VII. *Contributions to the Comparative Anatomy of the Reptilian and the Amphibian Eye, chiefly based on Ophthalmological Examination.*

By George Lindsay Johnson, *M.A., M.D.*

Communicated by Dr. H. Gadow, *F.R.S.*

(Received June 19,—Read November 20, 1924.)

(Plates 20–25.)

Contents.

Since the publication of my "Contribution to the Comparative Anatomy of the Mammalian Eye" ('Phil. Trans.,' B, vol. 194, p. 194 (1901)), I have supplemented this paper by similar investigations on the eyes of the lower classes of the Vertebrata, thereby hoping to extend our knowledge of the higher orders by comparison with those of the lower groups. As it was reasonable to expect in them incipient and simpler stages, where Mammals show highly complex or vestigial conditions, the hope seemed justified to approach the solution of various morphological and physiological problems.

Of course, the investigations should by rights begin with the Fishes, at least in theory. In practice, however, they present insurmountable difficulties to ophthalmological investigation, partly on account of the obstacles in the way of holding them in a fixed position, and of keeping them alive when removed from their natural element, and partly also on account of the refraction of their eyes, which are naturally adjusted for seeing under water, which causes their eyes to become enormously hyperopic when examined in air. Moreover, their crystalline lenses are almost invariably spherical, a condition which admits of only a minute portion of the fundus being examined at one time, whereby the difficulty of obtaining a complete view of the fundus becomes greatly increased. The examination of the eye after death, either by illuminating the interior with the

 Published February 15, 1927.

ophthalmoscope, or by dividing the eye equatorially and viewing the fundus through a microscope, is by no means a satisfactory procedure, since the post-mortem changes occur so rapidly that the picture is altogether misleading. For our present purpose, however, the fish's eye is of small importance.

The gap between the Fishes and Tetrapoda is enormous. We are no longer justified in looking for the Elasmobranchs as supplying the key for every morphological question of vertebrate structure, since it has become understood that instead of being in the direct line of descent, they represent an old and very divergent side-branch. Only a few Dipnoi and Polypteridæ could be suspected to bridge the gap, but they were unavailable. The Birds, which likewise are nowhere near the main line of descent, have been treated in a very efficient manner by the accomplished ophthalmologist Dr. CASEY WOOD, of Chicago.* There remain, therefore, only the Amphibians and Reptiles. Of these I have examined a sufficient number to venture on certain generalizations and deductions. With the sole exception of a paper by Prof. HESS, and another by Prof. SCHLEICH on the eyes of the frog, my communication presents an entirely new field of investigation.

In examining the fundus oculi, the direct method has invariably been employed, the manipulation and apparatus being practically the same as described in my previous paper (*q.v.*), but the smallness of the eyes and the minuteness of the pupils of the majority of the Reptiles and Amphibia rendered the work very difficult and laborious. Many Amphibians have pupils not exceeding 1 mm. in diameter, and quite a number of the Reptiles have as small, or even smaller, pupils. Moreover, in quite a number of cases the pupils are unaffected by mydriatics, so that there was no possibility of enlarging the pupils, as we know can be effected in nearly all the Mammalia. As it requires a pupil of from $1\frac{1}{2}$ to 2 mm. to obtain a satisfactory view of the fundus, it follows that all animals possessing smaller pupils than that are excluded from examination by the ophthalmoscope. Additional difficulties lay in the danger of a bite, especially when examining the poisonous snakes. The Chelonia also presented great difficulty owing to their invariably withdrawing their heads within their shells on the slightest attempt to get near them. For this reason the large land tortoises proved quite unmanageable. In the same way we (my artist and self) never succeeded in making a good sketch of a rattlesnake's fundus, although a sufficient view was obtained for comparison with the other snakes.

Most of the ophthalmoscopic work was made in the Zoological Gardens of London, and I wish to record my indebtedness to the Secretary and to the Curator for their kind assistance. Special thanks are due to Dr. GADOW for urging on and criticizing this research, which was begun soon after 1901, but suffered several long interruptions.

The following list contains an enumeration of the species examined (*cf.* Plates 20–25) :—

REPTILIA.

PROSAURIA ..	..	*Sphenodon punctatus.*
CHELONIA ..	CHELYDRIDÆ ..	*Chelydra longicollis.*
		,, *serpentina.*

* 'The Fundus Oculi of Birds' (Lakeside Press, Chicago (1917)).

CHELONIA	TESTUDINIDÆ	*Testudo radiata.*
		Cynixys erosa.
		Chrysemys scripta.
	TRIONYCHIDÆ	*Emyda granosa.*
CROCODILIA	.. ..	*Alligator sinensis.*
		,, *mississippiensis.*
		Crocodilus frontatus.
		,, *americanus.*
LACERTILIA	GECKONIDÆ	*Pachydactylus maculatus.*
		Hemidactylus turcicus.
		,, *cocteaui.*
	AGAMIDÆ	*Moloch horridus.*
		Chlamydosaurus kingi.
	IGUANIDÆ	*Anolis alligator.*
		Metopoceros cornutus.
		Conolophus subcristatus.
	ZONURIDÆ	*Zonurus giganteus.*
	ANGUIDÆ	*Ophisaurus apus.*
	VARANIDÆ	*Varanus bengalensis.*
		,, *gouldi.*
		,, *varius.*
		,, *acanthurus.*
	TEJIDÆ	*Tupinambis nigropunctatus.*
	LACERTIDÆ	*Lacerta viridis.*
		,, *galloti.*
		,, *simonyi.*
	SCINCIDÆ	*Lygosoma quoi.*
		Egernia cunninghami.
		Cyclodus nigroluteus.
		Macroscincus cocteaui.
		Chalcides ocellatus.
	PYGOPODIDÆ	*Pygopus lepidopus.*
	CHAMÆLEONTIDÆ ..	*Chamæleon vulgaris.*
OPHIDIA	BOIDÆ	*Boa constrictor.*
	COLUBRIDÆ	*Tropidonotus fasciatus.*
		,, *piscator.*
		,, *natrix.*
		,, *guttatus.*
		Heterodon madagascariensis.
	PROTEROGLYPHA ..	*Naia tripudians.*
	SOLENOGLYPHA	*Crotalus horridus.*

AMPHIBIA.

URODELA	SALAMANDRIDÆ	*Salamandra maculosa.*
ANURA	DISCOGLOSSIDÆ	*Bombinator pachypus.*
	CYSTIGNATHIDÆ	*Ceratophrys cornuta.*
	HYLIDÆ	*Hyla versicolor.*
		,, *cœrulea.*
	RANIDÆ	*Rana clamata.*
		,, *tigrina.*
		,, *catesbiana.*
		,, *esculenta.*
		,, *halecina.*
		,, *temporaria.*
	BUFONIDÆ	*Bufo boreas.*
		,, *marinus.*
		,, *melanostictus.*

NOTES ON THE EYES OF THE AMPHIBIA AND REPTILIA IN GENERAL, AND ON THE VARIOUS PARTS OF THEIR EYES.

Although attention has been paid chiefly to the ophthalmoscopic examination of the eyes of the Reptiles and Amphibia, I have included such observations on the eyes and adnexia bulbi as could be made on the living animal, so as to bring the description of the various parts into line with those made in my previous work on the mammalian eye. They will be found under the following eight headings :—

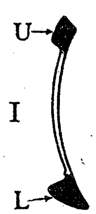
(1) Eyelids and their modifications—Lacrymal apparatus.
(2) The iris and pupil—Vertical groove.
(3) Movement, direction and refractive power of the eyes.
(4) The ophthalmoscopic appearance of the fundus oculi.
(5) Shape and colour of the disc.
(6) The pecten.
(7) Vascularization of the fundus.
(8) The colour sense of the lower vertebrates, and the adaptations in the retina of certain Reptiles for colour vision.

(1) EYELIDS AND THEIR MODIFICATIONS—LACRYMAL APPARATUS.

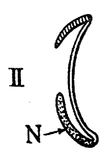
The eyelids are tegumentary duplications, or folds, of the skin. How far they surround and cover, and thereby protect, the corneal portion of the eye is largely a question of degree. As a rule the whole fold, more or less circular in its original indifferent condition, is modified into an upper and a lower lid, with a resulting horizontal slit. It is of great importance to note that there may be two successive folds, an inner and an outer (superficial) fold. Both may exist side by side fully developed, or either of them may by excessive development supersede the other, in which case it may be reduced almost to the vanishing point. It is fundamentally immaterial whether the inner or so-called "third lid" (or nictitating membrane) be considered as a primary lid, upon the outside of which a secondary fold is formed, thereby giving rise to the lower lid, or whether the lower lid arose first of all as a mere duplicature of its inner wall. The principle remains the same, namely, two successive folds, one of which is overlapped by the other. The third lid, or nictitans, arises almost universally from the nasal (or ventral) corner of the eye, whence with further development it spreads obliquely back and covers over the bulb.

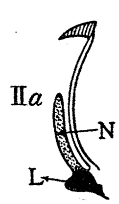
The following series of diagrams will obviate long and tedious descriptions, and will indicate the homologies of these lids in the various groups of Vertebrata. Although much has been written on the anatomy and development of the lids, their homologies and modifications have not been stated with sufficient clearness, or have been avoided by equivocal statements. Even the account in GEGENBAUR'S 'Vergleichende Anatomie' (vol. 1, pp. 945–7) is far from satisfactory.

The upper lid requires no special comment. I have designated the more superficial of the lower lids by L, and the deeper one by N. The more important conditions prevailing in the various groups of Vertebrates can be arranged as in the following series, with this important reservation, that this series does not necessarily represent the phylogenetic stages. It represents a morphological and polyphyletic arrangement, and not a continuous line.



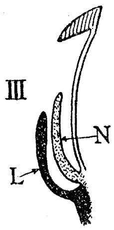
I. Lids indifferently divisible into an upper or dorsal half U, and a ventral half L, a stage perceptible in many Teleostei, also in Urodela, where it is hypothetical as a primary condition and undoubtedly pseudo-primitive, due to reduction.





II. An upper lid and a large ventral or lower lid, which is transparent and moves vertically upwards and not obliquely across the eye, thus forming a variety of the nictitans. In many Anura, and more especially in *Bufo,* we find a low outer fold arising like a broad rim from the base of the lid (L, fig. II*a*). This form of nictitans is not exactly homologous with the nictitans of the other Vertebrates on account of a unique mechanism which has been well described by MANZ, but the fold is undoubtedly homologous with, and equivalent to, the true lower lid (L). The simpler form without the fold may be considered as the primitive condition of the lower lid (II)

III



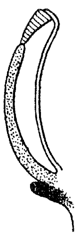
III. Strong development of an outer lower lid L, which covers the equally well-developed deeper lid which is transformed into a typical nictitating membrane by having its base shifted towards the nasal corner of the eye. It possesses a special development of muscles, usually two in number, which are derived from the palpebral muscles with trigeminal supply. This condition prevails in most reptiles, in all the birds, and in some mammals (more particularly throughout the Ungulata).

IV

IVa

IV. From the last form we find a departure in two divergent directions. Either we find, as in fig. IV, a reduction of the nictitans eventually degenerating to a *Plica semilunaris*, or, as in IV*a*, to complete reduction, as in *Lacerta simonyi*, and in most mammals. It is interesting to note that a parallel line of development of this nictitans already occurs in the Elasmobranchs, in some of which the nictitans is fully developed and active, in some cases even being furnished with a special muscle, while in others this third lid is much reduced, being then generally described as a fold of the inner lamella of the lower lid. It is, however, quite unwarrantable to interpret these elasmobranch conditions as being ancestral.

V



V. In this special form we find an excessive development and specialization of the nictitans, which becomes quite transparent, and by its free margin fuses with the inner lamella of the upper eyelid. The original lower lid is indicated either by a low rim throughout life, or it appears only in the embryonic stages, and disappears later on in life. This condition is typical of the Geckos. Similar conditions exist in a few specialized lizards, *e.g.*, Cabrita and Ophiops, but whether they are strictly homologous modifications must remain for the present an open question, for want of suitable material. The existence of proper and movable eyelids in the Eublephari sub-family of Geckos is sufficient indication that the apparently identical specializations of snakes and Geckos are cases of convergent analogy.

Detailed remarks on the eyelids, so far as these observations bear upon the interpretation given above :—

Among the Urodela movable eyelids exist only in the Salamandridæ, which means to say those newts which have, at least temporarily, a terrestrial life. In the absolutely aquatic forms, the Amphiumidæ, Proteidæ and Sirenidæ, the lids have by degeneration receded to immovable ridges or low folds. In the subterranean aquatic Proteus, and its counterfeit Typhlomolge in Texas, the eyes are completely covered by the skin. In

Typhlotriton spelæus of Missouri the eyes become concealed by the skin during metamorphosis.

The Anura possess eyelids, both an upper and a lower (ventral) one, variously called the nictitans or lower lid. It is of importance to notice that the nictitans invariably moves from below upwards, and not horizontally or obliquely from the inner angle across the eye, as is the case in all birds and many of the mammals. Moreover, the nictitans is more or less transparent, or at least translucent, so that the details of the iris can frequently be seen through it; but, on the other hand, it is never so thin as not to impair vision to some extent. The nictitans is usually bordered along its free edge with pigment of a brilliantly spotted bronze colour, but in some of the Hylidæ (*e.g.*, *H. cærulea*) the edge is bright green; in fact, this ventral lid behaves like a lower lid and nictitans combined. It may be remembered that in those sharks which possess a large nictitans, the outside of this membrane is covered with the same kind of minute placoid scales, as is the outer surface of the lower lid.

The Crocodiles have a well-developed typical nictitans, which moves obliquely backwards and slightly upwards. It is so exceedingly transparent that all the details of the iris can readily be seen through it. The free margin, which is slightly curved and convex, is bordered by three or four narrow bands of brown pigment. These animals often move the nictitans across the eye without closing the eyelids. In the act of closing the eye the lids, or rather the lower lid, closes after the nictitans has moved across the eye, and not simultaneously with it, as is the case in most other reptiles. The upper lid in the adult has a thick tough fringe-like membrane, which is split at the margin into about twenty short broad pieces, which gives it the appearance of a row of exceptionally thick eyelashes, which have become glued together and have then had the tips cut off. In an adult crocodile I found the fringe was about 6 mm. long with a base of 40 mm.

Lacrymal Secretion and Tears.—In the Saurians and Crocodiles the lacrymal gland is quite small in comparison with the size of the globe. As RATHKE first pointed out,* the Crocodilia possess three sets of lacrymal glands, the most important being the Harderian glands, but as he also discovered, the secretion passes straight into the lacrymal duct behind the conjunctiva, so that it entirely avoids the eyeball. Now I find that the other two sets, viz., the conjunctival glands and also the lacrymal glands, play a very insignificant rôle as far as the lubrication of the eye is concerned. My experiments entirely confirm the statements of RATHKE that the function of all these glands seems to be to lubricate the food, rather than to wash away foreign matter from the eyes. In fact the water which is their chief element performs this quite effectively. I made the experiment of squeezing the juice of an onion mixed with common salt into the eyes of four species in order to ascertain whether this irritating solution would excite any flow of tears, but it had no effect in increasing the moisture beyond the slight normal secretion. To my mind this is conclusive that the popular

* See C. RATHKE, 'Untersuchungen über die Entwick. der Krokodile' (1866).

notion of Crocodiles shedding tears is entirely a myth. The anatomical investigations of RATHKE,* CLOQUET,† DUVERNOY‡ and LEYDIG§ on the structure and function of these glands amply explain the absence of all external lacrymation in these animals.

Chelonia.—In the Chelonia all the three lids are likewise well developed, the nictitans being semi-opaque. Curiously enough, there are some aquatic members, *e.g.*, *Chelodina longicollis* and *Emyda granosa* (Burgoma river-turtle), in which the outer lids are transparent. This is especially the case on the centre of the lower lid. In the Burgoma turtle the lower lid closes against the upper one, and when the two meet the action still continues, the lower lid pushing the upper one back into the socket.

Lacertilia.—The eyes here are provided with eyelids as well as a nictitans. In many species both lids close at the median line as, for instance, in the *Anolis alligator*; in others *e.g.*, *Zacusa simonyi* and *Z. viridis*, the lower lid alone moves. In some desert forms, *e.g.*, *Cabrita* and *Ophiops*, the lower lid has a transparent disc like a window in the middle of it. This seems to be an initial stage leading to the condition of the skink Aplepharus, which seems to have arrived at the same modification described in the Geckos (page 320, fig. V). As a rule the nictitans is very active, and, as usual in the Lower Vertebrata, the upper lid remains nearly immovable, while the lower lid moves freely and rapidly upwards, the semi-circular edge of the lid flattening out into a straight line. At the same time the eyeball rotates and is pushed back by the lower lid, and in those cases in which the nictitans is freely developed, it simultaneously rolls across the eyeball from the inner canthus and then quickly retracts as the lids open, and the eye comes forward again.

In all animals which have a typical nictitans I noticed that the cornea is highly sensitive to the touch, and this is also the case in most of those which have only a trace of a nictitans, as in ourselves. On the other hand, in those creatures, *e.g.*, snakes, in which the nictitans has assumed other functions, and is itself not covered by eyelids, it is quite insensitive. In *Pachydactylus maculatus* (one of the Geckos) there are no eyelids but merely a thickened dermal fringe round the periphery of the eye. In many of the Geckos the eyes are covered by an external transparent skin as in the snakes.

