ON THE ELECTRICAL PHENOMENA OF THE EXCITATORY PROCESS IN THE HEART OF THE FROG AND OF THE TORTOISE, AS INVESTIGATED PHOTOGRAPHICALLY. By J. BURDON-SANDERSON, M.D., F.R.S., AND F. J. M. PAGE, D.Sc., F.C.S. Plates I.—VIII. (XIII.—XX.)

THE purpose of the present paper is to describe a method of obtaining photographic records of the phenomena of plant and animal electricity, as investigated by means of the capillary electrometer. The electrical changes which we have now succeeded in photographing are those we have described as regards the heart of the frog in a paper published in this Journal[1]. The apparatus employed is of the simplest possible character, the instruments and appliances being such as are to be found in most physiological laboratories. The electrometer was illuminated by a beam of light from an oxyhydrogen lamp, which was focussed on to the capillary tube by an ordinary condensing lens, having previously passed through a concentrated solution of alum. An enlarged image of the capillary tube is projected on a horizontal slit rather less than a millimeter in width at a distance of twenty inches, by means of a half-inch objective of A. Ross. The slit is inserted in a screen of thin wood of which the surface is blackened, about two feet high and a foot wide. The screen is not, however, vertical, but slightly inclined from the objective in the direction of the line of projection. About an inch behind the screen is a second screen parallel with it which carries on the surface facing the slit a railway, of which the rails run from top to bottom. On these rails a carriage runs which is supported on four brass wheels, and bears the photographic plate. Dry plates measuring four inches by ten inches were used. They were obtained from Messrs Wratten and Wainwright.

As the carriage descends, the sensitive surface of the plate passes at a uniform rate before the slit. Uniformity of motion is secured by the following arrangement:—On the middle spindle of a clock provided with Foucault's regulator (one of those used for recording purposes) is fitted a brass pulley round which a cord is coiled, its end being

[1] "On the time-relation of the excitatory process in the ventricle of the heart of the frog." *Journal of Physiology*, Vol. II. p. 385.

attached to the carriage. The whole is so arranged that by the motion of the clock the cord is slowly unwound so as to allow the carriage to descend. The pulley is furnished with a ratchet so that the carriage can be brought to its highest position without interfering with the clock. To prevent acceleration the pulley is acted on by a counterpoise which ascends as the carriage descends.

All the apparatus above referred to excepting the lamp, stands on a table in a room to which only non-actinic light is admitted. The lamp is in an adjoining room. The light passes through a tube (which can be closed by a cap) fixed in the partition between the two rooms.

In all cases the changes recorded were consequent on mechanical or electrical excitation. The moment of excitation was recorded by means of a Deprez' "signal" or chronograph, which was placed in the primary circuit of the induction apparatus when the excitation was electrical, or in the circuit of an electromagnetic apparatus used for mechanical excitation. The circuit was closed by means of a Ludwig's interrupting clock, the arrangement of which was, however, altered so that it produced instantaneous closure at regular intervals (in our experiments usually 5″) instead of instantaneous breaks. At each closure the marking lever of the chronograph rises so as to shut off or to open a portion of the slit, the effect of which is marked in the photograph by a black or white dot, as the case may be. By a similar arrangement a second chronograph which is in a circuit alternately closed and opened by a reed which vibrates twenty times in a second, marks the progress of time.

In all experiments the cooperation of two persons is essential, of whom one must be in the dark room, whose business it is to focus the capillary tube on the slit, to uncap and cap the tube which admits the light, to adjust the photographic plate on the carriage, and set it in motion at the proper moment. The second observer adjusts the light, and attends to the arrangements for leading off and for exciting the preparation.

The method of using the apparatus will be best understood from an account of our procedure. The preparation having been arranged and connected with the electrometer as described below, the first step is to adjust the light and carefully focus the image of the capillary tube. The electrometer is then unplugged, and any electrical difference between the surfaces compensated as usual; the light is then shut off by the cap, the photographic plate is placed in position, and the carriage brought up to its starting point. The carriage is then set in motion and the cap withdrawn. During the descent of the plate, it receives simultaneously three records—namely, that of the movements of the column of mercury in the capillary, and those of the two electromagnetic time-markers of which one vibrates 20 times per second and the other indicates the moments of excitation. As soon as the plate has descended, the cap is replaced and the photograph developed or placed in a light-tight box.

The experiments relating to the heart of the frog were made in August 1882. The heart was arrested by applying a Stannius' ligature. The preparation was placed on a well lacquered metallic surface of which the temperature is rendered constant (10^0 to 12^0 C.) by a stream of water (*loc. cit.* p. 395). The arrangement of the non-polarizable and exciting electrodes and their connections were substantially the same as those described in our previous paper (p. 394). The experiments will be described in relation to the photographs.

PLATE I[1]. FIG. 1.

The electrometer electrodes were in contact at *f* and *m* with the base and apex of the ventricle of an uninjured Stannius' preparation as shown in the diagram. In this and all other diagrams *f* designates the spot at which the electrode in connection with the mercury in the capillary is applied. The preparation was excited electrically at the apex *x*, the end of the platinum wires of the electrodes being one millimetre

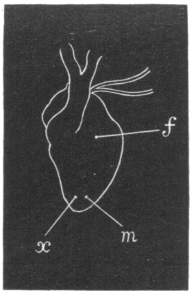


DIAGRAM 1.

apart. The photograph exhibits a narrow black band which runs from end to end and is broken at intervals of 3 to 4 centims. These breaks are produced by the motions of the lever of the time-marker and indicate the excitations to which the ventricle was subjected during the descent

[1] For the binder the plates are numbered from XIII—XX, but for the text they have an additional numbering from I—VIII.

of the plate, a period of about 30 seconds. Each break corresponds to a momentary closure of the primary circuit of the induction apparatus. Close to this is seen the faint tracing of the vibrations of the chronograph, marking[1] 20ths of seconds. On the opposite side of the excitation line the movements of the mercury column are recorded. The record is to be read from top to bottom. A movement of the column of mercury towards the point of the capillary is indicated by a protrusion of the black into the light space. Such a movement we designate, as in our previous papers, *negative*, meaning thereby that the electrode which is in connection with the sulphuric acid tube of the electrometer becomes negative to the other.

The photograph shows that the first phase of the electrical change follows the excitation at an interval of about 0·1″, the apex becoming suddenly and for an extremely short period negative to the base, that this is followed by a prolonged interval during which the electrometer is at zero, and that at the close of this period the apex becomes positive (second phase). In our former paper[2] a theoretical curve is given as the result of our observations with the rheotome and galvanometer. This curve will be found to correspond with the photographic record above described.

Plate I. Fig. 2.

The experiment corresponds with the preceding in every respect excepting that the exciting electrodes were applied to the base of the ventricle in proximity to the contact *f*. The electrometer record is the reverse of No. 1. The first phase is positive, the second negative. The interval between the excitation and the beginning of the electrical effect is the same as before. This is the photographic counterpart of the rheotome observation recorded *loc. cit.* p. 399. Experiments 5 and 6 severally correspond to Figures 1 and 2.

