscle les recueillements bien séparés les uns des autres.

On peut aussi conclure de la quantité de la nutrition d'après l'espace sur lequel la nourriture et l'oxygène sont obligés de se diffuser pour bien nourrir le muscle entier. Cet espace dépend du nombre de capillaires dans le muscle, ce qui dépend de leurs distances mutuelles et de leurs diamètres. L'espace de diffusion dépend aussi d'un autre fait. Si le muscle se trouve au repos, les vaisseaux capillaires se rétrécissent, s'il exécute un travail, les vaisseaux s'élargissent et leur distance mutuelle diminue (Krogh, Stoel).

La grandeur de la surface des capillaires par lesquels les muscles qui les entourent reçoivent la nourriture et l'oxygène, est un élément excessivement important pour la quantité de la nutrition. Pour la calculer on a mesuré dans des muscles différents le diamètre des capillaires remplis de matière colorante, et on a trouvé comme moyenne de 5 coupes pour *M. rectus lateralis* 8,3 μ, pour *V. parietalis* 9,8 μ et pour les muscles du globe de l'oeil 10,6 μ. On a mesuré seulement les vaisseaux coupés transversalement, qui avaient des contours exactement circulaires. A partir de là on a calculé avec la formule 2rwn (2r—diamètre, w—hauteur, n—le nombre des vaisseaux) que la surface globale des capillaires a 3,78 mm^2 pour 1 mm^3 de masse de muscle à faisceaux épais, tandis que dans le muscle à faisceaux minces cette surface est de 10,42 mm^2, et dans le muscle de l'oeil de 9,18 mm^2. Bien que le muscle de l'oeil possède beaucoup moins de capillaires que le muscle à faisceaux minces, cependant, comme on le voit, les surfaces des capillaires qui se trouvent dans 1 mm^3 de masse de muscle sont presque identiques pour les deux muscles. Cela reste en rapport avec un grand diamètre des capillaires des muscles du globe de l'oeil. Cependant les capillaires du muscle à faisceaux épais (3,78 mm^2) possèdent une très petite surface. Cela prouve que le muscle à faisceaux épais est moins bien nourri que les deux muscles nommés ci-dessus, car plus la surface des vaisseaux est grande, plus les vaisseaux diffusent.

La distance réciproque des capillaires est une chose non moins importante pour un approvisionnement convenable des muscles. La moitié de cette distance (R) est le rayon de la surface irriguée par chaque vaisseau. La grandeur de »R«, la grandeur de la surface des parois des capillaires et la pression qui y règne détermine la quantité de la nutrition du muscle et par consequent

son habilité. Comme exemple caractéristique on peut indiquer le muscle du globe de l'oeil de la Truite, où »R« oscille entre 39 et 105 μ, ce qui est causé par le groupement inégal de faisceaux des muscles épais et minces et par une grande quantité du tissu conjonctif localisé en plusieurs endroits. Chez la Truite le même »R« pour le muscle contenant des faisceaux minces, est de 33 μ, tandis que »R« pour le muscle composé de faisceaux épais est de 67 μ. Cet exemple montre aussi que le muscle à faisceaux minces possède de meilleures conditions de nutrition que celui à faisceaux épais.

En s'appuyant sur les mesures citées ci-dessus on a calculé aussi le volume des capillaires qui se trouvent dans une unité de volume de la masse du muscle, c'est-à-dire dans 1 mm^3. Pour le calcul on a pris la formule r^2 w n (w—hauteur d'une unité du volume, n—nombre de capillaires coupés transversalement dans l'unité de volume, r—rayon du vaisseau) Du calcul résulte, que le volume des capillaires dans 1 mm^3 de la masse du muscle à faisceaux minces est de 0,0216 mm^3, dans le muscle à faisceaux épais de 0,0092 mm^3, et dans le muscle du globe oculaire de 0,0243 mm^3. Le muscle de l'oeil, tout en étant moins vascularisé que le muscle à faisceaux minces, peut cependant avoir plus de sang, car le rayon de ces vaisseaux est plus grand et le volume des vaisseaux croît selon le carré du rayon. Le muscle à faisceaux épais est celui qui a le moins de sang dans ses capillaires.

Le sang qui coule dans les vaisseaux touche leur paroi, donc la même quantité de sang couvrira dans les vaisseaux fins une surface plus grande, que dans le gros vaisseaux. Les nombres calculés pour les capillaires étudiés ici sont tout à fait caractéristiques sous ce rapport, surtout en comparaison avec la surface du même volume de sang pris sous forme sphérique. La surface d'une goutte de sang sphérique de 1 mm^3 a 4,836 mm^2. La meme quantité de sang touche la paroi des capillaires sur une surface, qui pour le *M. rectus lateralis* est de 481,5 mm^2, pour le *M. parietalis* de 410,7 mm^2 et pour le muscle du globe oculaire de 387,8 mm^2. Cela prouve que la surface de contact de 1 mm^3 de sang s'accroît dans les capillaires 99,56 fois pour le premier muscle, 84,96 fois pour le deuxième et 78,11 fois pour le troisième.

Tous ces calculs montrent que le muscle le mieux approvisionné chez la Truite est *M. rectus lateralis*, car il possède le plus

grand nombre de capillaires, son R est le plus petit et la surface de contact de la paroi des capillaires est la plus grande.

Tout ce qu'on a dit des capillaires des muscles de la Truite peut être comparé aux calculs semblables faits chez d'autres vertébrés. Les résultats groupés sur le tableau ci-joint montrent que la quantité des capillaires est très variée, elle dépend de la nature du muscle, de l'animal et de l'espèce chez un même individu (la Truite 123 à 400, le Lapin 790 à 1550). Les différences sont

Les capillaires dans les muscles striées chez les vertébrés

L'animal	Le genre du muscle	r	N	P	V	R	p	L'auteur
		micron.	1 mm²	1 mm³	1 mm³	micron.	mm²	
la Myxine	les muscles axiales	16	56	5·68	0·0450		26·965	Herisch
la truite	m. parietalis	4·9	123	3·78	0·0092	67	84·965	Górkiewiczowa
„	les muscles du globe oculaire	5·3	276	9·18	0·0243	39—105	78·118	„
„	m. rectus lateralis	4·15	400	10·4	0·0216	33	99·564	„
la grenouille		7·5	400	18·8	0·0710	28	54·755	Krogh
le lapin	m. semitendinosus	2·6	790	12·9	0·0160	18	166·719	Stoël
„	m. adductor magnus	1·25	1550	12·2	0·0076	13	331·946	„
le chien	m. semimembranosus	3·6	2600	58·7	0·1060	11	553·800	Krogh
le cheval	m. gastrocnemius	2·75	1400	24·2	0·0328	15	152·571	„

Explication des signes. — r-rayon des capillaires, N-nombre des capillaires coupés transversalement sur la surface de 1 mm² du tissu musculaire, V-volume de capillaires dans 1 mm³ de tissu musculaire; P-surface de capillaires contenus dans 1 mm³ du tissu musculaire, R -espace de diffusion d'un capillaire, p-la surface de contact de 1 mm³ du sang contenue dans le vaisseau capillaire, calculée par rapport à une goutte de sang de même volume.

surtout nettes si l'on compare les mammifères (790 à 2600) aux animaux à sang froid (56 à 400). La quantité de vaisseaux dans une unité du volume et leur diamètre déterminent l'alimentation du muscle. La quantité de la nutrition est surtout mise en évidence par »R« (l'espace de la diffusion) et »p« (la surface d'attouchement). Plus l'espace pour l'irrigation exigé de chaque capillaire est petit et plus la surface de contact du sang est grande, plus les conditions d'alimentation du muscle sont meilleures. Les

conditions les plus avantageuses sous ce rapport existent dans *Musculus adductor magnus* chez le Lapin et *Musculus semitendinosus* chez le Chien.

Les recherches actuelles, encore peu nombreuses, ne permettent pas de tirer des conclusions plus générales. On peut seulement supposer, que des données quantitatives concernant des rapports vasculaires dans les muscles, étudiées systématiquement pour plusieurs représentants des divers groupes de vertébrés expliqueront leur habilité physique d'une manière plus sûre que les méthodes appliquées jusqu'ici. Il faut seulement se souvenir, que la quantité de capillaires n'est pas un caractère exclusif de l'espèce et que la grossesse et la gymnastique intense accroissent le nombre des capillaires dans le coeur et dans les muscles du squelette (Petren & Sjöstrand, Petren & Sylven).

Resumé

Dans ce travail on a décrit un certain nombre de vaisseaux longitudinaux et de vaisseaux métamériques du tronc de la Truite (*Salmo irideus* Gibb.) en se basant sur l'étude des vaisseaux injectés de matière colorante.

Outre les principaux vaisseaux longitudinaux (Aorte, *V. cardinalis posterior*) on a étudié des vaisseaux longitudinaux secondaires *A.* et *V. epigastricae* et *V. abdominalis*, bien connus chez les Elasmobranches, non mentionnés jusqu'alors chez les Téléostéens. Ces vaisseaux naissent de réseau vasculaire; on les trouve dans la région du muscle droit abdominal chez les embryons assez agés, mais seulement après l'absorption totale du vitellus.

On a décrit le parcours complet des vaisseaux métamériques avec toutes leurs branches les plus importantes (*Aa.* et *Vv. segmentales laterales*, *dorsales* et *Aa.* et *Vv. intercostales*).

La Truite, comme représentant des Poissons Téléostéens, possède dans son corps moins de veines longitudinales que les Elasmobranches, cependant son système de vaisseaux segmentaux rappelle le système des vaisseaux segmentaires chez les Elasmobranches.

Les capilaires sanguins se trouvent dans la couche conjonctive des faisceaux de muscles striés et sont à peu près parallèles à leur axe. Les myoseptes, qui coupent la continuité des fibres striées, forment aussi un insurmontable obstacle pour les capillaires.

On a compté par la méthode de Spalteholz et Krogh, les rapports quantitatifs des capillaires dans les muscles du tronc. Les calculs montrent, que les différents muscles de la Truite sont inégalement nourris par le sang. Plusieurs facteurs ont une influence sur l'intensité d'alimentation du muscle. Premièrement l'épaisseur des faisceaux musculaires et rayon des capillaires (r). Puis interviennent des facteurs secondaires comme la quantité de capillaires (N), l'espace de diffusion (R), la surface de diffusion des vaisseaux (P), la surface de contact du sang (p).

Les muscles de la Truite étudiée peuvent être classés au point de vue de la quantité des capillaires en une série décroissante de *M. rectus lateralis* à *M. parietalis*, en passant par le muscle du globe oculaire.

Je remercie ici chaleureusement Mr. le prof. Grodziński qui avec un si grand intérêt a suivi mon travail en m'aidant de ses précieux conseils.

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Explication des abréviations sur les figures

A — Anus
Ae — Arteria epigastrica
Af — „ femoralis
Ai — „ intestinalis
Aic — „ intercostalis
Ail — „ iliaca
Aisd — „ intersegmentalis dorsalis
Aisl — „ „ lateralis
Aisv — „ „ ventralis
Am — Aorta
Amp — Arteria muscularis prima
Ams — „ „ secunda
Amt — „ „ tertia
Asd — „ segmentalis dorsalis
Asi — „ subintestinalis
Asl — „ segmentalis lateralis
Cap — capillaires sanguins
K — vertèbres
Md — Musculus rectus dorsalis
Ml — „ „ lateralis
Ms — Myoseptum
Msb — Musculus parietalis subaxialis
Msp — „ „ supraxialis
Mv — „ rectus ventralis
N — rein
P — péritoine
R — moelle épinière
Sh — myosepte horizontal
Vab — Vena abdominalis
Vcp — „ cardinalis posterior
Ve — „ epigastrica
Vf — „ femoralis
Vi — „ intestinalis
Vic — „ intercostalis
Vil — „ iliaca

Visd — Vena intersegmentalis dorsalis
Visl — „ „ lateralis
Visv — „ „ ventralis
Vms — „ muscularis secunda
Vmt — „ „ tertia
Vsd — „ segmentalis dorsalis
Vsi — „ subintestinalis
Vsl — „ segmentalis lateralis
W — apohyses épineuses

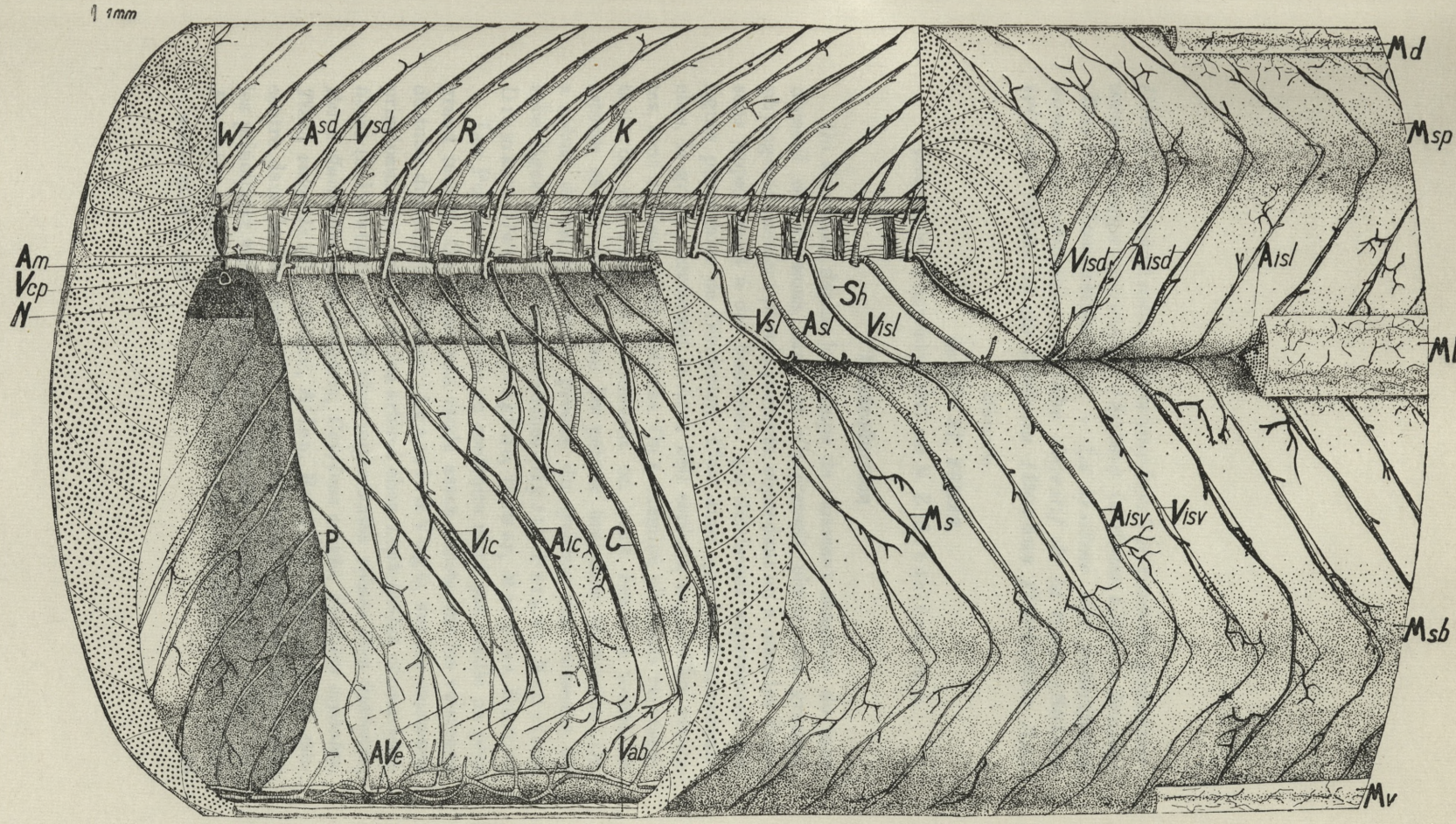

Fig. 1. *Salmo irideus.* Les vaisseaux du tronc sont tracés sur le fond des muscles et du squellette. Les artères sont indiquées par les lignes striées, les veines en lignes pointillées, les parties du squelette par le carreau oblique. La figure est faite de telle manière, que seul le côté droit montre tous les muscles après l'écartement de la peau. En passant du côté droit vers le côté gauche de la figure on voit les coupes de muscles de plus en plus profonds. A gauche on voit le péritoine et le rein qui luit à travers elle, et la colonne vertébrale et le myosepte horizontal du tissu conjonctif, qui sépare les muscles axiaux.

Układ głównych naczyń krwionośnych przewodu pokarmowego pstrąga tęczowego (Salmo irideus Gibb) i brzany (Barbus fluviatilis Ag). — Le système des principaux vaisseaux sanguins du tube digestif de la truite (Salmo irideus Gibb) et du barbeau (Barbus fluviatilis Ag).

Mémoire

de M^me^ ***ST. KONIAR,***

présenté le 10 Novembre 1947 par M. Z. Grodziński m. c.

L'introduction

On s'occupait depuis longtemps de vaisseaux sanguins du tube digestif des Poissons, mais on s'intéressait plutôt aux groupes phylogénétiquement plus importants, cependant on a omis les Poissons appartenant à des branches qui délaissent séparément des lignes principales de l'évolution. C'est ainsi que les Elasmobranches, le groupe contenant environ 280 espèces, aujourd'hui vivantes, sont suffisamment élaborés. On a examiné plusieurs représentants de ces Poissons et souvent on avait égard à toutes les artères et les veines avec les petites branches terminales. On a même donné une revue précise du système des vaisseaux du tube digestif à des Elasmobranches (Hyrtl, Parker, Neuville, Diamare, Daniel, O'Donoghue, Hower, Marples, Burne).

Les Poissons Téléostéens au contraire n'ont pas éveillé un plus grand intérêt. On a fait une étude assez exacte sur les vaisseaux du tube digestif du saumon (Agassiz & Vogt), sur les vaisseaux principaux des veines et des artères chez *Lopholatilus chamaeleonticeps* (Silvester), sur les plus importantes veines chez *Ophiodon*, *Perca fluviatilis*, *Lota vulgaris*, *Cyprinus carpio*, *Squalius cephalus*, *Tinca vulgaris* (Einstman, Allen, Rathke). Outre cela on rencontre dans la littérature les mentions moins exactes, concernant les principaux vaisseaux du tube digestif (*Lepadogoster* — Guitel *Fierasfer* — Emery, *Thynnus* — Frade, *Fistularia* — Junger-

sen, *Monopterus* — Volz) ou leurs certains segments (*Misgurnus* — Busnita).

Jusqu'à présent il n'y a aucune description des vaisseaux intestinales chez un représentant des Téléostéens, qui par sa précision serait égale aux descriptions, données aux représentants des Plagiostomes.

Tous les explorateurs sont d'accord, que trois artères et en certains cas quatre artères passent de l'aorte sur le tube digestif des Elasmobranches. L'une d'elles, *A. coeliaca*, vascularise la partie antérieure de l'estomac, le foie et la valvule spirale de l'intestin. La seconde, *A. mesenterica anterior*, approvisionne la partie postérieure de l'estomac, la rate et la paroi de l'intestin spiral. Cette artère peut se diviser en deux troncs qui sortent de l'aorte par soi-même et alors nous avons quatre au lieu de trois artères intestinales. La troisième artère, la plus petite, qui atteint seulement la partie terminale de l'intestin, est *A. mesenterica posterior*. Les veines accompagnent presque toutes les artères intestinales. Elles se joignent dans la région de la partie antérieure de l'estomac en un grand vaisseau *V. portae hepatis* et par sa médiation les veines arrivent au foie.

On est d'accord à cet égard qu'il n'y a qu'une artère *A. coeliaco-mesenterica*, qui parvient au tube digestif des Poissons Téléostéens. Elle se détache des derniers vaisseaux branchiaux *(Aa. epibranchiales)*, derrière l'aorte. La manière de détachement est très variée. La vessie natatoire n'existant pas chez *Elasmobranchii* exerce une certaine influence sur le mode de ramification artérielle. Il a une plus grande variété dans le système veineux. La façon d'union avec les vaisseaux du foie est compliquée, car au lieu d'une veine porte, *V. portae hepatis*, il y en a deux ou plusieurs. La veine caudale peut s'unir à celles de l'intestin (*Anguilla, Cyprinus, Lophius, Silurus* et d'autres) ce qui n'existait pas chez les Elasmobranches. Enfin les Téléostéens possèdent beaucoup de veines, qui n'accompagnent pas les artères.

Ce travail a pour but de donner la description du système des plus importants vaisseaux sanguins du tube digestif d'une carnivore truite (*Salmo irideus* Gibb) et du omnivore barbeau (*Barbus fluviatilis* Ag.).

Les truites servant d'expérience, dérivent d'un élevage de poissons de Ojców. On a choisi les poissons du genre masculin de 20

à 25 cm de longueur. Les barbeaux de la même taille provenaient de la pêche dans la Vistule. On a injecté de l'encre de Chine ou une solution aqueuse du bleu de Prusse et la masse rouge de la gomme laquée dans les vaisseaux sanguins à l'artère caudale. Les objets étaient fixés au formol. Leurs tubes digestifs furent préparés et rendus transparents dans la glycérine ou dans l'huile de cèdre. Les modeles étaient préparés et observés sous la loupe binoculaire. On a dessiné les préparations choisies en aide d'un appareil dessinateur d'Abbé. On a préparé également plusieurs coupes microscopiques des intestins d'une truite, de 18 micron d'épaisseur. On a coloré les coupes se servant de méthode van Gieson.

L'aspect du tube digestif de la truite et du barbeau

Le court oesophage de la truite (Fig. 1) se trouve au-dessus du coeur et s'élargit dans la cavité du corps en formant l'estomac qui, renfermé de deux côtés par les glandes génitales passe parallèlement à la longue axe de l'animal. L'estomac *(corpus ventriculi)* se courbe en anse à peu près au milieu de la cavité du tronc en descendant et passe plus loin en se rétrécissant comme partie pylorique *(pars pylorica)* vers la tête. Touchant la paroi ventrale du principal segment de l'estomac, il passe déjà comme intestin moyen à son côté droit et sur son dos. Là, en voisinant avec la vessie natatoire et les deux glandes génitales, il suit comme un mince tube jusqu'à la fin de la cavité du tronc, où derrière les nageoires abdominales il s'y termine par l'anus. Le mésentère passe entre l'intestin postérieur et la paroi abdominale *(Mesenterium ventrale)*. Dans son trajet, le tube digestif se courbe deux fois en une boucle de l'estomac et des intestins, rangée parallèlement à la longue axe du poisson. Un court conduit mène de segment final de l'oesophage et de sa paroi dorsale à la vessie natatoire. Des nombreuses évaginations en doigt de gant (Appendices pyloriques) sortent de l'intestin moyen dans le voisinage du *Pars pylorica* de l'estomac. Le foie se trouve entre l'estomac propre, sa partie pylorique, et l'anse de l'intestin moyen. C'est un produit court, trapu d'une forme d'un carreau, qui remplit hermétiquement l'espace mentionnée. Une petite vésicule biliaire s'ouvre vers l'intestin moyen. Sur le mésentère, au-delà du bord postérieur de l'estomac, se trouve la rate aplatie, avec un profil triangulaire.

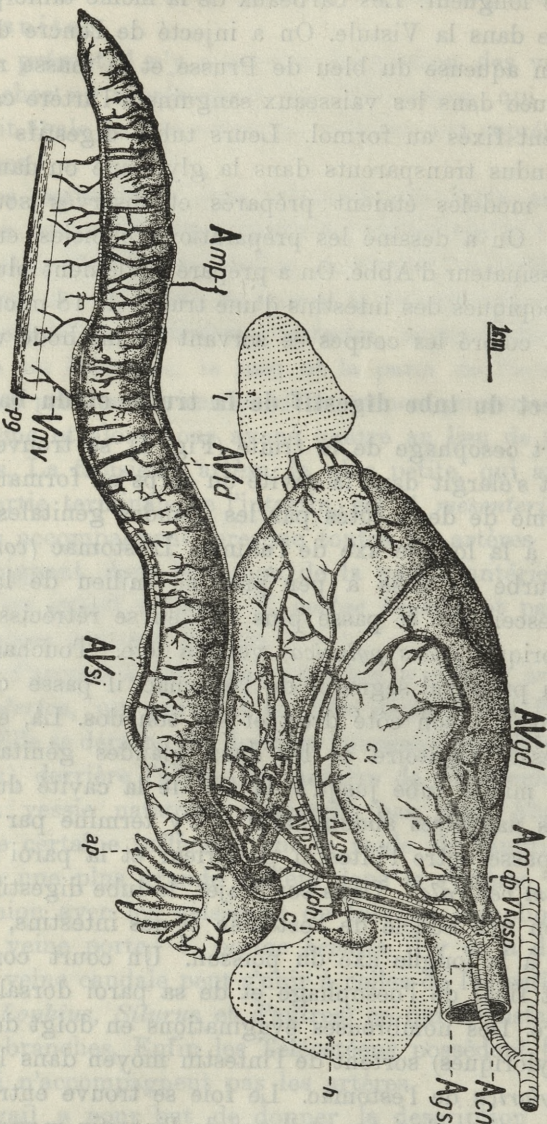

Fig. 1. Le tube digestif de la Truite (*Salmo irideus* Gibb).

Les parois intérieures du tube digestif sont couvertes de plis saillants de la tunique muqueuse, formés caractéristiquement dans leurs différents segments. Dans l'oesophage et l'estomac s'éten-

dent longitudinalement les simples plis de la tunique muqueuse au nombre de 12 ou 15, épais et larges dans le segment principal de l'estomac *(corpus ventriculi)*, moins épais dans l'oesophage et beaucoup plus nets étant plus hauts dans la partie pylorique de l'estomac. Les parois de l'intestin moyen sont couvertes de plis hauts, élancés et longitudinaux, très onduleux. Ces plis sont placés l'un près de l'autre, se touchent fortement l'un à l'autre, grâce à quoi ils se pénètrent réciproquement par leurs parois onduleuses. Dans le segment postérieur du tube digestif il y a 25 à 30 plis forts et circulaires, lesquels font saillie dans la lumière de l'intestin. Parmi ces principaux plis il y a des plis plus fins placés ainsi que dans l'intestin moyen. Grâce aux plis épais circulaires on peut déterminer exactement les limites de l'intestin postérieur, ce qui est très difficile à affirmer n'ayant pour base que la surface de l'intestin.

Le viscère chez *Barbus fluviatilis* est placé tout à fait autrement. Le tube digestif apparaît comme un long cylindre se rétrécissant graduellement du devant en arrière. Il n'est pas différencié à l'estomac et à l'intestin, car il n'y a aucun élargissement. Il forme cependant des longues circonvolutions, grâce auxquelles le tube digestif du barbeau est très long. Il y a trois circonvolutions dont deux longitudinales et une transversale. Trois forts lobes du foie couvrent l'intestin sur une espace remarquable. Des brefs segments de l'intestin terminal seulement passent du dessous du foie. La vésicule biliaire (Fig. 2, vf) se trouve dans lobe du foie à la hauteur de la circonvolution transversale. La tunique muqueuse de tout le tube digestif est arrangée dans les plis longitudinaux, qui passent en zigzag les uns près des autres.

Les vaisseaux intestinaux de la truite

Deux artères apportent le sang sur l'intestin de la truite, ce qu'on ne voit pas chez d'autres Poissons Téléostéens, L'une d'elles *A. coeliaco-mesenterica* (Fig. 1, Acm) passe de l'aorte à l'oesophage et atteint par ses branches tous les segments de l'intestin. L'autre *A. mesenterica primitiva* (Fig. 1, Amp) est moins importante, car elle unit l'aorte à une des branches de l'artère précédente, qui passe sur la surface de la partie postérieure de l'intestin.

A. coeliaco-mesenterica (Fig. 1, Acm) se sépare de la paroi ven-

trale de l'aorte *(Aorta mediana)* (Fig. 1, Am) derrière l'artère sous-clavière *(A. subclavía)*. Comme un vaisseau impair, elle achève le dos de l'oesophage et elle se dirige vers lui en arrière. Avant d'entrée à la base de la vessie natatoire elle se divise en deux branches, qui ont à peu près la même taille. L'une d'elles, *A. gastro-supraintestinalis* (Fig. 1, Agsp) vascularise la partie dorsale de l'estomac *(corpus ventriculi)* et la partie dorsale de l'intestin moyen et postérieur.