Chamæleontidæ.—In the chameleons the lids are rather more modified. They permanently cover most of the eye by one concentric fold, leaving only the pupil free, but when the animal is asleep and the eye is closed completely, the slit still assumes a horizontal position, the last indication of the original composition of an upper and lower lid. There is no nictitating membrane in these animals. Both lids of this lizard are exceedingly soft and thin, and close to form a horizontal slit as they apparently push the eye back into the socket. The eyes are nearly always seen open, the lids rarely closing.

* See RATHKE, *loc. cit.*

† CLOQUET, "Organisation des Voies lacr. chez les Serpents," 'Mémoire du Musée d'Hist. Nat.' (1821).

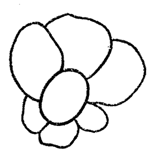
‡ DUVERNOY, 'Annales des Sciences Naturelles,' vol. 30 (1832).

§ LEYDIG, 'Max Schultze's Archiv für Mikros. Anat.,' vol. 9, p. 598 (1873).

Ophidia.—The greatest specialization of the lids has taken place in the snakes. The outer, upper and lower lids are completely reduced in the adult, with one exception to be mentioned presently. In the embryo, however, these lids are still represented by a low circular rim. The nictitans is transformed into an absolutely transparent membrane which covers the whole visible portion of the eye, and fuses early with the inner margin of the original margin of the lids, so that the eye is covered with a film like a watch-glass. This pellicle, of course, consists almost entirely of epidermal cells, at least all traces of the substratum of connective tissue of the nictitans seem to be lost. It forms a false cornea, while between it and the true cornea a lymph space is formed, or rather a space which is filled with another absolutely transparent fluid, possibly lymph, mixed with the secretions of the lacrymal glands. This fluid (the "tears") is drained off through the naso-lacrymal duct, without, of course, being able to come to the surface. When the snake sheds its skin—a process which takes place several times during the year—the false cornea, resembling both in size, shape and structure the true cornea beneath, comes away. Although this shedding of the "cornea," together with the connecting skin, seems to be easy of explanation, it is not so in reality, and exact information regarding the process will require further investigation.

As the snakes have no proper external eyelids, this hardened false cornea soon becomes dim and scratched by friction. It is quite insensitive to touch. The cobra, python, and other snakes all allowed me to touch it, and even polish it with a rag, so as to get a clear view of the fundus, without any attempt at resistance or even sign of discomfort. The thickness of the false cornea, which happened to be shed with the skin in a large python, I found the same throughout, viz., 0·1 mm.; but it seemed remarkable that although so exceedingly thin, the false cornea preserved its hemispherical form without any sign of collapsing. The same happened in the case of the small snakes, in which, of course, this film is naturally much thinner.

It is of considerable morphological importance that the Boidæ still possess well-developed lids, and corroborates the view taken here that the false cornea is not the result of the fused upper and lower lids, but the modified nictitans. These snakes are probably the most ancestral of all living snakes, a fact which is of interest in this connection. In *Python molurus* the false cornea is surrounded by an irregular circle of six scales, the three anterior of which are at least three times the size of the others (see drawing).



Drawing of scaly covering and false cornea of the eye of an adult python. (From life.)

These six scales are part of the scaly covering of the true outer eyelids, which have here combined to form a single concentric cover.

The edge of the hemispherical false cornea is not continuous with the epidermal scales, but is adherent to the scleral conjunctivæ of the eyeball, while the six scales of the python's are together with the central convex false cornea, about 1 mm. in front of its scleral attachment, so that when the skin is cast, the false cornea has a free ragged edge or border which projects internally where it was attached to the conjunctiva of the eyeball at the sclero-corneal junction. It is worth while mentioning that the eyeball moves freely in all snakes beneath this watch-glass cover.

(2) The Iris and Pupil.

The pupil of the frogs and toads is, relatively speaking, very large. The ratio-aperture,* *i.e.*, the ratio between the focal length of the optical system of the eye compared with the diameter of the pupil, is greater than the most rapid photographic lens, being equal to F/2 or even F/1, 5 as compared with F/4 of an ordinary Petaval portrait lens. In man the ratio-aperture varies between F/2 and F/8, although there are many exceptions to this rule. The large size in the Anura may be attributed, in many cases at any rate, to their amphibious habits, moreover, those animals which are nocturnal in their habits would, for obvious reasons, have a large ratio-aperture. It may be added that the ratio-aperture, and not the size of the eye, is what governs the intensity of light which reaches the eye, and, further, the size of the eye is no criterion of the size of the animal, many of the largest of the Amphibia possessing very small eyes.

Among the reptiles, many of the snakes and burrowing lizards have remarkably small eyes for their size. To this Sphenodon is a remarkable exception, but the factors influencing the size of the eye are altogether unknown, and at present we cannot form any theory on the subject.

Shape of the Pupil.—So far as I have ascertained, the shape of the pupil throughout the Amphibia, when fully dilated, is invariably either circular or a wide horizontal oval; but when contracted it may assume various shapes, all of which are characteristic of the various species, but not of the genera or families. As only relatively few species are to be met with in captivity compared with the immense number described, the statements concerning the shape and size of the pupils referred to in systematic works are by no means reliable, being for the most part taken from spirit specimens.

The pupil of the Anura may contract to a slit, or merely into a horizontal or vertical oval, but rarely into a lozenge-shaped pupil. Only rarely have I observed the pupil contract to a small circle, as is the case in some of the Mammals. As yet it is hopeless to assign names for these peculiar variations in shape. Most of the families of the Anura can be divided into two groups according to the shape and direction of the contracted pupil, which may be either horizontal or vertical. I have seen the pupil

* The ratio-aperture of any optical system may be expressed as a fraction: the numerator being the focal length of the lens, and the denominator the diameter of the aperture. This fraction expresses the intensity of the illumination, and, for the same focal length, varies directly as the square of the diameter of the pupil (or stop).

of *Rana clamata* (Noisy frog) contracting to a vertical slit, whereas it is described as being horizontal. Again *Ceratophrys cornuta* possesses a circular pupil, which remains circular, and is entirely unaffected by atropine or other drugs, and even light and electrical stimuli, and yet this animal is stated to possess a horizontally slit-shaped pupil. In the large-fingered frog (*R. halecina*) I noticed that the pupil contracted to a diamond shape, while in the *Bombinator bombinus* (Yellow-bellied toad) it assumes a heart shape. In the Bull-frog (*Rana catesbiana*) it is semicircular, the flat side being uppermost.

In the Chameleon, Scincidæ, Tejidæ, Varanidæ, Zonuridæ, and in the Iguanidæ, the pupil is invariably circular. In the Geckos it is likewise round, but closes to a vertical slit; in most species I have examined, *e.g.*, Fringed Gecko (*Pachydactylus maculatus*), Turkish Gecko (*Hemidactylus turcicus*) and Cocteau's Gecko (*H. cocteaui*), it closes to a vertical slit, but this slit is not a straight line, as in the domestic cat, but is interrupted by four, five or even more minute equidistant pinholes, or notches, so as to just permit a small amount of diffracted rays from direct sunlight to penetrate their eyes. The fact that these creatures are nocturnal hunters, and therefore extremely sensitive to bright light, affords a ready explanation for this modification of their pupils under the action of bright sunshine, in which they frequently bask. It is therefore all the more interesting that in the Green Gecko (*Hemidàctylus viridis*), a species which, by the way, is undoubtedly diurnal, the pupil remains circular, while sunlight and drugs hardly, if at all, affect it.

As a rule in the Geckos the pupil is exceedingly sensitive to light, and repeated observations seem to show that it is to a certain extent under the control of the animal, as we remarked was the case in the Otariidæ (eared seals and sea-lions).

In most snakes the pupil is round, or only slightly oval. In *Naia* it is lozenged-shaped, and vertically oval in all the *Boas*. In the Green Pit Viper (*Lachesis gramineus*) the iris closes to an exceedingly fine vertical slit or chink. In the Chelonia the pupil is circular and closes to a circle. In the Crocodilia the pupil expands to a circle under the action of atropin, but under the action of light it closes to a vertical button-hole or oat-shaped slit.

Lastly in the *Sphenodon* it is round or slightly oval, closing to a narrow line with a tiny dot-shaped aperture at each end, precisely as in the case in the domestic cat when the eye is turned towards the sun. The direction of the slit is, however, not vertical, as in the cat, but is directed downwards and backwards at an angle of about twenty degrees from the vertical.

A number of these curious variations will be found in my previous paper on the "Mammalian Eye" ('Phil. Trans.,' B (1901)). In the seals and sea-lions the narrow slit-like pupil has another use, namely, to overcome the enormously high astigmatism which invariably occurs in all marine amphibian mammals. (See above paper in these 'Transactions,' also my article in the 'Proc. Zool. Soc.,' in which the use of the tiny holes at each end of the slit in the cat's eye is referred to.)

Actions of Drugs and Light on the Pupil.—In the frogs and toads the pupil reacts slightly to both drugs and light, the sole exception I have met with being the Brazilian toad (*Ceratophrys cornuta*), upon which they had no effect. In this respect *Ceratophrys* agrees with the Iguanas and the Chelonia.

The eyes of the Crocodilia act freely to drugs, the pupil expanding from a vertical oat-shaped slit to a lozenge or round-oval shape, or even to a complete circle.

In none of the snakes does atropine or eserine have the slightest effect on the pupil. This is certainly due to the fact that the eye is shut off by the false cornea and its attachments to the surrounding epidermis at the sclero-corneal junction. In some snakes light has a marked effect, but again in others no effect is perceptible. Thus, in *Naia*, when the light of a lamp is focussed by means of a lens on the eye, the pupil contracts from about 2 mm. or 3 mm. to 0·75 mm. and instantly dilates to its former size the moment the light is removed. This return takes place much more rapidly than in a Mammal. The same effect occurs in various non-poisonous Colubrine snakes and to a somewhat less extent in the *Boa*, but in the pythons the contraction is only slight and then chiefly in a lateral direction. On the other hand, in the European grass-snake (*Tropidonotus natrix*) and in the sharp-nose snake (*Lioheterodon madagascariensis*) I found the iris was unaffected by light.

Colour of the Iris.—While, with the exception of Man, the mammalian iris shows very little variation in its colour, being of a uniform sombre light or dark brown shade, we find surprising variations both in colour and pattern in the iris of both Birds and Reptiles, and even, although to a much less extent, in the Amphibia. The colours are most striking and varied in the Birds, most diverse in pattern among the Reptiles, especially the Geckos. It is peculiar to the Amphibia and Reptiles that so many of them have an iris which is either adorned with a pattern, or else radiated, mottled or stippled with dark or metallic colours in a most artistic manner.

In most frogs and toads the iris is brilliantly coloured, often golden, as if dusted with golden or bronze powder, thus giving it the appearance of old gold or Japanese lacquer. This metallic lustre is due to the presence of tiny flakes of crystals of guanin, which is deposited within the chromatophore cells. In the giant toad (*Bufo marinus*) the iris, which is otherwise white or grey, has a brilliantly mottled streak along the upper border, and also a slight orange stippling all round it.

The Chelonia show a great variety of colours. In many aquatic forms the iris is very bright and mottled with various colours, while in the land tortoises it is usually brown. Gadow* draws attention to the fact that *Cistudo carolina* (one of the Testudinidæ) presents a remarkable case of sexual dimorphism, the male having a red iris, while the female has a brown one.

In many of the Geckos the iris is mottled in a peculiar way, showing a striped pattern of dark brown on a light yellow-ochre or grey background, giving a weird appearance to the eye, especially when the pupil is closed.

In *Lacerta viridis* (green lizard) the iris is of a brightly speckled gold colour. The

* 'Amphibia and Reptiles,' by Hans Gadow, Cambridge Nat. Hist., Series VIII, p. 329.

land iguana of the Galapagos possesses a remarkably brilliant iris, such as one may see in some of the parrots, *e.g.*, Palæornis, viz., a remarkably brilliant orange iris with a red or orange-red pupillary border. *Iguana tuberculata* has a most beautiful and artistically designed festoon pattern of gold and black fibres, which are exceedingly delicate in their outline.

Snakes.—The iris of the cobra is pale brownish yellow, speckled with gold. In the corn snake (*Coluber guttatus*) it is orange-red. In *Lachesis gramineus* we find a yellowish-green colour, which approximates to the general brilliant green hue of the animal. In the Indian river-snake (*Tropidonotus piscator*) the iris is bluish-grey with a golden yellow fringe at the true margin. And, lastly, the boa constrictor has a light straw iris mottled with light brown.

In the majority of Reptiles the colours are various shades of brown, and occasionally dull orange or yellow. The few examples given above, although most scanty, are sufficient to show the possibilities of iris coloration. Unfortunately, it is at present a hopeless task to correlate the iris colours with bionomic conditions. In some cases there is an approach to an effective harmony between the colour of the iris and the general colour of the body. In some instances there can be no doubt that the bright iris ring of differentiated colour seems to enhance the beauty of the animal's expression, but we are scarcely justified in dilating upon these æsthetic vagaries. Moreover, the so-called metallic colours appear to prevail in nocturnal creatures, but the examination of a long list of data makes it doubtful to decide what is the average condition, so as to determine which form the exceptions. We do not even know whether there is a definite object attained in the coloration of the iris, or whether even its most striking appearances are not mere incidental effects.

The simplest and most effective way to render the iris opaque to light would be by the deposition of black pigment, which one finds deposited all over the posterior layers of the iris and ciliary body in all, or certainly very nearly all, animals. But the metallic and other striking colours are deposited over the outer and visible layers. Whether these brilliant and beautiful colours are there for the purpose of attracting the opposite sex, as is certainly the case in many species of Birds, is an open question; but, as we can assign no other reason at present, we are justified, I think, in provisionally assuming this to be the cause. In the case of Fishes the problem becomes still more complicated, for, as HESS has repeatedly pointed out, fish appear to be colour-blind,* notwithstanding the fact that all fly-fishermen stoutly maintain the contrary. (See Section 8 on this point.)

It has been suggested that the pigmentary colours of the iris might form a selection filter to the various colours of light. I therefore made some tentative experiments

* "Untersuchungen über den Lichtsinn bei Fischen," CARL HESS, 'Arch. für Augenh.,' vol. 64, 1909. HESS points out, however, that fishes are sensitive to the ultra-violet rays, and become visibly fluorescent. See also as regards this point his paper "Untersuch. u. den Lichtsinn bei Rept. u. Amphibien," 'Arch. f. d. ges. Physiologie,' vol. 132 (1910).

by cutting out discs of various sizes from different coloured tissue-paper and holding the pieces of paper successively towards the sky and white clouds, and then towards trees and other opaque objects immediately in front. The only effect on looking through them was that after a second or two I observed the colour of the paper to spread beyond the edge of the aperture towards the centre, and to tint the objects looked at. Thus, on looking through the hole in a violet-tinted piece of tissue-paper, trees and other objects seen towards the edge of the hole appeared to be tinged with violet. On removing the paper this coloration at once disappeared.

The net result of these experiments convinced me that even if the pigments in, or in front of, the iris could be perceived by the animal's retina (which I am certain is an impossibility), the result would only confuse the animal and give it a wrong impression of the true colour of the objects looked at. A much more practical way, and the only one which Nature invariably adopts, is to place the pigment colours either immediately behind the retina in the substance of the choroid layer, or else in the layers of the retina itself, as is the position of the coloured oil globules in many of the Birds and a few of the Reptiles. By this means the light on entering the eye passes through the retina as well as the pigmented layer of the choroid (*tapetum lucidum*), and after reflection is projected as a sharply focussed image directly on to the terminals of the rods and cones.

Vertical Line and Groove.—In all Anura, but not in the Salamanders, the iris shows a straight pigmented stripe, which extends vertically downwards from the lower pupillary margin to the periphery of the iris. Occasionally a similar stripe may be noticed in the upper half of the iris as an individual variation. Amongst the Reptiles I have only noticed this pigmented stripe in *Varanus bengalensis* (Bengal monitor) and in *Iguana tuberculata*, in which animal it is very conspicuous. This curious formation is very frequently, if not always, connected with a slight vertical groove, which, although often very slight or shallow, can always be recognized with the naked eye both in the live animal and in horizontal sections of the iris. This groove occurs also in the monitor. Neither it nor the line of pigment extends beyond the base or external attachment of the iris, and therefore always ceases before reaching the ciliary processes.*

I have observed a similar pigmented furrow or ridge, and often in addition to it a well-marked notch, in a considerable number of the British river and sea fishes, viz., in the herring, smelt, trout, cod, carp, gurnet, starlet, *Salmo irideus* (rainbow trout) and the common minnow (*Leuciscus phoxinus*), the golden orfe (*Leuciscus idus*), and several other fish whose names I am not acquainted with. In the common mackerel there is a very pronounced irregular notch at the lower part of the pupil, but which differs entirely from the above-mentioned ridge, although situated in the same place, being much wider and more irregular in shape. This notch occurs invariably at the centre of the iris at the lower border of the pupil. It seems reasonable to refer this

* See in this connection my previous paper, "Contributions to the Comp. Anatomy of the Mammalian Eye," 'Phil. Trans.,' B, vol. 194 (1901).

vertical fold or gap to the effect of mechanical strain on the iris by its contractile elements. The occasional presence of a pigmented line on the opposite upper half of the iris indicates that the whole phenomenon started as a vertical slit, the right and left halves of the iris curtain being, as it were, drawn asunder, so that the muscles of the latter must have entered by the choroidal cleft. From this it would appear that the vertically slit pupil would be phyletically the oldest condition, and the round pupil the highest stage of development. The frequently occurring specializations, *e.g.*, a triangular, oval or even transverse opening, cannot invalidate this conception.