Plate I. Fig. 3.

In this experiment the exciting electrodes were applied not to the ventricle but to the right auricle immediately beyond the groove, the conditions being otherwise the same as in 2. The record resembles the last with this difference only, that the time-interval between excitation and electrical effect (first phase) is lengthened from 0·1″ to 0·45″.

[1] In the original negative this tracing is perfectly distinct.

[2] *loc. cit.* p. 428.

In our paper on the rhythmical motions, &c. of the heart published in 1878 (*Proceedings of the Royal Society,* Vol. 27, p. 411) we gave an experiment in which the interval between excitation and the beginning of the systole of the ventricle was longer by 0·3″ when the ventricle was excited through the auricle than when it was excited directly. It might be inferred from this fact that the interval between excitation and the beginning of the electrical disturbance of the ventricle would be prolonged to a similar extent by shifting the electrodes from the ventricle to the auricle. The comparison of the two tracings, Nos. 2 and 3, affords evidence that this is so. Although the distance between the two seats of application of the electrodes did not exceed 3 millims. the electrical interval was longer by 0·35″ in No. 3 than in No. 2

PLATE II. FIG. 4.

The contacts and seat of excitation were as in the first experiment (Fig. 1) but at the moment that the plate in its descent reached the slit, the apex of the heart was warmed by leading a current for three seconds through a coil of platinum wire placed at 3 millims. distance from the apex. This produces no modification of the electrical effect which follows the first excitation, but a marked increase of duration of the terminal phase at the expense of the equipotential interval. This modification passes off gradually in the 4th and 5th excitations and disappears entirely in the 6th which is normal. This photograph is the counterpart of the rheotome observation No. 17 (*loc. cit.* 416).

PLATE II. FIG. 5.

Fig. 5 was photographed immediately after Fig. 4 the same preparation being used, but the warming was prolonged so that the surface of the ventricle at the apex was permanently injured. The first phase is diminished and eventually disappears. The record can be best understood by comparison with No. 6.

PLATE II. FIG. 6.

The surface of the ventricle at the apex was further injured by bringing the hot wire into contact with it. The initial phase has entirely vanished. The apex is strongly positive, the electrical difference between the two contacts remaining constant or nearly so during the whole excitatory period. This result corresponds with rheotome observations Nos. 21 and 22 (*loc. cit.* pp. 420 and 421), the results of which are summed up as follows:—"In the inhibited ventricle, if either of the "leading off contacts is injured, the terminal phase disappears and the "initial phase is followed by an electrical condition in which the injured "surface is more positive or less negative, relatively to the uninjured "surface."

Heart of Tortoise.

The photographs of the electromotive changes in the ventricle of the heart of the Tortoise were made in October and November 1882. The method was in every respect the same as the experiments relating to the heart of the frog

PLATE III. FIG. 1.

The electrometer electrodes were in contact with the ventral surface of the ventricle at the points indicated in the diagram. The preparation was excited electrically, the electrodes being applied to the right auricle at *x*.

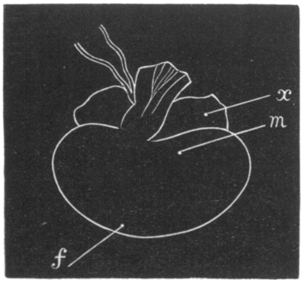


DIAGRAM 2.

The time was recorded as before, but in consequence of the increased rate of descent of the sensitive plate, the time record is more distinct. The moment of excitation is marked by a minute black dot, which is at a distance of 1½ centim. above the first prominence which indicates the first phase of the electrical effect. Consequently the time-interval between excitation and the first phase was as nearly as possible a second. The isoelectrical period lasts 2½ seconds. The second phase has the same character as in the ventricle of the heart of the frog.

PLATE III. FIGS. 2 AND 3.

The points of contact of the electrometer electrodes were as shown. The ventricle was excited mechanically, i.e. by a tap of the lever of the time-marker, which was furnished with a glass point for the purpose.

Photograph Fig. 2 was obtained when the seat of excitation was at *x*, Fig. 3, when it was at *x′*. It is seen that the two records are counterparts

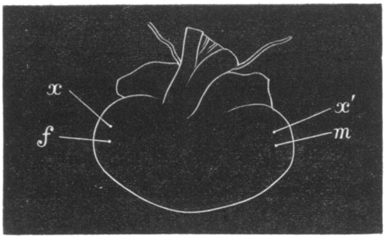


DIAGRAM 3.

of each other. The record is of value as showing that the negative wave of excitation is propagated from side to side of the ventricle, in the same way as from base to apex or from apex to base, and consequently that the character of the electrical disturbance is without relation to structural differences between base and apex; and further that in passing from side to side of the ventricle it is unaffected by the direction in which the propagation takes place. In comparing Figs. 2 and 3 with Fig. 1, it will be noticed that in the latter the time-interval between excitation and first phase is exceedingly short, not exceeding a tenth of a second. In this respect compare Plate I. Figs. 2 and 3.

PLATE IV. FIGS. 4, 5 AND 6.

Here the positions of the electrodes and the mode of excitation were the same as in the preceding experiment. In Fig. 4 the seat of excitation was at *x′*, in Fig. 5 at *x*. In these and in the preceding experiments the temperature of the surface on which the heart rested was 12° C. Fig. 6 shows the effect of increasing the temperature to 20° C.

PLATE V. FIGS. 7, 8 AND 9.

The three photographs relate to the same heart. In the experiments of which they represent the results, the electrode in connection with

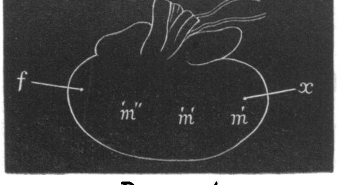


DIAGRAM 4.

the capillary was at *f*, but the other contact was at *m* in Fig. 7; at *m''* in Fig. 8; and at *m'* in Fig. 9. The seat of excitation was the same throughout, viz. close to *m*. The purpose of the experiment was to show first that in the normal heart the time at which the first phase begins depends upon the distance between *x* (the seat of excitation) and the *nearest* of the two leading off contacts (in this case the contact *m*, *m'* or *m''*), and secondly that the moment of the cessation of the first phase, i.e. the beginning of the isoelectrical period, is dependent on the distance between *x* and the furthest contact *f*—in other words, on the time occupied by the excitatory negative wave in passing from *x* to *f*. Consequently the duration of the first phase if *f* and *x* remain unaltered, depends entirely on the position of *m*. In Fig. 7, the moveable contact being at *m*, i.e. close to *x*, the interval between excitation and beginning of effect was short, less than a tenth of a second, the initial phase lasting four-tenths of a second and consequently terminating about half a second after excitation. In Fig. 8 the contact was at *m''* 0·8 centim. from *x*. The time-interval between excitation and first effect was correspondingly increased to three-tenths of a second. The duration of the phase was two-tenths, the phase terminating half a second after the excitation as in Fig. 7. As in Fig. 9 the moveable contact occupied an intermediate position between *m* and *m''*, the photograph is half-way between Fig. 7 and Fig. 8, as regards the time of beginning, and consequently as regards the duration of the first phase. These results are in complete accordance with the theory of the electromotive phenomena of the ventricle of the heart of the frog which is given on p. 428 of our former paper.