La seconde *A. gastro-subintestinalis* (Fig. 1, Agsi) vascularise la partie ventrale de l'estomac, toute sa partie pylorique et la partie ventrale de l'intestin moyen et postérieur. Les artères nommées ci-dessus se partagent en un nombre des branches, qui s'arrangent caractéristiquement dans les différentes parties de l'intestin et arrivent à des organes voisins, ainsi qu'à la vessie natatoire, aux glandes sexuels, au foie, à la rate (Fig. 1).

A. gastro-supraintestinalis (Fig. 1, Agsp) s'approche du conduit pneumatique de la vessie natatoire où elle se partage en trois plus grandes branches. Deux d'entre elles vascularisent le dos de l'estomac *(Aa. gastricae dorsales)*, la troisième *A. intestinalis dorsalis* (Fig. 1 Aid) passe sur l'intestin moyen et postérieur.

Les deux premières *(A. gastrica dorsalis sinistra* et *dextra)* (Fig. 1, Agd) entourent latéralement le conduit pneumatique de la vessie et vont du côté gauche et du côté droit sur le dos de l'estomac. Elles arrivent jusqu'à leur extrémité postérieure ou, ce qui arrive plus fréquemment, seulement derrière la moitié de sa longueur. Dans le premier cas elles ramifient dans la rate et mériteraient ainsi le nom *A. gastro-splenica*. Elles envoient sur la paroi de l'estomac des rares artères, irrégulières, et se ramifiant en arbre, lesquelles après un bref parcours se plongent dans l'épaisseur de la paroi.

La troisième branche *A. intestinalis dorsalis* s'abaisse directement à côté droit de l'oesophage derrière le foie (Fig. 1). En laissant à côté la partie pylorique de l'estomac, elle arrive sur l'intestin moyen immédiatement derrière la base des appendices pyloriques *(appendices pyloricae)* (Fig. 1, ap). Ici au dedans du mésentère et du tissu adipeux, elle passe dans la ligne médiane du dos de l'intestin et arrive comme un vaisseau longitudinal de l'intestin à l'anus. C'est alors un long tronc artériel, qui nourrit l'intestin moyen et postérieur, se ramifiant différemment dans

tous les deux segments mentionnés ci-dessus. Elle envoie à droite et à gauche dans l'intestin médian des courtes artères se ramifiant en arbre. Ces branches de l'intestin postérieur décrivent une courbe et s'unissent avec l'artère longitudinale au fond de ce segment du tube digestif. Grâce à cela il y a ici des vaisseaux, qui entourent l'intestin circulairement. Ils correspondent aux plis circulaires de la membrane muqueuse de l'intestin postérieur, dans la base duquel elles passent. Ces vaisseaux distinguent extérieurement l'intestin postérieur de l'intestin moyen.

A. gastro-subintestinalis (Fig. 1 Agsi) forme une seconde branche dérivant de l'artère principale du tube digestif, *A. coeliaco-mesenterica* (Fig. 1, Acm). Elle vascularise la partie ventrale de la paroi du tube digestif et en outre elle donne les branches à la vessie natatoire, au foie et à la rate.

Le tronc principal de l'artère se partage pareillement à *A. gastro-supraintestinalis* à deux artères de l'estomac et une artère de l'intestin. Leur trajet et la façon de l'embranchement rappellent beaucoup les rapports décrits ci-dessus; mais les premières artères se dirigent vers les parois dorsales et les secondes vers les parois ventrales du tube digestif.

Toutes les deux artères de l'estomac passent d'abord comme un tronc impair entre l'estomac propre *(corpus ventriculi)* et son segment pylorique. Après la bifurcation une branche va sur le sac principal de l'estomac comme *A. gastro-splenica* (Fig. 1 Ags), passe sur le pylore et arrive par les branches terminales à la rate. Les branches des artères nommées ci-dessus appartiennent à des types des vaisseaux courts et ramifiés en arbre. *A. subintestinalis* (Fig. 1 Asi) passe entre *Appendices pyloricae* à côté gauche de l'intestin et court plus loin comme un tronc longitudinal au milieu de sa paroi ventrale jusqu'à l'anus. Dans l'intestin postérieur elle se trouve dans la base du mésentère ventral, qui unit cette partie du tube digestif avec la paroi de l'abdomen. Les branches de l'*A. subintestinalis* (Fig. 1, Asi), différentes dans l'intestin moyen et l'intestin postérieur, se comportent comme les branches analogues d'*A. intestinalis dorsalis* (Fig. 1 Aid).

Il reste encore à dire quelques mots sur une artère mince *A. mesenterica primitiva* (Fig. 1 Amp), qui passe directement de l'aorte sur l'intestin postérieur à peu près au milieu de sa longueur. Elle ne joue qu'un rôle peu considérable pour l'alimenta-

tion du tube digestif, car elle unit l'aorte avec *A. intestinalis dorsalis*. Elle n'est qu'une anastomose artérielle. On la rencontre chez tous les poissons examinés comme un vaisseau constant, ce qui caractérise la truite, mais qui n'est nullement décrit chez les autres Téléostéens. On ne peut pas la comparer à *A. mesenterica anterior* ou *posterior* chez Elasmobranches, car les autres artères passent autrement et chacune d'elles se termine par un faisceau de branches.

Une lumière sur la signification de cette artère donnent les recherches du développement. Chez l'embryon de la truite, 9 mm de longueur (Grodziński), de l'aorte passe sur le dos de l'intestin postérieur un nombre de petites artères, qui pénètrent à travers les parois de l'intestin postérieur en réseaux. A part de cela elles forment une artère longitudinale dorsale de l'intestin, décrite chez les poissons adultes comme *A. intestinalis dorsalis*. Les anastomoses entre l'aorte et *A. intestinalis dorsalis* existent donc depuis l'origine. Durant leur développement toutes les artères disparaissent, sauf une qui survit des stades embryonnaires sans un plus grand changement jusqu'au moment, où les poissons sont adultes. C'est pour cela qu'elle mérite d'être appelée *A. mesenterica primitiva*.

Les veines du tube digestif de la truite accompagnent très exactement les artères et elles peuvent être situées près d'elles, au-dessous d'elles ou superposées. Les branches plus minces de l'artère sont accompagnées souvent par deux veines, qui les entourent des deux côtés. C'est seulement *A. mesenterica primitiva* qui ne possède pas la veine satellite. La divergence dans le système des artères et des veines se montre dans le segment antérieur de la cavité thoracique. Ici les artères émergent de l'aorte par un seul vaisseau, les veines cependant se réunissent par un seul vaisseau au foie.

La veine principale du tube digestif, la veine porte *V. portae hepatis* (Fig. 1, Vph) est un tronc court et épais, qui entre dans l'épaisseur du foie. La veine porte est formée par deux systèmes veineux, qui ont le même trajet que les artères. A cause de cela on peut les appeler du nom des artères voisines. Le premier système *V. gastro-supraintestinalis* (Fig. 1, Vgsp) se compose de *V. gastrica dorsalis* (Fig. 1, Vgd) *sin.* et *dextra* et *V. intestinalis dorsalis*. La deuxième *V. gastro-subintestinalis* (Fig. 1, Vgsi) se

compose de *V. gastrica ventralis*, *V. pylorico-splenica* (A. Vps) et *V. subintestinalis*. *V. subintestinalis* mérite une mention spéciale, car elle paraît déjà chez les très jeunes embryons comme une union immédiate entre la veine caudale et le coeur. Chez les embryons plus agés disparaît la continuité de ce tronc veineux dans la région de l'anus et le segment près du coeur. Et alors naissent de lui les vaisseaux *V. caudalis*, *subintestinalis*, *portae hepatis* et *hepatica* (Grodziński).

La veine la plus agée du tube digestif de la truite est *V. subintestinalis*. Toutes les autres veines sont nées plus tard et sont en réalité leurs branches latérales. Puisqu'elles parviennent à un très grand volume, on ne peut pas donner aux vaisseaux des Poissons adultes, les noms selon la hiérarchie du développement; leurs racines et leur volume servent de base de la nomenclature. De là aussi *V. subintestinalis* (Fig. 1, Vsi) apparaît dans la description anatomique comme une des branches de *V. gastro-subintestinalis* (Fig. 1, Vgsi).

A la frontière de l'intestin moyen et postérieur, parcourt une veine oblique sur le côté droit de la paroi de l'intestin, qui unit toutes les deux veines longitudinales et intestinales. Elle diffère des autres veines de cette région du corps par un parcours oblique et non pas perpendiculaire vers un axe long le l'intestin. Elle les surpasse par sa grosseur et chez tous les Poissons examinés elle est située asymétriquement seulement à côté droit du canal intestinal. Elle aurait été une des veines de la paroi de l'intestin postérieur mais un peu modifiée. En se basant sur l'image microscopique de l'intestin on ne peut rien dire de la cause d'une telle apparence.

Dans le mésentère ventral de l'intestin postérieur il y a plusieurs (vers 7) veines *Vv. mesentericae ventrales*, dont le commencement se trouve dans la paroi du ventre, et les segments terminaux se jettent dans *V. subintestinalis*.

Vv. mesentericae ventrales (Fig. 1, Vmv) particulières à la Truite doivent leur existence à la présence du mésentère ventral. Car nous savons que les artères du mésentère dorsal *(Aa. mesentericae)* de l'intestin chez une lamproie dépérissent en même temps que le mésentère (Hatter). Puisque les Poissons du genre *Perca*, *Clupea* possèdent également le mésentère ventral dans cette région du corps, il faudrait attendre, que là se trouveront aussi les vei-

nes analogues. Le mésentère ventral de l'intestin postérieur de la Truite n'est pas l'état primitif, car il est né (Boecke) comme une réunion secondaire; de là on ne peut pas attribuer aux veines du mésentère ventral une signification plus considérable au point de vue de l'anatomie comparée.

Les vaisseaux sanguins du tube digestif du barbeau

Le tube digestif du Barbeau et son système des vaisseaux sanguins sont tout à fait autres que celui de la Truite. Les artères et les veines analogues vont à part, tandis que chez la Truite elles passaient les uns à côté des autres ou les uns sur les autres. Le principal et l'unique tronc artériel de l'intestin passe de l'aorte sur le tube digestif: *A. coeliaco-mesenterica* (Fig. 2, Acm). Il arrive à l'oesophage, de là il passe sur d'autres segments de l'intestin, envoyant sur leur paroi un nombre de petites ou de plus grandes branches, se ramifiant en arbre. A la hauteur de la vésicule biliaire (Fig. 2, Vf) cette artère envoie une branche plus forte *A. intestinalis prima* (Fig. 2, Aip). Elle passe du côté droit de la vésicule biliaire, envoyant de plus petites artères sur sa paroi, elle se dirige ensuite sur la surface ventrale du segment antérieur de l'intestin et le vascularise presque jusqu'à sa courbure. Les petits rameaux de cette artère longitudinale se distribuent sur la moitié ventrale de l'intestin.

La seconde branche de l'artère *A. intestinalis secunda* (Fig. 2, Ais) aussi forte que la précédente, mais un peu plus courte, vascularise les parois dorsales du segment antérieur de l'intestin; c'est-à-dire toutes les deux ensemble avec l'artère précédente servent le même segment du tube digestif, en quoi la première se ramifie dans la partie inférieure et la seconde dans sa partie dorsale. La troisième artère *A. intestinalis tertia* (Fig. 2, Ait) sort perpendiculairement de *A. coeliaco-mesenterica* et croise le segment médian et postérieur de l'intestin, formant en même temps quelques plus petites artères, qui vascularisent les segments voisins du tube digestif. Dans une petite distance de l'artère perpendiculaire *A. coeliaco-mesenterica* se partage en deux artères presque de la même grosseur. L'une d'elles *A. intestinalis quarta* (Fig. 2, Aiq) court dans toute sa longueur sur la paroi du segment médian de l'intestin, formant quelques plus petites branches. La

seconde *A. intestinalis quinta* (Fig. 2, Aiqi) passe obliquement sur la paroi de l'intestin postérieur, et court sur lui jusqu'à l'anus.

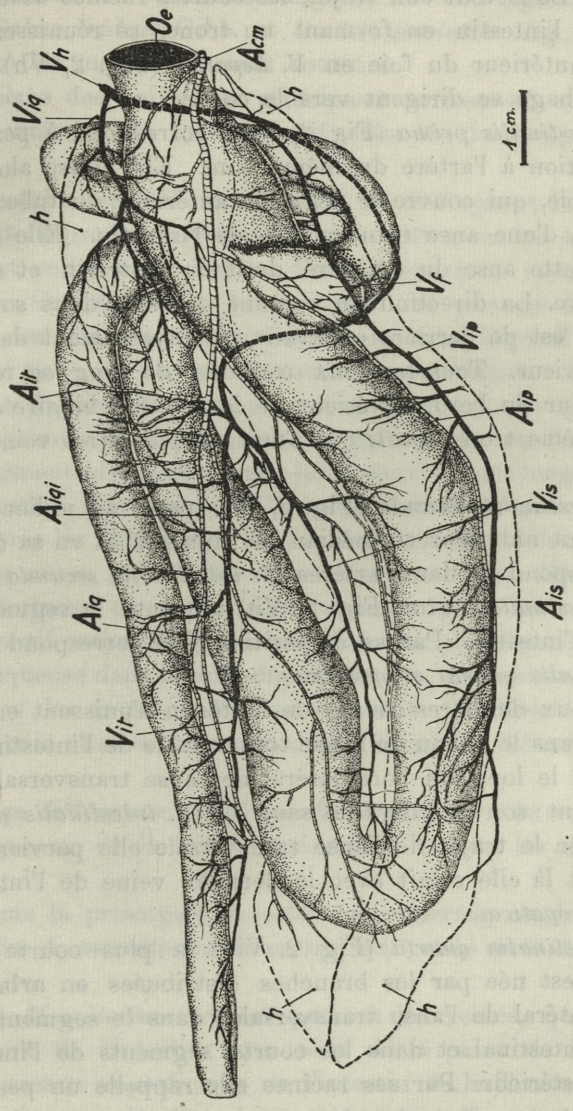

Fig. 2. Le tube digestif du Barbeau (*Barbus fluviatilis* Ag).

Dans tout son trajet elle envoie de plus petites branches sur la partie de l'intestin mentionnée ci-dessus.

Les veines du tube digestif parcourent comme les vaisseaux longitudinaux dans les lobes du foie, qui entourent les anses de l'intestin. Dans tout son trajet, les courtes racines descendent des parois de l'intestin en formant un tronc, se réunissent dans le segment antérieur du foie en *V. hepatica* (Fig. 2, Vh) et le long de l'oesophage se dirigent vers le coeur.

V. intestinalis prima (Fig. 2, Vip) correspond à peu près par sa disposition à l'artère du même nom. Elle passe alors dans le lobe du foie, qui couvre le segment antérieur du tube digestif et une partie d'une anse transversale de l'intestin. Elle ramasse le sang de cette anse du cylindre droit de l'intestin et de la vésicule biliaire. La direction du courant de sang dans son segment postérieur est de derrière en avant, va inversement dans le segment antérieur. Tous les deux courants de sang se rencontrent à la hauteur du bord postérieur de la vésicule biliaire et ils vont dans le même tronc court, qui s'unit avec d'autres veines de l'intestin.

V. intestinalis secunda (Fig. 2, Vis) passe au milieu de l'anse du segment antérieur et médian de l'intestin et vu sa disposition elle correspond à deux artères *A. intestinalis secunda* et *tertia.*

V. intestinalis tertia (Fig. 2, Vit) alimente le segment postérieur de l'intestin. Par sa disposition elle correspond à l'artère *A. intestinalis quarta* et *quinta.*

Les deux dernières veines de l'intestin s'unissent en un tronc commun dans le genou de l'anse transversale de l'intestin. Ce vaisseau court le long du bord latéral de l'anse transversale, en prenant durant son parcours le sang de *V. intestinalis prima.* En accord avec le trajet de l'anse transversale elle parvient sur l'oesophage et là elle s'unit avec la dernière veine de l'intestin, formant *V. hepatica.*

V. intestinalis quarta (Fig. 2, Viq) la plus courte veine de l'intestin, est née par les branches distribuées en arbre dans le segment latéral de l'anse transversale, dans le segment antérieur du tube intestinal et dans les courts segments de l'intestin médian et postérieur. Par ses racines elle rappelle un peu *A. intestinalis tertia.*

Les veines fines, ramifiées sur les parois du tube digestif et distribuées en arbre correspondent aux semblables artères.

Resumé

On a examiné les vaisseaux sanguins du tube digestif de deux Poissons *Salmo irideus* Gibb. et *Barbus fluviatilis* Ag., auxquels on a injecté les masses de deux couleurs.

Le système des vaisseaux principaux correspond exactement à l'aspect extérieur du tube digestif chez les deux espèces examinées.

Dans le tube digestif de la Truite se distinguent l'oesophage, l'estomac et le propre intestin. On voit nettement les artèrres de l'estomac et celles de l'intestin. Les artères sont accompagnées des veines. Correspondant au système des plis de la tunique muqueuse, les vaisseaux superficiaux du tube digestif se partagent en arbre ou entourent l'intestin circulairement.

Le tube digestif du Barbeau est un long cylindre qui s'amincit graduellement en arrière, sans se différencier en l'estomac et d'autres segments. L'intestin forme les circonvolutions longitudinales et transversales. Les artères de l'intestin sortent du tronc principal les unes après les autres dans les petites distances et elles se posent le long des anses intestinales en se distribuant sur elles par les branches formées en arbre. Ces vaisseaux sont les mêmes sur le tube digestif entier, ce qui correspond aux plis identiques de la tunique muqueuse dans le tube digestif entier. Les veines n'accompagnent pas les artères, elles ne reposent pas directement sur l'intestin, mais elles se trouvent dans l'intérieur d'énormes lobes du foie.

Outre les différences, résultant de la structure du tube digestif, les vaisseaux de la Truite présentent encore les différences suivantes:

1. Hormis la principale *A. coeliaco-mesenterica*, conduit le sang sur l'intestin *A. mesenterica primitiva*, qui est le reste du vaisseau embryonnaire.

2. Dans *Mesenterium ventral* passent les veines, qui unissent les vaisseaux de l'intestin avec ceux de la paroi de l'abdomen.

Les vaisseaux superficiaux de l'intestin de la Truite rappelent aussi les vaisseaux des Selachiens *(Mustelus)*. Tous les deux possèdent *V. subintestinalis*, outre cela les artères et les veines de l'estomac, les artères longitudinales et les veines de l'intestin propre

passent pareillement. Les vaisseaux sanguins du Barbeau diffèrent tout à fait par l'arrangement de la Truite et des Selachiens, ce qui s'explique par une autre structure du tube digestif.

Je veux ici remercier cordialement Mr. le prof. Grodziński de son grand intérêt à mon travail et de son aide considérable qu'il m'a apporté dans la préparation du présent travail.

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Explication des figures

Les figures sont faites à l'aide d'un appareil d'Abbé.

Les contours des lobes du foie sont marqués au moyen de courts traits. Les artères sont marquées par les lignes vergés, les veines par une ligne noire. Un trait ajouté à la figure, montre l'agrandissement linéaire de la préparation.

Signification de l'abréviation sur les figures

am — Aorta mediana
Acm — Arteria coeliaco-mesenterica
Agsi — „ gastro-subintestinalis
Aip — Arteria intestinalis prima
Ais — „ „ secunda
Ait — „ „ tertia
Aiq — Arteria intestinalis quarta
Aiqi — „ „ quinta
Amp — „ mesenterica primitiva
ap — Appendices pyloricae
AVgd — Arteria et Vena gastricae dorsales

AVgs — Arteria et Vena gastro-splenicae
AVps — „ „ pylorico-splenicae
AVgsp — „ „ gastro-supra-intestinales
AVid — „ „ intestinales dorsales
AVsi — „ „ subintestinales
cv — Corpus ventriculi
dp — Ductus pneumaticus
h — Hepar
l — Lien
pg — Paries abdominis
Vf — Vesica felea
Vh — Vena hepatica
Vip — „ intestinalis prima
Vis — „ „ secunda
Vit — „ „ tertia
Viq — „ „ quarta
Vmw — „ mesentericae ventrales
Vph — „ portae hepatis

Doświadczenia nad plastycznością instynktu u gąsienic topielki (Nymphula nymphaeata L.*) (Lepidoptera-Pyralidae). — Experiments on the plasticity of instinct in caterpillars of Nymphula nymphaeata* L. *(Lepidoptera-Pyralidae).*

Mémoire

de M^lle^ A. MIKŁASZEWSKA,

présenté le 10 Novembre 1947 par M. Z. Grodziński m. c.

Introduction

The concept of instinct, analysed since 2000 years from various points of view (Ziegler 1920) has become recently the object of an animated discussion. While formerly, the instinct was understood as acts performed by a species or race of animals strictly according some scheme, so as to repeat from one generation into another in a sort of unchanging automatism — later on, one came to the conviction that the acts of instinct are more or less plastic, and that the animals in their instinctive behaviour are able to adapt themselves in a certain degree to changed conditions. This plasticity of acts of instinct has induced some investigators as Loeser (1930, 1940) and Dembowski (1933 a, b, 1937) to utter the opinion that the concept of instinct is untenable and should be recognized obsolete. This point of view met with a warm protest from other authors (Garbowski 1935, Szuman & Skowron 1934). The discussion remained open.

To solve the problem of plasticity of instinct in a given species it is indispensable to acquaint oneself with some of its hereditary schemes and to know how far they can deviate under different conditions. To put it otherwise it is necessary to investigate the relation of instinct that is to say inborn psychic faculty to the ability of recognition or experiences acquired during the life of the individual. All this stands in close connection with reciprocal

relation of instinct and intelligence in animals (Garbowski 1936, Wojtusiak 1938).

The phenomena of the plasticity of instinct have been investigated lately on materials belonging to different groups of animals, that of invertebrates being represented by larvae of caddisflies *(Trichoptera)* repairing their houses (Gorter 1931, Dembowski 1933 a, b, 1937, Teyrovsky 1934, Frankhauser & Reik 1935). These investigations served to Dembowski as a basis for his above mentioned theoretical considerations. Adequate observations were made also on caterpillars of butterflies *Dicranura* and *Cerura* (Garbowski 1936) and *Cataclysta lemnata* L. (Natanson-Grodzińska 1932), and showed a prominent degree of plasticity of instinct in these insects as well as it has been established for bees, ants, termites a. s. o. (for more detailed literature see Maidl 1934).

Material

My experiments referred to the question of plasticity of instinct in caterpillars of *Nymphula (Hydrocampa) nymphaeata* L. living in fresh water and belongig to the family *Pyralidae.* The caterpillars of this species inhabit ponds and keep on the surface of water among the leaves of *Nymphaea alba* L., nenuphar (*Nuphar luteum* L.) or pond weed *Potamogeton natans* L. (Lampert 1925, Brehm 1926, Hering 1926). The leaves of these plants provide the caterpillars both with food and building material. In this respect their habits remember those of caterpillars of *Cataclysta lemnata* L. with that difference that the latter construct their houses from water lentil (*Lemna minor* L.) and accordingly to their respective age use from 2 to 50 leaves to make a single house. The caterpillars of *Nymphula nymphaeata* always construct their houses with only 2 oval pieces cut out of *Nymphaea alba* or other about mentioned species of plants and stuck together.

In their first stages of development the caterpillars of *Nymphula nymphaeata* drive canals inside the leaves (Hering 1935—37). In further stages they get out of their nourishing plant, cut a tiny oval out of the leaf and fix the small disk with their spinning to the underside of the leaf. Later on the upper disk is added to cover the house which is thus composed of two agglutinate pieces the upper and the lower one.

To secure most uniform possible results the experiments on caterpillars were confined only to the last stage of development, it is that one in which they construct their houses out of two eliptical disks.

The experiments were carried through in the year 1945 at the Department of Psychology and Ethology of Animals, Jagellonian University, under the guidance of Doc. Dr R. J. Wojtusiak.

Problem

The problem investigated was that of building instinct in caterpillars of *Nymphula nymphaeata* L. The house-building was observed under:

1. natural conditions or approaching to natural conditions in aquarium with leaves of *Nymphaea alba*,

2. artificial conditions it is such in which the caterpillars had no leaves of *Nymphaea alba* at their disposal but received instead other materials to build their houses either a) occuring in nature as other water plants, grasses or tree-leaves, or b) artificial products as coloured papers of different thickness, cork sheets and thread,

the ability to recognize the different building materials and the faculty of choosing them were tested by experiments, in which:

3. the caterpillars deprived of their houses were given a choice between natural and artificial building materials,

4. the caterpillars deprived of their own houses were given houses of other caterpillars belonging to the same species or paper houses different in shape and colour constructed by the author or glass tubes,

5. the caterpillars left in their own houses were given no other source of food than their own houses or those belonging to other individuals. The behaviour of caterpillars towards their own or foreign houses was then specially studied,

6. another set of experiments consisted in damaging intentionally the houses and observing how the caterpillars executed their repair,

7. special attention was devoted to the biological significance of the houses built by the caterpillars.

I. House building under natural conditions

From time to time the caterpillars leave their houses to build larger new ones. This takes place mostly after the larvae had shed their skin. The caterpillar begins its work of a new house by making an incision on the underside of a *Nymphaea* leaf, preferably near the edge or beginning at some accidental hole and proceeds so as to cut an elliptical disk (fig. 1 a, b, d, e). This

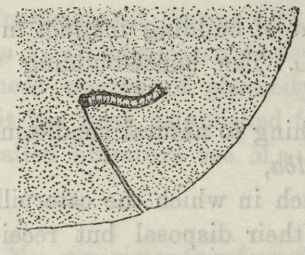


Fig. 1 a. Cutting of oval disk on the edge of *Nymphaea alba* leave.

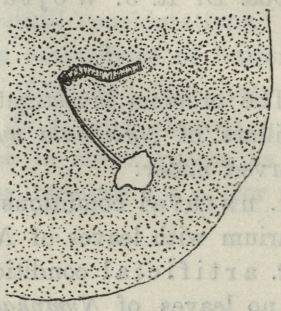


Fig. 1 b. Cutting of oval disk from the centre of leave from the hole eating by the other animals.

work takes relatively a long time, about two three hours, as the caterpillar stops its work from time to time with each stronger motion of the leaf or of the water. The disk forms a half of the future house. It is pulled by the caterpillar and fixed on the

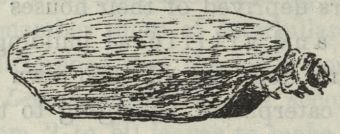


Fig. 1 c. House of caterpillar of *Nymphula nymphaeata* seeing from side and from the top (magnified).

underside of the leaf with thread secreted by the spinning glands. Between the disk and the leaf a little free space left serves for refuge to the caterpillar that remains there some time, the length of which differs with different individuals. The next stage of house building consist in cutting round the little disk in the leaf itself the upper half of the house which is as a rule larger than the lower disk (fig. 1 c).

The construction of the whole house takes from 12 to 48 hours.

II. House building under artificial conditions

This second group of experiments had for purpose to investigate whether the caterpillars are unable to use for house construction materials other than the *Nymphaea* leaves.

1. Materials existing in nature

Besides the *Nymphaea*, leaves of various species of water plants, grasses and trees have been used in the experiments. The

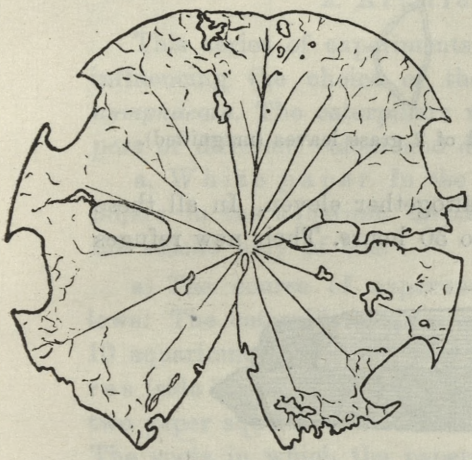


Fig. 1 d. Leave of *Nymphaea alba* from which the caterpillar had eaten sheats for the houses.