(3) Movement, Direction, and Refractive Power of the Eyes.

One should expect retraction of the eyes into the sockets to be a very common phenomenon in the Reptiles, on account of the immovability of the head, and the constant danger to the eyes from their position close to the ground; but apart from this retraction I have observed no movement in the eyes of the Amphibia. The axes are as a rule directed more forwards, *i.e.*, more towards the median line of the body than in the reptiles, but among the frogs and toads I have invariably met with a considerable divergence from the median line, amounting to 45 or 50 degrees.

In the lizards the axis of the eye is always nearly at right angles to the body; in fact, it may even exceed 90°, *i.e.*, the axis of the eye may be directed slightly backwards. For example, in *Lacerta simonyi* and *L. viridis*, it amounts to 100°. The *Sphenodon* possesses a divergence of 85 degrees.

The chameleons, as is well known, are able to turn either eye at will separately in any direction, so that one eye may be turned upwards, and the other downwards, so as to embrace an angle of as much as 160 degrees between them.

The axes of the eyes of the iguanas form an angle of about 85 degrees, *i.e.*, about 42 degrees for each eye, as measured from the long axis of the body.

In the snakes the eyes have a considerable range of movement. Generally speaking, they move through an angle of about 20 degrees each; in other words, the eye can travel backwards from 70 degrees, which is its normal position, to about 90 degrees; but the degree of lateral movement varies considerably in different genera. Thus, in the corn snake (*Coluber guttatus*), the axis may be directed forwards as much as 35 degrees, while in the python a range of at least 40 degrees was observed. The Crocodilia and Chelonia have their eyes directed nearly at right angles to the line of the body. It will thus be seen that the Reptiles possess a far greater amount of divergence than the vast majority of the Mammals, thus conforming to the general rule which I pointed out in my work on the eyes of the Mammalia, that the lower down the scale of the natural orders one descends the greater will the divergence become, and the greater the range between the two extremes in the natural order.

I have taken the refraction of a large number of species of the different families of both the Amphibia and Reptilia, both by the direct method with the ophthalmoscope and by means of retinoscopy, and I have noticed much less divergence from the normal condition than among the various families of the Mammalia. In nearly all cases I found the eye emmetropic or slightly hyperopic (one diopter or less), and only rarely did I come across any marked degree of astigmatism, *i.e.*, above 0, 5 or 0, 75 D. But the power of accommodation is usually very considerable. Thus, when examining the Geckos' eyes, I found the accommodation varied continually from 1 D to 6 or 7 D during the short time the eye was under examination. But this is just what one would expect, considering the semi-aquatic mode of life of most of the Amphibians and a large number of families among the Reptiles. Moreover, in searching for food it is essential for them to have a great range of vision, and more particularly of near vision.

(4) The Ophthalmoscopic Appearance of the Fundus Oculi.

A.—*In the Amphibia.*

Unfortunately, it has been possible to examine the fundus of only a very small number of this class, because only a very few families are to be found in the Zoological Gardens of Europe, and of these very few have sufficiently large pupils to allow of their being examined by the ophthalmoscope. I have therefore had to remain content with the examination of a few species belonging to four families, viz., the Ranidæ, Hylidæ, Bufonidæ and Salamandridæ. The first three families present a fundus entirely different from that of any other Vertebrate. They all exhibit an exceptionally well-developed vascular system, consisting of a characteristic *vena media* with lateral branches, which lie in the hyaloid membrane in front of the retina. The main trunk stands out in conspicuous relief, and passes vertically down in front of the disc. So large and prominent is it, that in several species, notably in *Rana catesbiana* (North American bull-frog), and *Hyla versicolor* (White tree-frog) the large red nucleated blood corpuscles can be seen with the ophthalmoscope quite distinctly streaming in single or double file through the lumen of the vessel. So beautifully clear are they that I cannot help calling attention to the fact that under a magnification of 16 or 20 diameters (which obtains when viewed through the ophthalmoscope by the upright image) these animals might prove of great utility for physiological experiments.

In all the species of Ranidæ and Bufonidæ the disc is long and narrow, and directed vertically downwards immediately behind the median vein. A similarly shaped disc may be seen in a large number of birds, but it differs in the latter in being invariably directed obliquely and not vertically downwards, and, moreover, it is always more or less completely hidden by the densely pigmented pecten, an organ which does not exist in any Amphibian which I have examined. But this is exactly what one would be led to expect, as I have pointed out in my previous work on the "Mammalian Eye" (pages 53–54), since the pecten is a secretory organ whose function is to supply nourishment for the inner layers of the retina and the vitreous when the retinal or hyaloid vessels are absent. Hence its presence would be quite unnecessary in an eye so abundantly supplied with blood as the Anura. Now, although there are a great many animals which possess an angiotic retinæ which are destitute of a pecten, the converse does not occur, in which a pecten exists along with retinal or hyaloid blood vessels, unless the pecten happens to be a mere vestigial relic, and therefore functionally inactive.

None of the Amphibia which I have examined, either ophthalmoscopically or by means of microscopic sections, possess any trace of a macula. The fundus in most of the species is uniformly the same throughout, both in colour and structurally, excepting, of course, at the disc and its immediate vicinity. The background is almost invariably of a slaty-grey colour, but this colour is largely if not entirely masked, either by opaque or semi-opaque nerve fibres, which radiate in immense numbers in all directions from the disc, or by a yellow, orange or pink superstructure, which appears to consist of an irregular closely meshed network of orange-red choroidal vessels, as in *Rana tigrina*. There is, however, a third form, in which the whole background is thickly strewn with orange-red or golden sago-like grains, in some of which a dark-coloured nucleus can be distinctly made out (see drawings of *Bufo* and *Hyla*).

In the Ranidæ the disc is long and narrow, and of a white or yellowish colour, giving it the appearance of a caterpillar with the body directed downwards. In the Hylidæ and Salamander the disc is circular. In nearly all cases the greater part of the disc is stippled with grey or occasionally black dots, as in the Giant toad and American bull-frog.

B.—*In the Reptiles.*

The fundi of the Reptiles bear no resemblance whatever to those of the Amphibia. Moreover, in the former the different Sub-classes, Orders and Sub-orders have each characteristic features, which at once distinguish them both from one another and from the fundi of Birds and Mammals.

To this there are two exceptions :—First, in the Geckos, it is interesting to note that the fundus bears a striking resemblance to that of the Apteryx. They all have a brick-red fundus, and circular, or nearly circular, disc, which is provided with a large conical pecten, resembling the thalamus of a raspberry, which fills the entire surface of the disc. No trace of blood vessels can be perceived in any of the Geckos' eyes, and there is certainly no trace of a macula, which is readily seen in close proximity to the disc in the Apteryx's eye. In fact, this is the one striking point of difference between the two. (See Plate 22.)

The other exception is that of the *Sphenodon*. The fundus of this animal possesses many of the characteristic features of the Bufonidæ, and also in a few points those of the Echidna. Thus the fundus in each case has a warm rather dark reddish-grey colour, to which in the *Sphenodon* and the Bufonidæ is added a mottling of gold spots or stippling.

These spots are very fine and cover the whole background. Again the disc in all three cases is a little below and behind the optic axis, and is long and narrow, the long axis being directed downwards. In *Sphenodon* its length is double that of its breadth, which latter is about a third that of the human disc. The disc itself is white in all these animals, and its margin nearly obscured by an immense number of opaque nerve fibres, which radiate outwards in all directions, and extend laterally for a considerable distance, to the periphery. Hence in the colour of the fundus, the gold mottling, the white disc covered with white nerve fibres, together with an absence of all trace of a pecten, the eye of the *Sphenodon* bears a striking resemblance to the toad's fundus. The one great difference lies in the fact that in the *Sphenodon* there are no blood vessels to be seen anywhere, which in all Anura form so prominent a feature in the hyaloid.

In the Echidna we find fewer opaque nerve fibres, and the fundus has a uniform lilac-red colour without any stippling, otherwise they are much alike. Thus the lowest living Reptile (nearest the level whence the Mammals have sprung from the hypothetical tree) bears a striking resemblance to the lowest living Mammal, whilst the other recent Reptiles reveal themselves as further developed side branches. It is just as, or rather better than, the phylogenist dared expect.

Briefly, the following are the main differences seen in the fundi of the various orders and families of the Reptiles :—

1. *Prosauri*.—(*a*) Represented by the single living form *Sphenodon*. Fundus dark reddish-brown, minutely mottled with fine gold stippling. Disc white, long and vertical. Three times as long as wide and situated just below and behind the optic axis. It is almost obscured by dense white opaque nerve fibres which emerge, turning to the right and left, from a vertical line through its centre. No trace of a pecten, or blood vessels, either retinal or choroidal.

2. *Chelonia*.—The following three families have been examined : Chelydidæ, Testudinidæ, and Trionychidæ. In all the different species examined, the background was either orange-red or Indian-red, modified in different ways. No retinal vessels exist. The disc is approximately a circle, often the margin is convoluted and irregular. There is no trace of a pecten beyond an irregular brownish patch in the centre of the disc of *Chelodina longicollis* and *Cinyxis erosa*, which some observers might possibly consider to be a vestigial trace of a pecten. In every case opaque nerve fibres are to be seen radiating over the greater part of the field, except in the single instance of *Chelodina longicollis*, in which they are very few and faintly marked.

Chelodina longicollis.—The fundus is light Indian-red, mottled over with darker red. The disc has an ill-defined margin of a whitish-yellow colour, with an irregular ring of brownish pigment in the centre.

Chelydra serpentina (Alligator terrapin).—Fundus a light mauve red, faintly mottled with black patches towards the periphery. The disc is yellowish, with a very conspicuous irregular white border. The opaque nerve fibres are very abundant, and almost completely hide the background.

Chrysemys scripta rugosa (Wrinkled terrapin).—The fundus is a light chocolate colour, irregularly mottled with darker chocolate patches. The disc is a dirty yellowish-white colour, and the opaque nerve fibres radiate from the centre for a considerable distance.

Testudo radiata (Radiate tortoise).—An Indian-red background stippled all over with innumerable minute orange oat-shaped dots. The disc forms a greyish-white well-defined white round disc, from the margins of which innumerable white nerve fibres proceed. As they are all of about the same length, they form a very elegant rosette. A similar rosette occurs in one or two of the marsupial eyes.

Cinyxis erosa (Eroded cinyxis).—The fundus is light Indian-red, faintly mottled with dark pigment. A large number of red choroidal vessels are visible all over the fundus, which are broken up into short lengths where they are hidden in the stroma. The disc is yellowish white, with an ill-defined margin, and a greyish centre. The opaque nerve fibres start from the centre of the disc. They are not very numerous and stop short before they reach the periphery.

Emyda granosa (Burgoma river-turtle).—Fundus brown-pink, mottled with reddish dots. The disc yellowish white, perfectly circular and with well-defined margin. Its size is larger than that of any reptile that I have examined, being at least three times (in area) of that of man. It is surrounded by a curious red choroidal ring which is mottled with darker red spots. I have never seen anything resembling it in any animal. One might almost compare it to a photograph of the solar corona, surrounding as it does this large yellowish-white disc.

The eye of the *Chelonia* has all the characteristics of what for want of a better definition I may call a "primitive fundus." By this I mean an eye consisting of a uniformly coloured background, with little or no differentiation beyond the presence of pigment, without any traces of blood vessels, either in the retina, disc, or hyaloid. Such an eye has a white, circular or oval disc, and if provided with a pecten, it is either a vestigial relic, or of the simplest possible type, *i.e.*, a simple unconvoluted cone or thalamus. Now I find that whenever an animal is specially protected by Nature against the attacks of its enemies, the fundus of the eye assumes a more or less primitive type, as is evident when examined by the ophthalmoscope.

Such a sweeping generalization may seem rash, but it is supported by the examination of several hundred different animals, among which I have found no striking exception to the rule. Thus we find this type of eye in the Rhinoceros, the Elephant,* the Armadillos, the Anteaters, the Porcupines, and Echidna, while in the Reptiles we find this primitive type in all the Chelonia, the Crocodilia, and in all the specially protected members of the great sub-order Lacertæ which I have examined, such as several of the Agamidæ (*e.g.*, *Moloch horridus*, *Chlamydosaurus kingi*) and Iguanidæ, and *Zonurus giganteus*.†

The converse of this rule is also true to a large extent. By the converse rule I mean to

* The elephant, it is true, has a mottled background, but otherwise it entirely conforms to my definition.

† This latter has a pecten, but it is a mere protuberance and quite inactive and useless.

say that only those animals which have primitive eyes are protected by Nature against the attacks of their enemies, and if they have not primitive types of eyes, they will not be found protected by Nature. Thus none of the birds have primitive eyes, since every bird (as far as we know) possesses at least one macula, and very frequently two, as well as a highly developed and differentiated choroid, while the disc is without a single exception covered by a physiologically active pecten, which latter is invariably highly developed and active.

The Salamanders with their primitive fundus are protected by their poisonous properties, and not a few possess warning coloration. The Urodeles have an eye so primitive that they have not yet a pecten.*

Crocodilia (*Alligator sinensis*, *A. mississippiensis*, *Crocodilus americanus*, and *C. frontatus*) all present the same characteristic features, viz., a light yellow background stippled all over with spots of brownish pigment and orange dots. The disc is circular, quite white, and covered with brownish pigment, almost black in *C. frontatus*. This pigment covering the disc resembles an abortive attempt at a pecten and is entirely functionless.

I have previously mentioned that a large number of those animals which seek their food at dusk, or night time, possess red, orange or yellow fundi, and the Crocodilia are no exception to this rule. It is difficult to assign a reason for this, since we know that as the light gets more and more feeble towards and after sunset, the spectrum becomes less and less visible towards the red end, so that the violet, blue, and greenish-blue colours alone remain visible, the red, orange, and yellow colours becoming dark purple, grey and black, and so more or less invisible. This law, known as PURKINJE's phenomenon, can be observed by every one, and according to my experience holds true for the panchromatic or colour-photographic plate as well. One would imagine that night animals ought to possess eyes with green and prussian-blue backgrounds, such as we find in the Ichneumon's eye, instead of the red and orange fundi peculiar to the dusk- and night-feeding animals.

4. Geckonidæ.—Three out of the four genera of the Geckonidæ examined, viz.: Hemidactylus, Pachydactylus, and Uroplates, have eyes with a red background. They are all nocturnal. The day-feeding Gecko, *Phleuma madagascariensis* (Green Gecko), has a *grey* fundus, which is rendered a still lighter grey by a dense layer of superimposed nerve fibres. This fact lends additional support to the above statement. All the Geckos have a large conical pecten which covers the entire disc. The background is mottled with dark red spots. No trace of blood vessels is perceptible.

5. Lacertæ.—(*a*) Iguanidæ.—The background varies greatly in colour. In *Anolis* the fundus is slate-grey, faintly mottled with light grey patches. The disc is circular, white, and covered with a deep black cushion-like pecten. In *Conolophus cristatus*, the

* The statement first made by Prof. OWEN, and since then copied in innumerable text-books, to the effect that the Apteryx does not possess a pecten, I proved to be erroneous in my "Comp. Anat. of the Mammalian Eye" ('Phil. Trans. R.S.' (1901)). See plate at the end of the work.

undus is dark grey, entirely covered with bright yellow spots. The disc is round, white, and covered with a very large fan-shaped pecten, having a highly ornamental crenated margin. In *Metopoceros cornutus* the upper half of the fundus is light grey, while the lower half is entirely covered with red and orange spots, like short rods. Disc is greyish white, bearing a large bifurcated black-pigmented pecten. Innumerable opaque nerve fibres proceed from the margin of the disc.

(*b*) Anguidæ.—These snake-like lizards possess fundi similar to those seen in the Scincidæ. *Ophisaurus apus* has a greenish-grey fundus covered with a brownish-black cushion-shaped pecten. Opaque nerve fibres radiate in all directions from the disc. In *Ophisaurus ventralis* (American grass-snake) there is a similar fundus, but the opaque nerve fibres are much coarser.

(*c*) Varanidæ.—All these animals have grey fundi mottled with dark grey or white spots as in the species *Varanus bengalensis*. The disc is very large, white and circular, and completely covered with a dense black pecten which projects far into the eye like a long spike. Abundant opaque nerve fibres almost obscure the fundus.

(*d*) Zonuridæ.—*Z. giganteus* is the only member of this family examined. The fundus is slate-grey, entirely covered with chalk-white spots. The disc is very large, white and entirely filled by a conical-shaped brown pecten, the conical part being covered by black pigment. Innumerable opaque nerve fibres proceed in all directions from the edge of the disc.

(*e*) Tejidæ.—The fundus is practically the same as that of the Glass-snake (*Ophisaurus apus*), one of the Anguidæ. It has no special feature.

(*f*) Lacertidæ.—The fundi of all this family are extremely dark, almost black in *Lacerta galloti*, slaty-grey in *L. simonyi*, and in all cases more or less completely covered with opaque nerve fibres. The circular disc is entirely hidden by a large black conical pecten. In *L. simonyi* the fundus everywhere is stippled with fine white dots.