Plate VI. Figs. 10, 11 and 12.

Photographs 10, 11 and 12 were taken consecutively, the contacts being as shown in diagram. Fig. 10 gives the normal variation consequent on electrical excitation at *x*. In Fig. 11 the platinum coil

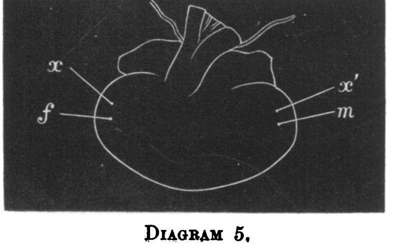


Diagram 5.

used in Plate II. Fig. 4 was brought into proximity with the contact *f*, and heated by the passage of a current for a few seconds before the descent of the plate. The effects of two excitations are seen of which the first shows a modification of the same kind as that previously photographed in the ventricle of the heart of the frog. The seat of warming being at the leading off contact furthest from the seat of excitation, the modification has an opposite sign to that shown in Plate II. Fig. 5. As regards the increased duration of the terminal phase at the expense of the equipotential interval, the two photographs correspond. In the second excitation shown, the modification is subsiding, but the terminal phase is still reversed as compared with the normal (Fig. 10), i.e. has the same sign as the first phase. This of course can be readily understood if it is assumed that, in consequence of the warming, the duration of excitatory change (negativity) at *f* is diminished that at *m* remaining unaltered. In Fig. 12 the effect of permanent injury of the surface of the ventricle at *f* is recorded.

PLATES VII. AND VIII. FIGS. 13—18.

The purpose of the series of experiments to which these photographs relate was to obtain further evidence that the character of the excitatory variation in the ventricle is dependent on the time-relation of the excitatory change (negativity) at the two leading off electrodes, and the rate of propagation of the negative wave. If, for example, a transitory block could be interposed between *m* and *f* so as to retard for a time the propagation of the negative wave the result ought to be that *m* would remain negative, i.e. the first phase would be protracted until the block was passed, and that the moment at which this happened would be indicated by a sudden change in the electrical relations of the two contacts. With a view to testing this deduction, it was evidently advantageous to increase the distance between *m* and *f* to the utmost, so as to prolong as much as possible the time-interval between the

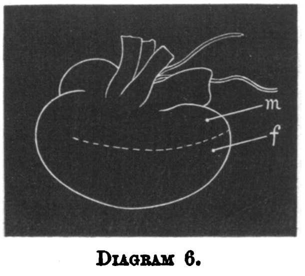


DIAGRAM 6.

beginning of excitatory change at *m*, and the arrival of the excitatory wave at *f*. The ventricle was therefore cut as shown in the diagram and a transitory block was produced half way between *m* and *f* by pressure.

This was effected by a weighted lever, the end of which rested on the preparation and was provided with an india rubber sheath, to avoid injury of the surface[1]. In this way the degree of pressure used could be regulated with precision. The contacts *f* and *m* were in the positions indicated in the diagram. The exciting electrodes were applied to the right auricle. Fig. 13 shows the (nearly) normal variation, its total duration is four seconds, of which the terminal phase is scarcely distinguishable. The short duration of the initial phase indicates that the contact *m* was close to its starting-point. The long interval between excitation and the first phase, which occurs when the ventricle is excited from the auricle, has been already explained. In Fig. 14 the modification of the variation due to cutting is seen. The direction and extent of the incision is shown by the dotted line. The cut was kept open

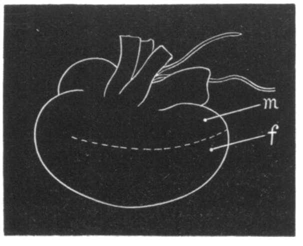


DIAGRAM 7.

by the insertion of a cork wedge, and the leading off and exciting electrodes were in exactly the same position as before. It will be observed first that the duration of the excitatory effect is longer by half a second, and that it consists of two phases, of which the first passes abruptly into the second without an isoelectrical interval.

The first phase lasts 0·55″ whereas before the section it lasted 0·25″. During the remainder of the excitatory period, *m* is positive to *f*. The next photograph (Fig. 15) shows a similar but more pronounced modification of the same kind produced in exactly the same way. Here the first phase lasts one second, passing abruptly as before into an electrical state of opposite sign.

[1] An ordinary myograph lever was employed. The distance between the axis of the lever and the point on which the weight rested was one third of the total length of the lever. Consequently the pressure was that of a weight one third of that actually used.

Plate VIII. Figs. 16, 17 and 18 refer to the same preparation. The contacts were as shown. The variation after section is recorded

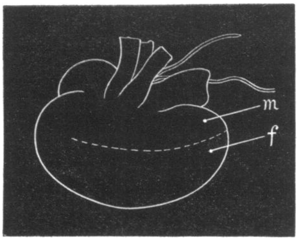


DIAGRAM 8.

in Fig. 16: it lasts less than three seconds. With the exception of the protracted first phase, of which the duration was 0·4″, it exhibits the characters of the normal excitatory effect. Fig. 17 shows the modification which resulted from the application of pressure at the point *v*[1]. The effect of the pressure (100 grammes) was, so long as it was continued, to *obstruct completely* the propagation of the excitatory wave, i. e. the auricular contraction was followed by a contraction of the part of the ventricle on the auricular side of the block—the rest of the ventricle remaining relaxed and motionless. The pressure was then removed and the preparation left to itself for half an hour—at the end of which period the photograph (Fig. 17) was taken. The period of exposure includes two excitations, in the first of which the negative wave passed the block, but failed to pass in the second. The photograph shows in the most striking way how the character of the electrical disturbance is affected by changes taking place at the more distant of the two leading off contacts. It is seen that after the first excitation, the contact *m* becomes negative and remains so for 1·7 second, i.e. until the excitatory wave has passed the block. The two contacts then remain equipotential for a short time, after which, *m* becomes positive in consequence of the arrival of the negative wave at *f*. In the second excitation the initial phase begins as before, but as the excitatory wave fails to pass the block, *m* remains negative to the end of the excitatory change, i.e. for 2·3 seconds; the part of the heart beyond serving as a physiologically inactive conductor. The terminal phase which follows the isoelectrical period in the first excitation is entirely absent in the second, it being the expression of the

[1] *v* (omitted in the Diagram by mistake) is at the junction of the two parts into which the ventricle is divided by the cut.