Fig. 1 e. Leaf of *Nymphaea alba* from which the caterpillars had eaten sheats for the houses and an natural house placed perpendicularly to the leaf (natural size).

caterpillars were with great care taken out of their houses and placed in a crystallizing bassin with a particular plant material.

a. Leaves belonging to various species of water plants *Nymphaea* excluded. The caterpillars deprived of their houses behaved in these experiments most recently, sinking to the bottom or coming up to the surface of water. After more than ten hours the construction began, such plants only being used whose leaves were large enough to cut out disks corresponding in size to disks made of *Nymphaea*. It seemed as if the

caterpillars were unable to build houses of a smaller size or to paste them together from smaller particles.

b. Grass blades. The behaviour was very similar to that of the former experiments. The caterpillars were uneasy and when past more than 10 hours they began to build their houses, they proceeded in a different way using according to their width two, three or even four grass blades to make one house (fig. 2 a, b, c).

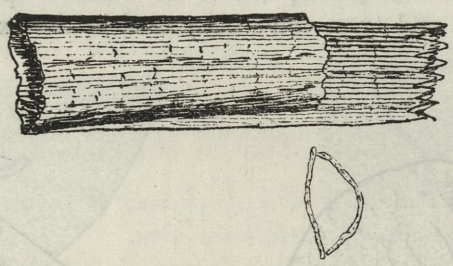


Fig. 2 a. The house build up by aid of 2 grass leaves (magnified).

The number of experiments was altogether eleven. In all these cases the house was ready in 25 to 30 hours. Their new refuges

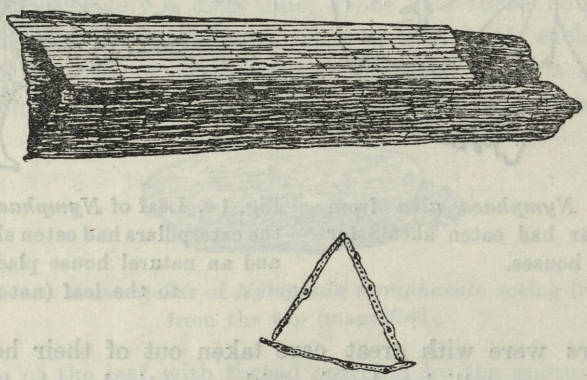


Fig. 2 b. The house build up by aid of 3 grass leaves (magnified).

served them for a longer time. During a fortnight — the time of observations all the caterpillars remained living.

c. Tree leaves. Caterpillars held in an aquarium into which mulberry leaves had been thrown showed also much restlessness but no attempt to build houses.

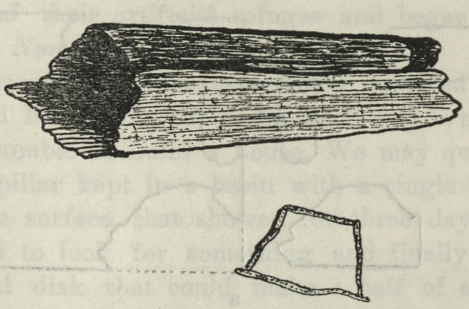


Fig. 2 c. The house build up by aid of 4 grass leaves (magnified).

2. Artificial materials

This series of experiments had the purpose to detect factors influencing the choice of the building materials in *Nymphula nymphaeata*. The caterpillars were offered artificial products: papers of different colour and different thickness, cork and thread.

a. White paper. In the first set of experiments the caterpillars in the aquarium disposed of several pieces of paper, in the second only of one.

a) The course of experiments was in the first case as follows: The caterpillars taken out of their houses were located in 10 aquariums containing each several white paper squares (side 3 cm). Within 12 hours each caterpillar pasted together two paper squares without cutting out of them any eliptical disks. The spots in which the papers were joined together by the glutinous spinning substance were disposed however so as to form a hind of elipse as is the case in a normal house. During the 12 following hours the caterpillars behaved differently. Some of them began to cut out eliptical houses from the paper squares (fig. 3 a, b, c, d), others preferred to remain in their provisory refuge between the paper squares.

After three days, the caterpillars residing in their paper houses were supplied with *Nymphaea* leaves. They began at once to feed intensely upon the leaves but though they had now their natural building material they did not change their houses. During 12 hours a certain number of caterpillars kept on feeding and remained in paper houses, the rest after a more or less longer

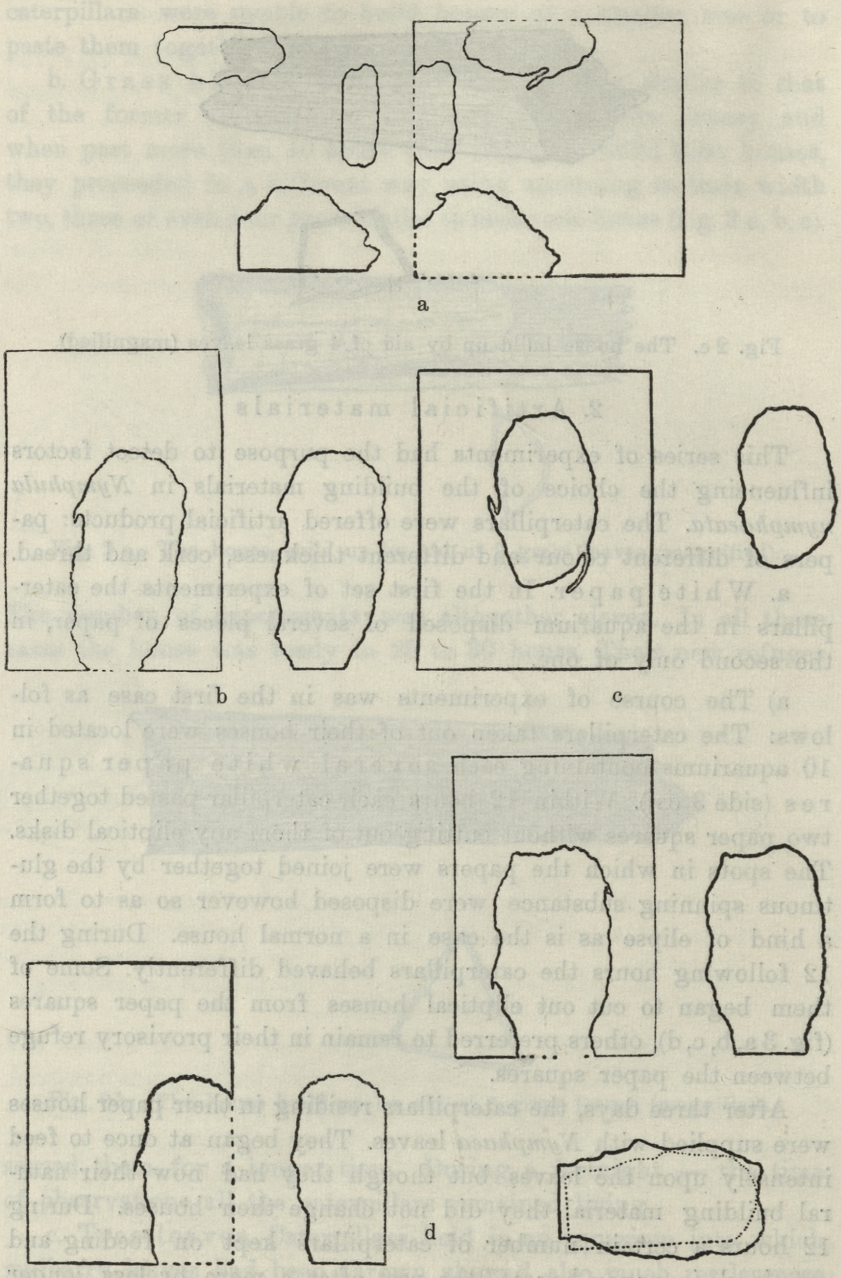


Fig. 3 a, b, c, d. Disks cut from white and coloured papers. On the fig. 3 d the manner of glueing of the disk is evident (natural size).

time abandoned their artificial refuges and began to build new ones from the *Nymphaea* leaves.

b) In the second case, the caterpillars deprived of their natural houses and having at their disposal only one piece of paper were unable to build a house. We may quote the example of a caterpillar kept in a basin with a single piece of paper floating on the surface, that showed for three days much excitement, seemed to look for something and finally began to cut out an eliptical disk that could make a half of a house. With this paper disk the caterpillar sank to the bottom of the basin and again emerged on the surface, repeating these trials many times until it had crawled upon the paper and remained there for eight hours without cutting it nor changing the position. Unfortunately the observations could not go as far as to tell what would be the behaviour of the caterpillar had she suceeded in getting under the paper. It is highly probable that sinking to the bottom and coming up to the surface are trials enabling the caterpillar to get under the paper and stick there the disk she had already cut. In such case the caterpillar would behave differently as in natural conditions in which the disk is slowly moved to the underside of the leaf where it is fastened.

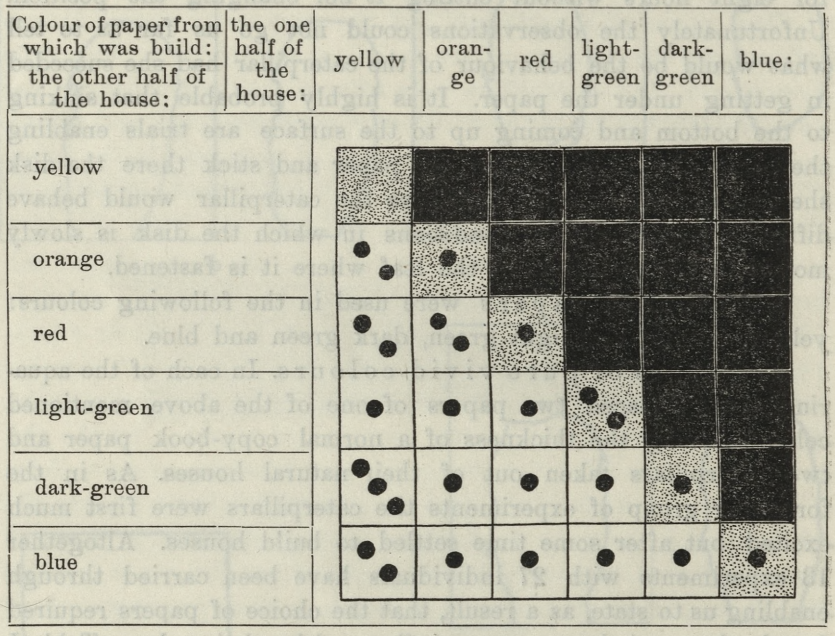
b. Coloured papers were used in the following colours: yellow, orange, red, light green, dark green and blue.

a) Papers of pure vivid colours. In each of the aquariums were placed two papers of one of the above mentioned colours having the thickness of a normal copy-book paper and two caterpillars taken out of their natural houses. As in the foregoing group of experiments the caterpillars were first much excited but after some time settled to build houses. Altogether 13 experiments with 27 individuals have been carried through enabling us to state, as a result, that the choice of papers required for the houses is by no means influenced by their colour. Table I gives the best illustration of the fact. As it may be seen each colour was used in regular succession. The various combinations of colours used in the construction by the caterpillars alternated with papers of a single hue. The quantity results are given in diagram, in which each »house« is marked by a black spot. Those of the dotted squares mean houses built of one colour paper.

TABLE I

Colour of papers:	yellow:	orange:	red:	light-green:	dark-green:	blue	Number of tests: 13
Number of the half of the »houses«:	9	9	9	10	9	8	Number of caterpillars: in 12 tests in each 2 caterpillars, in the first test 3 caterpillars; total 27 caterpillars
in %	16·7%	16·7%	16·7%	18·5%	16·7%	14·8%	Number of coloured papers in each test: 2

DIAGRAM I



b) Papers of pure vivid colours or with an admixture of white. In several other experiments the caterpillars were offered papers of pure vivid or pale-white satiated-colours. The intensity of colour seems to be of no importance. Houses were indiscriminately built both of pale or strongly coloured papers. In some cases one half of the house was pale, the other intensely coloured.

In order to ascertain what influence daylight or darkness may have upon the choice of colours some caterpillars were put into the aquarium with papers in the morning, some other in the evening. The results were verified generally at intervals of about 12 hours, for night experiments between 7 and 8 morning. As stated by former observations a caterpillar requires at least 12 hours to build a house. The experiments showed that the caterpillars proceed in the same way by day and by night, picking up papers at random and quite freely, unconcerned in their colour or the fact whether they are well lighted or remain in the dark.

c) Thickness of paper. Contrarily to the question of colours, the thickness and the quality of paper seem to play

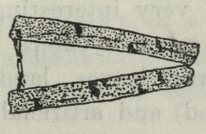


Fig. 4. House build from 2 cork sheats, in cross section (magnified).

a great role in house building. The experiments were analogous to those concerning colours. The caterpillars were offred three kinds of paper corresponding to tissue-, copy-book paper and a thin cardboard. Most houses were build of copy-book paper which was sufficiently resistent to water. Other sort of paper was used only when the »copy-book paper« was not there. Less resistent papers were of course never tried by the caterpillars as building material.

d) Thread. Having at their disposal thread alone the caterpillars did not try constructing houses.

e) Cork sheets were about 2 mm thick and had a surface of 1 cm^2. The caterpillars, after the habitual period of excitement caused by new conditions and known from previous experiments used them as building material and constructed within 24 hours new houses, composed each of two tiny sheets joined by thread so as to present some analogy with a slightly open book (fig. 4). The shape of these cork houses was rather irregular, the caterpillars using for their construction different »ready made« pieces of cork given to them.

After the houses had been completed the animals kept on showing great excitement, put themselves out of their houses almost entirely and sought for food. When a leaf of *Nymphaea* was placed in the aquarium a part of the caterpillars instantly left their cork houses while other began eating it eagerly without leaving their temporary »homes«. These latter abandoned the cork houses only after they had satisfied their hunger, leaving the house either at once, or replacing first, one of the cork halves of the house by a leaf cut side and then rejecting also the other cork side.

3. Materials existing in nature and artificial ones

a. Aquatic plants other than *Nymphaea alba* and coloured papers. A very interesting behaviour was that of caterpillars to which was given a choice between natural material (aquatic plants with narrow leaves, land grass blades on which the caterpillars never feed) and artificial material (papers of different colours). These experiments were carried through analogically to the former. Eight caterpillars were placed in an aquarium containing the above mentioned water plants plus some papers having the same colours as those used in the former coloured paper test. Past 24 hours each caterpillar constructed a house of its own, either from pure paper or from pure leaves. It was then that a *Nymphaea* leaf was presented to them. The caterpillars began feeding on it very intensely. After some time some of them left their houses (constructed with leaves other than *Nymphaea*). The houses were abandoned ot once or partially the two grass sides of the house being replaced gradually by *Nymphaea* leaf cuttings. It is highly characteristic that out of caterpillars residing in paper houses only one exchanged it against a natural *Nymphaea* leaf home. The rest i. e. four specimens remained in their former houses still for 3—5 days, what would confirm the conjecture that paper reminds the caterpillars the morphological structure of a *Nymphaea* leaf while narrow grass leaves are something quite foreign to them.

b. *Nymphaea alba* and coloured paper. Caterpillars placed in an aquarium with papers of many colours and *Nymphaea* leaves began after some time to build their houses from *Nymphaea* only.

Summing up the results of all these experiments, the caterpillars seem to be endowed with a special faculty to recognize artificial and natural building material. The materials used in the experiments have for the caterpillars a more or less pronounced degree of similarity to *Nymphaea* leaves. Copy-book paper is the most preferred building material. Next come the elongated narrow grass leaves and aquatic plants other than *Nymphaea*, while cork stands in the last place. All these building materials are used only when *Nymphaea* leaves are wanting. If this latter building material is put to their disposal the caterpillars make use of it without any hesitation. The thickness and the structure of the material, may be also its chemical properties seem to play a foremost role in *Nymphula nymphaeata* recognizing the proper sort of material. All these agents and may be still others which we did not analyse explain to a certain measure how the *Nymphaea* leaves are unmistakably distinguished by the *Nymphula* caterpillars from other materials as well natural as artificial.

III. The attitude of caterpillars to whom their own houses had been taken, towards ready made houses

The second problem dealt with was the behaviour of caterpillars of *Nymphula nymphaeata* whose houses had been replaced by ready made natural or artificial ones. The natural houses were made out of *Nymphaea* leaves. The caterpillars had abandoned them spontaneously or had been forced to do it. Grass made houses and artificial paper houses both abandoned by the caterpillars were used also in this experiment, as well as artificial houses of my own construction. These latter were made out of paper and sawn with thin thread.

1. Natural houses

a. Empty houses, no *Nymphaea* leaves. The caterpillars were placed in an aquarium with several different sized natural empty houses and no other building material nor *Nymphaea alba* leaves that could serve them for food. The caterpillars began at first to swim with great excitement, seemed to look for something, approached the houses, visiting and leaving them. After some time they began to occupy them, some of the caterpillars leaving

the houses again and trying to find other ones. The observations were carried for 12 hours. Out of the 9 caterpillars used in this experiment only one finally did not occupy a house.

b. Empty houses — *Nymphaea* leaves present. Done in the same way as the former, this experiment comprised 4 tests with 6 caterpillars each. In the first two tests the caterpillars were given to their disposal foreign houses, in the second two, they were offered their own houses. The observations lasted

TABLE II

Number of caterpillars:		Result of choice in caterpillars which disposed:		Relation of the choosing reactions in %	Number of caterpillars:		Result of choice in caterpillars which disposed:		Relation of the choosing reactions in %
in the I test:	6	the own house: 6	*Nymphaea* leaves: —	the own house: *Nymphaea* leaves: 100%	in the III test:	6	the foreign house *Nymphaea* leaves: 5	*Nymphaea* leaves: 1	the foreign house: *Nymphaea* leaves: 83%
in the II test:	6	6	—	100%	in the IV test:	6	4	2	66%

12 hours. The results are given in table II. It appears clearly that in most of the cases the caterpillars choose ready made houses instead of building new ones from the *Nymphaea* leaves. No mistakes commited in the I and II series of experiments in which the caterpillars had for disposal their own houses besides the *Nymphaea* leaves and 7% and 34% mistakes in experiments III and IV, in which the caterpillars were offered foreign houses besides the *Nymphaea* leaves, seem to point to the fact the caterpillars recognize their own houses and take them more readily than the foreign ones.

The observations showed that the houses are occupied immediately only by such caterpillars that were removed from them not long ago. If the houses out of which the caterpillars had been removed were left in water for a longer time and the caterpil-

lars could reach them only after a longer space of time, their behaviour was similar to that with foreign houses. The freshly abandoned houses must consequently possess a set of stimuli, probably of chemical nature which enable the animals to tell them as their »own« from other houses.

c. Empty grass houses. Experiments identical to the former with the exception that the houses were built of grass as in exqeriments of the series 1 b. The caterpillars occupied houses either in this case. After 12 hours *Nymphaea* leaves were offered to them. A part of caterpillars left the houses and began building new ones out of the leaves. Others leaving one half of the old grass house exchanged the other half against a newly built *Nymphaea* wall. An insignificant percent (one caterpillar) out of the 8 specimens used remained for over 24 hours in the old house.

2. Artificial houses

a. Glass tubes used for the experiment had an open space of 2—4 mm. Deprived of their own houses, the caterpillars took up glass tubes, but did not stay in them longer than two hours, most of them leaving the tubes in a much shorter space of time. The reasons were obviously the difficulty to move in the glass tube owing to its slipperiness and the rather heavy weight of the tube making it difficult to keep on the water surface.

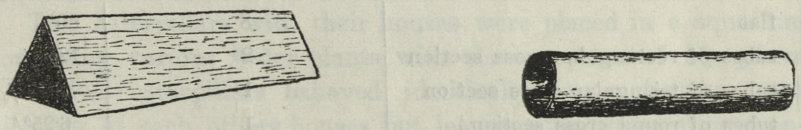


Fig. 5 a, b. Artificial houses constructed from the paper by the author (magnified).

It must be noticed that neither the transparency of the glass nor its colour does not play any role. In six experiments in which glass tubes covered with white or coloured paper were used the caterpillars entered them disregardful of their colour. Yet did not remain leaving them after a longer or shorter time.

b. Paper houses of different shape. The houses used for these experiments were about 2—3 cm long, had a triangular,

circular or rectangular cross section or were flat and similar to natural houses (fig. 5 a, b, c, d) sawn with thread of two paper oval pieces corresponding by their size to walls of a *Nymphaea*

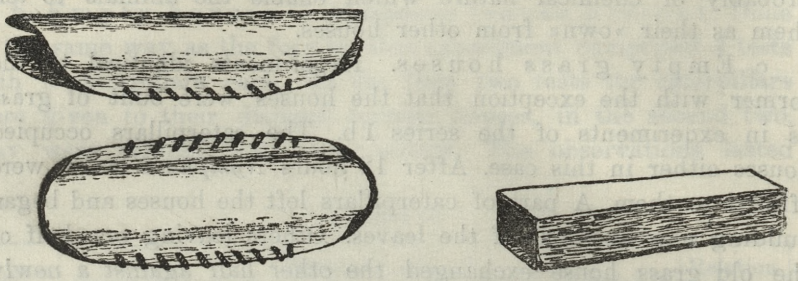


Fig. 5 c, d. Artificial houses constructed from the paper by the author (mugnified).

house. In sixteen tests, eight caterpillars took possession of flat paper houses, two entered houses with a rectangular, one a house with a triangular cross section and the last caterpillar occupied a circular paper tube (table III).

TABLE III

Caterpillars of *Nymphula nymphaeata* choosing and occupying paper houses of different shape. Number of tests: 16

Houses	Number of caterpillars	in %
flat	8	50%
tubes of rectangular cross section	2	12·5%
tubes of triangular cross section	1	6·25%
tubes of round cross section	1	6·25%
not occupied houses	4	25%

Some special tests proved that in this case also the colour nor its intensity did not play any role in the choice of a house.

IV. The attitude of caterpillars deprived of food towards *Nymphaea* houses

A special series of experiments was devoted to the problem of behaviour of caterpillars deprived of all sort of food but left in their natural houses.

a. A single caterpillar in a basin

In a simple rearing glass basin with no other plant food was placed one caterpillar with its house. The first four days the animal seemed very excited, emerged from the house and swam on the surface. The fifth day it began to gnaw round the edges of the house so that its surface was getting smaller and smaller It is to be noticed however that the caterpillar did not touch the central part of the house. Nine identical tests have been carried through. The caterpillars lived for ten days and their houses existed through strongly damaged.

b. Two caterpillars in one basin

Two caterpillars with their houses were placed in a basin. The first two days the caterpillars showed much excitement caused by a new surrounding and lack of food. The third day they began to prey upon each others houses. Eleven tests were carried through in all of which the caterpillars behaved identically, gnawing the houses of their companions but never touching their own houses. The houses were gnawed at first at the edges and then perforated in their upper central part; which the caterpillars never did preying upon their own »homes«.

c. Two caterpillars and water plants belonging to various species

Two caterpillars with their houses were placed in a aquarium containing various water plants with the exception of *Nymphaea alba*. The caterpillars bahaved identically as in former tests, nibbling at each others houses but leaving the water plants untouched. In these experiments as well as the former it has been stated that the size of the house or that of ceterpillar do not play a role when feeding. In some tests one caterpillar was much larger than the other. Consequently their respective houses were also of different size, and it was to be expected that the smaller caterpillars being weaker would have its house attacked first. It appeared however that the size has nothing to do here. Lerger caterpillar had their houses eaten much quicker than the smaller ones. Yet it was never observed that a caterpillar having to choose between two houses attacked its own one.

V. Repairing of damages

The forth problem referring to the plasticity of instinct in *Nymphula nymphaeata* was that the behaviour of caterpillars whose houses have been intentionally damaged. Different portions of the houses were most carefully cut out with sharp scissors so as to leave the caterpillar sitting inside uninjured. Operated in this way the houses with caterpillars were placed again in the aquarium.

1. Side of the house damaged. A piece of a lateral part of one half of a house has been cut so that the juncture of the two sides was damaged (fig. 6 a). After some time the cater-

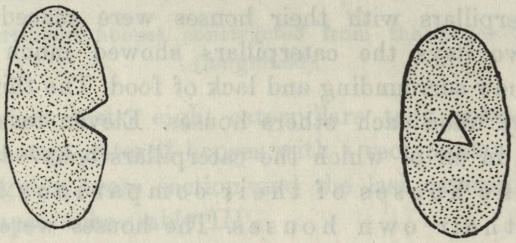


Fig. 6 a, b. The house disks cut out in the side (a), and in the midlle (b). (Near natural size).

pillars rejected the damaged half of the house and began to cut a new one in order to complete the wanting part.

2. Upper part of the house damaged. An opening was cut in the centre of the upper half of the house (fig. 6 b). As was in the former case the caterpillars after some time threw away the damaged upper part and made a new one.

3. Both upper and under part damaged. In this case the caterpillars abandoned the whole house and started a new construction from the *Nyphaea* leaves.

The first preliminary observations quoted above seem to show that the caterpillars reject rather than repair the damaged half of the house and make instead a completely new one. In this respect there is a visible difference between our caterpillars and the larvae of *Trichoptera*. A more detailed analysis of differences or analogies of behaviour in the larval stages of these two orders and a closer elucidation of the

plasticity of their building instinct may be brought by further special experiments which are planed to form the subject of a separate paper.

VI. The biological importance of house-building for the caterpillars of *Nymphula nymphaeata*

Constitutes the last problem to which our attention was devoted. According to the so far prevailing opinion, the house is a shelter against ennemies and unfavourable conditions of the environment (Doflein 1914). In order to investigate whether it has to fulfill also another role we made the following experiment:

A piece of wire, heavy enough was attached by means of a thin, soft thread to the lower part of a house, occupied by a caterpillar. Owing to the weight of the wire the house went down to the bottom. The caterpillar showed at first strong anxiety, tried to get back with the house to the surface and then after a relatively short time left the shelter. Six similar tests have been carried through and all caterpillars used in them behaved in the same way.

The results of these experiments as well as the observations made on caterpillars placed in glass tubes indicate that the *Nymphula nymphaeata* can live only in houses floating on the water surface. Only such houses can supply the caterpillar with the necessary amount of air to breathe. If the house is immerged more deeply water drives out the air and compels the caterpillar to leave the house. In a house floating on the surface of water the caterpillar is constantly surrounded by air.

Summary of results

The observations made on the building faculty of caterpillars *Nymphula nymphaeata* in their last developmental stages allow to state the existence of a well defined mode of behaving, whose inborn and hereditary character may serve as an ethological identifying feature of this species, based on the instinct. The caterpillars of this stage, placed in a water tank cantaining leaves of *Nymphaea alba* build flat houses of two oval pieces cut out of these leaves and stuck together at the edges by the spinning

substance. The leaves of *Nymphaea* serve at the same time for food.

This general mode of proceeding shown in normal conditions may deviate more or less when the conditions change what points to a rather vast plasticity of the instinct of building. In want of *Nymphaea* leaves the caterpillars use two, three or even four grass leaves and stick them together so that they take the shape of an irregular tube. In want of natural material, the caterpillars use for building purposes white or coloured strips of paper, more or less thick, cutting out together at the edge, so that the whole ressembles a natural house. In want of other material, the caterpillars use also cork. Having at their disposal *Nymphaea alba* and afore said artificial material, the caterpillars use only natural material i. e. the *Nymphaea* leaves. Only in the case when they have the choice between paper and grass leaves, paper is preferred. The choice among different substances is not influenced by their intensity of colour nor by the amount of white they contain but by structure, thickness, more or less extended dimensions and chemical properties of the material. Preferance is given to flat two dimensional substances, having the thickness of an ordinary copy-book and ressembling in some way their natural building material. In natural conditions these sort of factors combined with chemical stimuli of the feeding plants enable the caterpillars of *Nymphula nymphaeata* to find the adequate species of plant and to build the characteristic houses.

Deprived of houses and lacking all material to build, the caterpillars take willingly empty houses, preferring their own houses to alien ones. Artificial houses constructed by man are taken readily if only by their flat shape they resemble natural shelters.

Caterpillars occupying natural houses, placed in a tank with no other foot begin eating their shelters only in extreme necessity doing it only at the margins. Placed together with other individuals, they start eating houses of their companions gnawing not only at the margins but also at the central parts.

The caterpillars of *Nymphula nymphaeata* do not repair the damaged halves of their houses but throw them away and replace by new ones.

A house built of water plants has for the caterpillars of *Nymphula nymphaeata* a threefold importance, that of a shelter

and that of reserve food stock which the caterpillar exploits only in last necessity. The main role of a house is to assure the caterpillar a free breathing owing to the amount of air with which it is filled when floating on the surface. The caterpillars whose houses sink to the bottom because of an artificial weight attached to them, or which are compelled in want of other shelter to occupy a glass tube, heavier than water, are unable to remain long time under water, must leave their shelter and come up to the surface.