(*g*) Scincidæ.—I have examined *Lygosoma quoi*, CUNNINGHAM'S skink (*Egernia*) *Chalcides ocellatus*, and *Macroscincus cocteaui*. The fundus in all the skinks resembles that of the Lacertidæ in their main features, *i.e.*, a bluish-grey, light-grey, or greyish-black fundus. There is the usual circular disc entirely hidden by a large conical or cushion-shaped pecten, which is invariably densely pigmented with black pigment, with the exception of *Egernia cunninghami* (CUNNINGHAM'S skink), in which the pigment is of a deep brownish-red colour, and throughout the genus *Chalcides*, in which the pecten is almost flat and of a deep red colour. In COCTEAU'S skink (*Macroscincus cocteaui*) the pecten only covers the middle third of the disc. The usual radiate nerve fibres are invariably present.

(*h*) Pygopodidæ.—*P. lepidus*, or limbless lizard. This animal has a grey fundus faintly mottled all over with brown-pink stippling. The disc is much smaller than that of the other members of the group. It is entirely covered by a dense black pecten. The nerve fibres are so fine as to be barely visible.

Sub-order CHAMÆLEONTIDÆ.—The only member of this sub-order examined is

Chamæleon vulgaris. The fundus closely resembles that of *Pygopus* just described. The disc is very large for so small an eye. It is quite circular, and almost entirely hidden by a dense black conical pecten which projects right into the vitreous. This Reptile possesses a macula ; this forms a well-defined conical pit, with a fovea closely resembling the human one, both microscopically in prepared sections and in the living animal by the ophthalmoscope. It may be seen with the ophthalmoscope by the upright image as a faint depression in the axis of vision, about three disc breadths to the outer side of the disc, which agrees with the position in our own eyes. (See Plate 24, fig. 39.)

To see the fundus in so small an eye it is necessary to have the room made quite dark, and to use a very short-focus concave mirror with a small aperture. The most important point is to allow the rays to enter the observed eye as obliquely as possible, so as to obtain as large an angle as can be effected between the entering and the reflected pencils. If these points are not attended to it will be found impossible to see the macula of any eye in which the pupil is less than 1·5 mm. in diameter. On removing the eye, immediately after being killed, and treating it with alcohol or a solution of chromic acid, it becomes much clearer and more visible as a deep pit without any floor, measuring 1·5 mm. vertically by 1 mm. horizontally. Microscopic sections, of which I have made some hundreds, show an entire absence of rods even at the periphery of the macula, which is never the case in the human eye. Although it is probable, from physiological considerations, that the macula lutea exists in some of the other Reptiles, the Chameleon is the only one in which I have detected it with certainty.

Order OPHIDIA.—The snakes possess very broad and conspicuous blood vessels, which enter and emerge from the disc, which in many species extend far beyond the visible limits of the fundus, even to the ora serrata. Choroidal vessels somewhat resembling those seen in the human eye are conspicuous in certain snakes (notably the python) and traces of these vessels are frequently present in those snakes which possess red fundi. This is almost invariably the case in the Birds.

COLUBRIDÆ.—(1) *Aglypha. Coluber guttatus* (Corn snake).—Fundus a light warm grey, covered all over at regular intervals with white spots. The disc is very large, more than double the diameter of the human disc, and of a light grey colour, with a chalky-white centre. From the edge of this central disc four large arteries emerge at right angles to each other and extend to the periphery. A rosette of long semi-transparent nerve fibres radiates from the disc.

Heterodon madagascariensis (Sharp-nosed snake).—The fundus is pale brick red, mottled all over with pale brown spots. Disc very large, white, with a black pigmented centre, about a third the diameter of the disc. This is most probably the vestigial remains of a pecten which has become lost for want of use. Three well-developed arteries emerge from the edge of this functionless pecten, and a very large vessel (vein or artery ?) enters or emerges from the disc close to it. It is impossible to tell by means of the ophthalmoscope whether these vessels are veins or arteries, as, unlike the vessels in the Mammals, they all have a bright scarlet colour. The only difference is in the size, as one of the vessels (presumably the vein) is usually two, three, or sometimes even four or five times the size of the remaining vessels. All the vessels, both veins and arteries, have a wide central lumen. In this snake the nerve fibres are very faint and inconspicuous.

Tropidonotus piscator (Indian river-snake).—Fundus a pale pink, covered with dark grey dots. Three vessels, probably arteries, emerge from the edge of the pecten. This latter is bright red, and forms a cushion which fills the central third of the disc. It is covered with a small amount of black pigment. Whether it is an active organ or not I cannot be certain. The disc is light grey, and exceedingly large, being at least three times the diameter of the human disc, *i.e.*, nine times as large as ours (!)

Naia tripudians (Indian cobra).—Disc brownish pink, faintly mottled with dark grey spots. Disc very large, round, and has an abortive pecten-like growth occupying its central third. It is irregular in shape and nearly flat. It is covered with pigment but obviously functionless. From its upper border two vessels arise which proceed towards the periphery of the retina. At the lower part of the pigment patch an immense vein (?) enters the disc.

(3) Boidæ. *Boa constrictor* (Common boa).—Fundus is a brilliant light red, very faintly mottled with a slightly deeper shade of red. The disc is exceptionally small, and horizontally oval. It is surrounded by a white ring. Five or six small white discs are arranged round the inside of the parent disc. Each has a small black dot in the centre. I have no idea as to their function. I have never met with anything in the least resembling these small discs. There is no trace of a pecten. Three very thin vessels emerge from the inside of the disc, and proceed to the periphery. Fine opaque nerve fibres radiate outwards.

Python molurus (Indian python).—A full grown specimen. The fundus is light Indian-red, faintly mottled. The disc, like the Boa's, is very small, round and mottled with yellowish patches. There is not the slightest trace of a pecten, or, indeed, of any pigment on the surface of the disc, except a single small white disc, having a central black dot, similar to those just described in the Boa's eye. Three minute vessels, probably arteries, emerge from the upper part of the disc, but they entirely disappear a very short distance from it. A small vein (?), but considerably larger than the arteries, enters the lower part of the disc. This eye is remarkable inasmuch as it shows a considerable number of well-defined choroidal vessels along the upper part of the fundus some distance above the disc. That they are choroidal vessels is evident from their deep orange colour, their characteristic branching, and from the fact that the nerve fibres can be seen spreading over them.

(5) Shape and Colour of the Disc.

In the Amphibia the disc shows much greater variety than in the Reptiles.

(1) Urodela (*Salamandra maculosa*).—This animal exhibits the simplest, and apparently the most primitive condition of the disc. It is quite round, and very small, being only

about a third or a fourth that of the majority of the Anura. It is dull white in colour, and is not covered by anything, nor is there pigment or differentiation of any kind, nor the slightest trace of any vessels, either hyaloidean or discoidal.

(2) Anura.—The disc of the Anura is bisected vertically by the main hyaloid vessel into which the chief branches enter, and is known as the *vena media*. The Hylidæ possess the usual round disc, whereas the Bufonidæ and Ranidæ have a long vertical disc resembling a broad white worm, its length being from five to ten times its width. It is placed almost exactly in the axis of vision. The disc in the Bufonidæ differs from that in the Hylidæ in being shorter and more irregular in outline. The difference between the round disc in the Hylidæ and the long disc in the other two families finds a striking analogy in the Sciuridæ, where we find a round disc in the Flying Pteromys, but ribbon-shaped and stretched horizontally across the fundus in every one of the ordinary Squirrels and Marmots.

The colour of the disc in Anura is almost invariably chalky white or light grey, but this colour is often obscured by a dark grey pigment, or even black, as in *Bufo marinus* (Giant toad). In none of the Anura does the pigment cover the whole disc, as is the case in the majority of the Reptiles and Birds, the margin being free from pigment. This pigment merely spreads over the disc in a thin layer.

Reptilia.

Prosauria (*Sphenodon punctatus*).—The disc of this animal, the lowest of living Reptiles, forms a narrow oval, about three times as long as it is broad, the long axis being directed downwards. It is the smallest disc of any animal that I have examined, being only half the length of the human disc, and about two-thirds that of the Salamander's disc, and a fourth of its area. There is no trace of a pecten, or even of pigment. It is quite possible that the pecten had not commenced to be evolved in these primitive Reptiles. Unfortunately, it is the only living representative of the Prosauria, so that we have nothing to guide us in this matter.

The nerve fibres spread out across the fundus like a fan, starting from a grey streak which passes down the centre of the disc, resembling a person's hair parted in the middle. Above and below the fibres are very sparse.

Chelonia.—The disc in these animals is circular, often with an irregular wavy or crenated border. The disc is often covered with a layer of pigment, which may be light or dark, particularly over the central area, of a radiate appearance like a star-fish. In *Chelonia longicollis* (Long-necked chelodine) I noticed some heaped-up pigment covering the centre of the disc, which appeared to me to be the vestigial remains of a pecten, and in *Emyda granosa* (Burgoma river-turtle) in the centre of the disc there was a short blind and bloodless vessel (see Plate 21). I have observed a similar vessel attached to the centre of the disc in several of the lower mammals, especially among the Rodents (Alactaga, Castor, Agouti, Gerbille). In the diagrams of the primitive and retrograde forms of the pecten at the end of my work on the "Mammalian Eye," one will at once perceive the significance of such a vessel in such a position.

Crocodilia.—The disc of the Crocodilia undoubtedly shows a relationship to that of the Chelonia, but in the Crocodiles we see the pigmentation covering the disc has become decidedly more marked, and is already approaching the condition of a pecten, although much too primitive to be functional. The pigment overlying the disc entirely covers a large number of exceedingly short and fine imperfectly formed vessels, which give the surface of the disc a mossy appearance. This is better developed in the Crocodiles than in the Alligators. In the former the pigment is dense black and the pigmented vessels so matted together as to leave no interstices, whereas in the Alligators the structure appears to be more completely formed, so as to bear some resemblance to a functional pecten of a primitive type.

Lacertilia.—A further advance in the same direction is to be found in the Lacertilia. Throughout this immense group this vascularized pigmented structure has at length apparently become an actively secreting organ, which projects forwards (usually in the form of a cone) right into the vitreous. But although the pecten is invariably present throughout the Lacertilia, there are no traces of blood vessels to be seen anywhere throughout the fundus. It is only when we come to the Ophidia, the highest and most specialized group of the Saurian stock, that the first signs of blood vessels begin to appear.

Ophidia.—The Ophidian disc is invariably round, or nearly so, but it varies immensely in size. Thus the disc of the Mocassin snake (*Tropidonotus fasciatus*) is at least nine times in area that of the huge adult *Boa constrictor*. The disc of the latter is only about a third of the area of the human disc, whereas the former far surpasses in area the disc of any other order among the Reptiles, and if we consider only round or oval discs, it surpasses in area that of any Vertebrate; even those belonging to the huge eyes of the Cetacea, which occasionally measure as much as 20 inches in circumference!

Every Ophidian disc which I have examined is white or light grey, excepting the Boidæ, in which the disc may be pink. In those discs in which there is no trace of a pecten or pigment, the central portion of the disc is dazzlingly white, which makes the grey part of the disc a deeper shade by contrast. In *Naia, Heterodon, Tropidonotus,* the central third of the disc is heaped up with black pigment, which forms a low smooth cushion, and not irregular and mossy like the pigment deposits in the Crocodilia. This pigmentary deposit is probably a vestigial relic of the true Lacertilian pecten. In certain closely allied forms, however, *e.g.*, *Tropidonotus fasciatus*, *Coluber guttatus* (Corn snake) the disc has no trace of pigment. In Boidæ the pigment is entirely confined to a few round spots of black pigment placed around the margin of the disc. These spots are always surrounded by a white area. Nothing has been suggested as to their purpose and morphological signification. Blood vessels are invariably present in every one of the Ophidia. These vessels are often of remarkable size, especially the vessel which passes vertically downwards and enters the disc at its lower margin. All the vessels either enter or emerge from the disc, and do not merely pass over it, as is the case in all the Anura.

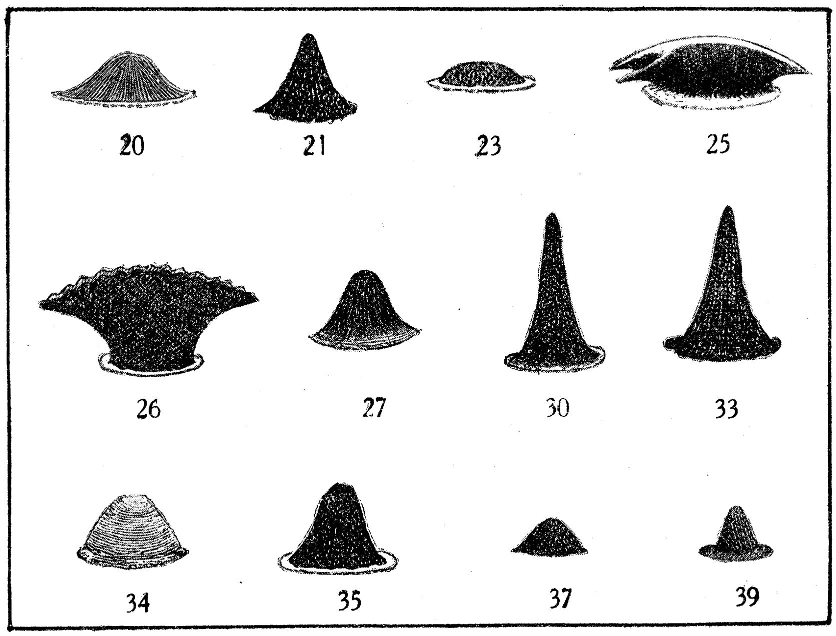
It is remarkable that, so far as my present observations go, each of the main groups of the Reptiles and Amphibia can actually be diagnosed by the condition and form of their discs, the characteristic features being the shape, the presence or absence of pigmentation, the presence or absence of the pecten, and of the blood vessels. When the blood vessels are present, we find a large median vessel with independent lateral branches, all of which either enter or leave the disc (Ophidia), or a complete vascular supply, which passes in front of the disc and retina along the hyaloid. It will also be clear that most of these characters present cases of convergent analogies, not blood relationship or true homologies in the various groups, *e.g.*, the vascularization of Anura and snakes, the lens-shaped disc of the *Sphenodon* and various Anura, etc.

(6) The Pecten. (See accompanying figures.)

No trace of a pecten can be found in any Amphibian eye, unless we choose so to call the patch of grey pigment which is very commonly to be seen spread over the greater part of the disc of the Anura and Salamanders. But this light grey pigment is quite different in appearance from that which begins to assert itself in the various families of the Chelonia. In the Amphibia the disc merely appears as if it had received a wash of grey paint. There is no heaping up of pigment as one observes for the first time in *Chelodina longicollis*. There is no trace of vascularization, which one also meets with for the first time in *Emyda granosa* (Burgoma river-turtle), or any sign of differentiation. In some of the Ranidæ which form the highest family among the Amphibia (as, for example, in *Rana catesbiana*), the pigment coating is certainly black and not grey, but even then it is impossible to associate it with either a vestigial relic or the commencement of a pecten. The fact that one never finds a pecten in any eye which is provided with either retinal or hyaloid blood vessels, unless it is a mere vestigial relic, such as one frequently meets with in certain families of the Marsupials and very occasionally among the Rodents (*e.g.*, Agoutis), seems sufficient reason for doing so. Moreover, if we trace the growth of the pecten from its source, we find a gradual increase in the amount of pigment and fine blood vessels or capillaries, which at first form tiny functionless loops, become more and more enveloped in pigment, and as they progress form first a mossy cushion, as in the Crocodilia, and then as they fill up with secreting cells they coalesce, and thus prepare the way to form a prominent functional pecten which occupies the greater part of, or the whole of, the disc, and ultimately protrudes far into the vitreous.

This we find, first of all in the Geckos, and better developed in the next higher group, the Lacertæ, which have a perfectly active pecten, although often of a still somewhat primitive form. In the Iguanidæ the pecten becomes more complex, by being crenated or folded, which gives it an increased secreting area, as we find to be the case in the Alligator Lizard (*Anolis alligator*). Finally, it undergoes dichotomous division (Black Iguana, *Metopoceros cornutus*).

The Iguanidæ have undoubtedly the highest and most developed form of pecten of any reptile which I have examined, and, indeed, the pecten of *Conolophus cristatus* (Galapagan Iguana) bears a strong likeness in its fan-shaped form and crenated margin to that of the American Coot (*Fulica americana*), *vide* fig. 84 in Dr. Casey Wood's Atlas ('Fundus Oculi of the Birds'). In like manner the pecten in all the Geckos' eyes bears a remarkable likeness to that of the Apteryx, which is figured in my former work on the "Mammalian Eye" previously quoted. As a rule, however, the Birds have a pecten which exhibits a far greater complexity of structure, becoming vastly more convoluted than any pecten one meets with among the Reptiles. These convolutions afford a far greater secreting surface than can possibly be obtained from the simple cone-shaped pecten of the Reptilian eye.



20. *Pachydactylus.*	21. *Hemidactylus.*	23. *Anolis.*	25. *Metopoceros.*
26. *Conolophus.*	27. *Ophisaurus.*	30. *Lygosoma.*	33. *Lacerta.*
34. *Egernia.*	35. *Macroscincus.*	37. *Pygopus.*	39. *Chamæleon.*

Side views of pecten in various genera—numbered to agree with figures on Plates 20 to 25.

Although the Ophidia are the most highly specialized branch of the Reptiles, they have either no pecten at all, or, if present, a very degenerate form; in other words, a mere vestigial relic. This may be accounted for by the fact that the blood vessels of the optic nerve, which divided up into capillaries and supplied the pecten, are now more profitably employed in supplying the retina instead.