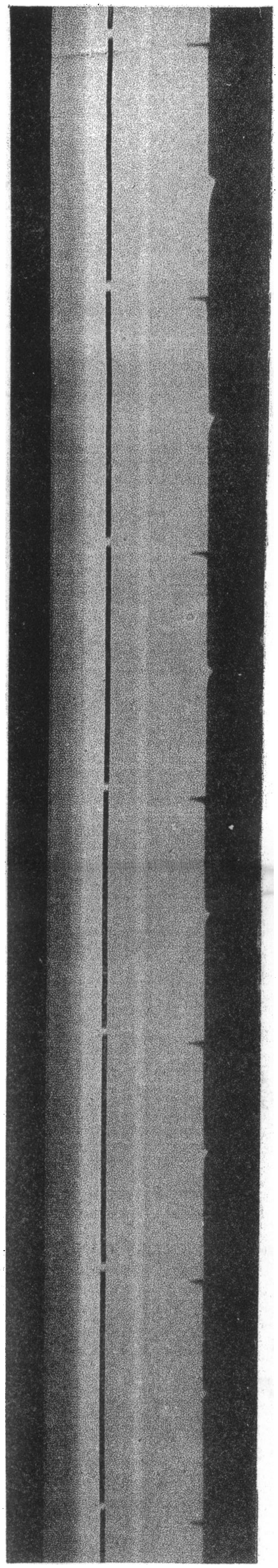
excitatory process in the part of the ventricle beyond the block. In Fig. 18 the excitatory effects are given of two successive excitations, both of which failed to pass the block.

As the photographic records commented on in the preceding paragraphs confirm in every respect the conclusions of our former paper as to the nature of the electrical phenomena which accompany the excitatory process in the ventricle, it is unnecessary to set them forth again in full. It is sufficient to note that the photographs afford the strongest evidence in favour of the most important of those results namely (1) that the electrical excitatory change instead of lasting a fraction of a second as supposed by all previous observers (its maximum duration according to Engelmann being half a second) lasts at ordinary temperatures about two seconds, and (2) that in all cases the character of the electrical variation may be satisfactorily explained as resulting from the time-relations of the electrical processes which have their seats at the two leading off electrodes during the period that the excited state of the ventricular tissue lasts.

The photographs which exhibit the modifications produced by heating and injury will now be seen to admit of no other explanation than the simple one previously given, namely, that the effect of both consists in diminution of the physiological activity of the parts which are the seats of their influence, the difference between them being that one is transitory, the other permanent.

The experiments on the effects of pressure, which it may be noted were frequently repeated, show that this acts in a manner strictly comparable to that of heat, i.e. a bit of ventricular tissue has its function (as evidenced by its electrical reaction to excitation) depressed, just as if it had been heated. And, as in the case of heating, the injury is transitory when slight, permanent when more intense, so the effect of slight pressure passes off entirely, whereas more severe pressure deprives the compressed part both of its power of conducting the excitatory wave and of its excitability.

The results of our experiments appear to us to establish the applicability of the Capillary Electrometer as an instrument of physiological investigation and the value of the photographic method as a means of recording electrical changes in living structures. The imperfections which are obvious in the plates now published (all of which are untouched photo-lithographic reproductions of the original negatives) will, we are confident, be got rid of by improved apparatus which is now in process of construction.



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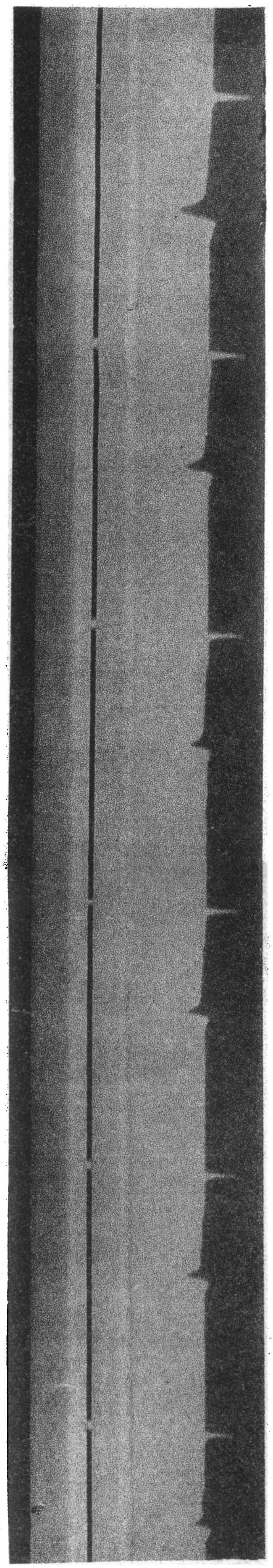

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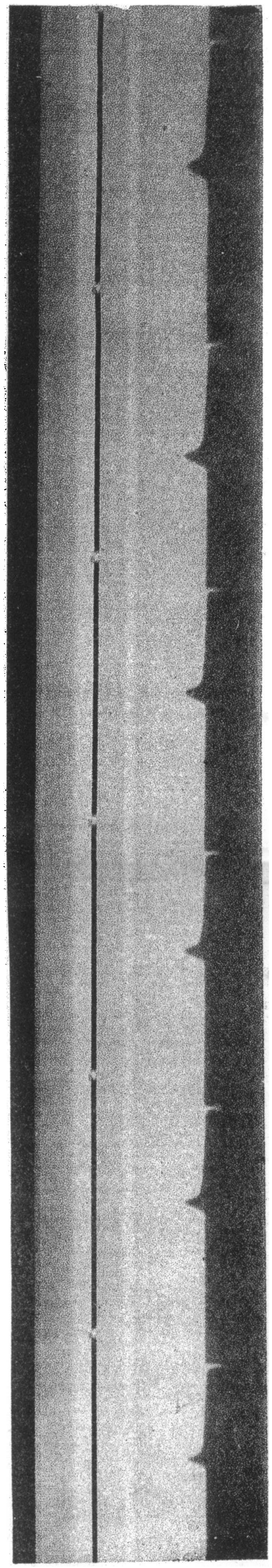
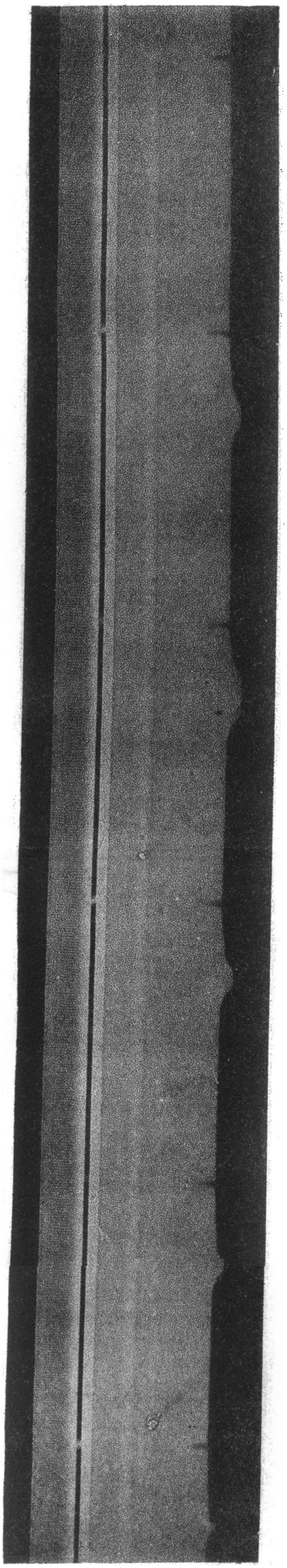


3.

HEART (Frog)

Plate I.