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Okolica graniczna tułowia i głowy u Salmo irideus Gibb., ze szczególnym uwzględnieniem układu krwionośnego — The Bordering Region of the Head and Trunk of the Salmo irideus Gibb. (with special references on its vascular system).

Mémoire

de M^me^ *L. SIKOROWA,*

présenté le 1 Décembre 1947 par M. Z. Grodziński m. c.

Problem and Material

The bordering region of the head and trunk of fishes have up to now seldom been the subject of separate study. Uniform territories, e.g. the head or the trunk, were more often described. It is however in this region that the principal circulatory organs of fishes are grouped, and here they enter the heart. Here the fins and the gills are placed.

The task undertaken was to describe the bordering region of the head and trunk of *Salmo irideus* Gibb, special attention was to be laid on the blood vessels of this region and on comparing them with the corresponding organs of the *Selachii.* The material for this work consisted of specimens of trout with the blood vessels filled with Prussian blue and red shellac injection dye. The specimens, about 20 cm in length, came from the trout-nursery in Ojcow. After having been injected from the caudal vessels the specimens were fixed with 10% formalin. To fascilitate the understanding of the circulatory system, the ventral wall of the trunk of a trout embryo, 22 mm in length, with its blood vessels injected, was made transparent in cedar oil. Adult trouts were fixed, prepared and observed through binocular microscope. In the course of dissecting numerous diagrams were made, which

later on were combined by several into final diagram. Owing to this method many details fixed in the drawings were not blurred by the further preparing process, even if they had been destroyed in the specimen itself. In order to compare the parts of the blood vessels already prepared with their topography and entire course, one head of a *Salmo*, made transparent in cedar oil, has been observed trough binocular microscope.

Topography of the region of the heart

The region of the heart, cone-shaped, is limited in its caudal part by the elements of the shoulder-girdle, and laterally by the gill chamber. The shoulder-girdle forms the protective cover of the heart from the ventral, the cleithrum from the lateral sides. The skeleton of the pectoral fins is connected with the shoulder-girdle.

The ventral muscles of the heart region are attached to the base of the ventral fins and to the shoulder-girdle. Their fibres are running straight and parallel to each other forming the *M. rectus abdominis* which completely covers the heart region from the outside. A longitudinal septum of connective tissue divides it into a left and right part. Between the *M. rectus* and the ribs are placed the oblique muscles, *M. obliquus externus et internus.*

The heart is surrounded from all sides by sturdy membranous sac called pericardium which tightly envelopes the heart walls. The external surface of the pericardium is grown together on all sides with the adjacent muscles, by which is made taut, and only its caudal part forming the *Septum pericardiaco-peritoneale* rests freely on the liver. In two places, at the front and at the back, where respectively the principal veins open into the heart and the *Truncus arteriosus* leaves, the pericardium is joined to the heart. For the rest the heart lies freely in the pericardium. The space between the heart wall and the pericardium forms the most cranial section of the body cavity, separated from it by the *Septum pericardiaco-peritoneale.* Immediately adjoining the septum at the back is the liver connected with the heart by the tube of the hepatic vein.

The vascular system of the ventral wall of the body

In the ventral wall of the trunk of the *Salmo irideus* Gibb. occur vascular trunks runnig longitudinally, according to the axis of the body. They are the big *V. abdominalis* running along the middle ligne of the abdomem immediately below the epidermis and lateraly to it the *A.* and *V. epigastricae* (Grodziński), situated immediately below the peritoneum. Besides these longitudinal vessels there occur small ventral branches of segmental vessels. The *V. abdominalis* of an adult trout ramifies in the region of the pectoral fins into two vessels, of which the right branch a stunded one, reaches the dorsal border of the pericardial sac. It does not exceed in length the laterally running *A.* and *V. epigastricae.* The left branch of this vessel encircles laterally the pericardial sac and, running along its wall forms an arch towards the back and enters the *Ductus Cuvieri* (Fig. 1. Va). In its entire course the *V. abdominalis* receives the small branches of the dermal veins and the small ventral branches of the segmental veins.

The *A.* and *V. epigastricae* connect the region of the shoulder-girdle with the region of the pelvis. They run on both sides of the trunk between the peritoneum and the muscles, on the upper lateral edge of the *M. rectus abdominis.* Almost throughout their course the walls of the artery and of the vein adjoin each other.

Their course, both of the vein and the artery, is undulating. In my material the *A. epigastrica* is in its entire course sturdier than its homonamic vein. In some individuals the situation may be reversed (Górkiewiczowa). In the region of the shoulder-girdle both vessels diverge from the middle abdominal line in the direction of the pectoral fins and at their base join the *A.* and *V. subclavia* system. In one specimen the *A epigastrica* of either side joins the *A. subclavia* by means of the *A. coracoidea* while the *V. epigastrica* runs down in a curve and opens into the *Ductus Cuvieri* (Fig. 1. Ve. Ae).

The subclavian vascular system

The *Aa. subclaviae* of the *Salmo irideus* Gibb. are strong branches of the aorta ramifying approximately at the height of the *Apex cordis* to both sides and running in an arch towards the ventral side under the coracoid. Here they divide into bran-

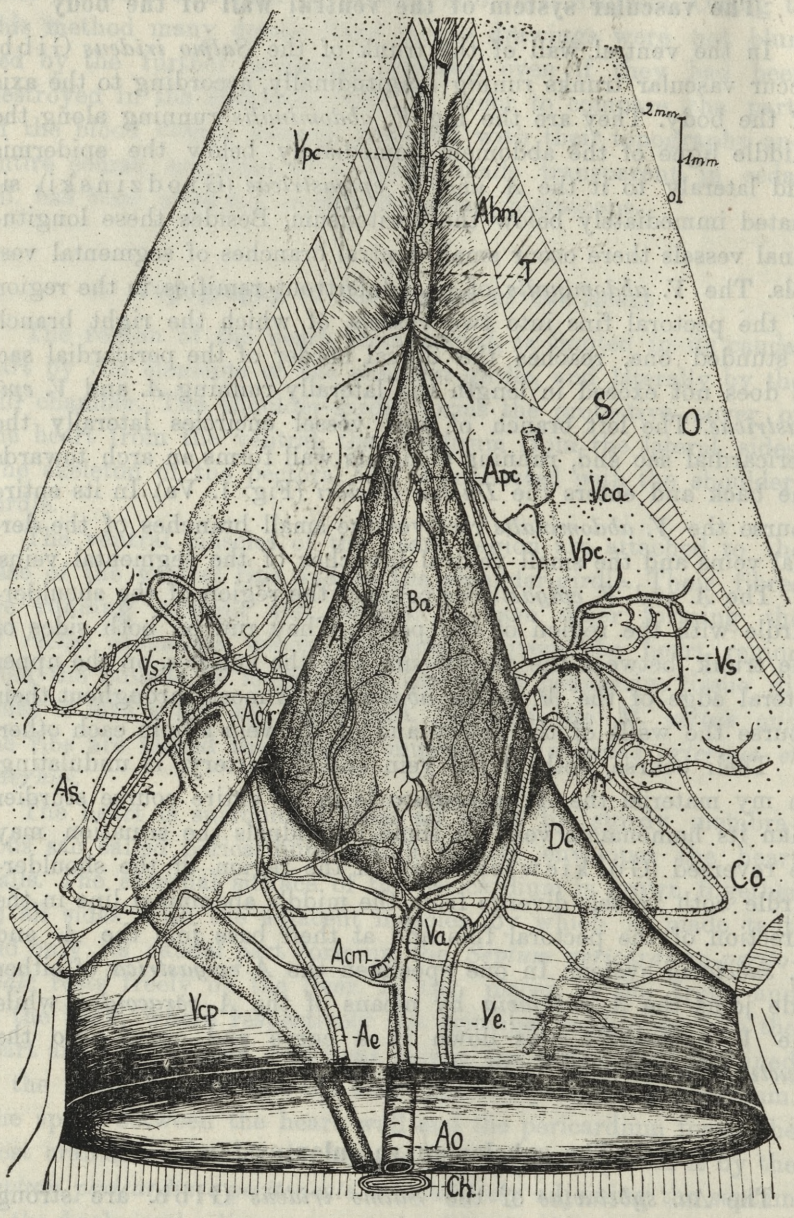

Figure 1. Coracoid and the heart with the blood-vascular system as seen after removal of skin and muscles.

ches running to the free fins, and into others which supply the shoulder-girdle muscles. By means of the *Aa. coracoideae* they are joined to the hypobranchial system and to the vascular system of the ventral wall (*Aa. epigastricae*). The *Aa. coracoideae* are extensively ramified and their branches spread in the muscles lying above and below the coracoid (Fig. 1. As. Acr. Ae). The extensively ramified veins of the fin muscles of the trout unite into one trunk, the *V. subclavia*, which enters on the left side the *V. abdominalis* loop and with it the *Ductus Cuvieri*. On the right side the veins of the subclavia system join the *V. epigastrica* close to the entrance of the *Ductus Cuvieri* (Fig. 1. Vs. Va. Dc). The former veins also collect the small branches spreading on the pericardium.

The hypobranchial system

The vascular system of the heart region feeding the organs situated below the gills has been called the hypobranchial system. The principal vessels of the hypobranchial system are composed of numerous longitudinal and transversal vessels, rooted in the ventral segments of the *Aa. branchiales efferentes*. Here belong the *Aa. hypobranchialis lateralis* and *medialis* and the *Aa. commissurales*. From the *A. branch. eff.* of the third branchial arch of the left side of the body of the trout there ramifies an unpaired *A. hypobranch. med.*. It runs along the pericardium into arteries passing over the heart: *Aa. coronariae ant.* and *post.* and into arteries supplying the pericardium: *Aa. pericardiales* (Fig. 1. Apc. Fig. 2. Apc. Acs. Acd.).

The lateral trunks of the hypobranchial arteries, viz. *Aa. hypobranchiales laterales* present the largest variety of ramifications. They run between the trunk muscles in the direction of the pectoral fin, where they join the *A. epigastrica* and the *A. subclavia* as *Aa. coracoideae* (Fig. 1. As. Acr. Ae.). Along the middle line of the head of *Salmo irideus* runs a single unpaired *V. jugularis inferior*. It runs between the *Truncus arteriosus* and the muscles of oesophagus, as a sturdy vessel, somewhat widened at the entrance. The *V. jugularis inferior* flows immediately into the *Sinus venosus*, opening somewhat asymmetrically towards the right *Ductus Cuvieri* (Fig. 3. Vj.). Laterally it receives the branches of the thyroid gland and of the pharyngeal muscles. Besides the just

mentioned branches the *V. jugularis inferior* receives also small branch from the pericardium. This branch, the *V. pericardiaca* has numerous ramifications on the pericardium covering the car-

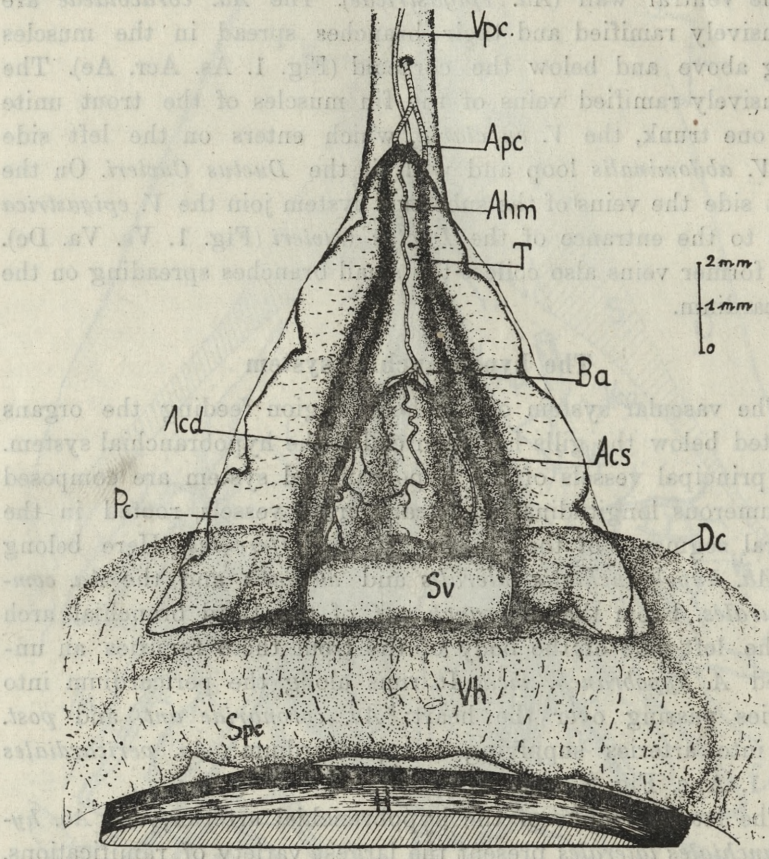

Figure 2. The heart as seen in the open pericardial sack.

diac ventricle. Curving lightly to the right it passes first to the *Bulbus art.*, then to the *Truncus art.*. Here it intertwines with the *A. hypobranch. med.* and on the level of the fourth branchial arch it turns to the right and enters the *V. jugularis inferior* (Fig. 1. Vpc).

The hepatic vascular system

The hepatic system appears early in the embryo. From the *V. caudalis* the *V. subintestinalis* ramifies, which running along

the ventral wall of the intestine passes through the liver and enters the *Sinus ven.* of the heart. It loses the connection with the *V. caudalis* very early. Running anteriorly it ramifies in the

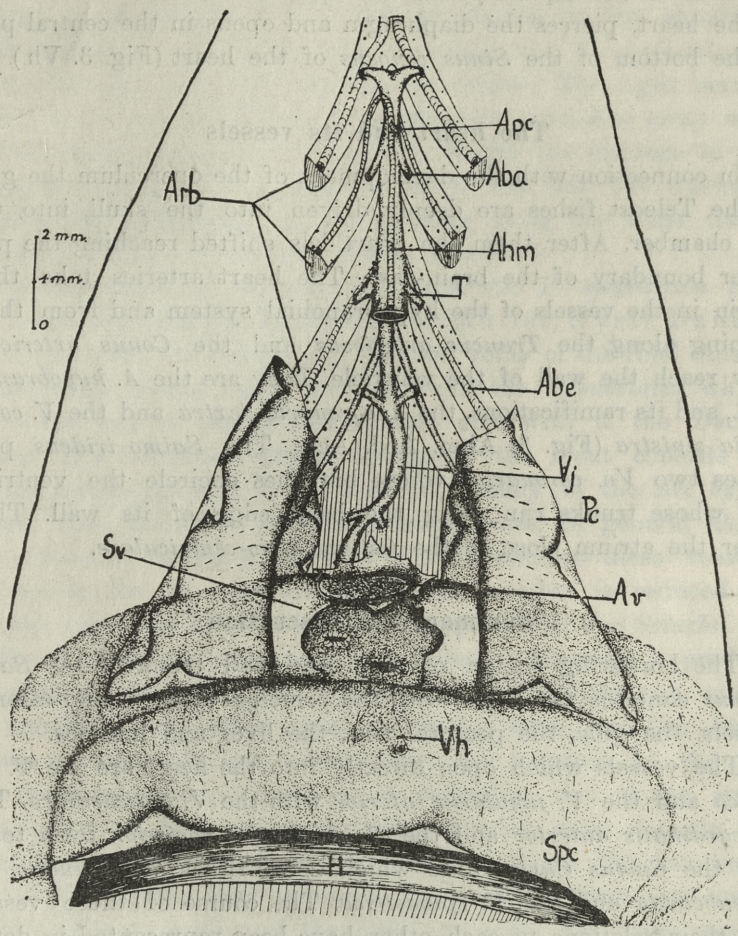

Figure 3. The bordering region after removal of the heart.

liver lobes and changes into capillaries, thus breaking its continuity for the second time. It is therefore divided into two sections: an anterior one placed between the liver and the heart — it is the *V. hepatica*, the posterior one carries blood from the bowels to the liver — it is the *V. portae hepatis*. Thus both *V. hepatica* and *V. portae hepatis* originate from the *V. subintestinalis*

(Grodziński). The *V. hepatica* of the *Salmo irideus* consists of two branches merging into one trunk on the surface of the liver, posterior to the *Septum pericardiaco-peritoneale*. This trunk turns to the heart, pierces the diaphragm and opens in the central part of the bottom of the *Sinus venosus* of the heart (Fig. 3. Vh.).

The heart and its vessels

In connection with the development of the operculum the gills of the Teleost fishes are deeply driven into the skull, into the gill chamber. After them the heart has shifted reaching the posterior boundary of the brain-case. The heart arteries take their origin in the vessels of the hypobranchial system and from there running along the *Truncus arteriosus* and the *Conus arteriosus* they reach the wall of the ventricle. They are the *A. hypobranch. med.*, and its ramifications, the *A. coronaria dextra* and the *V. coronaria sinistra* (Fig. 3. Ahm. Acd. Acs.). The *Salmo irideus* possesses two *Vv. coronariae* whose branches encircle the ventricle and whose trunks run along the back edge of its wall. They enter the atrium close to the *Ostium atrio-ventriculare*.

Summary and discussion

The bordering region of the head and trunk of the *Salmo irideus* contains the heart with the principal afferent and efferent vessels, the gills, the pectoral fins, the liver and muscles.

The vessels which open directly into the heart are the *V. hepatica* and the *V. jugularis inferior* with the V. *pericardiaca*. The *V. cardinalis anterior* and the *V. cardinalis posterior* form together the *Cuctus Cuvieri* into which opens the *V. abdominalis*, the *V. subclavia* and the *V. epigastrica*. The course of these vessels and their relations to each other have been represented in detail. They have been moreover compared with the corresponding vessels of the *Selachii*. It follows from this comparison that owing to the evolving of an operculum and the concentration of gills, the bordering region of the *Teleostei* was considerably shifted forward, shortened and completely separated from the abdominal cavity by the *Septum pericardiaco-peritoneale*. The *Selachii* possess a secondary connection between the cavity of the body and the pericardial cavity as a so called *Canalis pericardiaco-perito-*

nealis (Hochstetter). The pericardial sac of the *Selachii* is spacious, while that of the *Salmo* tightly envelopes the heart walls.

The *V. abdominalis* of the *Selachii* divides in the shoulder-girdle region in two equal arms entering the *V. epigastrica* of either side and with them the *Ductus Cuvieri.* The right branch of the *V. abdominalis* of the trout partially dwindles away with a blind ending, it does not exceed in length the distance to the laterally running *Aa. epigastricae* while the left one encircles laterally the pericardial sac and running along its walls forms a dorsal arch and enters the *Ductus Cuvieri.*

Vv. subclaviae of *Selachii* unite with the *V. epigastrica* into one vein which enters the *Ductus Cuvieri* (Müller, Hyrtl, Daniel, Parker), while the extensively ramified veins of the final muscle of the *Salmo irideus* unite into one trunk, the *V. subclavia* which enters the loop of the *V. abdominalis* and with it the *Ductus Cuvieri.* The subclavial arterial system of the trout consists of the same units as that of the *Selachii*, namely of the *Aa. hypobranch. med.* and *later.*, and *Aa. commissurales.* In general there is a noticeable tendency towards a reduction of these vessels, particularly the *Aa. commissurales* whose number is reduced to one pair with the *Teleostei* against four pairs with the *Selachii.*

The *V. jugularis inferior* of the *Salmo* is likewise a product of reduction. The paired *Vv. jugulares* of the *Selachii* run within the mandible and either open as paired veins into the *Sinus venosus* or unite into one vessel before the entrance. In the hepatic venosus system a tendency to reduction also shows itself for the two *Vv. hepaticae* of the *Selachii* either enter directly the *Sinus venosus* or flow into the wide hepatic sinus. The two branches of the hepatic vein in *Salmo* flow together into one trunk on the anterior surface of the liver and enter the *Sinus venosus* as a single vessel the *V. hepatica.* From among other *Teleostei* the *Lota*, *Perca*, *Lopholatilus* have two, the *Gadus* three, the *Periophalmus*, *Lepidosteus*, *Amia* — one *V. hepatica.*

Beside the two *Vv. coronariae* one can distinguish on the heart of the *Selachii* also a *V. cardiaca,* carrying blood from the dorsal wall of the ventricle. This one is missing in the *Salmo.*

Kraków. Institute of Comparative Anatomy in the Jagellonian University. Director: Prof. Dr Z. Grodziński.

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Description of figures

The figures were drawn with the aid of Abbé's apparatus from preparations studied under the binocular microscope. Arteries are cross-striped, veins dotted. Each figure is provided with a line showing the enlargement.

Abbreviations for all figures

A — Atrium.
Aba — Arteria branchialis aff.
Abe — „ branchialis efferens.
Acd — „ coronaria dextra.
Acm — „ coeliaco-mesenterica.
Acr — „ coracoidea.
Acs — „ coronaria sinistra.
Ae — „ epigastrica.
Ahm — „ hypobranchialis medialis.
Ao — Aorta.
Apc — Arteria pericardiaca.
Arb — Arcus branchiales.
As — Arteria subclavia.
Av — Septum atrio-ventriculare.
Ba — Bulbus arteriosus.
Ch — Chorda dorsalis.
Co — Coracoid.
Dc — Ductus Cuvieri.
H — Hepar.
O — Operculum.
Pc — Pericardium.
S — Gills.
Spc — Septum pericardiaco-peritoneale.
Sv — Sinus venosus.
T — Truncus arteriosus.
V — Ventriculus.
Va — Vena abdominalis.
Vca — „ cardinalis anterior.
Vcp — „ cardinalis posterior.
Ve — „ epigastrica.
Vh — „ hepatica.
Vj — „ jugularis inferior.
Vpc — „ pericardiaca.
Vs — „ subclavia.

O zdolności odróżniania barw u puszczyka (*Strix aluco aluco* L.). — *On the Ability of Colour-Discrimination of the Tawny Owl* (*Strix aluco aluco* L.)

Mémoire

de M. *B. FERENS,*

présenté le 1 Décembre 1947 par M. Z. Grodziński m. c.

(Plate 10)

The aim of this work was to investigate the colour sense of the tawny owl *Strix aluco aluco* L., and to compare this sense with the ability of colour-discrimination of diurnal birds and other Sauropsida.

Sauropsida are characterised by the presence in their retinas of coloured fat corpuscles, which play the part of a colour-filter (Waelchli 1883, Kühn 1927, 1929). The diversity in the colouring of these corpuscles within various groups of Sauropsida is the cause of the difference existing in the colour sense of lizards (Wagner 1933), tortoises (Wojtusiak 1933), and birds with regard to the colour sensitivity of human beings.

Hitherto a knowledge of the colour sense in birds has been acquired chiefly by investigating species having diurnal habits of life. Katz and Revesz (1909) in domestic fowl, C. Hess (1911) in domestic fowl, turkeys, domestic pigeons, and also in the kestrel *Falco tinnunculus* L. and common buzzard *Buteo buteo* L., and Laurens (1923) in pigeons, all of them by using different methods ascertained that in birds there exists a restriction of sensitivity in the short-wave part of the spectrum, namely with regard to blue and violet, in comparison with the colour sense in man, and an intensification of sensitivity in the long-wave part, with regard to red and orange. These results were

confirmed by the investigations of Henning (1920), Honigmann (1921), Riekel (1922), Ehrhard (1924), Heinroth (1925) and Blässer (1926). Owing to the presence of red-orange and yellow fat corpuscles in their retinas, diurnal birds presumably see their surroundings as does a man looking through a red-yellow filter which suppresses short-wave radiation, and causes it to lose its saturation and to grow grayishlike. The fat corpuscles, acting like lenses concentrating long-wave rays, are at the same time presumably the cause of the higher sensitivity of diurnal birds with regard to this part of the spectrum in comparison with man.

A deviation from such a colour sense is shown by undulated grass-parroquets *Melopsittacus undulatus* Shaw., which have in their retinas fat corpuscles differently coloured. They are distinguished by possessing the highest degree of sensitivity on the one hand to yellow and yellow-green, on the other hand to violet, and the lowest sensitivity to orange and dark-green. The colour sense is here in distinct relationship with the parroquets' coloration, making possible the recognition and discovery of the separate sexes.

Differences in the colour sense, existing between the representatives of various groups of diurnal birds, suggest that in this regard nocturnal birds must also evince peculiar characteristics, resulting from a distinct mode of life and the histological structure of the eye. Coming into consideration here are alike the difference in the colouring of the fat corpuscles, which in nocturnal birds are said to be chiefly yellow and brown (C. Hess 1911), and the quantitative proportion of rods and cones in the retina. In diurnal birds the cones exceed quantitatively the rods. In owls one encounters the reverse. In accordance with the theory of a separate function of the two retinal elements (Schultze 1866, Kries 1923, Frisch 1925), it is to be expected that owls, possessing a smaller number of cones, ought to perceive colours in a weaker degree than diurnal birds do, but on the other hand they should have a better perception of shades of gray.

The problem concerning the colour sense in owls was hitherto taken up by Abelsdorff (1900), Piper (1904) and C. Hess (1911). The latter carried out investigations on the long-eared owl *Asio otus* L., the European owlet *Athene noctua* Scop., and

the tawny owl *Strix aluco aluco* L. In the second of the above-mentioned species it was possible to determine in the short-wave section of the spectrum that sensitivity is slightly higher than it is in diurnal birds. Within the field of blue and violet however, visibility was said to be in spite of this weaker than in man. These results, obtained by the method of observing in what colours birds see food best, and in what colours worst, do not allow of an exact characterisation of the colour sense of these birds. The author therefore undertook the problem of investigating the ability of colour-discrimination in the tawny owl *Strix aluco aluco* L. by a method of training. The results arrived at by applying such a method make it possible to carry out an accurate comparison of the tawny owl's colour sense with that of other Sauropsida.

The herewith presented work was begun iu 1936 in the Psychogenetic Department of the Jagellonian University, under the guidance of the late Prof. Dr Tadeusz Garbowski who did not live to see its termination, on account of his tragic death in the German concentration camp at Sachsenhausen in 1940. For inducing me to take up this problem, as well as for suitable suggestions, I most cordially thank Dr Roman Wojtusiak. For experimental material I am indebted to Dr J. Żabiński, Director of the Zoological Garden in Warsaw, and to him also I owe my cordial thanks.

Material and methods

Four tawny owls *Strix aluco aluco* L. were used for the experiments; they are convenient material for experimenting on, on account of their seeing well both in daytime and at night. The birds were kept in a cage measuring $170 \times 120 \times 82$ cm, and divided into three storeys. In each section one owl was kept. The fourth, a very tame one, passed most of its time outside the cage. The birds did not see one another. The cage stood at a distance of four metres from a window which faced southeast. During the experiments the owls were fed mostly horse-flesh, but from time to time apart from this the birds received sparrows, pigeons, mice, and similar small vertebrates, such food being every now and then a manifest necessity. In such cases

a break was made in the experiments for two or three days. The experiments were conducted twice daily, in the forenoon and afternoon. At first the feeding presented certain difficulties, but as time went on the owls became so tame that they approached to take food from the experimenter's hand.

The training took the following course. For feeding the owls a two-pronged wire fork was used, about 20 cm long, the two prongs being parallel and 3 cm distant from each other. A piece of meat was placed on one prong, and on the other a coloured paper square (4 × 4 cm), which formed a background for the food. The coloured square together with the food was well illuminated with daylight.

For making the squares Ostwald's coloured papers were used; they are arranged in a 24-degree scale of colours, passing from yellow (No 1—3) to orange (4—6), then to red (7—9), violet (10—12), blue (13—15), light-blue (16—18), green (19—21), yellow-green (22—24), and back to yellow (1). For training the owls eight colours of this scale were used: yellow (2), orange (5), red (7), violet (11), blue (15), light-blue (17), green (20), and yellow-green (23). When training to gray colours, Hering's papers were used; they have a scale composed of 17 degrees, No 1 being white, and No 17 black. Strict attention was paid when conducting the experiments to see that the coloured squares on the forks used for training were not soiled or damaged. As soon as defects of any kind were noticed the squares were replaced by new ones.