I have briefly referred to a small cæcal bloodless vessel springing from the otherwise naked disc in the *Emyda granosa* (Burgoma river-turtle). This projects forward towards the vitreous. The exact nature of this blood vessel or lymphatic is uncertain; it may be the vestigial remains of an artery, or CLOQUET'S canal, just as we find in certain of the Marsupials and Rodents (*vide supra*), or it may have some relation to the permanent ligament which stretches from the disc to the posterior capsule of the lens, as in some of the Cervidæ. (See Plate 28 in my Mammalian work previously quoted.)

Along with the reduction of this central structure we find, as if to compensate for its loss, a development of numerous minute vessels covered with pigment, which give rise to a moss-like structure, which covers the greater part of the disc in the Crocodilia. This is the next stage towards the formation of the pecten, and is typical of the Lacertilia, in which the central vessels of the disc form a densely branched framework of minute vessels entirely covered with black pigment. This we have already described as forming a cone which projects far into the vitreous. The whole process of the formation can be seen at a glance in the previously mentioned plate (Plate 28), in the various species of the Kangaroos, in the Perameles, and among the Rodents in the Agoutis, in which family a perfect conical pecten can be seen with the ophthalmoscope, or quite readily with the naked eye in a spirit specimen, which has been opened.

As previously mentioned, the highest development of the pecten in the Reptiles occurs among the Iguanidæ (see especially *Conolophus* and *Metopoceros*), which show the first commencement of a definite plication, which becomes transformed into an organ of great beauty and perfection in the Birds. It may be worth mentioning that we find this conical primitive pecten in the Ostrich, and particularly in the Apteryx, in which owing to degeneration or other cause we find it even less highly developed than among many of the Lacertæ. Whether the size of the pigment cone has any direct relation to the night or day habits of the animal, I have been unable to decide, for want of sufficient material.

Ophidia.—As the Ophidia have all a retinal circulation, although an imperfect one, one could not expect to find a pecten, or, to be more exact, a functionally active one. And that is the case. Thus, in *Coluber guttatus* (Corn snake), *Tropidonotus fasciatus* (Mocassin snake), and *T. natrix* (Common European snake) we find no trace of pigment, the disc being quite naked. The Boidæ likewise have no trace of a pecten, for the few scattered pigment dots seen near the margin of the disc have apparently nothing in common with a pectinate relic. In certain other families an imperfectly formed and obviously functionless pecten vestigial relic can be clearly seen. Thus, in *Naia tripudians* (Indian Cobra) a large black mossy-looking patch, somewhat raised, may be seen in the centre of the disc. A similar but smoother one exists in *Heterodon madagascariensis* (Sharp-nosed snake) and a more developed brownish disc is met with in *Tropidonotus piscator* (Indian river-snake). I imagine that these Ophidia have arrived at this condition through atrophy from disuse of pectinate structures. Their descent from Lacertilia-like creatures makes this view plausible. Further, in favour of this view, arguing from the Mammals by analogy, the direct central hyaloid supply by pectinal vessels is rendered unnecessary, owing to the existence of a retinal supply of vessels in the Ophidia, and a system of hyaloid blood vessels in the Anura, in the same way as Mammals have lost their pectinal supply of vessels, and with them their pectens, through the formation and, generally speaking, high development of their retinal system of blood vessels.

This theory, that one kind of supply has been superseded by another in the Reptiles and Mammals, is of great interest from a morphological and physiological point of view, although one can hardly dare to base any phylogenetic conclusions on so frail a foundation. The eye, although it affords considerable contributory evidence, does not unfortunately allow us to draw any conclusions as to the descent of the Mammals, either from the Amphibia or the Reptiles. Within the same groups we find a struggle between the development of the pecten and that of a retinal vascular system. It is possible that a highly developed pecten is the more suitable organ for animals requiring excessively rapid accommodation, such as we find in the Birds, which have to adapt the focus of the eye from infinity to an inch or so in the fraction of a second, while the vascular form of supply is more suited for embracing a wide expanse of view while requiring a much less active accommodation; but I only throw this out as a suggestion.

Lastly, the very primitive condition of the fundus of *Sphenodon* is remarkable. The entire absence of all traces of the pecten, which is so largely developed in Reptiles, points strongly to the supposition that the pecten did not exist at all in the older groups of Reptiles, but was formed at a later stage during the development of the Reptilian eye, and reached its highest and complete development as a perfect organ in the Birds. In the lower mammals, which seem to claim affinity as the direct descendants from the Reptilia, we find retrogressive traces of the pecten in the Marsupials and certain Rodents, notably in the Agouti family, among which we may see the final traces of a nearly or quite functionless organ.

(7) Vascularization of the Fundus.

As the vascularization of the fundus has been very minutely described by Hess, Schleich, and a number of other writers, I shall merely describe it so far as necessary to elucidate the connection between the vascular systems and the hyaloid artery and pecten.

The Anura show no traces of blood vessels in the retina itself. There are, however, many large hyaloid vessels and peripheral vitreous vessels, both arteries and veins. The chief characteristic of their vascular supply lies in a very large *vena media* which passes vertically downwards over the fundus. This vessel is fed by a large number of lateral branches which pass horizontally across the disc.

In the Urodela there is not the faintest trace of a vessel. In the lowest living Reptile (*Sphenodon*) there is likewise no trace of vessels, but the commencement of a vascular system in the small network of capillary vessels which are restricted to and cover the disc more or less completely, which usually takes the form of a capillary network. These vessels are restricted to the disc, where they are fully developed and clothed with secreting pigment cells. They project forwards, forming the organ known as the pecten. In the Trionyx genus, *Emyda*, I found the remnant of a small hyaloid vessel which is probably the remnant of CLOQUET'S canal.

Lacertilia.—In these animals there is no trace of retinal vessels, but, on the other hand, there is a remarkable development of pectinal capillaries and actively secreting pigment cells.

Ophidia.—All these animals have an imperfectly developed retinal system of vessels, and in the Python (not in the Boa) a large number of well-developed choroidal vessels. There are always three and sometimes four vessels, all of which either enter or leave the disc, but curiously enough all the vessels have the colour and calibre of arteries and not veins. The two superior vessels are undoubtedly arteries, while the inferior trunk, which is, as a rule, much larger than any of the others, indeed often as large as all the other three put together, has been described as a vein, but on careful examination with the ophthalmoscope, one may generally see the blood corpuscles streaming from the disc towards the periphery, thus proving its arterial origin. In addition to the three (or four) main trunks, I discovered an immense number of fine hair-like branches which spread obliquely outwards from the main trunks. These minute arterial vessels are perhaps the "Vasa hyaloidea" which HYRTL described as lying in the limitans interna layer. Moreover, HANS VIRCHOW has described choroidal, retinal and hyaloid vessels as existing together in the eye of the Viper.

It is evident that we have to deal with three distinct groups of vessels, viz., (1) Hyaloid, (2) Retinal, and (3) Choroidal vessels.

(1) *Hyaloid.*—These are divided into (*a*) *Hyaloidea centralis*, which originally passed to the lens in the *Canalis Cloqueti*. This we find permanently present in many of the adult Cervidæ, *e.g.*, Reindeer, and also in the Indian Jerboa, and the Guinea-pig; and (*b*) *Vasa superficialia*. These are divided as follows :—

1. *Peripheral.*—These vessels run all over the periphery of the vitreous. They are the first to disappear in the human embryo.
2. *Discoidal.*—These vessels are entirely restricted to the area of the disc, upon which they form a special development, leading to concentration and specialization of,
3. *Pectinal*, which are to be found in their most perfect form in the Birds, in a transitional form in the Sauria, and in a still more vestigial form in a few Marsupials and Rodents.

(2) *Retinal. Angiotic and Pseudangiotic.*—These are originally vessels which come in with those of the nerve sheaths, which vessels then secondarily anastomose with the previously existing central and choroidal vessels. They ultimately form a proper Arteria centralis retinæ, the main stem passing into the substance or more often the axis of the optic nerve.

(3) *Choroidal.*—They have, like the Hyaloids, come into the eye through the Choroidal fissure. In the Mammals they still supply the retinal layers from the hexagonal pigment layer to the outer molecular layer, clearly seen in the Python and the Viper (H. VIRCHOW).

According to O. SCHULTZE (' Festsch. für KÖLLIKER,' 1892) the retinal vessels of the Mammalia are not derived from the vessels which pass through the optic nerve sheath, but from the posterior ciliary arteries. The communication between these ciliary derivatives and the nerve sheath to vitreous vessels is a secondary process. In the Anura and Snakes, some Teleostei, and in embryonic Mammals the retina is supplied from the superficial hyaloid vessels, either osmotically or directly by vessels entering the retina (Eels, Snakes). In Urodela, most Fishes, Reptiles (except Snakes), Birds, and apparently many Mammals, the retina is still entirely dependent upon osmosis from the vitreous. This itself is originally supplied by the hyaloidea centralis, superseded by peripheral hyaloids.

(8) THE COLOUR SENSE IN THE LOWER VERTEBRATES, AND THE ADAPTATIONS IN THE RETINA OF CERTAIN REPTILES AND BIRDS FOR COLOUR VISION.

The problem of the colour sense in the lower Vertebrates is an unusually difficult one. Physiologists and ophthalmologists have obtained chiefly negative results in their experiments on the colour sense in these animals, but I think I shall be able to show that the colour sense is by no means absent in any of the Vertebrata, for, as LUBBOCK remarks, " Negative results prove nothing as to the colour vision of an animal."* The majority of the experiments above mentioned were conducted by placing food along troughs or tanks and illuminating various sections of the feeding ground by means of different parts of the spectrum, and thereby ascertaining the number of animals which visited the different coloured areas in search of food.

As regards the Fishes, the results of various experimenters are very conflicting. GRABER,† one of the earliest investigators (1884), obtained only negative results. HESS, who made a large number of very carefully thought-out and quite original experiments, came to the conclusion that all fishes were totally colour-blind. WASHBURN and BENTLEY,‡ ZOLOTNITZKI,§ and REIGHARD¶ arrived at more or less the same result, although some of their experiments pointed to a slight perception of red, by the fact that the fish were more attracted to that colour than to any of the other colours, but

* LUBBOCK, ' On the Senses, Instincts, and Intelligences of Animals,' London (1888).

† GRABER, ' Grundlinien zur Erforschung des Hell- u. Farbensinnes der Thiere,' Leipzig (1884).

‡ WASHBURN and BENTLEY, ' Jour. of Comp. Neur.,' XVI (1906).

§ ZOLOTNITZKI, ' Archiv. de Zool. Expér.,' IX (1901).

¶ REIGHARD, ' Carnegie Instit. Washington,' II, p. 257 (1908).

that may possibly have been due to the increased intrinsic brightness of the red sensation. HESS* in a series of admirably thought-out papers, attributed their preference to certain colours entirely to the brightness, and not to the colours themselves.

On the other hand, we have, in the first place, the unanimous opinion of all fly-fishermen that fish have a decided preference for certain colours, and even certain definite shades or hues of colour, especially green, red, orange and various browns, which latter shades are almost entirely independent of their brightness. In the second place, we have only to visit the museums, or even the fish markets or aquariums, to see what a number of fishes have spots or patches of very bright and varied colours. As fishes have very few enemies outside their own class, it is reasonable to assume that their coloration either serves for protection or sexual attraction. But there are many cases of coloration which cannot be explained in this way, which renders the whole subject obscure and difficult of solution.

Amphibia and Reptiles.—There can be no doubt that as we ascend the scale colour perception becomes more evident, and we find the physiologists entirely in agreement as to Reptiles having some degree of colour sense. It is true they have arrived at this conclusion chiefly by food experiments, or by illuminating successive areas by different portions of the solar spectrum. As regards the Amphibia, the results are not altogether convincing, although the reddish fundus, often combined with brightly coloured dots (which details can be perceived when the fundus is illuminated by means of light from any part of the visible spectrum), affords, to my mind, ample evidence of colour perception. But it is among the Reptiles and Birds that we find positive evidence of colour perception, as I shall proceed to show. I have already referred to the case of sexual dimorphism which may be seen in the different colour of the iris in the male and female of the tortoise *Cistudo carolina*, and which points strongly to colour perception.

If we examine a Lumière autochrome photographic plate with a magnifying glass, after having stripped off a small piece of the sensitive film, we notice that the entire surface is covered with a mosaic of red, green and blue-violet dots, about the size of a human blood corpuscle. These dots are merely starch grains mechanically stained with the three primary colours. Now, as I have pointed out in my former paper on the "Mammalian Eye," the fundus is almost invariably very brightly coloured, and for the most part in two or three zones of different colours, the chief exceptions being those cases in which the fundus is of a bright red colour (as is the case in the human eye, the primates, lemures, rodents, etc.). In all these latter cases light from every part of the visible spectrum is reflected, since we can see every detail of the fundus by means of the ophthalmoscope, no matter what part of the spectrum we employ to illuminate it with. This is by no means the case in all Birds and Reptiles, since many of the latter have a grey, or occasionally a very dark brown or slate-coloured, fundus.

* HESS, 'Das Sehen der Nied. Tiere,' Gustav Fischer, Jena, in which references to his other papers will be found.

In many of the Birds and some of the Reptiles we find the retina provided with a mosaic of oil globules. These latter are tiny droplets of a highly refracting coloured substance, which are placed in regular parallel rows close to where the rods and cones penetrate the external limiting membrane, and consequently immediately in front of the sensitive layer, *i.e.*, the tips of the cones, where they receive the impact of the wave-front after reflection from the choroidal mirror. Their position will be seen to be almost in contact with the pigment-laden filaments which pass and move about between the conical sheaths which envelop the nerve terminals of each rod and cone.* It will be also noticed that these coloured drops are about four or five times the diameter of the Lumière starch grains. They form four rows—or, rather, parallel layers: first (on the outer or choroidal side) a yellow, then a red, then another yellow, and, lastly, a green row. In the Chelonia it has long been shown that there is an additional blue-violet row. Thus LUMIÈRE's brilliant invention had, ages ago, been forestalled by the Birds and Reptiles!

But why should there be invariably a yellow layer of dots? Are not the three primary colours enough? By mixing coloured lights or separate spectroscopic colours, CLERK-MAXWELL, and subsequently HELMHOLTZ, ABNEY and others, proved that the three primary colours, red, green, and blue-violet, were sufficient by mixing to produce all the various hues and tints of colour. But the perception of colour by the eye differs in one respect from the purely physical production of colours. In the latter case yellow is produced by the mixture of red and green in certain proportions. In the eye, however, yellow is a distinct colour sensation, for we can readily match a pure yellow (such as is obtained by transmitting a narrow strip of the spectrum around the D line) with a mixture obtained by transmitting a red and a green beam and superposing them. Moreover, we can certainly perceive a yellow flower, or the yellow tints of the sky at sunrise, neither of which contain a trace of green.

Lastly, I have demonstrated that the fovea and the greater part of the macula region, both in man and all the true monkeys, is of a pure canary-yellow colour. I discovered this by examining the macula through the ophthalmoscope when illuminated by light filtered through a pure spectrum-blue glass, a fact that has since been independently rediscovered by Prof. VOGT† by the same method of experiment. KÜHNE demonstrated the same thing by the chrome-alum method as long ago as 1890.

I think I am therefore justified in stating that in the eye there are four primary colour sensations, and from what I have stated above we have reason to believe that colour sensations can be perceived in a more or less perfect degree in all Vertebrate animals, although to a less degree in the Fishes than in the Amphibia and Reptiles, and considerably less in the latter than in Birds and Mammals.

* See figure in my 'Photography in Colours,' 3rd Edit., London (Routledge), 1919.

† Dr. ALFRED VOGT, "Ophth. Beob. u. die Mitbeteil. der Netzhaut," 'Klin. Monatsbl. f. Aug.,' vol. 59 (1917); also Dr. ED. KOBY, 'Rev. gén. d'Ophtal.' (January, 1920).

SUMMARY OF CONCLUSIONS.

(1) Eyelids and their Modifications.—Lacrymal Apparatus.

The eyelids in the Amphibia may be classed under six distinct types :—

(1) Imperfectly formed lids, indifferently divisible into an upper or dorsal and a ventral lid. Urodela (and many Teleostei).

(2) A primitive upper and a large lower lid, which is transparent and moves vertically upwards, forming a variety of the nictitans. In Anura this has an additional fold at the base, which is very conspicuous in *Bufo*.

(3) The lower lid is transformed into a typical nictitans, having its base shifted to the nasal corner of the eye. A second well-developed outer lid overlaps the nictitans. This is the common condition throughout the Reptiles, in all the Birds, and in some of the Mammals.

(4) The nictitans now forms a plica semilunaris, or becomes entirely suppressed, as in *Lacerta*, and many Mammals.

(5) The nictitans becomes enormously developed, fusing with the upper eyelid, the lower lid forms a mere ridge, or disappears entirely, as in the Geckos, Cabrita and Ophiops. Among the Uredela we only find movable eyelids among the Salamanders, that is, in those newts which have a temporary terrestrial life. In the true aquatic forms the lids have degenerated into mere ridges. In Proteus and Typhlomolge the eyes are completely covered up by skin.

The Anura have an upper lid, and a lower lid or nictitans which is quite transparent and moves directly upwards. It is usually ornamented along its upper border by coloured pigment.