Hanhart imp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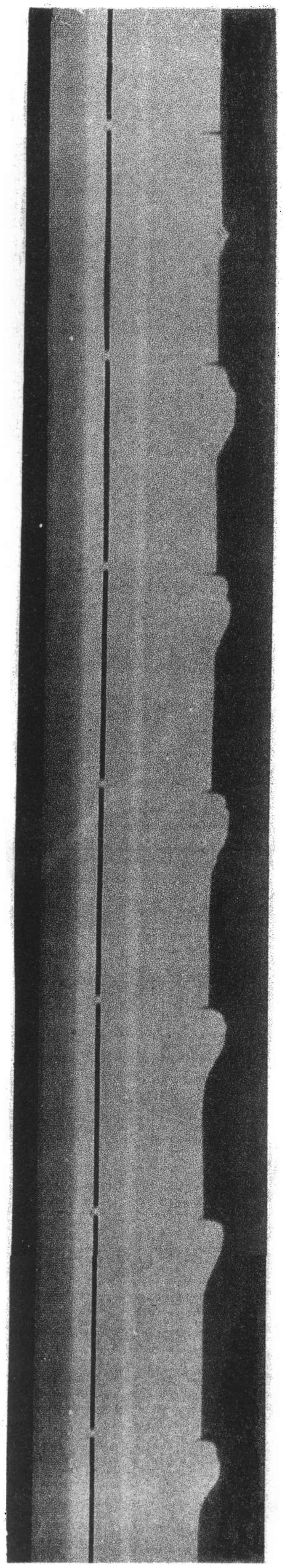
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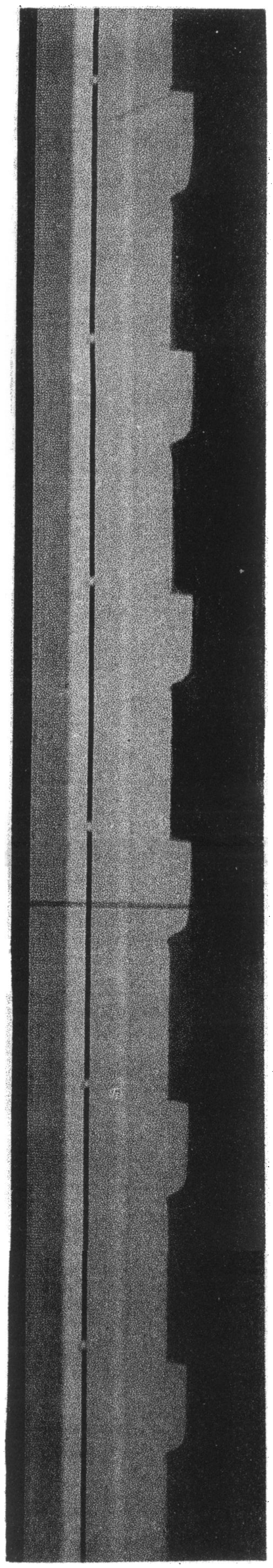
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HEART (Frog)
Plate II.

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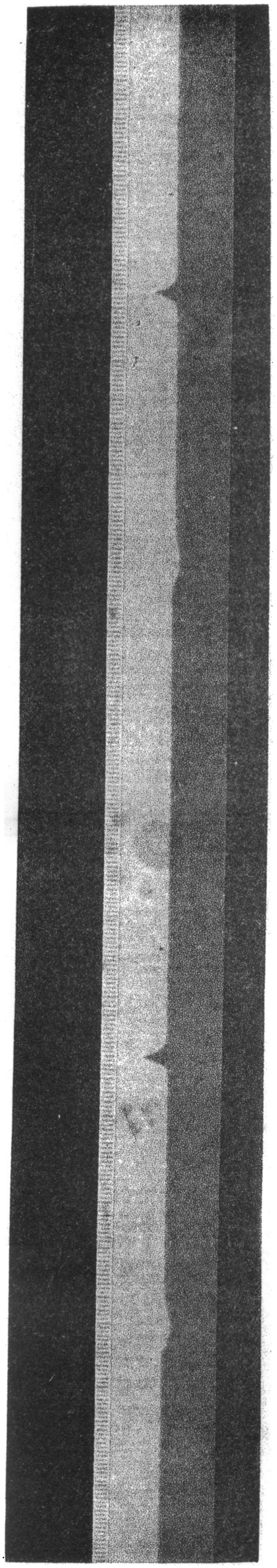

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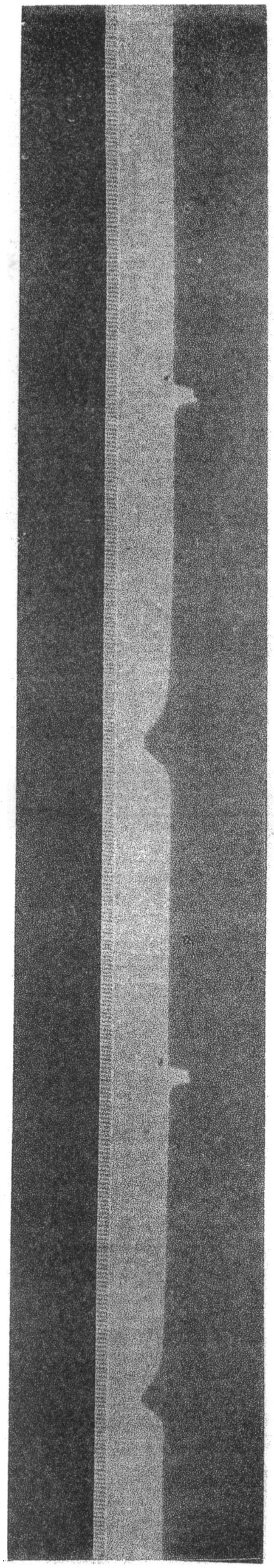

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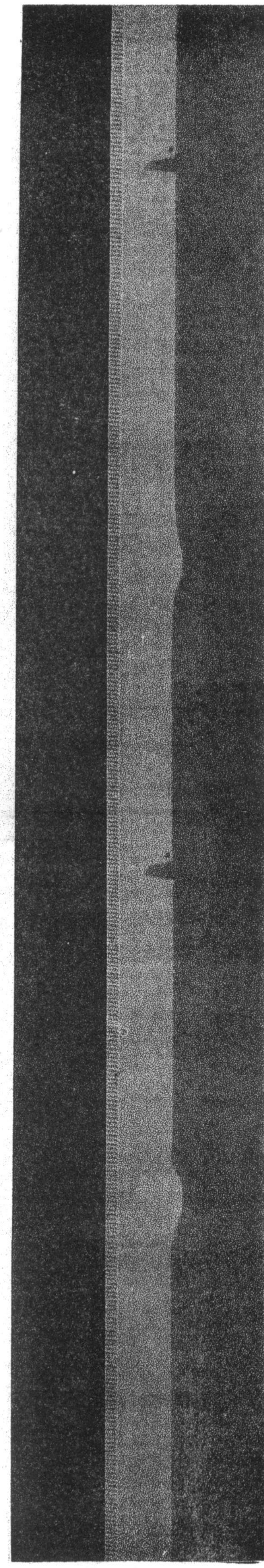

3.