Each owl was first trained to one of the above-mentioned spectral colours of Ostwald's scale. An owl was offered food from the fork on a background of a given »training« colour until the bird became accustomed to that colour; then the bird was given a choice, on two forks, of two coloured squares, one of which was of the 'training' colour, while the other had a strange colour. In order to avoid training of the animal to the spatial position of the coloured square, the »training« square was transferred from time to time in the course of the experiments from the right-hand side of the fork to the left, and vice versa. The animal was allowed to eat the food only if it had made a correct choice. Otherwise the fork was withdrawn without permitting the owl to remove the meat from it. Grasping reactions with regard to the coloured squares were recorded only when they had a decided

character, whereby reactions towards the »training« square were marked in the records with a plus sign (+), and towards the negative square with a minus sign (—). It was frequently noticeable that an owl, having approached the food, would cast a distinct glance at one and the other coloured square before making its choice, which in such cases was almost always correct. Such behaviour of the birds was appropriately noted in the records. The results of all tests were grouped ten together, and every ten was marked on the axis of abscissas in a graph. The percentage of positive reactions in every group of ten was calculated and marked on the axis of ordinates. When the curve connecting the various points passed between the 50% and 100% lines, the animal was assumed to discriminate the given colour. If the curve displayed oscillations on both sides of the 50% line, this would be proof that owls have no colour-discrimination.

In order to determine in what degree owls discriminate between a particular colour and other spectral colours, forks were used which had five pairs of prongs; on these, apart from the square with the »training« colour, one could place four other squares with neighbouring colours from Ostwald's scale. For instance, if the »training« colour was No. 5, then the adjacent Nos. 3, 4, 6 and 7 were placed alongside, and the animal was to distinguish, from among the five colours, the »training« colour. A count was made of the number of grasping reactions with regard to each of the five colours. In the course of the experiments the order of succession of the colours on the fork would be changed, in order to avoid training the birds to the position of the »training« colour. The results of this series of experiments are presented graphically in the form of curves in such a manner that the colour numbers from Ostwald's scale are marked on the axis of abscissas, while on the axis of ordinates is marked the number of grasping reactions with regard to each colour calculated in percentages. A similar procedure was followed in experiments whose point was to investigate the birds' ability of discriminating between various degrees of gray.

Having at my disposal only four owls, it was necessary to train the birds over and over again several times, in relation to successively new colours. No great difficulties were experienced in training the birds over again. A several days' interval was

introduced into the experiments, during which the owls were fed with small vertebrates. After such a period, feeding of the owls was resumed on a background of a new colour; later on, simultaneously with the new coloured square, a square of the previous colour would be displayed, now as a negative one. At first the owl would tend to grasp even more frequently the food appearing on a background of the previous »training« colour. However upon receiving no food in connection with the old colour, it would soon learn, after several trials, to recognise the new value of the old coloured square, and it would react positively towards the new »training« square.

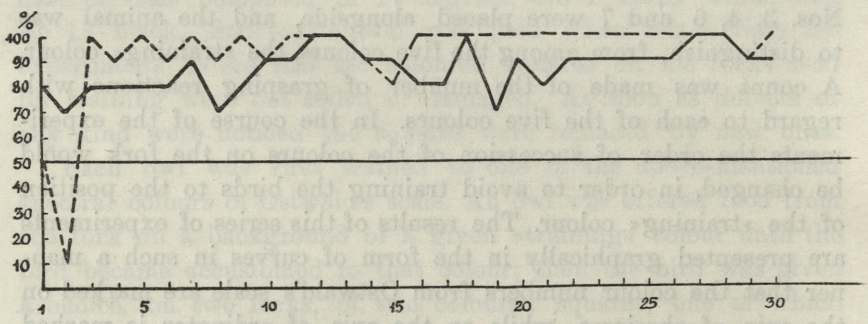
A more detailed explanation of the graphs and tables is to be found in the text.

Account of the Experiments

1. Preliminary experiments

Preliminary experiments were carried out with all four owls in the following manner.

The first owl (owl No 1) was fed at a yellow-coloured square (colour No 2 of Ostwald's scale) for six days' time. Subsequently



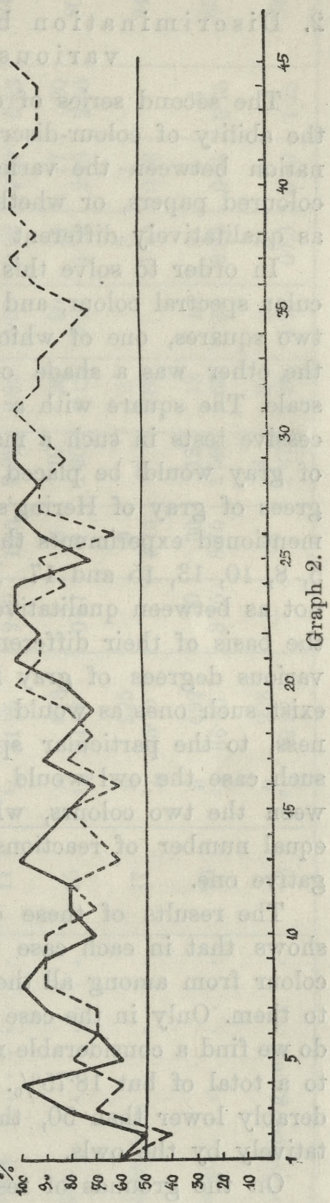
Graph 1.

both the above-mentioned coloured square and a blue one (No 15) were offered to the bird to choose from. The result was positive, the fact being that in the 300 tests which were carried through, only forty of the owl's grasping reactions were negative, while in 86·6% of the cases the bird chose the colour at which it had been fed. The herein included graph 1 (continual line) confirms that the owl discriminates between yellow and blue.

The second owl (owl No 2) was fed, also for six days, at a blue-coloured square (colour No 15), after which the bird was offered both the latter colour and yellow (No 2). The result of this experiments confirmed our expectations in a still more convincing manner. The owl executed only 22 negative grasping reactions in the 300 tests which were carried out. Graph 1 (broken line) displays oscillations on both sides of the 50% line only at the beginning of the experiments; later, however, it rises steeply and maintains itself steadily between 80% and 100%. Its mean value is 92·6%.

The third owl (owl No 3), trained to red (colour No 17), also for six days, was then to discriminate between this colour and blue (No 15). In this experiment in 300 tests the animal executed 47 negative grasping reactions. The mean value of positive reactions was 84·3%. (Graph 2, continual line).

The last owl (owl No 4) was fed for eleven days at a green-coloured square (colour No 20); then it was confronted with an orange-coloured square (No 5). This owl, in 450 tests, executed the largest number of incorrect grasping reactions, i. e. 67. The corresponding curve shows at first that a plainly visible process of learning is going on in the animal. At the beginning this curve oscillates on both sides of the 50% line, then it gradually rises and maintains itself steadily between 60 and 90%. Its mean value amounts to 85·1%. (Graph 2, broken line).



Graph 2.

All the preliminary experiments demonstrated, therefore, that owls do discriminate between colours.

2. Discrimination between spectral colours and various degrees of gray

The second series of experiments was to determine, whether the ability of colour-discrimination of owls is based on discrimination between the various degrees of brightness of Ostwald's coloured papers, or whether these birds perceive various colours as qualitatively different sensations.

In order to solve this problem, owls were trained to a particular spectral colour, and then they had to discriminate between two squares, one of which was of the »training« colour, while the other was a shade of gray from among those of Hering's scale. The square with a shade of gray was changed in the successive tests in such a manner that each time a different degree of gray would be placed on the fork. From among the 17 degrees of gray of Hering's scale, for the purpose of the above-mentioned experiments the following numbers were chosen: 1, 3, 5, 8, 10, 13, 15 and 17. If owls discriminated between colours not as between qualitatively different sensations, but merely on the basis of their different brightness, then among the series of various degrees of gray in Hering's scale there would have to exist such ones as would correspond, with regard to their brightness, to the particular spectral colour from Ostwald's scale. In such case the owl would have to be unable to discriminate between the two colours, which fact would manifest itself by an equal number of reactions to the »training« colour and the negative one.

The results of these experiments are listed in Table I. It shows that in each case the owls distinguished the »training« colour from among all the degrees of gray which were displayed to them. Only in the case of the violet »training« colour (No 11) do we find a considerable number of mistakes, amounting however to a total of but 18·75%. Inasmuch as this percentage is considerably lower than 50, this colour was also discriminated qualitatively by the owls.

On the grounds of results arrived at in this series of experiments, it can be stated that owls discriminate all colours from

TABLE I

Distinction of colours from the greyness of different degree

Training colour	Number of the Ostwald's scale	Numbers of the positive reactions: n = total; % = percentage	Number of catching reactions on the degree of greyness 1—17 according to scale of Hering								Joint number of tests;
			1	3	5	8	10	13	15	17	
Yellow	2	n 761	12	8	9	6	3	—	1	—	800
		% 95·15	1·50	1	1·12	0·75	0·36		0·12		
Orange	5	n 214	1	4	2	2	9	2	2	4	240
		% 89·17	0·42	1·67	0·83	0·83	3·75	0·83	0·83	1·67	
Red	7	n 690	7	11	14	9	21	10	21	17	800
		% 86·25	0·87	1·37	1·75	1·12	2·63	1·25	2·63	2·13	
Violet	11	n 195	7	3	5	7	8	7	6	2	240
		% 81·25	2·92	1·25	2·08	2·92	3·33	2·92	2·50	0·83	
Blue	15	n 679	7	8	10	25	20	14	17	20	800
		% 84·88	0·87	1	1·25	3·12	2·50	1·75	2·13	2·50	
Light-blue	17	n 225	—	9	—	2	—	3	1	—	240
		% 93·75		3·75		0·83		1·25	0·42		
Green	20	n 692	30	30	12	13	10	5	2	6	800
		% 86·50	3·75	3·75	1·50	1·62	1·25	0·63	0·25	0·75	
Yellowish-green . . .	23	n 223	—	—	4	3	3	2	2	3	240
		% 92·92			1·67	1·25	1·25	0·83	0·83	1·25	

Ostwald's scale qualitatively, and not on a basis of differences in their brightness.

3. Discrimination of spectral colours

The aim of this group of experiments was to determine in what degree owls discriminate various spectral colours. For this purpose the owls were offered, on a five-pronged fork, a square with the »training« colour, and four squares with colours of adjacent numbers from Ostwald's scale, two from the left-hand side and two from the right. The order of succession of the squares was frequently changed. For the purpose of training the birds in this respect, eight colours were chosen from Ostwald's scale: yellow (2), orange (5), red (7), violet (11), blue (15), light-blue (17), green (20), and yellow-green (23). In order to ascertain what individual differences occur in colour-discrimination, three owls were trained to each colour. One hundred tests were conducted with each bird.

The respective graphs comprise the results of experiments with all three birds, and therefore present the average of 300 tests. The graphs show that the owls distinguished very well the »training« colour from other colours, inasmuch as the largest percentage of grasping reactions always falls on the former. In comparison with the »training« colour, adjacent colours were chosen less frequently. For each »training« colour we therefore obtained a curve, the highest point of which falls on the »training« colour. The height and dispersion of each curve give a picture of the discrimination ability and sensitivity of the owls with regard to various colours.

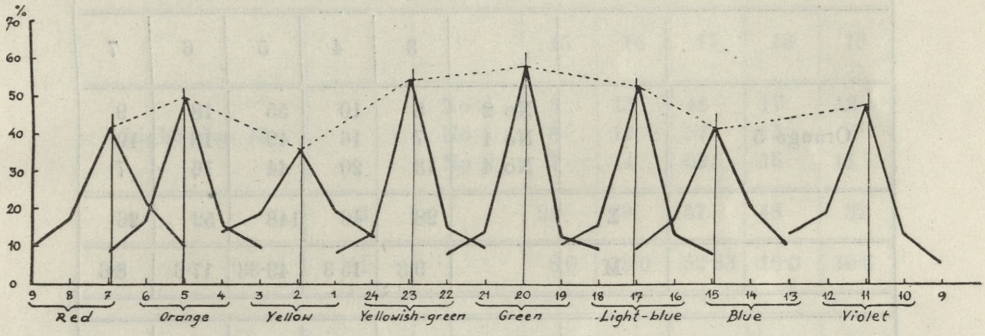
The results of this series of experiments, reviewed in the sequence of colours of the solar spectrum, from red to violet, are as follows:

Trained to red (No 7) were the owls No 1, 2 and 3 (Graph 3 and Table II). The apex of the curve obtained attains 41·33%, its dispersion amounts to $\pm$ 1·52. The curve's mean value in relation to the modal value appertaining to the »training« colour is slightly shifted, by 0·08 class units, towards orange. The curve rises and descends almost symmetrically on both sides.

Eight ordinate units higher reaches the apex of the curve for orange No. 5 (Graph 3 and Table II), obtained from experiments

with the birds No 1, 2 and 4. It reaches up to 49·33%. The dispersion of this curve amounts to ± 1·42. In comparison with the previous one, this curve rises and descends much more steeply. Its mean value is shifted in relation to the modal value in a still weaker degree, only 0·026 class units towards red.

The curve obtained for the yellow »training« colour No 2 (Graph 3 and Table II) is very flat and almost symmetrical. Its apex reaches up to 35·67%. This curve is the lowest, and its dispersion, amounting to ± 1·60, is bigger than for all other curves; this testifies that of all colours yellow is discriminated worst by tawny owls. The mean value of this curve is shifted 0·03 class units, in relation to the modal value, towards yellow-green.



Graph 3.

The curve pertaining to the yellow-green »training« colour No 23 (Graph 3 and Table III) rises steeply and symmetrically on both sides. Its apex reaches up to 54·00%, while its dispersion amounts to ± 1·33. Its mean value is shifted 0·04 class units, in relation to the modal value, towards green.

Very closely related to the latter curve, in many respects, is the following curve, appertaining to the green »training« colour No 20 (Graph 3 and Table III). It rises and descends very steeply and symmetrically on both sides. Its apex reaches up highest, up to 57·33%, while its dispersion is smallest, only ± 1·30. Its mean value conforms to the modal value, being equal to 0.

Up to 52·33% reaches the apex of the curve for the light-blue »training« colour No 17 (Graph 3 and Table III). The character of this curve approximates very closely to that of the two previous ones. Its dispersion amounts to ± 1·35. Its mean value is

TABLE II

Training colour	Σ = total M = mean	Specimens of owls	Catching reactions on separate numbers of Ostwald's coloured papers:				
			24	1	2	3	4
Yellow 2		No 1	15	18	37	16	14
		No 2	11	17	41	21	10
		No 3	11	22	29	20	18
	Σ		37	57	107	57	42
	M		12·3	19·0	35·67	19.0	14·0
			3	4	5	6	7
Orange 5		No 2	8	10	55	18	9
		No 1	7	16	49	18	10
		No 4	13	20	44	16	7
	Σ		28	46	148	52	26
	M		9·3	15·3	49·33	17·3	8·6
			5	6	7	8	9
Red 7		No 3	12	19	36	20	13
		No 1	11	21	42	17	9
		No 2	7	24	46	15	8
	Σ		30	64	124	52	30
	M		10·0	21·3	41·33	17·3	10·0
			9	10	11	12	13
Violet 11		No 1	7	17	46	18	12
		No 4	8	16	42	22	12
		No 2	3	9	54	19	15
	Σ		18	42	142	59	39
	M		6·0	14·0	47·33	19·6	13·0

TABLE III

Training colour	Σ = total M = mean	Specimens of owls	Catching reactions on separate numbers of Ostwald's coloured papers:				
			13	14	15	16	17
Blue 15		No 2	15	16	36	21	12
		No 3	11	20	44	17	8
		No 1	4	26	46	15	9
	Σ		30	62	126	53	29
	M		10·0	20·6	42·00	17·6	9·6
			15	16	17	18	19
Light-blue 17		No 4	9	13	48	17	13
		No 1	8	12	57	15	8
		No 2	7	14	52	16	11
	Σ		24	39	157	48	32
	M		8·0	13·0	52·33	16·0	10·6
			18	19	20	21	22
Green 20		No 1	9	14	57	15	5
		No 4	8	11	61	14	6
		No 3	10	12	54	13	11
	Σ		27	37	172	42	22
	M		9·0	12·3	57·33	14·0	7·3
			21	22	23	24	1
Yellowish-green 23		No 4	10	16	51	14	9
		No 1	8	14	59	12	7
		No 2	10	14	52	15	9
	Σ		28	44	162	41	25
	M		9·3	14·6	54·00	13·6	8·3

shifted, in relation to the modal value, 0·006 class units toward green. It can be generally stated that the last three colours (yellow-green No 23, green No 20, and light-blue No 17) are discriminated best of all colours, and the apexes of their sensitivity curves pass the 50% line.

The curve for the dark-blue »training« colour No 15 (Graph 3 and Table III) has features which approximate markedly to those of the curve for the red »training« colour No 7. The apex of the curve in question reaches up to 42%, its dispersion amounts to $\pm$ 1·51, while its mean value is shifted 0·066 class units, in relation to the modal value, towards violet.

The last curve, appertaining to the violet »training« colour No 11 (Graph 3 and Table II), displays a distinct asymmetry, and descends steeply towards red, while towards blue it descends much more gently. Its apex reaches up to 47·33%, while its dispersion amounts to $\pm$ 1·44. Its mean value, in relation to the modal value, is shifted 0·026 class units towards red. Its mean value and dispersion liken this curve to the one for orange colour No 5.

4. Discrimination of various degrees of gray

For the purpose of training the owls to various shades of gray, use was made of three degrees of gray from Hering's scale, namely numbers 6, 10 and 14. Each of the above-mentioned degrees of gray, employed for training purposes, was contrasted with the following gray shades from Herings's scale: for the »training« gray No 6 Nos. 3, 9, 12 and 15; for the »training« gray No 10: Nos. 1, 4, 7 and 13; and lastly, the owls had to discriminate between the »training« gray No 14 and the Nos. 2, 5, 8 and 17 (Table IV).

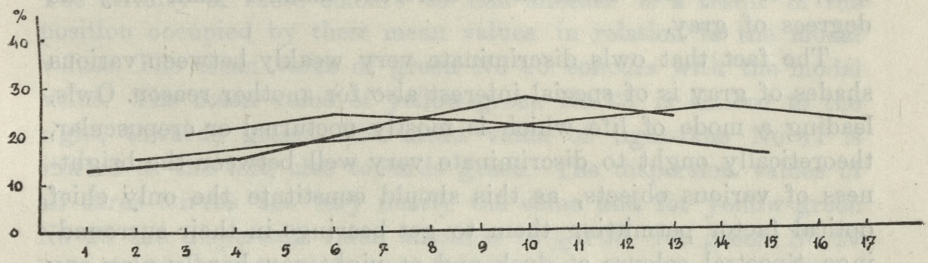
The experiments were conducted with three owls, one hundred tests with each. Mean values were calculated from the results arrived at from 300 tests conducted with all the owls, and presented in the form of a curve (Graph 4); degrees of gray from 1 to 17 according to Hering's scale are marked on the axis of abscissas, while the percentage of grasping reactions is marked on the axis of ordinates. Comparing the three curves obtained for each of the »training« shades of gray, it is noticeable that they differ from one another in a minimal degree. These curves

are flat. The apex of the curve obtained for gray No 10 barely reaches up to 27%, for gray No 14 up to 25%, and for gray No 6 merely up to 24%. The difference in height between the

TABLE IV

Training on the degree of greyness according to scale of Hering:	Catching reactions on separate numbers of Hering's grey papers:				
	3	6	9	12	15
6	20	24	22	19	15
	1	4	7	10	13
10	13	15	22	27	23
	2	5	8	14	17
14	15	18	20	25	20

highest and lowest curve barely amounts to 3%. Dispersion of the several curves is also considerable. For gray No 6 it amounts



Graph 4.

to $\pm$ 5·9, for gray No 10 it is $\pm$ 4·7, and for gray No 14 it is $\pm$ 5·4.

Of the eight curves appertaining to spectral colours and discussed in the previous chapter, the largest dispersion is displayed by the curve for yellow No 2. It amounts to $\pm$ 1·60. It is, therefore, very small in spite of the fact that the animal had to

discriminate between the most proximal colour degres from Ostwald's scale. In comparison with the dispersion of curves representing the result of training to degrees of gray, it is obvious that the ability of discriminating between spectral colours is incomparably greater than the ability of discriminating between various degrees of gray. This difference is brought into prominence so much stronger when we consider that in the experiments with degrees of gray the owls had to discriminate between far-removed classes in Hering's numeration, differing distinctly as to their brightness. Owls, therefore, are able to discriminate plainly, but in a relatively weak degree, only between the most extreme classes of gray, i. e. white and black.

The latter fact is of far-reaching significance when studying the problem whether these birds discriminate between spectral colours qualitatively. If they discriminated between them not qualitatively, but on the basis of differences in their brightness, then the curves from both groups of experiments would display a similar course. We see, however, that the dispersion value for yellow No 2, the biggest from among all the spectral colours, is incomparably small in relation to the smallest dispersion value of the curve for the »training« gray No 10. Tawny owls discriminate, therefore, between spectral (pigment) colours qualitatively, and not quantitatively on the basis of differences in their brightness, i. e. they see them in a different manner than they do degrees of gray.

The fact that owls discriminate very weakly between various shades of gray is of special interest also for another reason. Owls, leading a mode of life which is mostly nocturnal or crepuscular, theoretically ought to discriminate very well between the brightness of various objects, as this should constitute the only chief optical factor permitting them to get bearings in their surroundings. Spectral colours at dusk and at night can hardly play any role. This appears to be supported by the fact that in the ocular retina the number of rods exceeds that of cones. However, sensitivity to shades of gray is unexpectedly small, and for the time being there is no explanation for this fact. The possibility cannot be ruled out that it is related to the sensitivity of these birds to infra-red rays. This matter has been lately a subject of discussion (Vanderplank 1934, Matthews L. H. & Matthews B. H. C.

1939, Hecht S. & Pirenne M. H. 1940) and it passes beyond the scope of this work.

5. Discussion of results

Having presented in succession all the experiments carried out on tawny owls, we can now proceed to discuss the results and to draw therefrom conclusions concerning the colour-discrimination ability of these birds. In order to acquire a knowledge of the sensitivity to differences in the shades of particular colours, we have put together in Graph 3 all the curves obtained for Ostwald's »training« colours, discussed in detail in Chapter 3. They have been presented in the sequence in which they occur in the solar spectrum.

In the whole complement of colours the maximum sensitivity is noticeable at the green colour No 20. Such sensitivity, however, is not restricted to this one colour; indeed, it includes three adjacent colours: yellow-green No 23, green No 20, and light-blue No 17. The group of these yellow-green-blue colours dominates the whole graph, and the curves which make it up pass with their apexes the 52% line (for yellow-green No 23—54%; for green No 20—57·33%, and for light-blue No 17—52·33%). The difference in the height attained by the apexes of these three curves oscillates in a relatively slight degree, from 3·33% to 5%. The affinity of these colours to one another is a result of the position occupied by their mean values in relation to the modal values. The mean value of green No 20 concurs with the modal value. The mean value of yellow-green No 23 is shifted to the right, towards green. The mean value of light-blue No 17 is shifted to the left, also towards green. The dispersion values of all three curves are very nearly the same and for yellow-green No 23 the dispersion value amounts to $\pm$ 1·33, for green No 20 it is $\pm$ 1·30, and for light-blue No 17 it is $\pm$ 1·35 (Graph 6). These characteristics distinctly attest the affinity of these three colours in Ostwald's scale, and they demonstrate that tawny owls perceive them in an almost equal manner.

Within Ostwald's scale the minimum of sensitivity exists with regard to but one colour: yellow No 2. The curve for this colour deviates considerably by its nature and characteristics from the remaining curves shown in the graph under discussion. It barely

reaches upward to 35%, while its dispersion, bigger than that of all the other curves, amounts to as much as ± 1·60. Its mean value is shifted towards yellow-green. The colour in question bears, therefore, a bigger resemblance to shades of green than it does to orange colours.

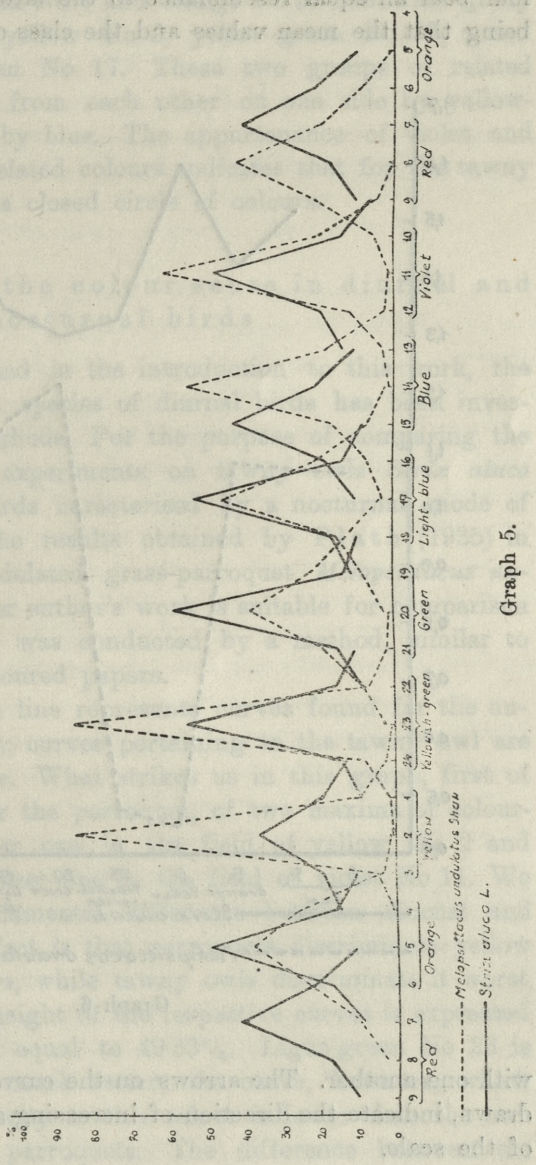
In the long-wave portion of the colour scale there still remain to be considered the curves for red No 7 and orange No 5, while in the short-wave portion the curves for violet No 11 and blue No 15. In the two outward-lying groups of curves a distinct resemblance is noticeable. Thus the curve for red possesses as though its counterpart on the other side of the spectrum in dark-blue No 15. The apexes of these curves differ in their height by as little as 0·67%, while their dispersions are ± 1·52 and ± 1·51 respectively, therefore almost the same. The mean values of these curves in relation to their modal values are in both cases shifted towards the short waves, therefore red displays a resemblance to orange, and dark-blue to violet. Within the two colours we encounter two minima of sensitivity which, however, are weaker than in yellow.

On the other hand the curve for orange conforms to the one for violet. The difference in height of their apexes amounts to 2%, while dispersien is nearly the same: ± 1·42 for orange and ± 1·44 for violet. The mean values of the curves under discussion are numerically equal to each other, but they have opposite signs. Both are shifted, in relation to their modal values, towards red. Therefore, orange and violet are similar to red. These similarities are illustrated by the graph 7 which shows the differences between the mean and modal values of the curves in question. Within orange and violet there lie two further maxima of sensitivity; they are, however, lower than the maximum lying within green.

By comparing the dispersion of the curves for the »training« colours, we obtain a much more distinct and accurate picture of the tawny owl's sensitivity to colours. A graph of dispersion values of the curves is presented in Graph 6. On the axis of abscissas we have marked here the »training« colours from Ostwald's scale in the order in which they occur in the solar spectrum, while on the axis of ordinates we have dispersion values for the several curves. In this graph there show up very dis-

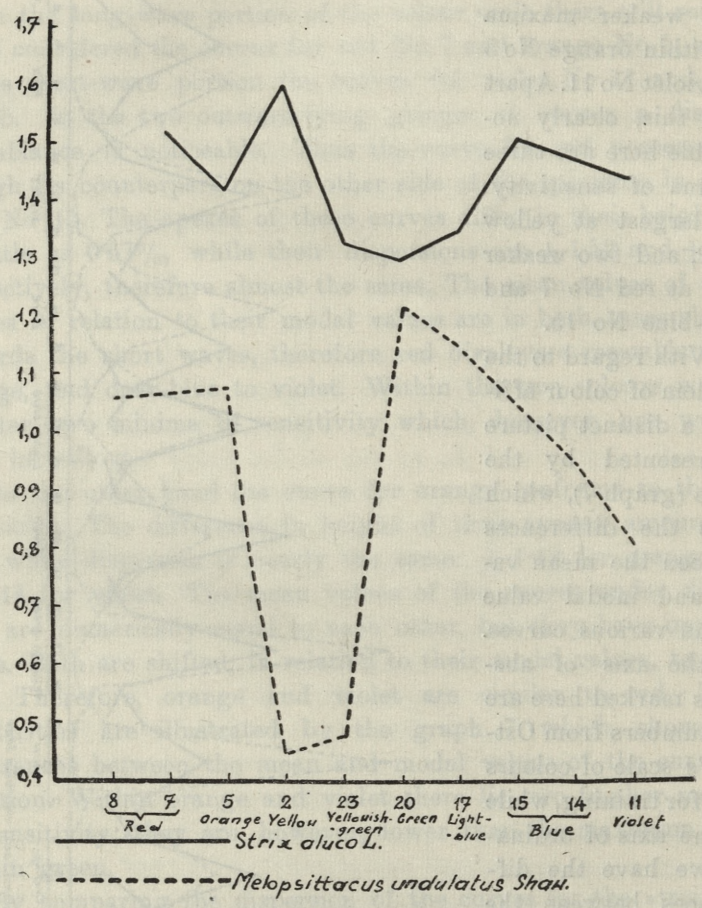
tinctly three maxima of sensitivity, characterised by small dispersion of the curves. One maximum, the largest, lies within the group of yellow-green-blue colours, with its apex at green No 20. Two weaker maxima lie within orange No 5 and violet No 11. Apart from this, clearly noticeable here are three minima of sensitivity: the largest at yellow No 2, and two weaker ones at red No 7 and light-blue No 15.