The Crocodilia have a well-developed perfectly transparent nictitans, which moves obliquely backwards and upwards. When the animal closes its eye, the lower lid closes after the nictitans has moved across the eye. This is not the case with most of the other Reptiles. The lacrymal secretion passes behind the conjunctiva, for the purpose of lubricating its food, and therefore never moistens the eyeball.

Lacertilia.—They possess both eyelids and a nictitans. In some the lower lid alone moves. In some desert forms the lower lid has a transparent window in the middle.

In all animals which have a typical nictitans, as well as those which have only a trace of a nictitans (as in ourselves), the cornea is highly sensitive.

Chamæleontidæ.—In these animals the lids form a concentric fold which covers the greater part of the eye, leaving only the pupil free. These animals have no nictitans, and the eye is rarely closed by the lids.

Ophidia.—The outer upper and lower lids are completely reduced in the adult, with the exception of the Boidæ, which possess well-developed lids, and support the view that the false cornea is not the result of fusion of the upper and lower lids, but is merely a modified nictitans. This latter is quite insensible to the touch. The eye can be seen to move freely behind it.

(2) The Iris and Pupil.

The light intensity in all frogs and toads is remarkable, the ratio-aperture being as much as F/1·5, or more than double that of a rapid portrait photographic lens. Many of the snakes and burrowing lizards have extremely small eyes for their size, but I can assign no reason for it.

The shape of the pupil varies enormously among the Reptiles. This is not the case in any of the other Vertebrates, although the shape of the pupil in the Amphibia varies very considerably when compared with that in the Fishes, Birds and Mammals.

I find a great range of activity of the pupils as regards light in the snakes. Thus, in *Naia*, *Boa*, and various Colubrines the pupil responds rapidly to the action of light, whereas in the Grass snake and Sharp-nosed snake the pupil was entirely unaffected by light. The pupil of the Brazilian Toad was likewise unaffected, as I found the case in many other Reptiles (Chelonia, Iguanidæ). In none of the snakes did atropin or eserine have any effect. This is certainly due to the so-called false cornea shutting it off from the eye.

Colour of the Iris.

With the single exception of Man, the mammalian iris shows very little variation in colour, but in both Birds and Reptiles, and to a less extent in Amphibia, we find a surprising diversity, both in colour and pattern. The colours are most striking and varied in the Birds, and most diverse as regards pattern in the Reptiles, especially the Geckos. The Amphibia are remarkable in that they frequently exhibit irides sprinkled over with dark or brilliant colours. In most of the Anura the iris is dusted over with a golden or bronze powder resembling Japanese lacquer. In *Cistudo* we have an example of sexual dimorphism, the male having a red iris, the female a brown one.

Vertical Line and Groove.—In all Anura, but not in all the Salamanders, the iris shows a straight pigmented stripe, which extends vertically downwards from the lower pupillary margin to the periphery of the iris. Occasionally a similar stripe may be seen in the upper half of the iris as an individual variation. Among the Reptiles I have only observed this stripe in *Varanus bengalensis* and in *Iguana tuberculata*, in which latter animal it is very conspicuous. This curious formation is usually connected with a slight vertical groove, which, although often very slight, can always be recognised by the naked eye. This groove also occurs in the *Monitor*. Neither the groove nor the line of pigment extends beyond the base of the iris, and therefore ceases before reaching the ciliary processes. I have observed a similar pigmented furrow or ridge, and very often a well-marked notch as well, in a number of the British river and salt-water fishes, *e.g.*, Herring, Smelt, Trout, Cod, Carp, Gurnet, Starlet, etc. The occasional presence of a pigmented line on the opposite side of the iris indicates that the whole phenomenon started as a vertical slit, the right and left halves of the iris curtain being as it were drawn asunder, so that the muscles of the latter must have entered by the choroidal cleft. From this it would appear that this vertically slit pupil would be phyletically the oldest condition, and the round pupil the highest stage of development. The frequently occurring specializations of various shaped openings cannot invalidate this conception.

(3) Movement, Direction, and Refractive Power of the Eyes.

One should expect retraction of the eyes into their sockets to be a very common phenomenon, on account of the immovability of the head and the danger to the eyes from their approximation to the ground, but this is by no means the case. Apart from this I have observed no movement of the eyes in the Amphibia. The optic axis is much nearer to the middle line than in the Reptiles—usually amounting to about 45 or 50 degrees. The deviation of the optic axis from the median line of the body amounts to 70 degrees or more in the Reptiles. In the snakes it varies from 70 to 90 degrees, while in the *Lacerta* it often reaches 100 degrees. It will thus be seen that Reptiles possess a far greater amount of divergence than is the case in the vast majority of the Mammals, thus conforming to the general rule, which I pointed out in my former work on the "Mammalian Eye," that the lower the position in the ancestral tree the greater will be the divergence, and also the greater the range between the two extremes in the Natural Order.

In nearly all cases I found the refraction to be either emmetropic or slightly hyperopic, and only in very rare cases did I come across any marked degree of astigmatism such as one invariably finds among the marine Mammals. The power of accommodation is usually very considerable, especially among the Amphibia and amphibious Reptiles.

(4) The Fundus Oculi.

A.—*In the Amphibia.*

I have had the opportunity of examining the fundus of only a very few families of this class, as, outside the Ranidæ, Hylidæ, Bufonidæ and Salamandridæ, there are very few families to be found in any of the Gardens of Europe, and those which are represented have either eyes which are too small to be examined or they are impossible to handle. They all exhibit a fundus entirely different from that of any other Vertebrate. The first three have a well-developed vascular system, consisting of a large *vena media* with numerous lateral branches, all lying in the hyaloid membrane just in front of the retina.

In *Rana catesbiana* and *Hyla versicolor*, the lumen of the main vessel is so transparent and large that a double file of blood corpuscles can be seen with great distinctness under a magnification of 16 to 20, which the direct examination with the ophthalmoscope affords. I have mentioned in the text that these animals might be used with great advantage for physiological experiments, since every corpuscle can be watched as it travels along the vein.

The disc is long and narrow, directed vertically downwards, and to a very superficial observer it might present some resemblance to that of many of the birds, but a closer examination shows that it differs in two fundamental particulars, viz., that in the Amphibia there is no trace either of a macula or of a pecten.

B.—*In the Reptiles.*

The fundus of all the Reptiles differs from that of any other Vertebrate, with the possible exception of that of the Geckos, and that of the *Sphenodon*. The former has many features in common with that of the Apteryx, the chief difference being the presence of a macula in the latter, while that of the *Sphenodon* bears some resemblance to that of the Bufonidæ, and even to the Echidna. The great family of the Lacertidæ are nearly all characterized by a slaty-grey fundus, almost entirely covered by opaque nerve fibres, which radiate in all directions from a central circular white disc, more or less obscured by a densely pigmented pecten. The Ophidia are peculiar among the Reptiles in possessing a broad and very conspicuous system of retinal blood vessels. A few small capillaries are often seen in connection with the disc in other families, but they never reach the retina.

(5) The Shape and Colour of the Disc.

In the Salamandridæ we find a primitive white circular disc without any trace of vessels. In all the Anura, on the other hand, we find a long, vertical, rather broad disc, thus forming a striking analogy to the two forms of disc in the flying and the ordinary squirrels and marmots.

With the single exception of the Boidæ, all the Reptiles possess either a white or occasionally a dark grey disc, but never a pink one, as is almost invariably the case in the Mammals. The size of the disc has no relation whatever either to the size of the animal or to the eye. Thus the Mocassin snake has a disc at least nine times that of the huge Boa constrictor, which latter is only about a third that of the human disc in area.

No trace of blood vessels can be seen until we come to the Ophidian eye, where we find it in every one. These vessels, which either enter or emerge from the disc, are often of remarkable size. They also penetrate the disc, and do not merely pass over it, as happens with all Anura.

(6) The Pecten.

The pecten is a secretory organ (lymphatic) whose function is to supply nourishment for the inner layers of the retina and the vitreous when retinal and hyaloid vessels are absent (*cf.* p. 330 (4), A).

No trace of a pecten occurs in any amphibian eye. Although the Ophidia are the most highly specialized branch of the Reptiles, they likewise are destitute of a pecten, or, if it does occur, it is either in a very primitive or very degenerate form. It is among the *Lacertæ* that we find the highest development of the pecten among the Reptiles. In them it is usually in the form of a cone which dips into the vitreous.

(7) Vascularization of the Fundus.

The Anura show no trace of blood vessels in the retina itself, but there are large hyaloid vessels and peripheral vitreous arteries and veins. Neither in the Urodela nor in the *Sphenodon* can we find any blood vessels. In all the lower Reptiles we find a small network of capillary vessels which are restricted to and cover the disc more or less completely. These become covered with pigment cells, thus forming the pecten. It is only when we come to the Ophidia that we find an imperfectly developed vascular system in the retina. In the python we find visible choroidal vessels. In Urodela, most Fishes and Reptiles (excepting the snakes), also in the Birds and many Mammals, the retina is dependent on osmosis for its blood supply.

8) The Colour Sense in the Lower Vertebrates and the Special Adaptation in the Retina of Certain Reptiles and Birds for Colour Vision.

All the experiments made by physiologists go to show that fishes are totally colour blind, but the united opinion of all fly-fishermen tends to the opposite conclusion. In this paper the reasons for and against fishes being sensitive to colour are discussed. The writer is in favour of a certain degree of colour perception in all Vertebrates, and that colour perception increases as we ascend the scale. The use of the oil globules in the retina of certain Reptiles and Birds is explained and their close analogy with the coloured starch grains in the Lumière autochrome colour plate pointed out. The writer has further shown that this evidence is strongly in favour of there being four primary colours, and not three, as is usually held to be the case. For although, from a physical point of view, Clerk-Maxwell's three-colour theory holds good, it does not do so from a physiological standpoint. Moreover, the writer has demonstrated that the macula, both throughout the Simiæ and in Chamæleon, is normally of a canary-yellow colour, which is therefore not a mere post-mortem change, as physiologists maintain.

DESCRIPTION OF PLATES.

Plate 20.

1. *Rana clamata.*
2. *R. tigrina.*
3. *R. catesbiana.*
4. *Salamandra maculosa.*
5. *Sphenodon* (for comparison).
6. *Bufo boreas.*
7. *B. melanostictus.*
8. *B. marinus.*

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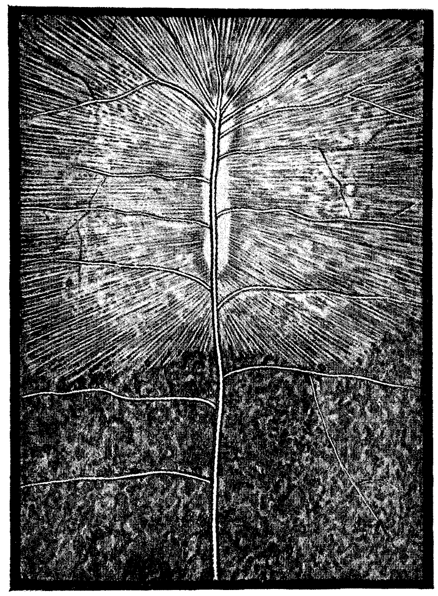

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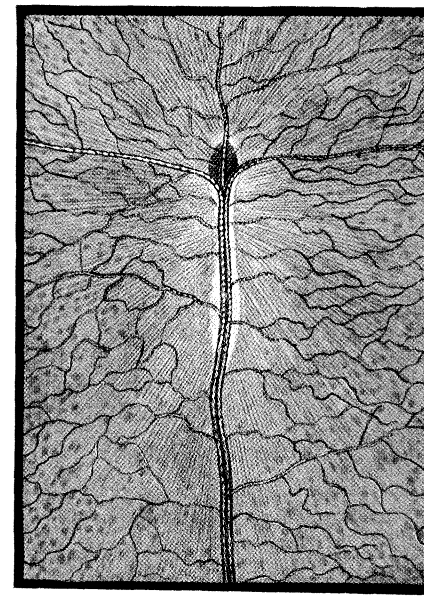

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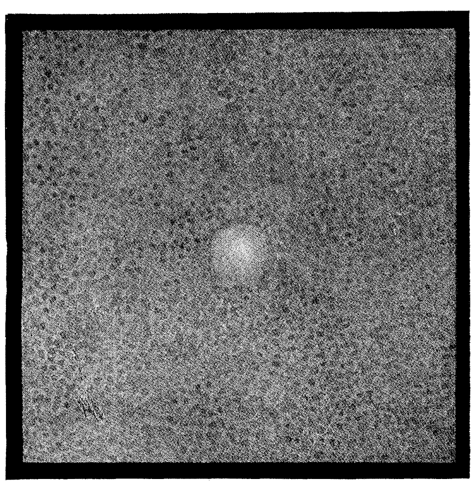

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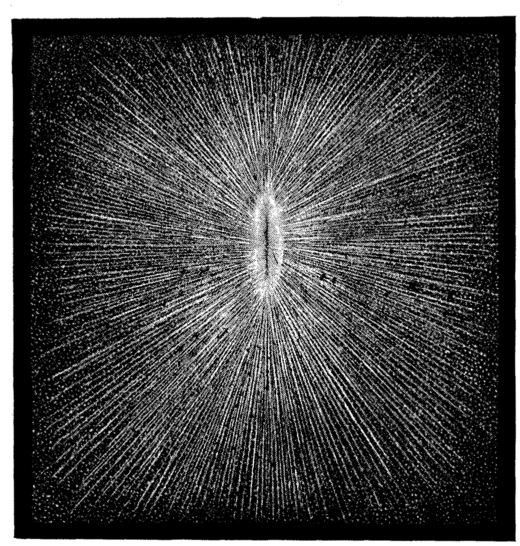

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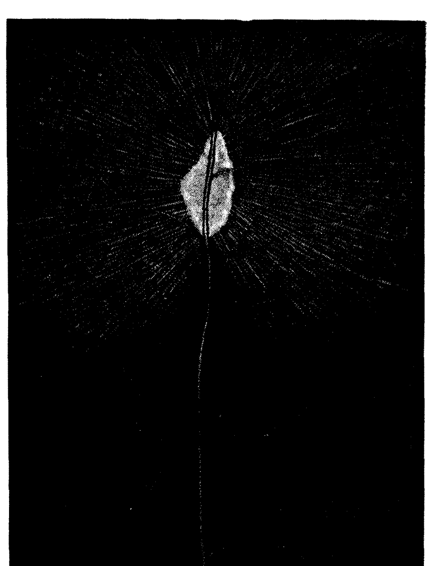

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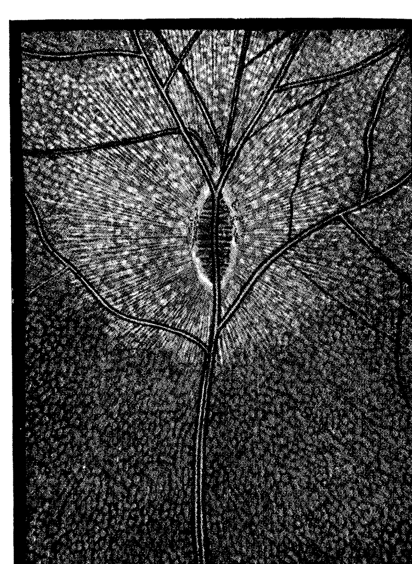

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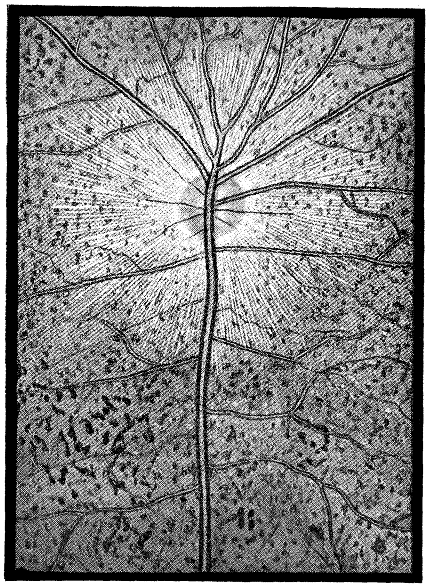

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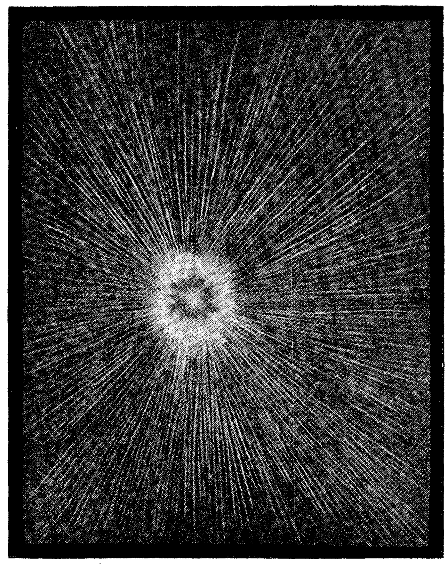

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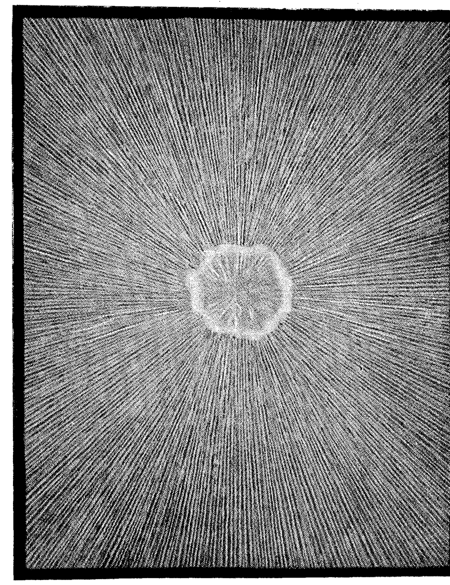