HEART (Tortoise)
Plate III.

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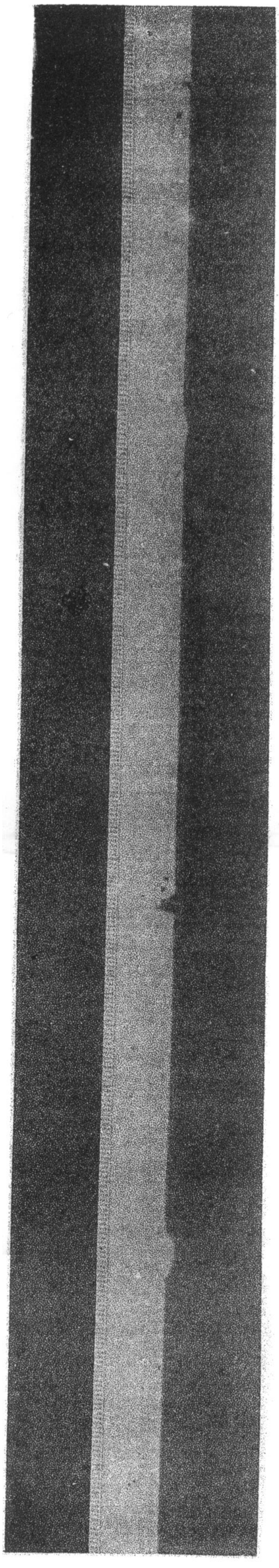
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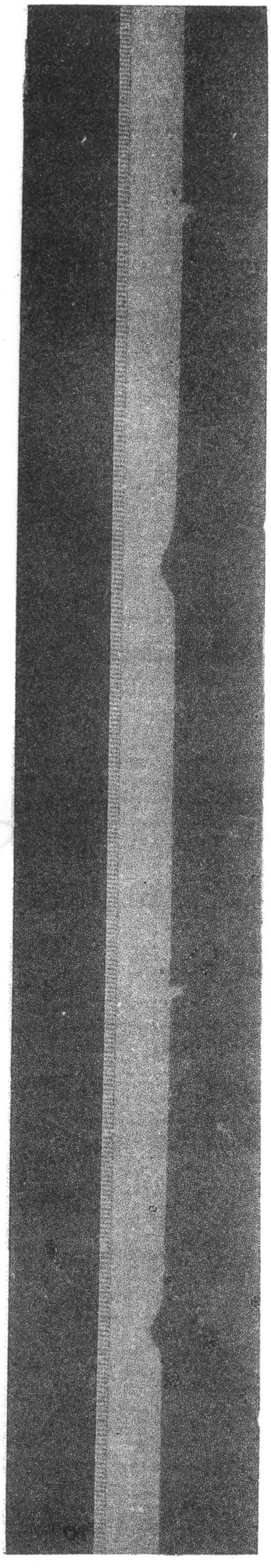
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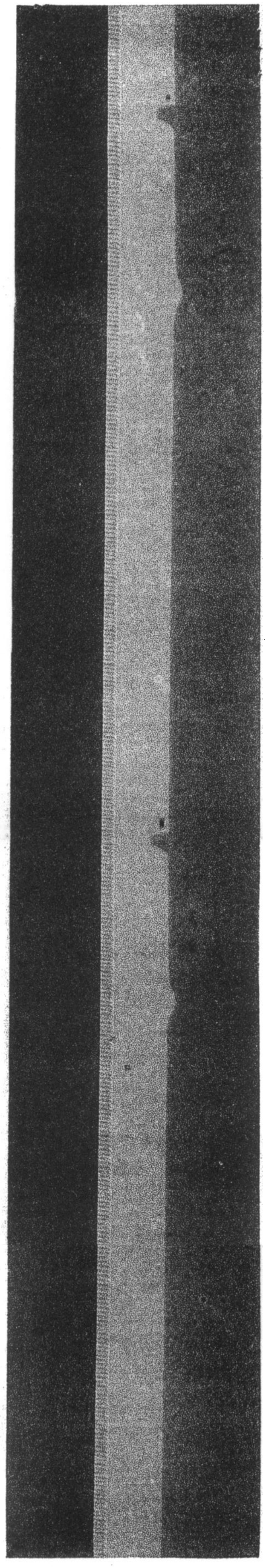
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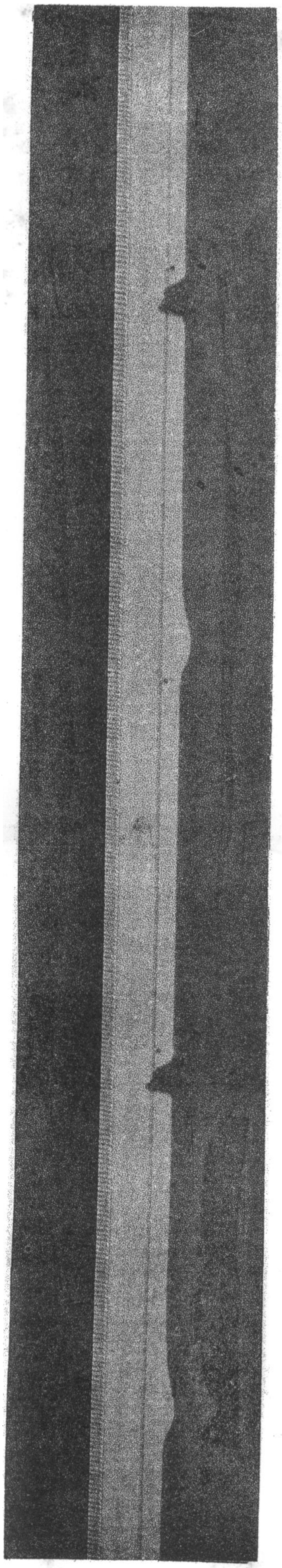
HEART (Tortoise)
Plate IV.

Hanhart imp



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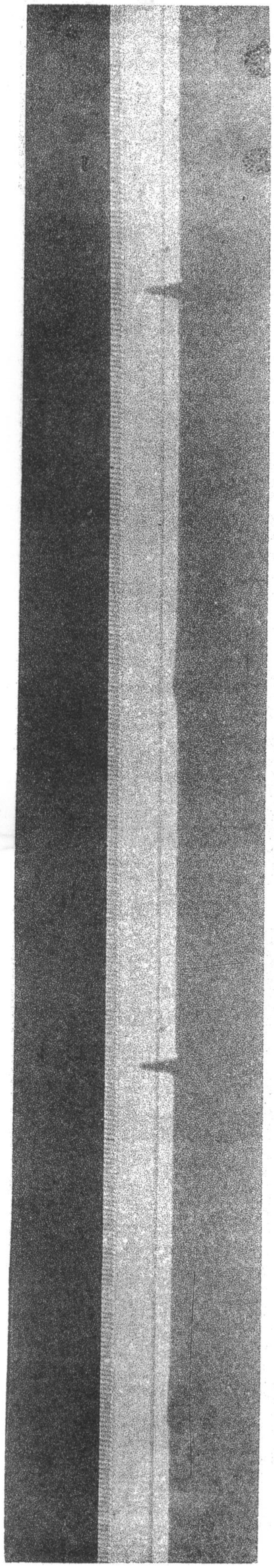