With regard to the problem of colour affinity, a distinct picture is presented by the curve (graph 7), which hows the differences between the mean value and modal value of the various curves. On the axis of abscissas marked here are the numbers from Ostwald's scale of colours used for training, while on the axis of ordinates we have the differences between the mean value and modal value of each curve. Mean values shifted towards the long waves received the plus sign, while those shifted towards the short-wave portion of the spectrum were given the minus sign. The points at which the



Graph 5.

curve intersects the zero line, mark those places in the colour scale where colours adjacent on both sides to the »training« colour bear an equal resemblance to the latter, the reason therefore being that the mean values and the class of modal value coincide



Graph 6.

with one another. The arrows on the curve, which has been thus drawn, indicate the direction of increasing affinity between colours of the scale.

The graph shows in a distinct manner that as far as tawny owls are concerned there exist within Ostwald's scale two prin-

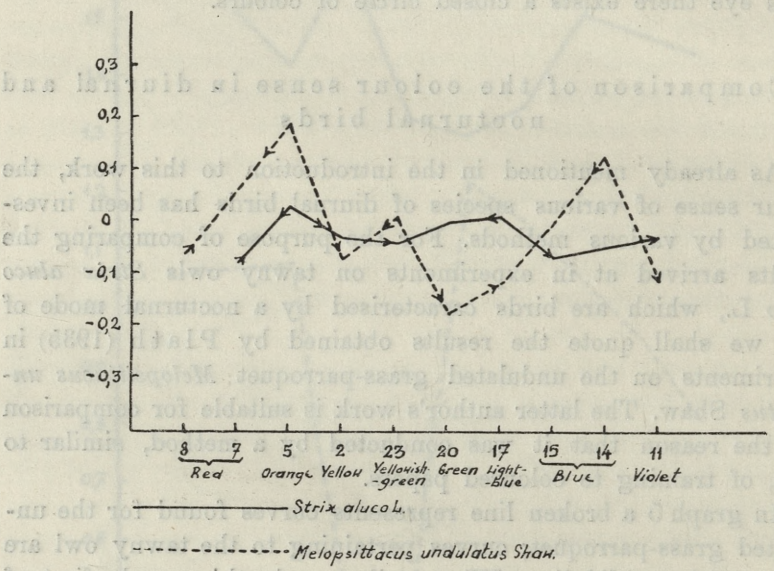
cipal groups of related colours. The first group includes the following colours: blue No 15, violet No 11, and, from the other end of the spectrum, red No 7 and orange No 5. The other group includes the colours: yellow No 2, yellow-green No 23, green No 20, and light-green No 17. These two groups of related colours are separated from each other on one side by yellow-orange, on the other by blue. The appurtenance of violet and red to one group of related colours indicates that for the tawny owl's eye there exists a closed circle of colours.

6. Comparison of the colour sense in diurnal and nocturnal birds

As already mentioned in the introduction to this work, the colour sense of various species of diurnal birds has been investigated by various methods. For the purpose of comparing the results arrived at in experiments on tawny owls *Strix aluco aluco* L., which are birds caracterised by a nocturnal mode of life, we shall quote the results obtained by Plath (1935) in experiments on the undulated grass-parroquet *Melopsittacus undulatus* Shaw. The latter author's work is suitable for comparison for the reason that it was conducted by a method, similar to ours, of training to coloured papers.

In graph 5 a broken line represents curves found for the undulated grass-parroquet; curves pertaining to the tawny owl are shown with a solid line. What strikes us in this graph, first of all, is the existence, for the parroquet, of two maxima of colour-discrimination: a higher one in the field of yellow No 2 and light-green No 23; a lower one in the field of violet No 11. We encounter here a fundamental difference between diurnal and nocturnal birds. The fact is that parroquets discriminate yellow No 2 best of all colours, while tawny owls discriminate it worst. The difference in the height of the respective curves is expressed by a numerical value equal to 49·33%. Light-green No 23 is discriminated by owls much better; the curve, however, which represents their sensitivity to this colour is lower than the corresponding curve for parroquets. The difference between the apexes of the two curves amounts to 30·25%. Worthy of pointing out is the fact that the latter colour is one of those which

are discriminated best by tawny owls, constituting as it does one of the three colours belonging to the maximum of sensitivity. In order to obtain a more complete picture of the differences existing between the colour sense of owls and of diurnal birds, it should be briefly mentioned that for hens the maximum of sensitivity falls on yellow, orange, and red (Honigmann 1931), therefore in somewhat other regions of the spectrum, namely in those of longer wave-length, than for undulated grass-parroquets.



Graph 7.

Investigations on other diurnal birds having been conducted by a different method, we point to them only in a general way.

The other lower maximum of sensitivity for the undulated grass-parroquet lies within violet No 11. It corresponds to a similar third maximum within violet for owls. The corresponding curve for the latter birds is lower by 13·42% than it is for parroquets.

The zones of weakest colour-discrimination for parroquets lie within orange No 5 and dark-green No 20. Both these colours are discriminated better by tawny owls. The difference in the height of curves obtained from training to orange amounts to

11·58% in fawour of owls. Within green the curve is higher by 19·83% for owls than is the corresponding curve for parroquets.

Sensitivity of parroquets to red No 8 is the same as that of owls to red No 7. The difference in favour of diurnal birds here barely amounts to 1·42%. Light-blue No 17, which is one of the three colours discriminated best by owls, is discriminated by parroquets in a slightly weaker degree. The apexes of the respective curves differ by 7·08%. The last colour of the scale, blue No 14, is discriminated better by parroquets than is the adjacent colour, blue No 15, by owls. The apex height of the curves differs here by 12·5%.

With regard to colour affinity Plath demoustrated (graph 7) that for parroquets there exist three groups of related colours, namely: one group of red (No 8) and orange (No 5); a second group of yellow (No 2) and light-green (No 23); and a third group including dark-green (No 20), two shades of blue (No 17 and 14), and violet (No 11), the latter colour linking up with one another the colours belonging to the first and third group. It constitutes for the uudulated grass-parroquet, as a sensation, a transition to colours of long wave-length. Also for these diurnal birds, as a matter of fact, Plath ascertained that there exists a closed circle of colours within Ostwald's colour scale.

In order to demonstrate the resemblances and differences within the various groups of related colours in parroquets, as representatives of diurnal birds, and in tawny owls, as representatives of nocturnal birds, we have put together in Graph 7 the curves of differences between the mean and modal value of »training« curves for the two species. In owls the first group of related colours is made up by orange No 5, red No 7, violet No 11, and blue No 15. This group is separated from neighbouring groups on one side by a zone of yellow-orange colours, on the other by blue. In parroquets this group comprises a somewhat smaller portion of the spectrum, inasmuch as blue colours pass to another group. The boundary is formed here on one side, as in owls, by yellow-orange, on the other side by blue-violet. The second colour group in owls consists of yellow No 2, yellow-green No 23, green No 20, and light-blue No 17. In parroquets we have within this group yellow and yellow-green. Green and blue-green in parroquets form together with blue the third group of related colours,

separated on one side from the second group by light-green, and on the other side from the first group by blue-violet. Consequently, in owls we have only two well-defined groups of related colours, while in parroquets there are three. Parroquets, therefore, as diurnal birds, have a more highly differentiated world of colour sensations than have owls, the latter as representatives of nocturnal birds.

Wishing to demonstrate in a more forcible manner the differences existing between the colour sense of diurnal birds and that of nocturnal ones, we have shown side by side in respective graphs the curves of the dispersion value (graph 6) for the tawny owl and the undulated grass-parroquet. In a similar manner we have also put side by side curves representing the differences between the mean and modal value for both species of birds (graph 7). In the graph showing the dispersion values (graph 6) it is noticeable that dispersion values for curves of »training« colours for owls are bigger than those found by Plath for parroquets. Consequently the entire curve for owls lies above the one for parroquets, intersecting it at no point. On such a basis we are entitled to draw the conclusion that in comparison with diurnal birds owls do indeed possess a considerably weaker sensitivity to colours.

The establishment of the aforesaid facts brings forth the question of whether it is possible to associate the colour sense of owls with the anatomico-histological peculiarities of these birds' eyes. It is known that in the retina of diurnal birds the number of cones is bigger, while in the retina of crepuscular and nocturnal birds *(Striges, Camprimulgi)* rods are more numerous (Heinroth 1933). This fact conforms to the theory of a double function of the histological elements of the retina; this theory considers that cones are for perceiving spectral colours, while rods are set for seeing various shades of gray, i. e. differences in brightness of given objects. A diminished sensitivity to spectral colours in owls would thus be the consequence of the quantitative relation of rods and cones in the retina of these birds, which are characterised by a prevalence of the former. In diurnal birds sensitivity to colours is greater on account of a prevalence of cones.

To this peculiarity we must ascribe, according to Stresemann (1934), the fact that the plumage of owls *Striges* and

goatsuckers *Caprimulgi* is devoid of spectral colours and constitutes a mixture of gray shades and brown ones. This characteristic is of great biological importance to owls which lead a nocturnal mode of life. The fact is that the frontally located eyes (Plate 10), on account of a sideward restriction of its fi ld of vision, expose the owl in daytime to many risks which become dangerous when the enemy approaches noiselessly. The above-mentioned plumage and a great ability for assuming poses resembling tree-bark, may be of protective importance to owls. On account of the abundance of rods in their retinas, swallows *(Hirundinidae)* and swifts *(Micropodidae)* resemble owls. Neither of the aforementioned families, however, have been hitherto investigated as to their colour sense.

In contradistinction to the ability of discriminating between spectral colours, incomprehensible in owls is the very feebly developed ability of discriminating between shades of gray. Rods predominating, the birds should from a theoretical point of view distinguish very well differences in the brightness of papers; however, something opposite is indicated by the results of experiments. Up to the moment we do not know how to explain this fact. We have already pointed out that it may be associated with the problem of infra-red perception in owls. However, until this problem is solved, it is difficult to arrive at any conclusions.

With regard to the fat corpuscles which are situated in front of the sensory cells in the retina of birds, with regard to their colour and significance, the references in literature are rather meagre. We have discussed the significance of these corpuscles in the introduction to this work. According to Stresemann (1934) and Hess (1913) their colour in diurnal birds is mostly ruby, orange, yellow, or pale yellow, while in owls of the genus *Athene* and *Bubo*, and in the swift *Micropus* it is pale yellow and bluish-green. This conforms completely to the colour sense of both groups of birds. The highest maximum in owls falls on colours of the spectrum from yellow to light-blue, while with regard to orange and violet we encounter a sensitivity which is considerably lower than it is in diurnal birds. The highest sensitivity of the latter birds concerns colours of long wave-length: red, orange, and yellow, while they are less sensitive to colours discriminated best by owls.

There is a lack of detailed anatomical data concerning the differences which exist in the retinal structure of owls leading a nocturnal and diurnal mode of life. The fact is that not all owls are crepuscular or nocturnal animals. For instance, the owls *Nyctea* and *Surnia*, and some species of the genus *Glaucidium* hunt in full daylight. Owls which lead a diurnal mode of life have much smaller eyes than the species which hunt at dusk or at night. This fact is obvious and understandable. It would be interesting to discover the anatomico-histological differences which exist in the retinas of owls which lead a nocturnal mode of life and of those which lead a diurnal one, as well as to investigate by the training method the colour sense of both groups and to compare this sense in the two groups.

On the basis of the preceding considerations it is easy to notice that in spite of ascertaining the existence of well-defined differences between the colour sense of tawny owls *Strix* and that of parroquets *Melopsittacus*, one cannot generalise them for all diurnal birds and all owls. Parrots *Psittaci* and owls *Striges* occupy as orders completely separate systematic positions. Parrots do not display any relationship to other orders of birds; they form a group which is well separated from all others, nevertheless they are considerably specialised group, particularly as regards their habits. Not all of them are diurnal birds. The genera *Geopsittacus* from Australia and Tasmania, and *Stringops* from New Zealand lead a mode of life which is mostly nocturnal. Of their colour sense we can say nothing for lack of appropriate investigations. Even if we confine ourselves to the already discussed parroquets, we observe in them the occurrence of well defined differences in comparison with the colour sense of other diurnal birds. Owls *Striges* constitute in the system also a compact group of raptorials which, as already stated above, also display both diurnal and nocturnal forms. In order, therefore, to acquire a detailed knowledge of the colour sense of birds, we are in need of more detailed investigations concerning whole groups, or even particular species differing not only phylogenetically and systematically, but also ethologically.

Summary of results

1. Tawny owls *Strix aluco aluco* L. can be trained at least to eight colours from Ostwald's scale of 24 coloured papers, namely: red No 7, orange No 5, yellow No 2, yellow-green No 23, green No 20, light-blue No 17, blue No 15 and violet No 11. The training was conducted with the help of the positive colour signalizing food.

2. Tawny owls discriminate colours qualitatively, one from another, and from various degrees of gray.

3. Tawny owls can be also trained to particular degrees of gray from Hering's 17-degree scale of papers. The ability of discriminating between degrees of gray is considerably weaker than the ability of discriminating between spectral colours.

4. The maximum of sensitivity lies in the field of green No 20, the minimum in the field of yellow No 2. A second weaker maximum exists within orange, a third one within violet; a second weaker minimum lies in red, a third one in blue.

5. The author succeeded in establishing within Ostwald's scale two groups of related colours. One of them includes the colours: blue, violet, red, and orange; the other: yellow, yellow-green, green, and light-blue. They are separated one from the other on one side by yellow-orange colours, on the other side by blue.

6. The author succeeded in determining the existence of a closed circle of colours in the tawny owl's colour sense.

7. In comparison with the colour sense of the undulated grass-parroquet *Melopsittacus undulatus* Shaw., well defined differences proved to exist as to colour sensitivity in various parts of the spectrum, as well as to the number and placement of groups of related colours. The colour sense of the tawny owl, in comparison with diurnal birds, is developed in a oonsiderably weaker degree, this being associated with the anatomico-histological structure of their eyes.

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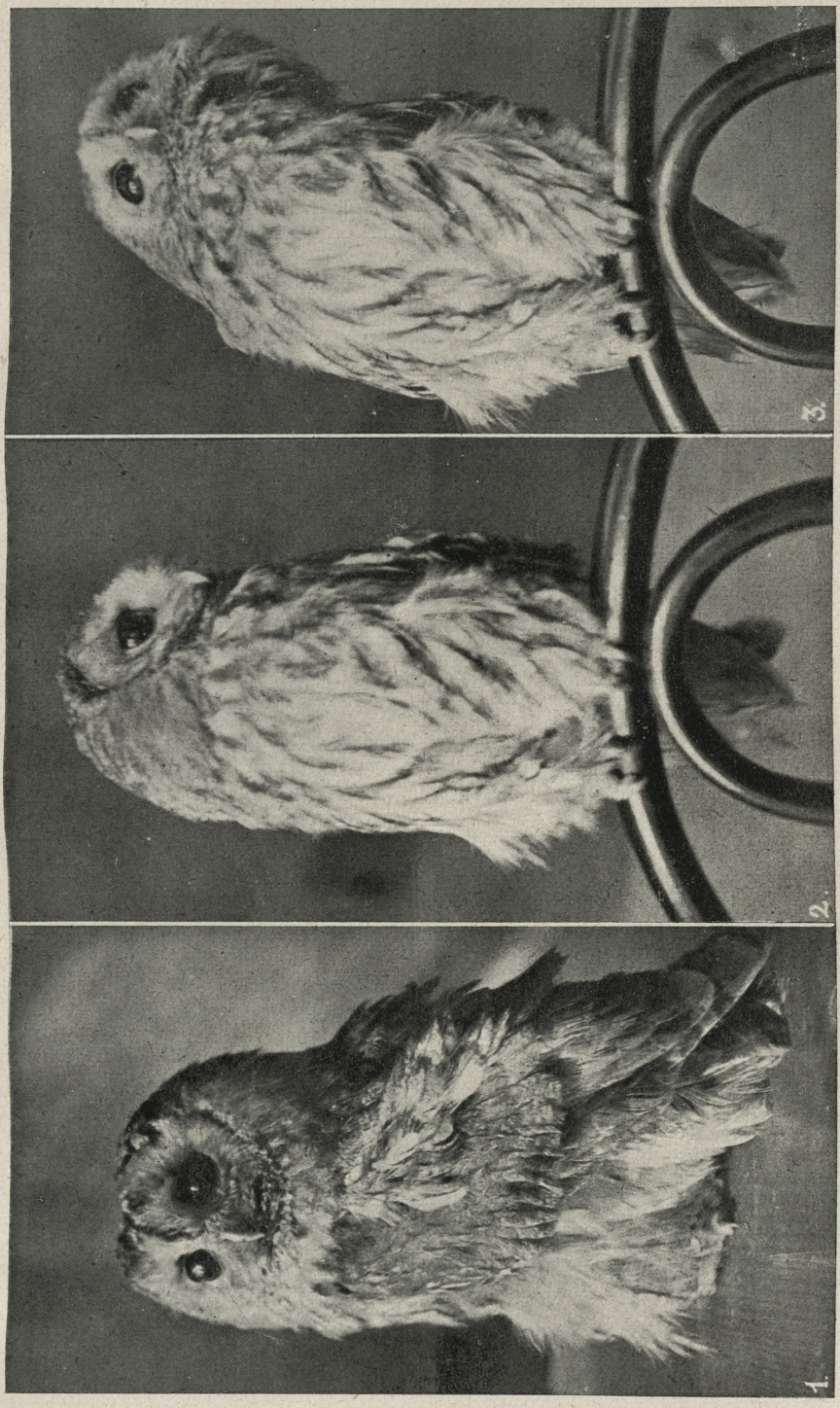
Explanation of plate 10

Phot. 1. The specimen No 1. The frontal situation of the eyes in the owls head.

Phot. 2. The specimen No 4. The turn of the head towards the noticed object.

Phot. 3. The specimen No 4. The observation of the pigeons passing behinde the window.



B. Ferens phot.

Rozwój zatok podstrunowych u Lampetra Wilderi. *The Development of the subchordal sinus in Lampetra Wilderi.*

Mémoire

de MM. ***E. KURZMANN*** et ***M. PASCHMA***[1]),

présenté le 1 Décembre 1947 par M. Z. Grodziński m. c.

The subchordal vascular-system of the lamprey has since long been the object of investigations of several authors who agree in the description they give of it, but differ in their opinion as to its significance. All investigators agree in describing the aorta running right under the noto-chord, flanked by the large veins on both sides *(v. cardinales)*. All authors find ventrally from the mentioned vessels some sinus-like formations that follow them the whole length from heart to tail. These vascular sinuses are always filled with a liquid, containing a varying quantity of erythrocytes.

The presence of erythrocytes accounts for the fact that many investigators interpreted these subchordal sinuses simply as blood vessels (Rathke, Klinkowström, Neuville). But already J. Müller and later Langerhans and Vogt assumed them to be lymphatic. Możejko ascribes them a mixed veno-lymphatic character.

[1]) The material was collected in the year 1929 in USA by Prof. Dr. Z. Grodziński, who injected the blood vessels of animals with indian-ink. Before the war E. Kurzmann prepared from this material several excellent series of microscopical sections and described the development of lymphatic vessels. In the year 1941 E. Kurzmann was killed by the German, the manuscript was lost. M. Paschma studied again the sections and did the graphical reconstructions, what facilitated greatly the understanding of developmental processes.

Lately, the problem has been taken up by Hoyer, who give an accurate description of these sinuses, discussed their relation to the veins and having recognised them as lymphatic vessels called them the lymphatic subchordal sack. This sinus extends, in adult specimens, from heart to the end of the coelome, ventrally from the aorta and the cardinal veins. Its walls are thin and delicate especially the ventral wall bordering on the kidneys and forming many protrusions. Its interior is cut here and there by thin trabeculae which multiply in its lateral parts. Here they are more densely set and form a sponge-like tissue.

The communication between the »subchordal sac« and the cardinal veins is secured laterally and medially. According to Hoyer each row has about 25 apertures, each of the last having a valvule hindering the back-flow of blood from the veins into the subchordal sac. The segmental ventral arteries pierce the sac running to the kidneys and gonads.

Our task has been to study the development of »the lymphatic sac« from its earliest stage ap to the moment of metamorphosis of the lamprey. The study has been carried on the larvae of *Lampetra Wilderi* of various sizes (6, 9, 49, 79, 132, 164 mm) whose vessels had been injected with indian-ink through the caudal artery. The larvae were preserved in formalin or Bouins liquid. Microtome cutting was considerably difficult on account of the small degree of permeability of the tissues for paraffin. The skin had to be removed and skinned specimens were kept in paraffin for over ten hours. Suitable sections of the larvae at different stages of development served for a graphical reconstruction of the noto-chord and the adjacent vessels.

Stages of development of the lymphatic subchordal sinus

In the youngest larvae examined (6 and 9 mm) the lymphatic system is not present. Under the notochord however the aorta and two cardinal veins running along it, are already perfectly developed. The diameter of the veins is twice as large as that of the aorta. Ventrally to the main veins are situated the kidneys (Fig. 1, Mh) and the intestine lies below already without a mesentery. According to Hatta in earlier stages than the one we have started with, the intestin is stil provided with a mesentery,

that disappears during farther development. Besides that there exist segmental arteries and veins (Fig. 1, As, Vs) and ventral arteries running from aorta to kidneys Fig. 1, Av).

The older larvae (49 mm) show changes in their cardinal veins. Both unite namely medially from the aorta on their whole length. Properly speaking, there exists but one large vein, its lumen being strongly narrowed beneath the aorta and widened in its lateral sectors, which belonged primarily to both cardinal veins.

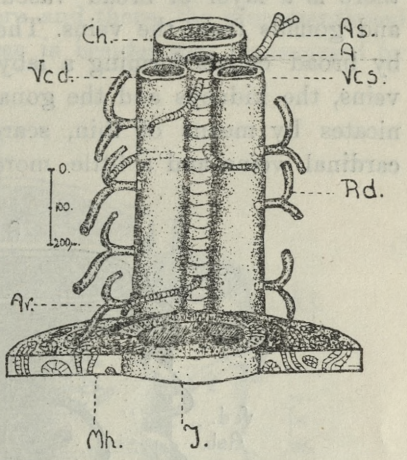


Fig. 1. Larva 9 mm. No trace of lymphatic vessels nor connections between the cardinal veins are visible.

In the flattened middle sector a small number of the bars, connecting the dorsal wall of the vessel with the ventral one are noticeable. From the middle part of the vessel i. e. from the newly formed, numerous little sinus-like vessels run towards the gonads and the kidneys (Fig. 2).

Further conspicuous changes in the vascular system are met with in larvae of 79 mm. First of all the middle sector of the newly formed vessel situated below the aorta begins to separate from the cardinal veins. This part bears the character of an independent vascular duct which we are going to design as *Truncus intermedius* (Fig. 3, Ti).

The *Truncus intermedius* is a wide tube situated between both cardinal veins. It communicates with them by means of larger or smaller apertures situated in rows closely to each other. The numbers of trabeculae connecting the ventral and dorsal walls of the *Truncus intermedius* increase considerably. The sinus-like little vessels from the *Truncus intermedius* and from the adjacent sectors of cardinal veins increase considerably in number. Similarly to the former stage these vessels grow into the kidneys and gonads and their number becomes finally so great as to form an intricate tangle of vascular ducts (Fig. 3).

The anatomic relations in the larvae of 132 mm length point to important changes of the development. Ventrally to the veins there is a layer of broad vascular ducts separating the kidneys and gonads from the veins. They are connected with each other by broad canals forming a labyrinth of big vessels between the veins, the kidneys and the gonads. This labyrinth again communicates by means of thin, scarce, irregular openings with the cardinal veins and a little more frequently with *Truncus inter-*

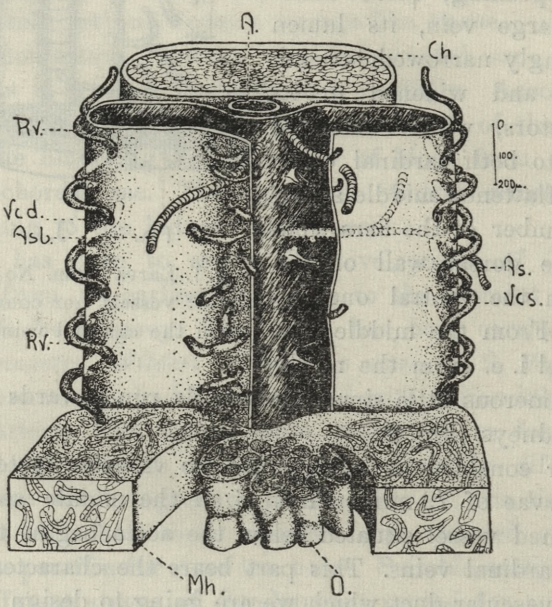


Fig. 2. Larva 49 mm. Connections between the cardinal veins appear, sinus-vessels begin to germinate.

medius. The *Truncus* itself is smaller in size compared with the former stage and similar in appearance to other vessels composing the labyrinth. Its initial connection with the cardinal veins is maintained (Fig. 4).

In big larvae (164 mm) standing close before metamorphosis the lymphatic subchordal sinus is very much like that of adult specimens. Between the kidneys and the gonads from on side and the main blood vessels situated below the notochord on the other extends a large vascular sac. Its dorsal side gently curved in the

middle adheres closely to the walls of the cardinal veins and the aorta.

The ventral side forms sac-like protrusions towards the basis of the gonads. Inside the sac, here and there, the aforementioned thin trabeculae are found. The sac is besides that transversed by

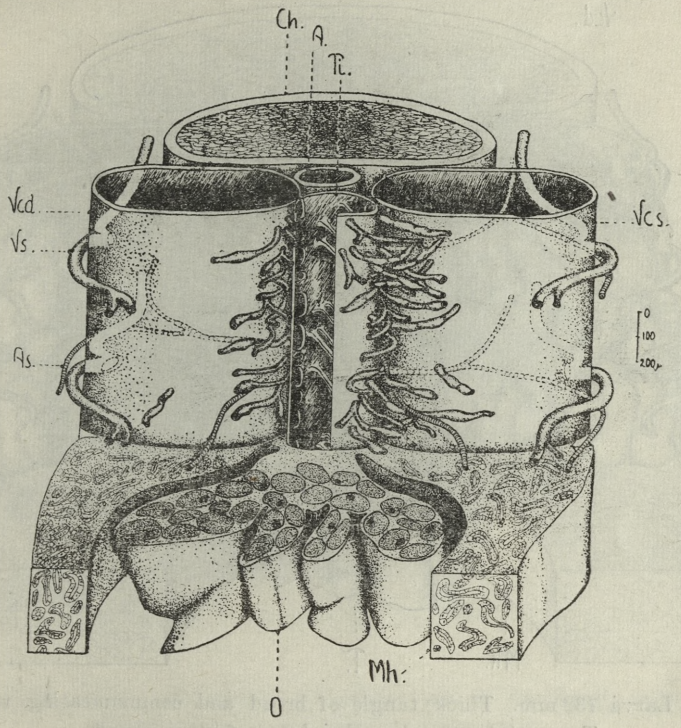


Fig. 3. Larva 79 mm. *Truncus intermedius* in formation. The sinus-like vessels grow considerably in number.

arteries running from the aorta to kidneys and gonads. The lymphatic sac is provided on its dorsal side with 4 rows of apertures, that connect it with *Vv. cardinales*. Two of them are situated laterally and two medially. The lymphatic sac is connected with each cardinal vein by means of two rows of apertures (Fig. 5). The apertures provided with valvules and forming in adults the connection between the lymphatic sac and the veins are found in the same region, but are far less in number. The connections with the veins are also narrower than those of young specimens.