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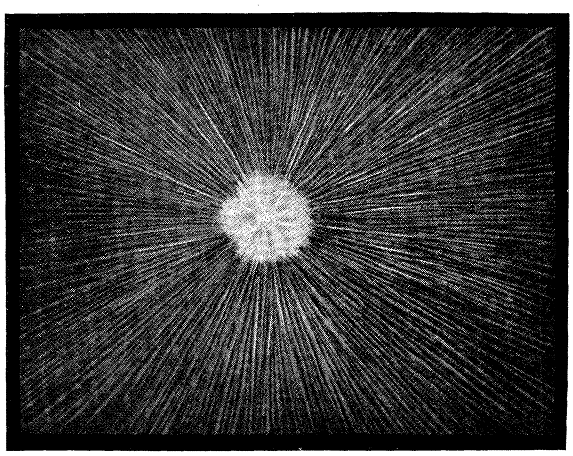

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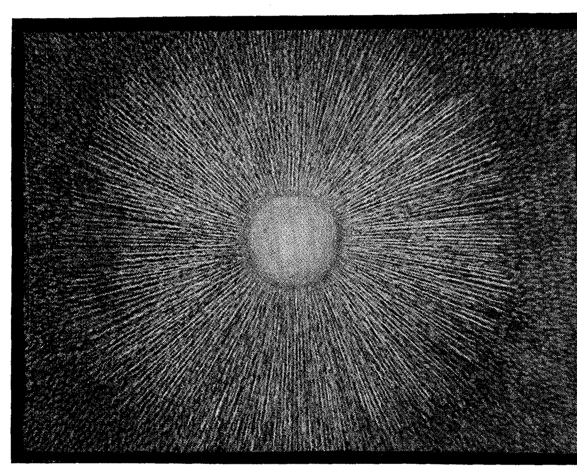

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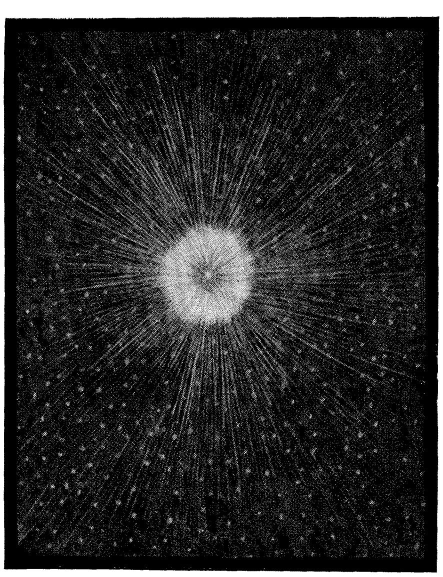

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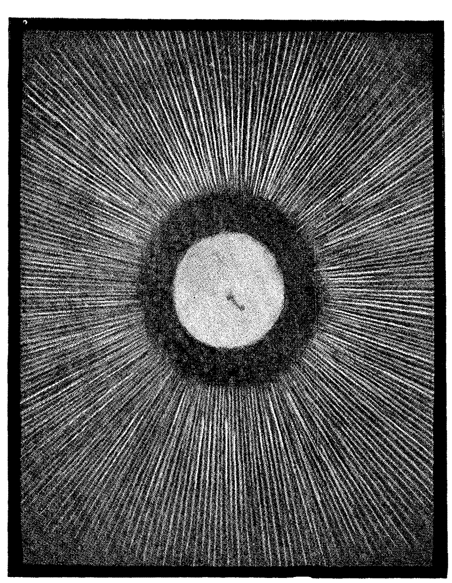

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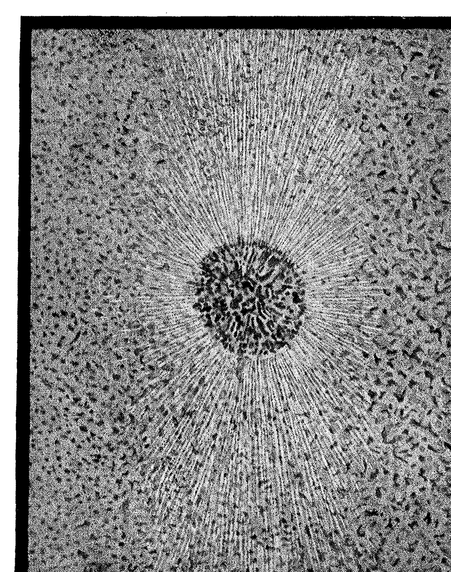

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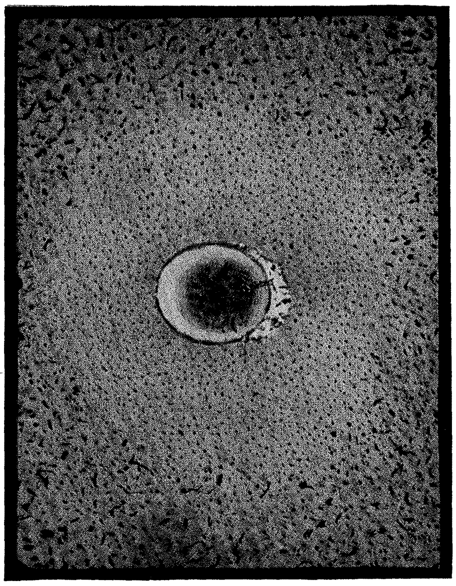

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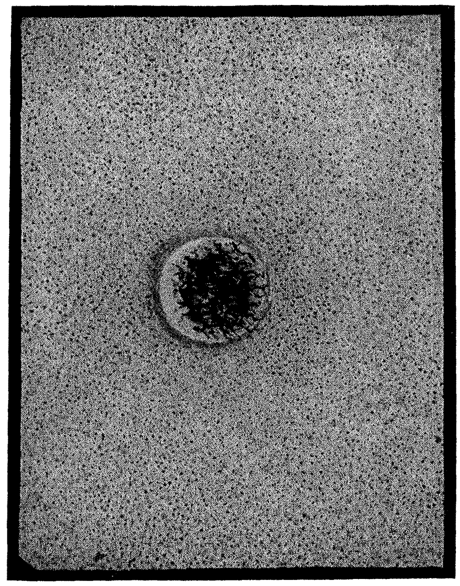

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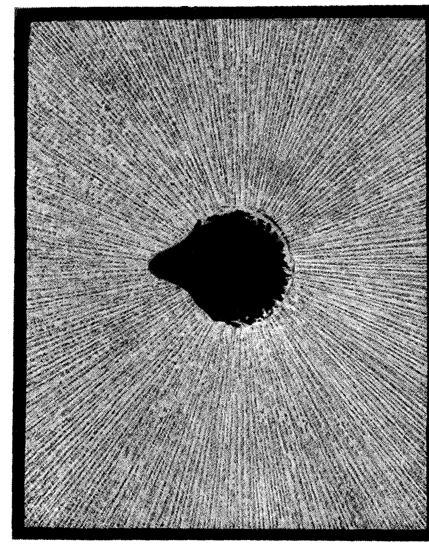

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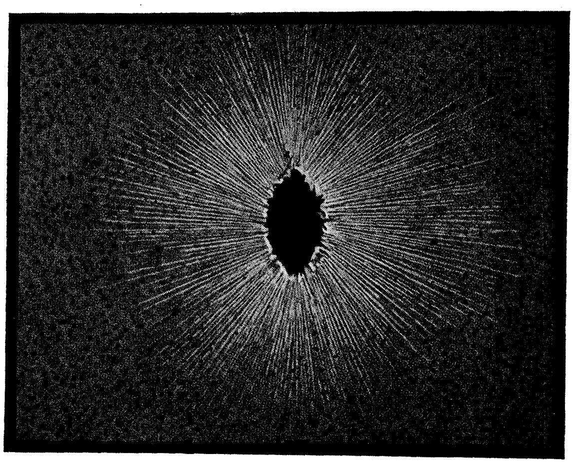

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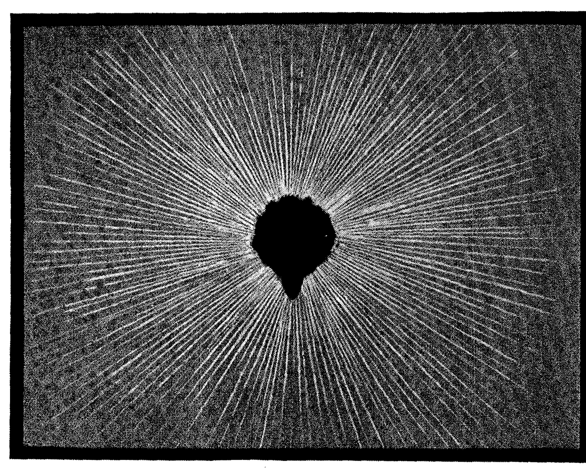

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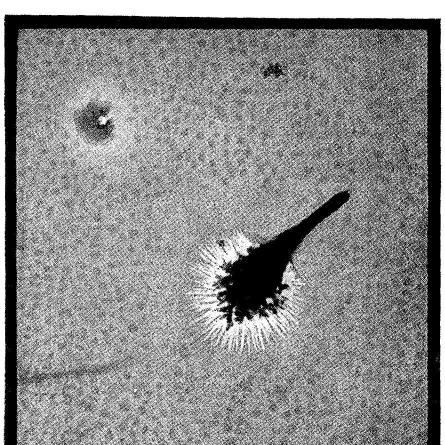

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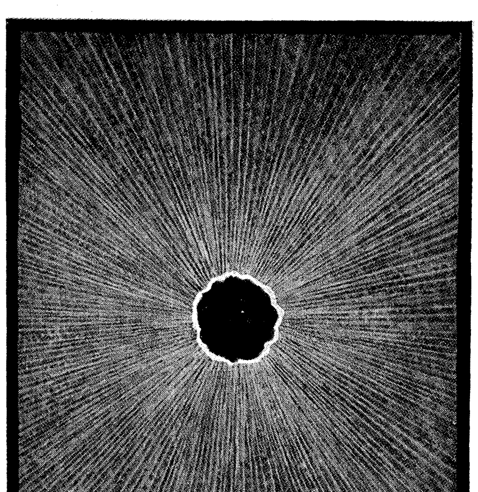

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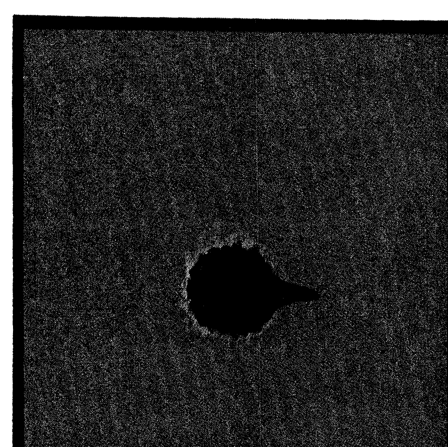

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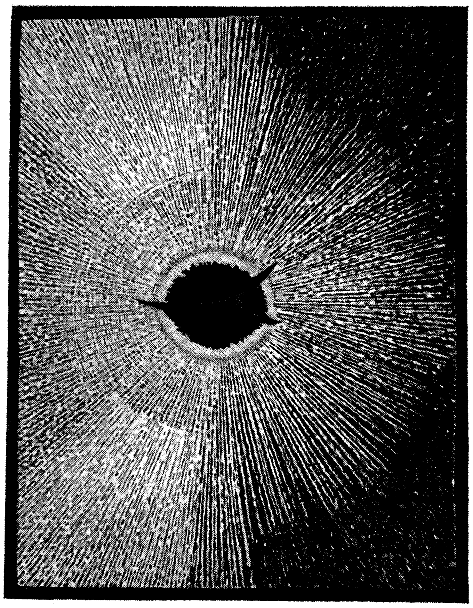
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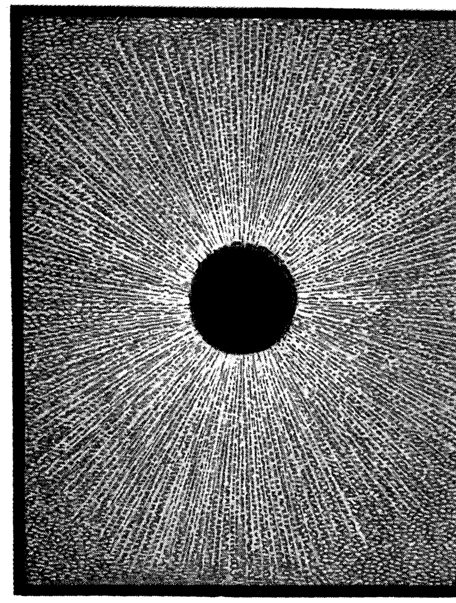
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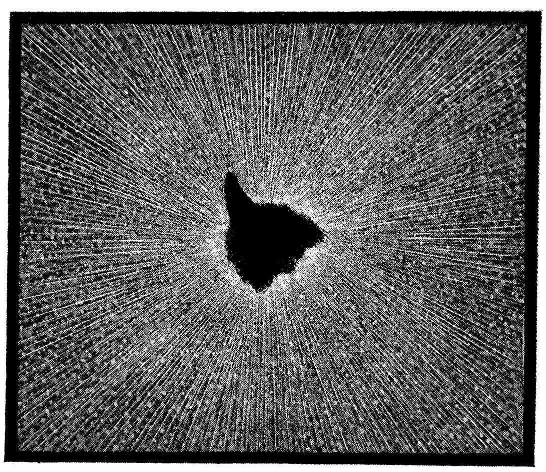
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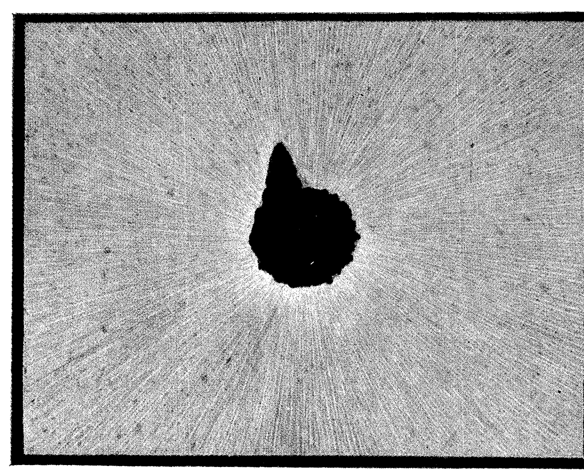
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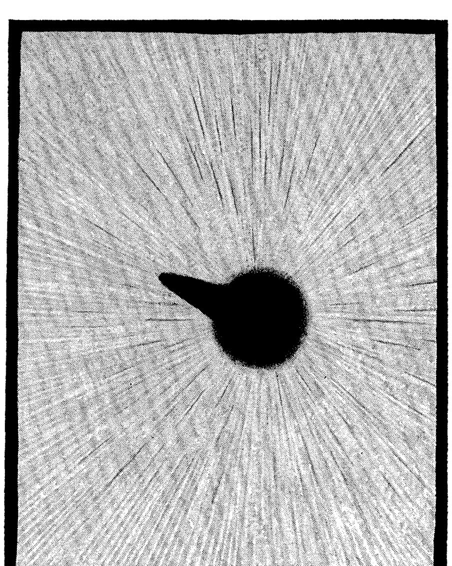
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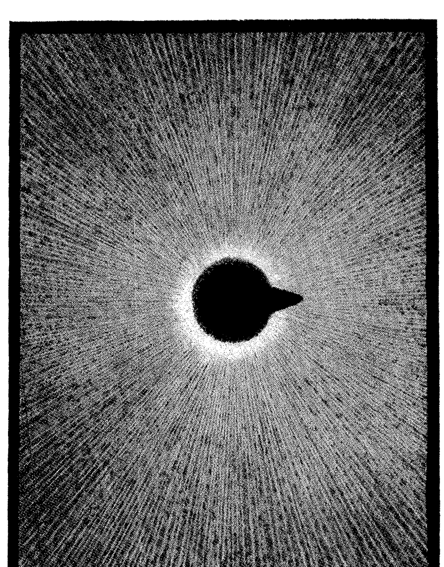
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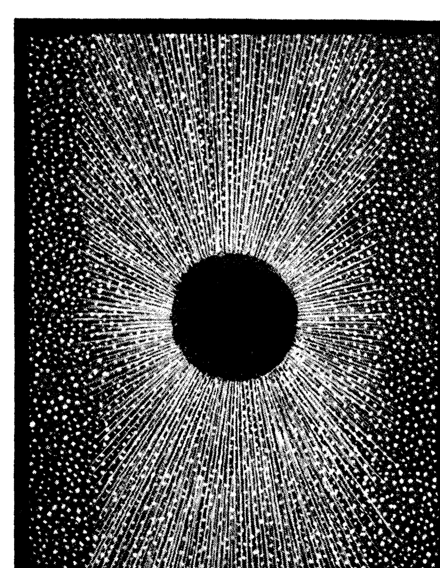
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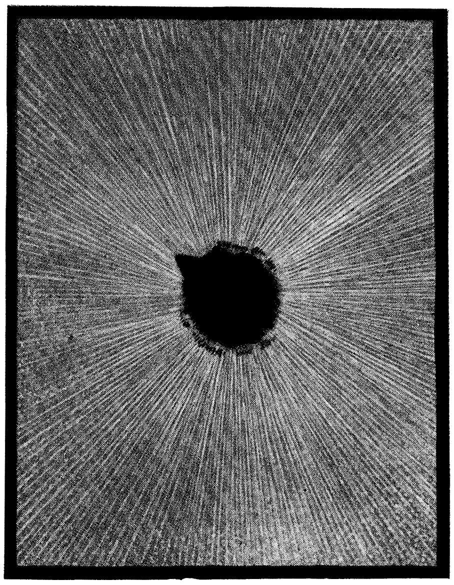