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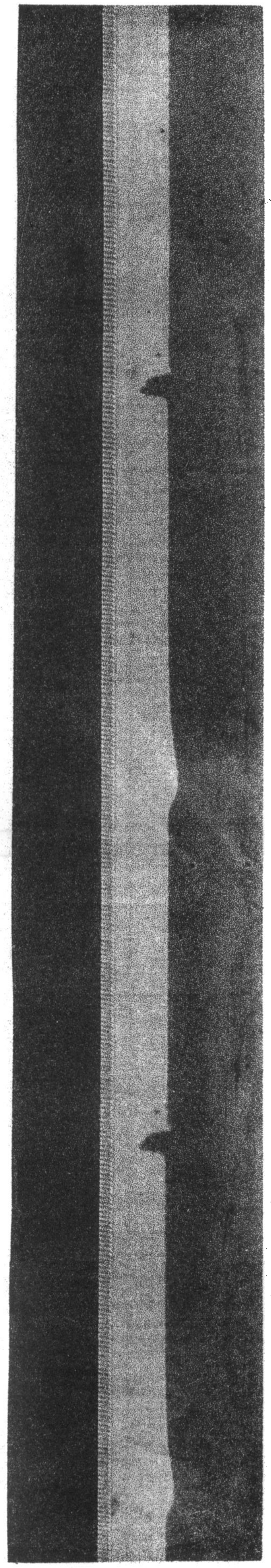

9.

HEART (Tortoise)
Plate V.

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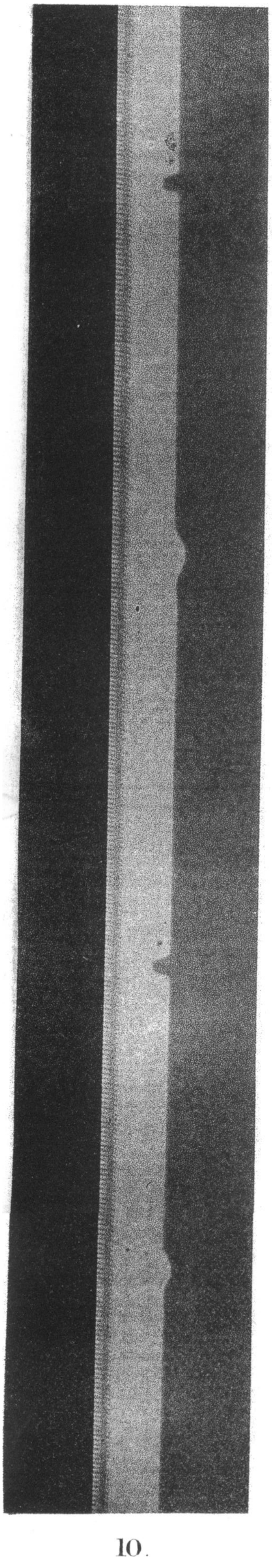
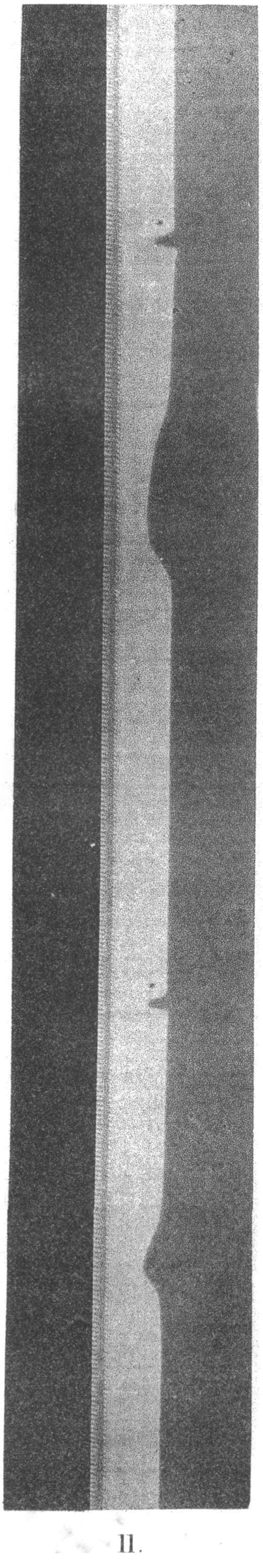


10.



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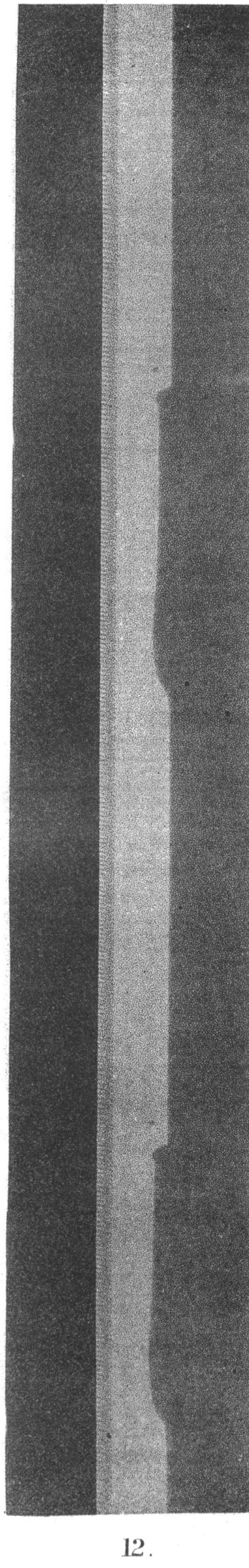
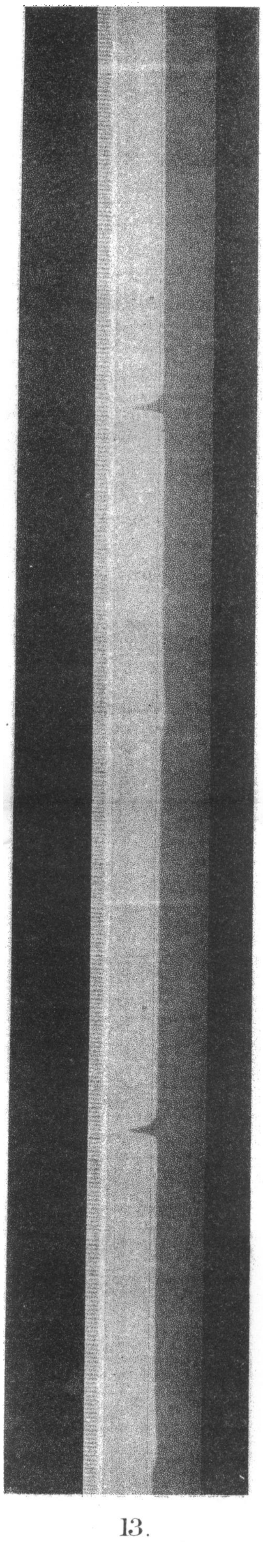


12.