The medial ones are larger and longer than the marginal ones. The shape of the sac undergoes in adults a slight change. The gonads namely move ventrad and draw with them the sides of the

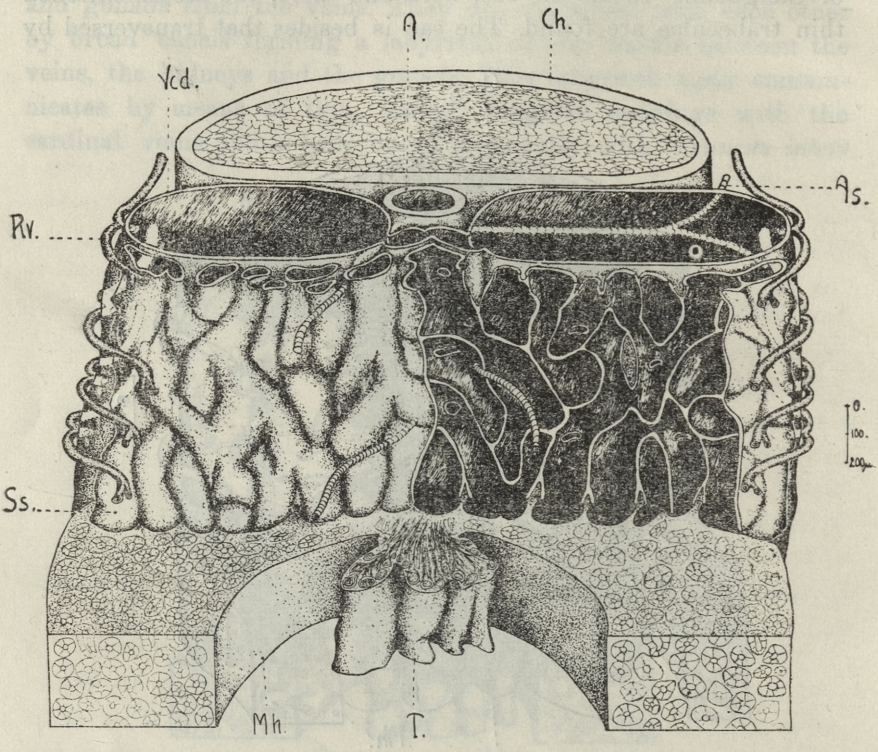


Fig. 4. Larva 132 mm. Thick tangle of broad and communicating vessels. *Trunc. interm.* takes the shape of other canals.

median part of the sac and form two falds along the gonads, whereas medially the sac flattens somewhat in a dorso-ventral direction

The process of the formation of the subchordal lymphatic sac

On the baais of the a forementioned observations the development of the lymphatic sac may be hypothetically traced as follows: Both cardinal veins approach ventrally from the aorta and fuse into one large vessel; from the central sector small sinuses begin to germinate growing in the direction of the gonads. The number of the sinuses augments with the develop-

ment of the embryo. Simultaneously, between the cardinal veins, the central canal *(Truncus intermedius)* begins to form, remaining in connection with them by means of numerous apertures. The diameter of the sinuses, formed below the veins, grows larger, they multiply and get in contact with each other; finally they

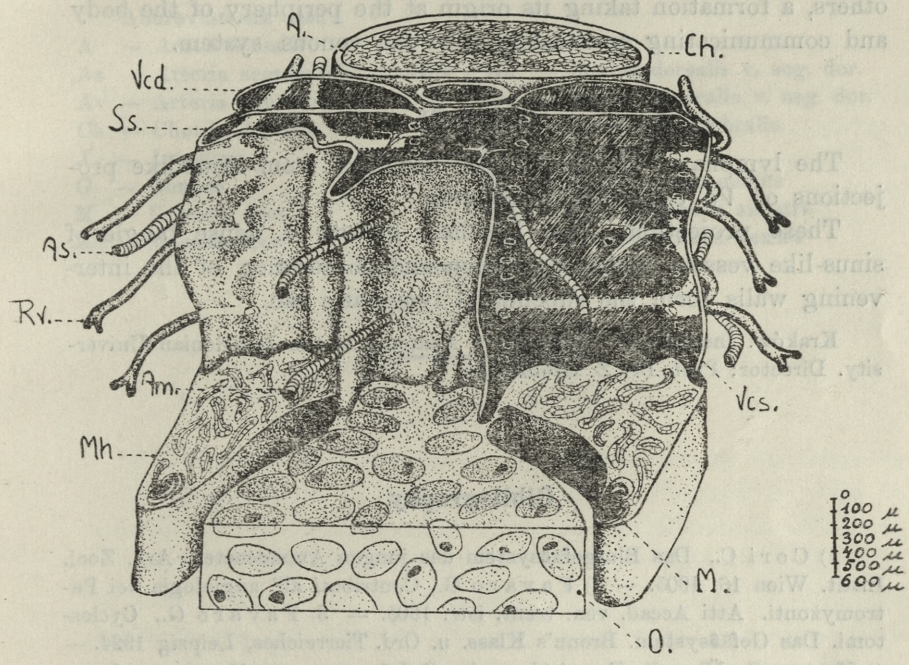


Fig. 5. Larva 164 mm. Subchordal lymphatic sac is developed, with the system of apertures leading to the veins.

form a thick net of vessels situated between the cardinal veins the kidneys and the gonads.

The partial obliteration of the walls of these sinuses forms a connection between them. *Truncus intermedius* assumes the shape of the sinus and separates almost completely from the cardinal veins. In this way a labyrinth of sinuses is being formed. A further obliteration of the walls and the fusion of sinuses into larger vessels gives rise to an uniform lymphatic sinus similar to the one found in adult specimens. Irregular connections with the cardinal veins disappear leaving a system of communication in the shape of four rows of apertures (Fig. 5).

The description we gave of the development of the subchordal lymphatic sinus, illustrated in the adjoined figures supports the thesis, that the lymphatic vessels are a secondary formation, developed from the vein-system (Hoyer, Favaro, Tretiakow, Sabin, Clarc); and is not, as supposed by Vialleton and others, a formation taking its origin at the periphery of the body and communicating secondarily with the venous system.

Summary

The lymphatic subchordal sac develops from sinus-like projections of *Vv. cardinales posteriores.*

These projections form by their growth a dense tangle of sinus-like vessels, which by fusion and obliteration of the intervening walls form the subchordal lymphatic sac.

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Explanation of figures

The figures represent a graphical reconstruction of the subchordal organs of the lamprey *Lampetra Wilderi* in the abdominal part, situated backwards to the heart. The notochord is covered with vessels, the terminal section of which are covered by kidneys and gonads.

Abbreviations used:

A — Aorta dorsalis
As — Arteria segmentalis dorsalis
Av — Arteria ventralis
Ch — Chorda dorsalis
J — Intestine
G — Gonads
M — Urinary duct
Mh — Mesonephros
O — Ovary
Rd — Ramus dorsalis v. seg. dor.
Rv — Ramus ventralis v. seg. dor.
Ss — Sinus subvertebralis
T — Testicle
Ti — Truncus intermedius
Vcs — Vena cardinalis sinistra
Vcd — Vena cardinalis dextra
Vs — Vena segmentalis dorsalis.

Nowa grupa związków organicznych modyfikujących wzór skrzydeł motyli metodą injekcji Zaćwilichowskiego. Un nouveau groupe de composés organiques modifiant le dessin des ailes des Lépidoptères d'après la méthode d'injection de Zaćwilichowski.

Mémoire

de M. ***J. RYMAR***,

présenté le 1 Décembre 1947 par M. Z. Grodziński m. c.

(Planches 11—12)

Dès l'époque de la découverte dans l'hémolymphe des Lépidoptères qui se fonce au contact de l'air, du ferment oxydant la tyrosine en un pigment sombre, pareil aux mélanines (Fürth), on a souvent attribué l'origine du dessin des ailes des Lépidoptères à la présence de la tyrosinase, ou à celle d'autres ferments oxydants englobés sous le nom général de chromooxydases (Oppenheimer).

En soumettant les chrysalides à l'action des hautes et basses températures pendant les 48 heures qui suivent leur métamorphose, on est à même d'obtenir des formes de Lépidoptères au dessin fort modifié. Les formes ainsi obtenues à l'aide des températures semblent en général plus riches en mélanine que les formes normales.

Zaćwilichowski a obtenu des variétés identiques à ces dernières, en injectant à l'hémolymphe des jeunes chrysalides deux composés chimiques aux effets à peu près semblables: l'acide phosphorotungstique *(acidum prosphorowolphranicum)* et l'acide phosphoromolybdénique *(acidum phosphoromolibdenicum)*.

Il est donc possible, dans une certaine mesure, d'agir expérimentalement sur la quantité et le placement de la mélanine dans l'aile du Lépidoptère. Zaćwilichowski assure que l'apparition

des modifications de formes a pour cause fondamentale les bouleversements opérés dans les processus chimiques des composés albumineux d'un Lépidoptère en développement et qui ont lieu sous l'influence des agents extérieurs.

Mes recherches personnelles m'ont convaincu que l'injection à l'organisme de la chrysalide — d'après la méthode de Zaćwilichowski — de divers polyphénols, doit entraîner les modifications du dessin des ailes pour autant que ces composés, dans l'organisme de la chrysalide, s'oxydent en produits se rapprochant de la mélanine des écailles. J'ai pu constater en injectant des composés de phénol que les modifications du dessin obtenues par la méthode d'injection ne sont point comparables aux variétés obtenues sous l'action des températures; et qu'au contraire, il est aisé d'obtenir des transformations qui ne le cèdent en rien aux résultats de Zaćwilichowski, en utilisant pour les injections les produits foncés d'oxydation de ces mêmes phénols.

Les premières injections faites étaient des solutions paramétha- et ortho-phénols, ainsi que du tannin dont les molécules contiennent des restes bigalloliques. En outre, j'ai fait certaines observations sur l'activité des extraits végétaux contenant du tanin.

Au cours d'expériences ultérieures, ces mêmes composés ont été soumis à l'oxydation et leurs produits injectés aux chrysalides. L'oxydation s'effectuait de deux manières, soit grâce à l'oxygène de l'air dans une solution ammoniacale, soit également au contact de l'eau oxygénée en employant une préparation de péroxydase de racine de raifort.

Dans les expériences de contrôle j'ai introduit des colorants: bleu de méthylène et coccinine (*Coccinin* Grübler) pour savoir jusqu'à quel point l'injection des colorants est à même de changer le fond et le dessin des ailes. Voilà pourquoi j'injectais, à l'occasion, bien d'autres composés chimiques, qui, d'ailleurs, n'ont fourni aucun résultat permettant de conclure à une spécificité chimique du mécanisme particulier de l'apparition des modifications du dessin sur les ailes des Lépidoptères.

Les chrysalides utilisées ici de préférence ont été les »*Vanessa urticae* L.«, espèce aisément accessible et bien explorée s'il s'agit des modifications du dessin. Bien d'autres espèces de Lépidoptères de jour et de nuit ont été, en outre, étudiées, afin de connaître leur aptitude à créer des variétés.

Méthode et matériaux

Le premier groupe des réactifs chimiques comprend des solutions à 1% de tannin, de pyrogallol (1, 2, 3, trioxybenzène), de pyrocatéchine (ortho-bi-hydroxybenzène) et de hydroquinone (para-bi-hydroxybenzène), ainsi que des solutions saturées d'acide protocatéchique (acide ortho-bihydroxy-carbonique), d'acide caféïque (acide ortho-bi-hydroxy-cinnammonique) et d'acide gallique (1, 2, 3, trihydroxy-carbonique).

Les composés d'hydroxybenzène cités plus haut, fournissent, mélangés à une solution à 1% de chlorure de fer, des produits chimiques colorés. Le pyrocatéchine et l'acide protocatéchique se colorent en vert, le pyrogallol et l'acide gallique en bleu, le pyrogallol en surabondance en rouge, le tannin en grenat, l'hydroquinone en jaune. Ces composés ne sont point actifs.

Par contre, on obtient des produits actifs en oxydant ces mêmes composés dans une solution d'ammoniaque. Ces produits d'oxydation sont des composés noir-brun qui ne se colorent point au contact du chlorure de fer, mais font se foncer visiblement la solution dans laquelle, au bout d'un certain temps, se forme un sédiment noir-brun informe.

A ces solutions de 1 à 2% ou à ces solutions saturées, ajoutons de l'ammoniaque concentré (soit 25% de NH^3) dans la proportion de: une part de NH^4OH pour trois parts de la dite solution. Elles s'oxydent ensuite sur de larges verres de Petri au contact de l'air pendant vingt-quatre heures à la température de la chambre. Pour éviter la complète évaporation d'ammoniaque, il convient de verser de temps à autre dans la solution oxydée, de modestes quantités d'ammoniaque concentré. A la première addition d'ammoniaque les composés prennent rapidement une teinte foncée. Quand, au bout de vingt-quatre heures d'oxydation, aucune altération de couleur n'a plus lieu, malgré l'addition dans une petite épreuve du composé, de ces petites doses d'ammoniaque, on fait sécher les composés oxydés sur une plaquette à l'étuve à la température de 50 à 60° C. Ces résidus noir-brun servent à former des solutions à 3% que l'on enferme dans des ampoules. L'hydroscopie de certaines de ces préparations rend difficile leur conservation à l'état sec.

L'oxydation enzymatique des polyphénols cités s'obtient en ajoutant aux 5 cc des solutions 3 gouttes d'extrait de péroxydase et 1 cc d'eau oxygénée à 3%. Au bout d'une heure, on peut injecter aux chrysalides *V. urticae* L. les produits brun-clair de l'oxydation. Ces solutions prennent, grâce au chlorure de fer, des teintes qui dénoncent la présence de certains groupes inoxydés d'hydroxyles.

Pour obtenir de la péroxydase, on recourt aux extraits de la racine du raifort. Du raifort broyé, mis dans un linge de toile, on extrait soit à la main, soit à la presse hydraulique, la sève que l'on ne filtre qu'après vingt-quatre heures de décantage à la température de la chambre. Cela donne un liquide transparent, légèrement opalescent, jaunâtre.

On y ajoute de l'alcool étylique à 96%, soit environ 1 part de C^2H^5OH pour 3—4 parties d'extrait. Après avoir filtré le résidu qui en provient et en avoir fait évaporer l'alcool à une température de 40° C, on obtient une matière apte à la préparation des solutions actives. Pour juger de la force active de l'extrait, on lui fait subir l'épreuve de la benzidine (benzidine utilisée dans des solutions aqueuses): si l'extrait est réussi, la benzidine prend rapidement au contact de l'eau oxygénée une teinte d'un bleu-foncé.

Un autre groupe d'expériences exige des extraits végétaux qui contiennent des depsides et qui, en contact avec le chlorure de fer, se colorent en vert. Soumis à l'influence de la péroxydase du raifort et de l'eau oxygénée, ces solutions se foncent. C'est de cette façon que j'apprêtais mes extraits de grains de café et de pétales de rose rouge.

Les grains bien broyés de café non torréfié trempent pendant 12 heures à la température de la chambre, dans de l'eau distillée, en raison plus ou moins de 1 pour 3; l'extrait est pressé dans un morceau de toile et puis filtré. Le liquide recueilli accuse de l'albumine, de la péroxydase et des tannins dont la présence est décelée par des réactions chimiques. Pour éliminer les albumines, soumettre à une courte ébullition, puis filtrer. L'extrait originel ainsi obtenu donne, avec le chlorure de fer, une teinte accentuée noir-vert que l'on utilise dans les injections de contrôle.

Dans l'extrait originel de grains de café non torrifié versons de la sève de raifort, dans une proportion de 1 à 4—5. A ce

mélange ajoutons par portions, au bout d'une demi-heure, de l'eau oxygénée à 3% dans la proportion de 1 pour 3 jusqu'au moment de la formation d'un mélange trouble à teinte sombre rouge-brun qui conserve sa couleur malgré l'addition du reste de l'eau oxygénée. Ce produit opaque est essentiellement toxique. Après l'avoir exposé 24 heures à la température de la chambre, puis filtré bien méticuleusement, ou tout moins, après l'avoir séparé par centrifugation du sédiment brun, on obtient un liquide clair-jaune d'or qui, au contact du chlorure de fer, devient vert-olive et ne contient pas de péroxydase. Il est parfois malaisé de filtrer ou de centrifuger ces sédiments bruns; il faut alors décanter le liquide qui, en trois semaines au moins, se détache des résidus. Il peut arriver que, dans la préparation il reste encore de la péroxydase. Pour l'éliminer, il suffit d'ajouter un peu d'extrait originel de grains de café non torrifié et de filtrer à nouveau.

Quant aux pétales de la rose rouge Sherlock Holmes, après les avoir fait tremper dans de l'eau distillée, il faut les faire bouillir une heure environ, sans omettre d'ajouter de l'eau distillée au fur et à mesure de l'évaporation. L'extrait filtré encore chaud se condense par évaporation et devient rouge-foncé. Après la condensation et le filtrage, l'extrait originel rouge foncé est utilisé dans les injections de contrôle.

Si on mélange cet extrait originel avec de la péroxydase, en une proportion d'environ 1 à 4, le liquide, de rouge, devient gris-violet et trouble. Deux heures après, on y ajoute de l'eau oxygénée à 3% dans la proportion de 1 à 4. Quelques heures plus tard, on filtre le liquide rouge foncé, l'extrait originel devient vert au contact du chlorure de fer; traité à la péroxydase et l'eau oxygénée, il devient brun-olive.

Injectons à présent ces solutions de composés chimiques aux chrysalides à l'aide d'une mince canule de verre passée à la flamme, toujours suivant la méthode de Zaćwilichowski. La dose de solution injectée varie entre 5 et 10 mg pour les chrysalides *V. urticae* L., pesant 0·23—0·25 gr, c'est-à-dire qu'elle équivaut à 2—4% du poids de leur corps. C'est donc $^1/_{10}$—$^1/_5$ de goutte normale (0·05 cc) pour les chrysalides *V. urticae* L. La dose moyenne d'injection équivaut à $^1/_{30}$ du poids du corps de la chrysalide. La quantité de substance active dans l'injection d'une solution à 3% à une chrysalide, se monte, dans les grandes doses, à en-

viron 0·3 mg, ce qui equivaut à 1 mg pour chaque 1 gr du poids de la chrysalide. Ces mesures ont pu être établies en pesant les chrysalides avant et après l'injection.

C'est la même proportion qui a été observée dans les injections aux chrysalides des autres espèces employées ici.

En pratique, il convient de distinguer la petite dose (d'environ 5 mg) de la grande (10 mg environ), suivant les réactions de la chrysalide pendant l'injection. Ainsi, sous l'action des grandes doses, les segments abdominaux s'élargissent quelque peu; dans les petites au contraire, la chrysalide ne subit aucune modification. La concentration des diverses solutions injectées oscille entre 2 et 5%: j'utilisais à l'ordinaire des composés à 3%. Lorsque j'injectais des extraits actifs, la question du pourcentage ne pouvait être définie.

Les chrysalides recevaient les injections entre 4 et 24 heures après leur métamorphose, la plupart entre 12 et 18 heures.

Dans les expériences, j'ai utilisé de préférence les chrysalides des Lépidoptères *Vanessa urticae* L., ainsi que, parmi les espèces apparentées: *V. io* L., *V. Polychloros* L., *Pyrameis atalanta* L., *Polygonia C album* L. Parmi les autres espèces j'ai également utilisé les *Phytometra gamma* L.

Les nids des chenilles *Vanessa urticae* L. ont été recueillis, la plupart du temps, au moment de leur dernière mue, ou à peu près déjà mûrs. Les essaims cultivés avaient leurs boîtes larges et à ouvertures garnies de mousseline et vivaient à la température de la chambre.

Classification des variétés de *Vanessa urticae* L.

Mes recherches m'ont permis d'obtenir des exemplaires de *Vanessa urticae* L. qui montrent, sur une grande échelle, les modifications du dessin des ailes. Pour plus d'ordre, j'ai choisi comme base de ma classification l'aspect macroscopique de la surface supérieure des ailes antérieures et postérieures. Je ne me suis point arrêté à l'analyse minutieuse de la variabilité des divers éléments du dessin, comme l'ont fait Köhler et Feldotto. Je me suis contenté du système qualitatif qui distingue les variétés: *var. polaris* Stgr., *ichnusa* Bon., *atrebatensis* Boisd., *ichnusoides* Sel., et *conjuncta* Neub. Au cours du travail, il est apparu néces-

saire de distinguer encore une variéte: »*faible*« et une autre »*très faible*«.

La classification employée est, jusqu'à un certain point, facultative. Quant aux formes transitoires, elles ont été classées d'après la prépondérance de leurs caractéristiques.

La planche 11 présente une série de formes allant de la *Vanessa urticae* L. normale, phot. 1, à la variété *ab. conjuncta* Neub.

Les variétés très faibles. Ce sont les Lèpidoptères qui tout en conservant tous les éléments de la surface supérieure de l'aile antérieure, montrent sur leur aile postérieure un léger agrandissement des taches bleues. Il peut, en outre, arriver que la tache claire du rebord antérieur de l'aile postérieure s'assombrisse. De même, il peut se produire un infime agrandissement de la tache sombre à la naissance de l'aile postérieure sans que le contour nettement dessiné de la tache fondamentale en soit atteint (phot. 2).

Les variétés faibles. Elles sont caractérisées par l'agrandissement à la surface supérieure de l'aile postérieure, de la tache sombre à la naissance de l'aile. De plus, ce qui n'a point lieu chez les variétés très faibles, la ligne du rebord extérieur de la tache fondamentale est effacée et ne se dessine pas nettement sur le fond clair, surtout dans sa partie antérieure. Les taches bleues sont nettement allongées et agrandies, tandis que la tache claire sur le rebord antérieur de l'aile postérieure se fonce nettement. Sur l'aile antérieure, tous les éléments du dessin restant intacts, les taches bleues du ruban ocellé peuvent être plus allongées en leur partie antérieure (phot. 3).

Les variétés polaris Stgr. Les traits caractéristiques en sont le coloris foncé du fond des ailes, ainsi que l'agrandissement des taches noires. La tache centrale du rebord antérieur de l'aile rejoint la tache du milieu. Ce trait d'union n'est jamais aussi foncé que les taches noires des ailes, et sous la forme d'une S, peut être plus ou moins visible. Les variétés obtenues dans les expériences avaient, à coté des caractéristiques zoologiques relevées plus haut, des veines plus foncées (phot. 4).

Les variétés ichnusa Bon. J'ai classifié sous ce vocable toutes les variétés qui, à la surface supérieure de l'aile antérieure ne portaient point les deux taches, ou n'avaient que la tache antérieure, la tache postérieure étant à peine marquée. Sur l'aile postérieure, le coloris foncé qui se trouve à la naissance de l'aile

atteignait partiellement le ruban de la bordure ou restait dans les limites normales (phot. 5).

Les variétés atrebatensis Boisd. On y relève à la surface supérieure de l'aile antérieure, en plus de la disparition totale ou presque des taches jumelles, une coloration foncée de l'espace entre la tache du rebord et celle du centre sur la bordure avant de l'aile. Cette teinte n'est jamais aussi foncée que les taches elles-même; c'est quelque chose entre le foncé des veines (m^1 et m^2) de cet espace et le coloris sombre non moins accentué des taches de l'aile antérieure. L'espace foncé du rebord postérieur de l'aile est, en général, plus grand que dans les variétés *Ichnusa* Bon. On constate souvent également chez les *atrebatensis* Boisd., la disparition partielle du ruban ocellé fortement marqué à l'aile antérieure. La tache blanche qu'elles portent s'élargit et prend souvent la forme d'une demi-lune, alors que chez les *Ichnusa* Bon., cette tache n'est guère plus large que la normale (phot. 6).

Les variétés ichnusoides Sel. Elles se distinguent par la fusion complète ou presque en un tout homogène à l'aile antérieure, de la tache du centre et de celle du rebord à l'avant de l'aile, tandis que l'aile postérieure est toute entière foncée. Parfois cependant, le rebord arrière de cette dernière est plus clair. De plus, à l'aile antérieure les taches jumelles font toujours défaut et la tache blanche est presque toujours agrandie en demi-lune. Parfois, la bande ocellée est sauvegardée, mais pas typiquement, surtout à l'aile postérieure (phot. 7).

Les variétés coniuncta Neub. Sur leur aile antérieure on remarque la fusion totale entre la tache caractéristique des variétés *Ichnusoides* Sel. et la tache quasi-centrale du rebord avant de l'aile. Cette fusion est ou totale, ou parfois, simplement nettement marquée. La teinte noire de l'aile postérieure est encore bien plus intensive que chez les *Ichnusoides* Sel. (phot. 8).

Certains Lépidoptères, sous l'influence de l'agent chimique, n'éclosaient pas d'eux-mêmes et restaient dans leur coque de chrysalide (exuvium). D'autres ne parvenaient pas à déployer leurs ailes. La pincette y aidait les uns et les autres. Je les ai classés tout comme les Lépidoptères normalement venus, dans la mesure où leur classification était possible. Dans mes expériences, sur tout le matériel expérimental il y avait 4% environ de Lépi-

1.

VANESSA URTICAE

5.

VAR ICHNUSA BON.

2.

VAR. TRÈS FAIBLES

6.

VAR. ATREBATENSIS BOISD

3.

VAR FAIBLES

7.

VAR. ICHNUSOIDES SEL.

4.

VAR POLARIS STGR.

8.

VAR. CONIUNCTA NEUB.

J. Rymar phot.

doptères *Vanessa urticae* L. anormalement éclos et environ 15% de non éclos.

I-er groupe d'expériences: l'action des composés hydroxyaromatiques et de leurs produits d'oxydation

Ces expériences ont été divisées en trois séries. Dans la première j'ai injecté des composés hydroxyaromatiques inoxydés; dans la deuxième, les produits de l'oxydation enzymatique de ces composés; dans la troisième, les substances noir-brun obtenues par l'action de l'oxygène sur les hydroxybenzènes dans un milieu ammoniacal. Les résultats sont exposés à la table Ia.

Les expériences de la première série démontrent qu'aucune transformation du dessin des ailes n'a suivi les injections faites avec les composés tri- et bi-hydroxydes dérivés du benzène, et qui figurent à la table Ia.

Quelques changements »*très faibles*« et »*faibles*« ont eu lieu dans la deuxième série de chrysalides (table Ib) sous l'action des produits d'oxydation enzymatique. Ce sont surtout des trihydroxydes dérivés du benzène: le pyrogallol, l'acide gallique et le tanin qui, dans ses molécules, contient des restes bigalloliques. Par contre, les produits bi-hydroxybenzènes, oxydés enzymatiquement, ne provoquent aucun changement chez les *Vanessa urticae* L.

Les produits les plus actifs sont ceux qui proviennent de l'oxydation des composés hydroxyaromatiques dans un milieu ammoniacal. Ils donnent naissance à toutes sortes de variétés: les formes *polaris* Stgr., *ichnusa* Bon., *Atrebatentis* Boisd., *ichnusoides* Sel., et les *coniuncta* Neub. (table Ic).