HEART (Tortoise)
Plate VI.

Hanhart imp.



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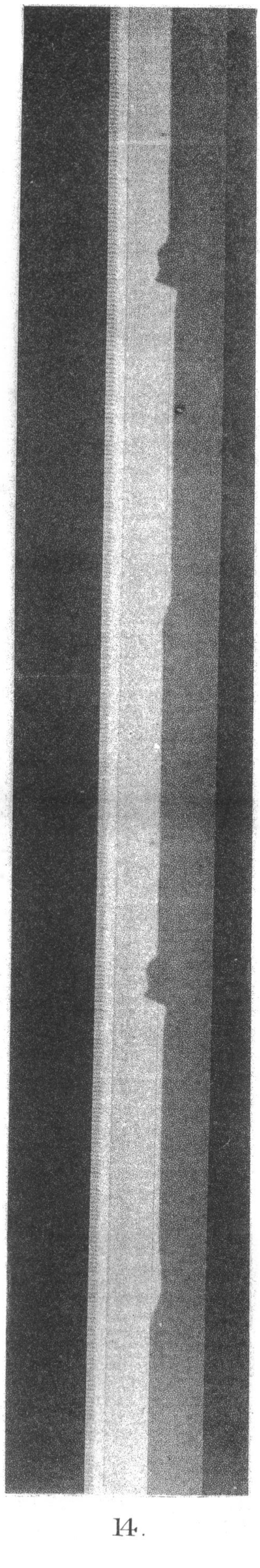

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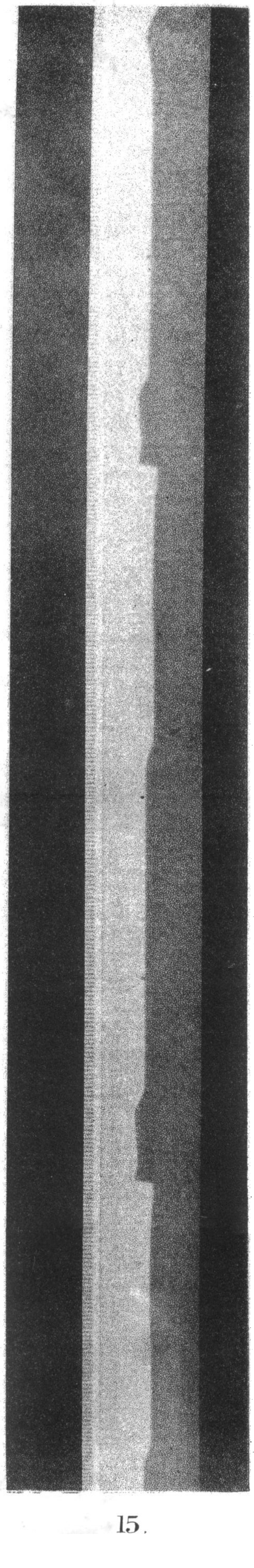
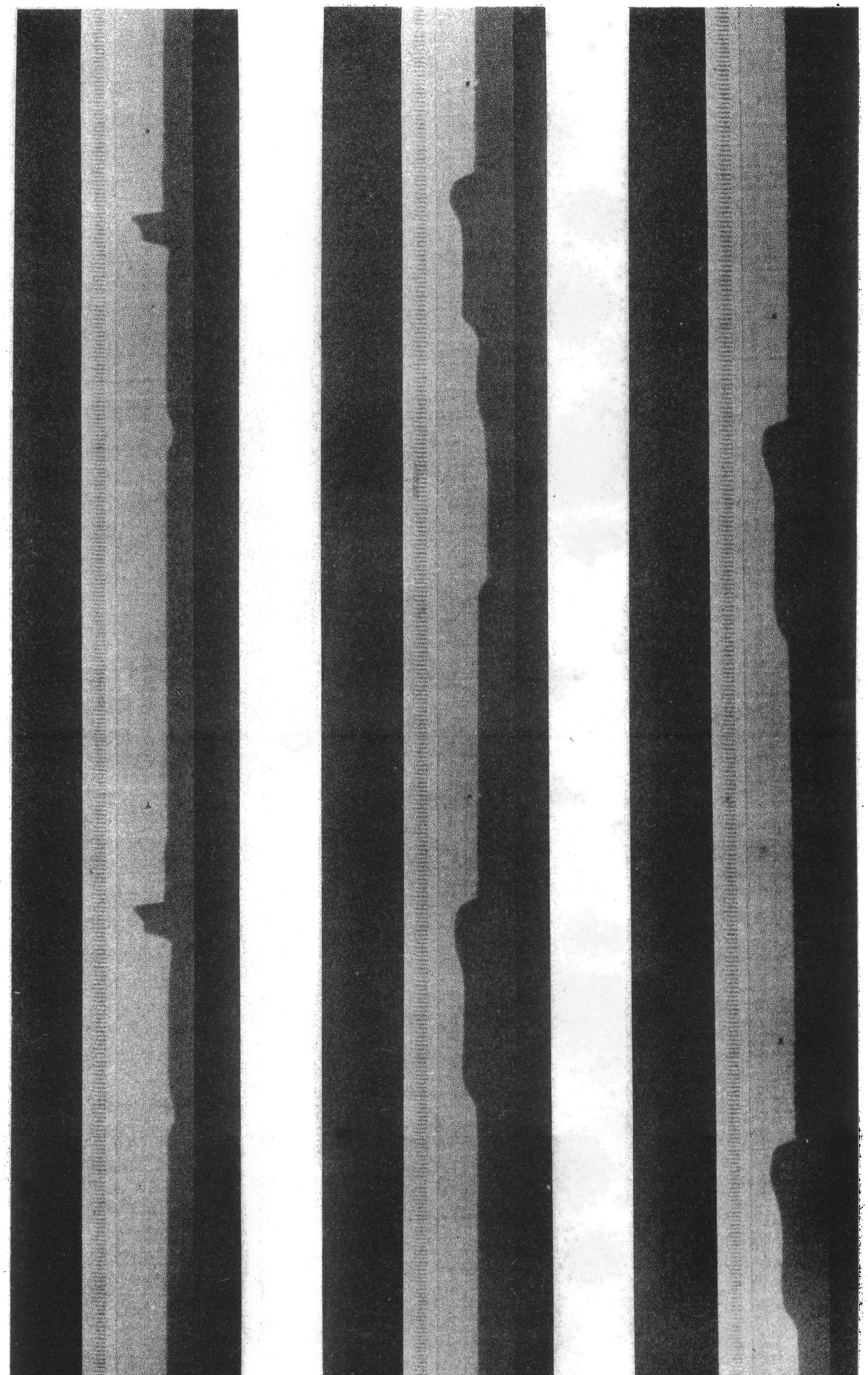


15.

Hanhart imp.

HEART (Tortoise)
Plate VII.



16. 17. 18.

HEART (Tortoise)
Plate VIII.

Hanhart imp.