II-e groupe: Expériences sur l'action des extraits végétaux oxydés

Jusqu'à présent, ce ne sont guère par conséquent que les polyphénols oxydés dans un milieu ammoniacal à l'oxygène atmosphérique qui se sont montrés actifs. Les produits d'oxydation enzymatique se sont révélés très peu actifs; c'est peut-être que le degré d'oxydation des composés hydroxyaromatiques n'était pas assez avancé, vu les conditions d'expérimentation. Il faut, par contre, relever comme particulièrement actifs les extraits aqueux

TABLE Ia

Expériences faites sur *Vanessa urticae* L. — Action des composés hydroxyaromatiques non oxydés

Préparations	Nombre	Mortalité	Sans changement	Changements très faibles	Changements faibles	Var. polaris	Var. ichnusa	Var. atrebatensis	Var. ichnusoides	Var. coniuncta
Pyrogallol	20	6	14	—	—	—	—	—	—	—
Acide gallique	20	5	15	—	—	—	—	—	—	—
Tanin	20	5	15	—	—	—	—	—	—	—
Pyrocatéchine	20	3	17	—	—	—	—	—	—	—
Acide protocatéchique	20	3	17	—	—	—	—	—	—	—
Acide caféïque	10	—	10	—	—	—	—	—	—	—
Hydroquinone	20	10	10	—	—	—	—	—	—	—

TABLE Ib

Action des composés hydroxyaromatiques enzymatiquement oxydés

Pyrogallol	20	3	16	1	—	—	—	—	—	—
	10	—	9	1	—	—	—	—	—	—
Acide gallique	20	3	16	1	—	—	—	—	—	—
	10	1	9	—	—	—	—	—	—	—
	15	5	7	3	—	—	—	—	—	—
Tanin	45	10	25	9	1	—	—	—	—	—
Pyrocatéchine	20	5	15	—	—	—	—	—	—	—
	10	2	8	—	—	—	—	—	—	—
Acide protocatéchique	10	1	9	—	—	—	—	—	—	—
Hydroquinone	20	14	6	—	—	—	—	—	—	—

TABLE Ic

Action des composés hydroxyaromatiques oxydés dans un milieu ammoniacal

Préparations	Nombre	Mortalité	Sans changement	Changements très faibles	Changements faibles	Var. polaris	Var. ichnusa	Var. atrebatensis	Var. ichnusoides	Var. coniuncta
Pyrogallol	10	1	—	—	2	—	3	4	—	—
	40	5	—	—	2	—	14	17	2	—
	61	27	—	—	—	—	—	—	6	28
	38	—	—	—	8	8	7	11	4	—
	15	5	—	—	—	—	—	—	8	2
	90	20	—	—	—	1	1	7	52	9
Acide gallique	20	4	—	—	—	3	4	6	1	1
	50	8	—	—	1	4	7	17	13	1
	20	8	—	—	—	1	1	3	3	4
	20	16	—	—	—	—	—	—	—	4
Tanin	75	6	—	—	2	2	5	36	24	—
	25	9	—	—	13	—	2	1	—	—
	25	11	—	—	2	—	—	11	1	—
	30	7	—	—	2	—	9	13	5	—
Pyrocatéchine	21	3	—	—	3	14	1	—	—	—
	23	—	13	—	9	—	1	—	—	—
	30	8	3	—	18	—	1	—	—	—
Acide protocatéchique	20	3	—	—	9	3	—	5	—	—
	10	—	—	—	2	1	3	3	1	—
	25	1	—	—	14	—	1	6	3	—
	20	11	—	—	5	—	—	4	—	—
	26	5	—	—	9	—	5	5	2	—
	25	2	2	—	18	—	3	—	—	—
	32	3	3	—	24	—	1	1	—	—
Acide caféïque	10	1	—	—	1	—	1	3	3	1
Hydroquinone	20	6	—	—	2	4	6	1	1	—
	25	4	—	—	7	11	3	—	—	—
	20	4	1	—	10	—	4	1	—	—
	30	26	—	—	1	—	2	1	—	—
	22	10	—	—	2	—	3	6	1	—
	10	2	—	—	1	3	4	—	—	—

des grains de café non torréfié, ainsi que les pétales de rose rouge, après oxydation à la péroxydase et à l'eau oxygénée (table II).

Les extraits végétaux originels, non oxydés, sont très peu actifs, tandis qu'après leur oxydation enzymatique ils se sont montrés aussi actifs que les plus puissants produits noir-brun obtenus des polyphénols. Il n'a pas été possible de déterminer

clairement, dans les expériences faites avec les extraits végétaux, quelles sont les substances les plus propices à l'oxydation par la péroxydase; c'est que, probablement, on n'a traité que les depsydes dont les produits d'oxydation dans un milieu peu acide et sous l'action de l'eau oxygénée et de la péroxydase du raifort,

TABLE II

Action des extraits végétaux: de grains de café brut et de pétales de rose rouge

Préparations	Nombre de chrysalides	Mortalité	Sans changement	Changements très faibles	Changements faibles	Var. polaris	Var. ichnusa	Var. atrebatensis	Var. ichnusoides	Var. coniuncta
Extrait premier de grains de café brut	15	2	6	5	2	—	—	—	—	—
	15	3	4	7	1	—	—	—	—	—
Extrait premier enzymatiquement oxydé	10	1	—	—	1	—	3	3	2	—
	50	2	—	—	15	—	4	6	21	2
	15	1	—	—	3	—	2	5	3	1
	15	—	—	—	1	—	2	5	7	—
	20	10	—	—	—	—	1	2	—	7
	43	4	—	—	7	1	4	11	14	2
Extrait premier de pétales de rose rouge	20	9	8	3	—	—	—	—	—	—
Extrait premier de pétales de rose rouge enzymatiquement oxydé	11	1	—	—	2	—	3	3	2	—
	20	3	—	—	12	—	4	1	—	—

aboutissent à la formation de composés biologiquement actifs. Les résultats ainsi obtenus sont exposés pour plus de clarté en pourcentage à la table III.

Celle-ci fait clairement apparaître que les produits d'oxydation des tri-hydroxyphénols (pyrogallol, acide gallique et tanin, qui d'après Fischer contient cinq restes bi-galloliques) sont biologiquement plus actifs et donnent un pourcentage plus élevé de Lépidoptères *Vanessa urticae* L. à teinte noire, que les produits

TABLE III

Influence des composés hydroxyaromatiques oxydés dans un milieu ammoniacal et des extraits végétaux enzymatiquement oxydés. Expériences faites sur *Vanessa urticae* L.

Préparations	Nombre de chrysalides	Mortalité	Sans changement	Changements faibles	Var. polaris	Var. ichnusa	Var. atrebatensis	Var. ichnusoides	Var. coniuncta
Pyrogallol oxydé à 3%	254	22·8%	0·0%	4·7%	3·5%	10·0%	13·0%	**28·4%**	**15·4%**
Acide gallique oxydé à 3%	110	32·7%	0·0%	0·9%	7·6%	10·0%	**25·6%**	**15·0%**	9·0%
Tanin oxydé à 3%	155	21·3%	0·6%	12·2%	1·3%	6·4%	**39·2%**	**19·4%**	0·0%
Acide protocatéchique oxydé à 3%	158	15·8%	3·1%	**50·0%**	2·5%	8·2%	**15·2%**	3·8%	0·0%
Hydroquinone oxydé à 3%	127	40·8%	0·7%	**18·1%**	14·2%	**17·3%**	7·0%	1·6%	0·0%
Pyrocatéchine oxydé à 3%	74	14·9%	21·6%	**40·5%**	**19·0%**	4·0%	0·0%	0·0%	0·0%
Extrait de grains de café enzymatiquement oxydé	153	12·0%	0·0%	17·5%	0·6%	10·4%	**21·0%**	**37·7%**	7·8%
Extrait de pétales de rose rouge enzymatiquement oxydé	31	13·0%	0·0%	**45·0%**	0·0%	**22·0%**	13·0%	6·4%	0·0%

d'oxydation des bi-hydroxyphénols (pyrocatéchine, acide protocatéchique et hydroquinone). C'est ainsi également que les extraits végétaux enzymatiquement oxydés sont plus actifs que les produits d'oxydation des bi-hydroxyphénols.

Dans les expériences d'orientation, les produits noir-brun d'oxydation de la résorcine (1, 3 bi-hydroxy-benzène), les produits rouges de l'adrénaline (derivée 1, 2, de bi-hydroxy-benzène, position 4), ainsi que ceux de la D. O. P. A. (dérivées 1, 2, de bi-hydroxy-benzène, position 4), n'ont point montré cette activité qu'on en attendait après les expériences faites avec la pyrocatéchine (1, 2, bi-hydroxy-benzène). C'est ainsi également que, à l'encontre de ceux du pyrogallol (1, 2, 3, tri-hydroxy-benzène), les produits foncés d'oxydation de la floroglucine (1, 2, 5, tri-hydroxy-benzène) n'étaient pas actifs.

Il apparaît encore plus nettement que l'activité biologique dépend de la préparation utilisée dans l'injection, quand on compare le pourcentage de Lépidoptères inchangés avec ceux devenus très foncés (*var. atrebatensis* Boisd., *ichnusoides* Sel., *conjuncta* Neub.), et ceux faiblement modifiés (variétés très faiblement changées, faiblement modifiées, *var. polaris* Stgr., *var. ichnusa* Bon.) pris en gros — diagramme I. Il ressort du diagramme que les composés oxydés tri-hydroxy-aromatiques fournissent presqu' un pourcentage cinq fois plus grand d'exemplaires fortement foncés que les composés oxydés bi-hydroxy-aromatiques. La mortalité qui, chez les chrysalides, est une preuve de la toxicité et non de l'activité de la préparation, est à peu près la même dans les deux groupes.

Le pourcentage des exemplaires modifiés est approximativement égal quand on les soumet à l'action des composés oxydés bi- et tri-hydroxy-aromatiques; c'est uniquement l'intensité de l'assombrissement qui depend de la préparation employée. Un certain nombre de chrysalides, soumis à l'action des composés oxydés bi-hydroxy-aromatiques, ne change pas de dessin.

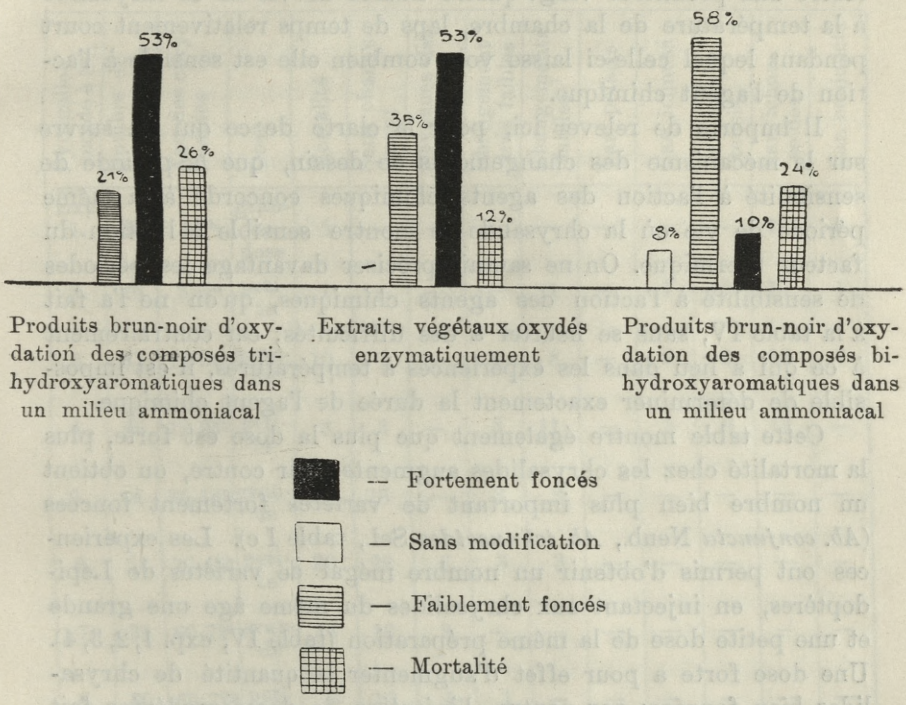
Lorsqu'on utilise les extraits végétaux oxydés enzymatiquement, la mortalité des chrysalides est deux fois moindre que dans les deux groupes de composés hydroxy-aromatiques. Le pourcentage des formes assombries sous l'action des préparations végétales est proche de celui des composés tri-hydroxy-aromatiques.

Les différences d'activité sont probablement dûes à la consti-

tution chimique différente des produits d'oxydation utilisés pour les injections. Les résultats fournis ci-avant ne sauraient cependant servir de preuve décisive de l'activité spécifique — constitutive des composés, car nous ne connaissons la constitution chimique d'aucun des composés examinés.

DIAGRAMME I

Les differences en % des variétés obtenues grâce aux agents chimiques chez *Vanessa urticae* L.



Il y a parallélisme entre l'activité de la préparation et son aptitude à l'oxydation dans un milieu ammoniacal. En effet, les produits caractérisés par une activité très intensive, se forment très rapidement du pyrogallol, de l'acide gallique et du tannin, traités à l'ammoniaque. Les solutions absorbent immédiatement l'oxygène et passent à vue d'oeil par toute une échelle de couleurs: jaune, vert, brun-clair, rouge-brun, pour aboutir à une teinte définitive noir-brun. Par contre, les préparations dérivées du bihydroxy-benzène s'oxydent sensiblement plus lentement à l'air; la

pyrocatéchine, par exemple, et l'acide protocatéchique mélangés avec une solution ammoniacale, deviennent verts, puis au bout d'un certain temps brunissent — l'hydroquinone devient jaune-brun, puis assez longtemps après, noir-brun. Il semble que l'activité de la préparation injectée est en proportion même de son aptitude à absorber l'oxygène dans un milieu ammoniacal.

Il y a une dépendance marquée entre la dose de préparation active et le degré de modification du dessin (table IV). Cela se réfère aux premières vingt-quatre heures de vie de la chrysalide à la température de la chambre, laps de temps relativement court pendant lequel celle-ci laisse voir combien elle est sensible à l'action de l'agent chimique.

Il importe de relever ici, pour la clarté de ce qui va suivre sur le mécanisme des changements de dessin, que la période de sensibilité à l'action des agents chimiques concorde à la même période de vie où la chrysalide se montre sensible à l'action du facteur thermique. On ne saurait préciser davantage les périodes de sensibilité à l'action des agents chimiques, qu'on ne l'a fait à la table IV, sans se heurter à des difficultés; car contrairement à ce qui a lieu dans les expériences à températures, il est impossible de déterminer exactement la durée de l'agent chimique.

Cette table montre également que plus la dose est forte, plus la mortalité chez les chrysalides augmente. Par contre, on obtient un nombre bien plus important de variétés fortement foncées (*Ab. conjuncta* Neub., *Ab. ichnusoides* Sel., table I c). Les expériences ont permis d'obtenir un nombre inégal de variétés de Lépidoptères, en injectant aux chrysalides du même âge une grande et une petite dose de la même préparation (table IV, exp. 1, 2, 3, 4). Une dose forte a pour effet d'augmenter la quantité de chrysalides bien foncées; par contre, l'injection de doses modérées fait avoir des formes moins foncées (*Ab. atrebatensis* Boisd.) et des formes non foncées (*Ab. ichnusa* Stgr.), ainsi que des variétés faibles de *Vanessa urticae* L.

On peut donc poser en principe, que chez les chrysalides *Vanessa urticae* L., les modifications dépendent non seulement de leur période de sensibilité comme Köhler et Felldotto l'ont démontré dans leurs expériences à températures, mais également, comme l'attestent les expériences chimiques, de la dose de préparation injectée. Dans les expériences faites suivant la méthode

d'injection, c'est non seulement l'âge de la chrysalide qui influe sur la naissance d'une variété déterminée, c'est surtout la quantité injectée de substance active (0·15—0·3 mg) ainsi que son activité chimique spécifique.

TABLE IV

Dépendance réciproque entre l'activité de la dose et les périodes de sensibilité sur la formation des variétés chez *Vanessa urticae* L. et influence de la dose sur la formation des modifications

Pyrogallol oxydé à 3%	Nombre de chrysalides	Age des chrysalides	Dose	Mortalité	Sans changement	Devenues claires	Changement très faibles	Changements faibles	Var. polaris	Var. ichnusa	Var. atrebatensis	Var. ichnusoides	Var. coniuncta
Exp. 1.	26	3-6^h	grande dose	5	—	—	—	—	—	—	—	12	9
2.	26	3-6^h	petite	1	—	—	—	1	—	1	10	12	1
3.	47	12-24^h	grande	10	1	—	1	8	—	2	2	16	7
4.	46	12-24^h	petite	3	3	—	3	11	—	5	8	13	—
5.	44	36-48^h	grande	23	16	—	3	2	—	—	—	—	—
6.	54	36-48^h	petite	20	22	6	3	3	—	—	—	—	—
7.	32	60-72^h	grande	14	16	2	—	—	—	—	—	—	—
8.	30	60-72^h	petite	6	19	4	1	—	—	—	—	—	—

Dans le laps de temps de 36 à 72 heures, on n'obtient aucune variété (exp. 5—8); on n'a guère que des papillons *Vanessa urticae* L. normaux ou faiblement changés ou très faiblement changés ou devenus plus clairs. Ces derniers montraient des éclaircies locales du fond qui, de rouge-orange, était devenu jaune-clair. La période de sensibilité donnant naissance aux modifications chimiques se place entre 0 et 24 heures qui suivent leur métamorphose; l'extrême limite ne dépasse point 36 heures.

Dans la vie de la chrysalide âgée de 0 à 72 heures, il est deux périodes pendant lesquelles celle-ci réagit à l'action de l'agent chimique: entre 0 et 36 heures, la modification apparaît; entre 36 et 72 heures, on observe l'apparition de teintes claires ou l'absence de réaction. C'est que probablement l'agent chimique, trouve dans la chrysalide des conditions physiologiques différentes pendant la première et la deuxième période de son développement.

III-e groupe d'expériences: Résultats obtenus sur d'autres espèces de Lépidoptères

Les préparations qui ont agi sur les *Vanessa urticae* L. ont également donné des résultats positifs chez quelques autres espèces apparentées comme par exemple les *L. polychloros* L., *V. io* L., *Polygonia* C. *album* L. et les *Pyrameis atalanta* L. (planche 12).

1. Les *V. polychloros* L. soumises à l'action de l'extrait oxydé de grains de café, fournissent des *ab. dixeyi* Stdfs., *ab. testudo* Esp., ainsi que de nombreuses formes intermédiaires (phot. 2, 3).

2. *V. io* L.: l'extrait enzymatiquement oxydé de pétales de rose rouge, ainsi que l'extrait enzymatiquement oxydé de grains de café fournissent des *ab. fisheri* Stdfs., *ab. antigone* Fschf., et des formes intermédiaires (phot. 5, 6).

3. ***Polygonia C. album*** — sous l'action de l'extrait enzymatiquement oxydé de grains de café, on obtient des *ab. F. album* Sp. (phot. 13).

4. ***Pyrameis atalanta*** L. Les injections: d'extrait enzymatiquement oxydé de grains de café, de pétales de rose rouge, de tanin oxydé et de pyrogallol oxydé dans un milieu ammoniacal, donnent des *ab.* Klemensiewicz et Schille, *ab. merifieldi*-Stdb. (phot. 8, 9) ainsi que bien d'autres formes intermédiaires. *L'ab.* Klemensiewicz et Schille, obtenue grâce aux injections d'extrait enzymatiquement oxydé de grains de café, se différencie nettement des exemplaires normaux par le changement du dessin et la colorisation de la surface intérieure des ailes (phot. 11).

Ces mêmes procédés expérimentaux m'ont permis d'obtenir des changements du dessin sur les ailes des *Vanessa*, ainsi que quelques dizaines de variétés de *Phytometra gamma*, en injectant exclusivement, dès les premières heures après leur métamorphose,

de l'extrait enzymatiquement oxydé de grains de café, à des chenilles receuillies dans la nature.

Le dessin de la paire antérieure des ailes se simplifie considérablement, le signe du gamma s'estompe et s'allonge en une tache triangulaire jaune-clair qui occupe l'espace foncé sur lequel apparaît, dans les conditions normales, le signe du gamma. Le sommet de la tache jaune-clair est orienté vers la naissance des ailes. La base de la tache triangulaire n'est point nettement délimitée; elle fusionne au contraire avec le foncé de la partie distale de l'aile (phot. 18). Les exemplaires plus faiblement transformés laissent voir un gamma agrandi aux bras plus ouverts (phot. 16, 17). Sur les ailes postérieures, la bande colorée de la bordure s'élargit sans perdre son teint gris foncé.

Les modifications obtenues chez la *Phytometra gamma* après l'injection d'une préparation de café non torréfié, sont caractérisées par une tache triangulaire allongée à la place du gamma; ce qui permet de la considérer comme une *ab. gartneri Scala* (Seitz). Il est fort probable que l'étude de matériaux expérimentaux plus nombreux amènera à de nouvelles modifications encore inconnues. Cela facilitera en outre l'analyse minutieuse du dessin modifié des ailes.

IV-e groupe: Les expériences de contrôle sur les *Vanessa urticae* L.

Action des colorants. Le bleu de méthylène provoque chez les *Vanessa urticae* L. la transformation du fond soit rouge soit jaune en gris-vert; les autres éléments du dessin des ailes restent inchangés. De nombreux exemplaires non éclos et cependant développés montrent les transformations décrites plus haut. La coccinine (Coccinine de Grübler) est très toxique pour la chrysalide. On relève chez les rares Lépidoptères éclos un changement de la teinte rouge du fond qui devient brun, alors que les taches jaunes du rebord antérieur de l'aile supérieure deviennent brun-jaunâtre. Le dessin des ailes reste inchangé.

Action des acides. Les acides à 1%: hydrochlorique, sulfurique, phosphorique, azotique, sulfosalicilique, urique, taurocholique, glycocholique et nucleïnique n'ont aucune influence sur les changements du dessin chez les *Vanessa urticae* L. Il en est de même de certains acides aminés tels le glycocole, la cystine,

l'asparagine, l'alanine, la tyrosine, dans des solutions neutres ou acides; ils n'ont aucune action sur le dessin chez les *Vanessa urticae* L. Quant à l'histamine, la bi-jodo-tyrosine, elles agissent tant soit peu sur le fond rouge qu'elles changent en fond jaunâtre.

Action des divers composés organiques. Les alcaloïdes comme le nitrate de strychnine, l'apomorphine, la crotine, le sulfate de quinine, n'agissent point sur les *Vanessa urticae* L. Les autres composés: la caféïne de soude, l'albuminate de tanin, la quinoléïne, la résorcine, la floroglucine, la suprarénine, ainsi que les préparations de diastase et de pepsine et l'extrait de péroxydase n'ont également aucune influence sur le dessin des ailes des *Vanessa urticae* L.

L'eau distillée, l'eau oxygénée à 3%, la solution de chlorure de soude à 1·2%, n'ont aucune influence sur la coloration de ces mêmes *Vanessa.*

Les expériences de contrôle attestent qu'il est imposible d'obtenir un changement du dessin des ailes chez les *Vanessa urticae* L. avec quelque autre produit chimique que ce soit; dans de rares cas cependant, un éclaircissement du fond a lieu et, si l'on utilise des colorants, le fond des ailes passe au verdâtre soit même au brun. Cette coloration verdâtre ou brune des ailes est l'effet de l'arrangement mécanique des colorants dans les ailes. Ces transformations n'ont pas été étudiées histologiquement; on peut seulement extraire à nouveau partiellement les colorants par l'extraction aqueuse.

Les injections de tyrosine, de suprarénine ainsi que des composés hydroxyaromatiques dont il a été parlé dans la première catégorie d'expériences, malgré leur caractère chromogénique, ne modifient en rien le dessin des ailes des *Vanessa urticae* L. Il semblerait donc que la formation du dessin des ailes n'a rien de commun avec le caractère du chromogène injecté artificiellement à la chrysalide; elle dépend uniquement d'un autre agent.

Les acides organiques et inorganiques qui, tout comme les composés hydroxyaromatiques oxydés et les acides phosphoro-tungstique et molybdénique (Zaćwilichowski) précipitent l'hémolymphe, n'entraînent point de modification du dessin des ailes; l'apparition d'une modification n'est donc pas en rapport direct avec le phénomène de détérioration des albumines dans l'hémolymphe.

L'histamine et la bi-iodo-tyrosine ont, quoique faiblement, une influence dans l'éclaircissement du fond rouge-orange des ailes. Cela n'a point lieu après l'injection des autres composés biologiquement actifs, cités ici.

Il se peut que l'éclaircissement du fond des ailes chez les *Vanessa urticae* L. soit un phénomène d'un autre genre que les modifications du dessin des ailes sous l'influence de certaines subtances. Cette question n'a pas été davantage étudiée ici.

Discussion des résultats

Toutes les substances qui, jusqu'ici dans mes expériences, ont montré une activité biologique, étaient des substances colorées obtenues par l'oxydation des composés hydroxy-aromatiques, éventuellement des extraits de depsides végétaux.

Il n'y a point de différence entre les changements obtenus par Zaćwilichowski sur les *Vanessa urticae* L. et ceux auxquels je suis parvenu dans mes expériences. Il faut donc admettre que l'action des acides phosphoro-tungstique et phosphoro-molybdénique se fonde sur le même mécanisme que celle des produits d'oxydation des composés hydroxy-aromatiques. De même, les variétés obtenues sous l'action des températures extrêmement hautes et basses montrent une ressemblance quasi-identique avec les formes obtenues par la méthode d'injection.

Toutes les préparations connues jusqu'à présent précipitent l'hémolymphe de la chrysalide. Il m'est cependant arrivé, au cours de mes expériences, de rencontrer des composés qui précipitent l'hémolymphe sans pourtant modifier le dessin des ailes (le tannin, l'acide nucléïnique, l'acide sulfosalicilique, l'acide taurocholique, l'acide glycocholique, les acides minéraux). Aucune raison par conséquent de supposer que la précipitation des albumines de l'hémolymphe est une condition suffisante pour provoquer les changements du dessin des ailes. Le résultat caractéristique de l'action des agents tant chimiques que thermiques n'est pas uniquement fondé sur la »mélanisation«, c'est-à-dire sur l'augmentation de la quantité de mélanine dans les ailes, mais bien sur la perturbation du plan normal de la localisation des écailles foncées et claires. En général, la perturbation se manifeste par l'apparition d'écailles foncées aux endroits où, normalement, se trouvent

des écailles claires. De même et inversement, chez la plupart des variétés chimiques, à la place des écailles foncées (appelées taches jumelles) apparaîssent des écailles claires. Zaćwilichowski a obtenu des variétés qui, à la place des écailles foncées de la tache du milieu, portaient des écailles claires. Le même facteur peut, en divers points de l'aile et en même temps, provoquer des résultats inverses.

Sous l'influence des agents chimiques, tout comme d'ailleurs dans les expériences à températures, le changement du dessin des ailes chez les *Vanessa urticae* L. va en se simplifiant quant à sa structure: les taches jumelles disparaîssent, celles qui se trouvent sur le rebord avant de l'aile antérieure se fondent en un tout homogène, le contour aigu en bordure de la tache qui se trouve à la base de l'aile postérieure s'efface; jamais cependant, jnsqu'ici, il ne s'est formé aucun élément nouveau du dessin, isolé du reste. Il semble que le mécanisme qui règle la formation du dessin, riche en détails, de l'aile normale, a cédé à un bouleversement. Le germe de l'aile, après que le mécanisme a été endommagé, reproduit le dessin mais d'une manière simplifiée. On pourrait d'autre part accepter que le germe de l'aile est doué d'un pouvoir prospectif qui, à l'ordinaire, ne se réalise pas sous notre climat, de former des dessins — pouvoir que l'on est à même de faire agir grâce à certains composés chimiques, ainsi que sous l'action du froid et du chaud.

Quelle que soit celle de ces deux hypothèses qui soit juste, dans l'un comme dans l'autre cas, on a affaire à l'action des composés chimiques spécifiques, sur la différenciation des germes des ailes des Lépidoptères.

Je considère comme un devoir très doux d'adresser tous mes remerciements à Mr. le Professeur Hugon Kowarzyk pour ses précieux conseils et l'aide qu'il m'a gracieusement apportée dans le présent travail.

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Explication de la planche 12

1. Vanessa polychloros L. — exemplaire de contrôle.
2. Var. dixeyi Stdfs.
3. Var. testudo Esp.
4. Vanessa io L. — exemplaire de contrôle.
5. Var. fischeri Stdfs.
6. „ antigone Fschr.
7. Pyrameis atalanta L. — exemplaire de contrôle
8. Var. merifieldi Stdfs.
9. „ Klemensiewiczi Schille.
10. Pyrameis atalanta L. exemplaire de contrôle, l'aile vue d'en-dessous.
11. Var. Klemensiewiczi Schille — l'aile vue d'en-dessous.
12. Polygonia C album L. — exemplaire de contrôle.
13. Var. F album.
14. Phytometra gamma.: exemplaire de contrôle.
15. 16, 17 Phytometra gamma.: exemplaires faiblement changés.
18. Phytometra gamma var. gartneri Scala.

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