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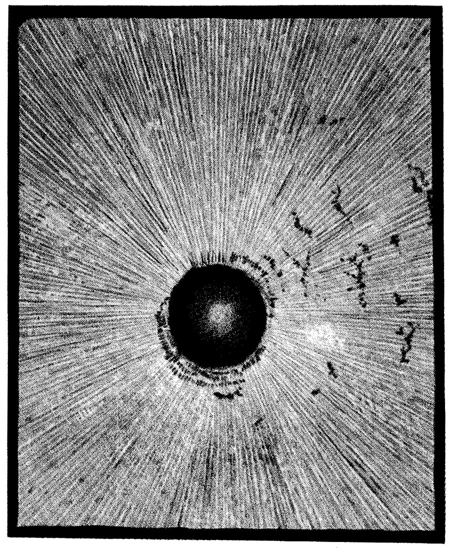

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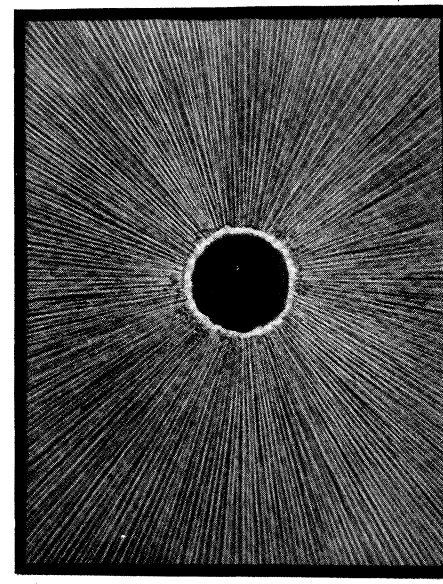

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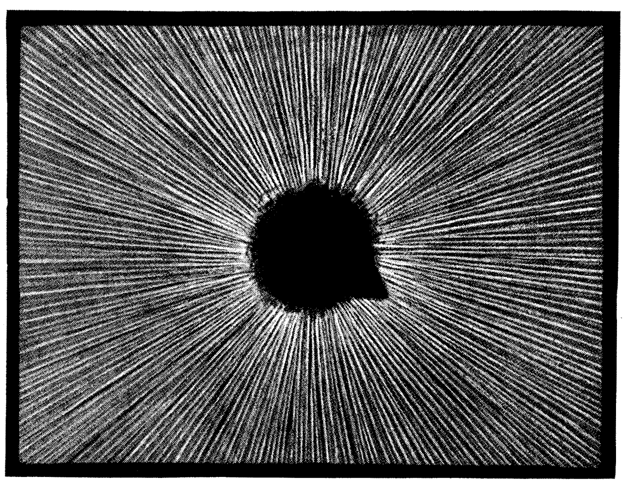

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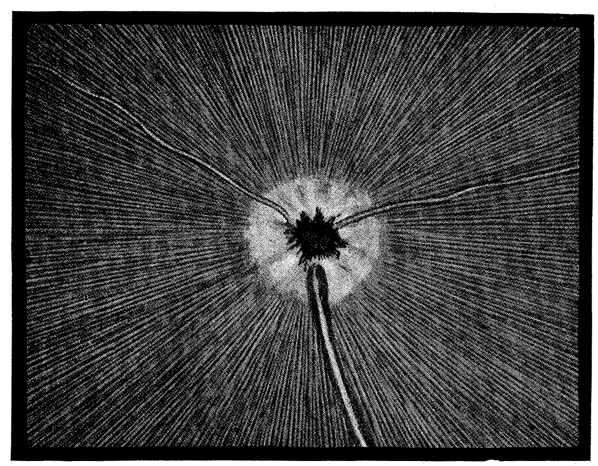

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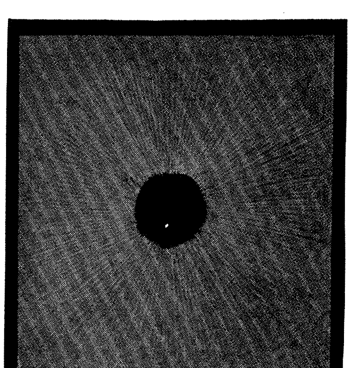

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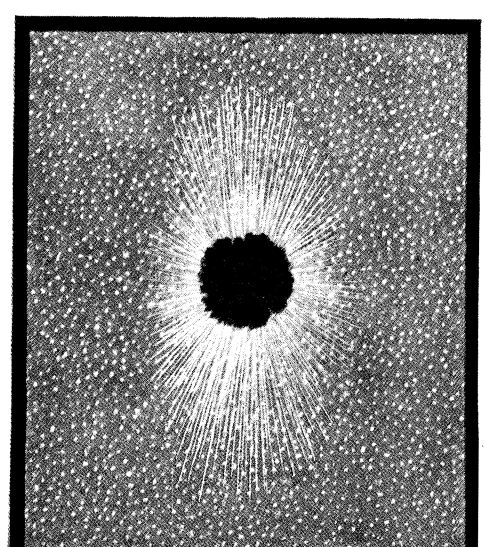

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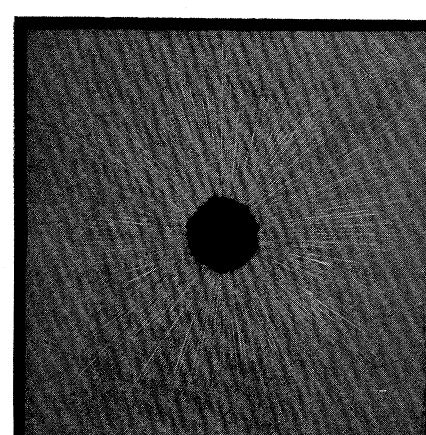

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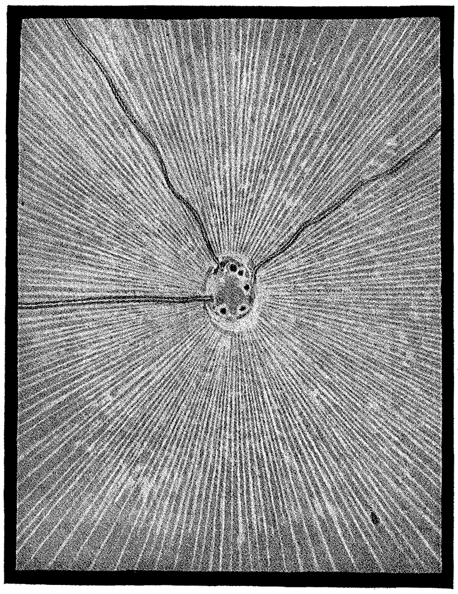

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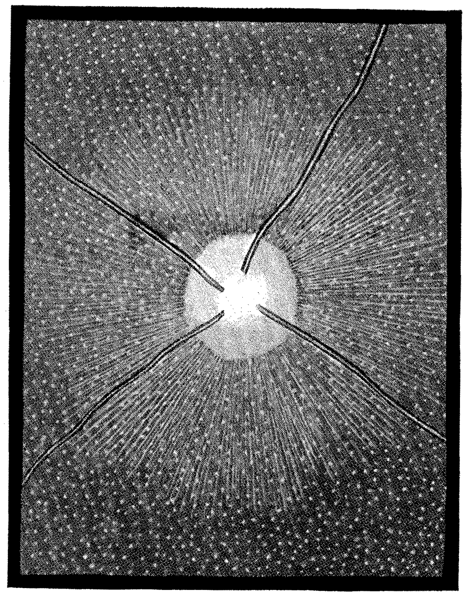

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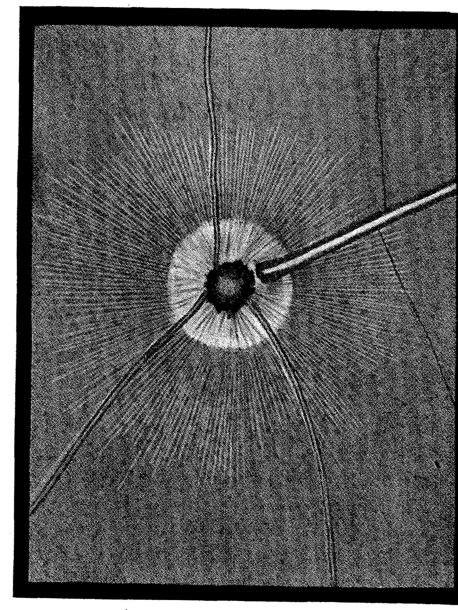

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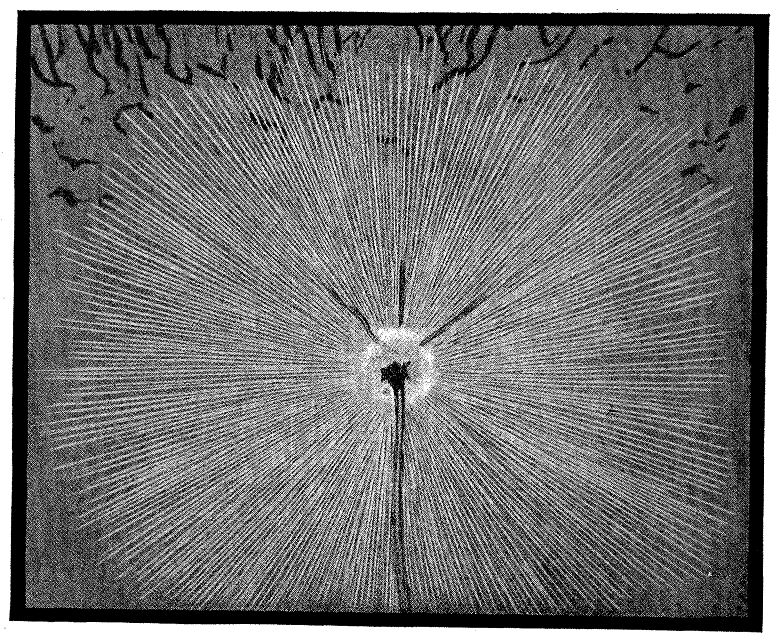

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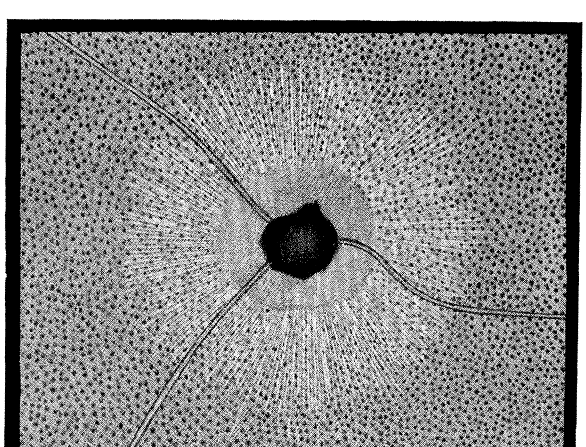

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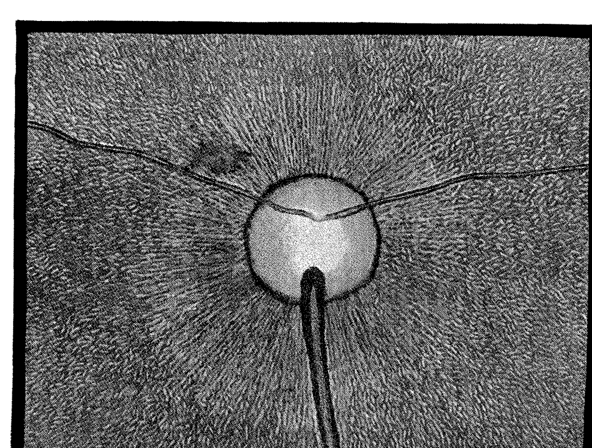

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PLATE 21.

9. *Hyla cærulea.*
10. *Chelodina longicollis.* (Turned.)
11. *Chelydra serpentina.* (Turned.)
12. *Chrysemys scripta rugosa.*
13. *Testudo radiata.*
14. *Cinyxis erosa.* (Turned.)
15. *Emyda granosa.* (Turned.)
16. *Alligator mississippiensis.* (Turned.)

PLATE 22.

17. *Alligator chinensis.* (Turned.)
18. *Crocodilus frontatus.* (Turned.)
19. *Phleuma madagascariense.* (Turned.)
20. *Pachydactylus maculatus.*
21. *Hemidactylus turcicus.*
22. *Apteryx* (for comparison). (Turned.)
23. *Anolis alligator.* (Turned.)
24. *Uroplates fimbriatus.* (Turned.)

PLATE 23.

25. *Metopoceros cornutus.* (Turned.)
26. *Conolophus subcristatus.* (Turned.)
27. *Ophisaurus apus.* (Turned.)
28. *Varanus bengalensis.* (Turned.)
29. *Varanus Gouldi.*
30. *Lygosoma Quoyi.* (Turned.)
31. *Tupinambis nigropunctatus.* (Turned.)
32. *Lacerta Galloti.* (Turned.)

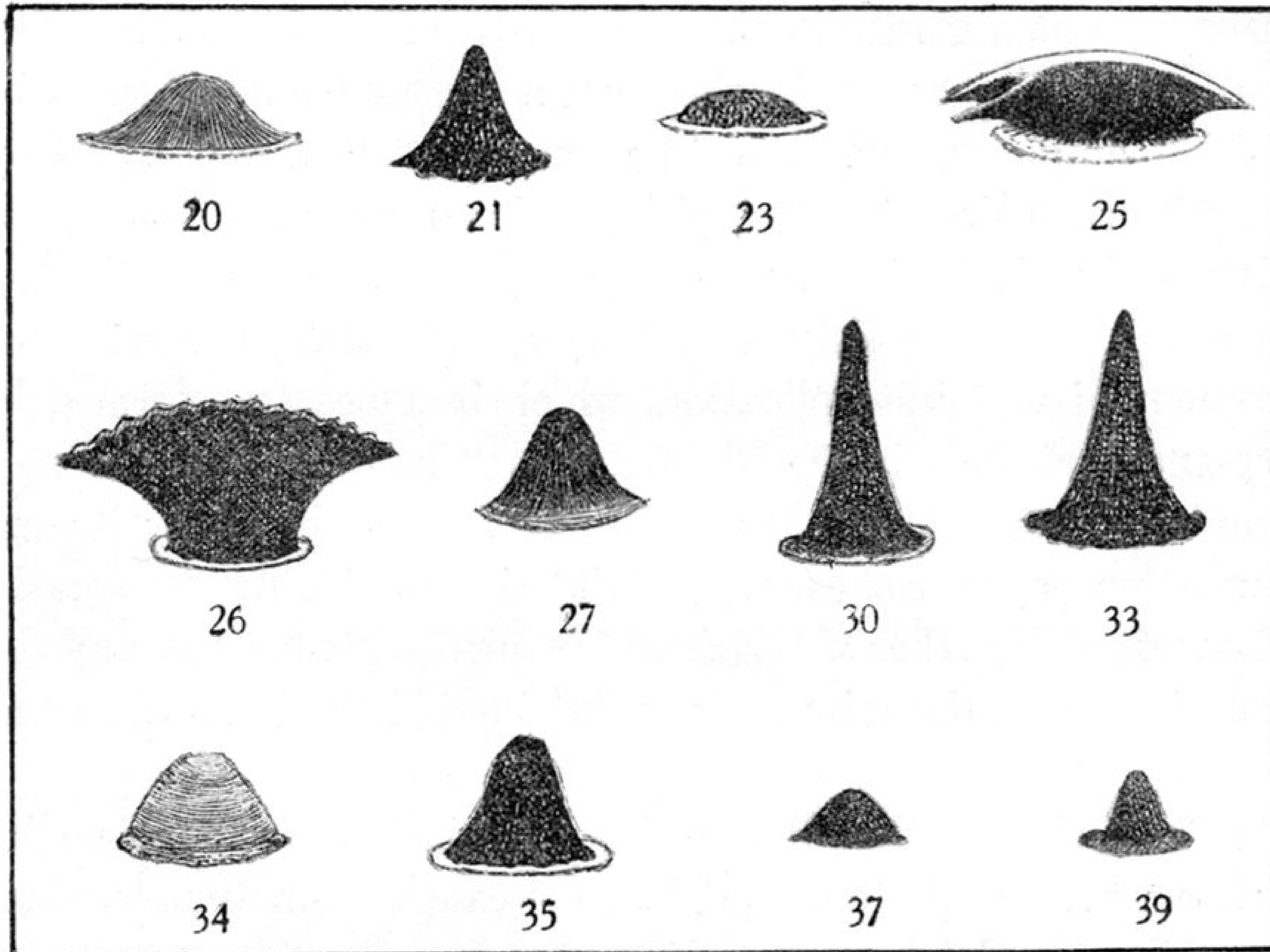
PLATE 24.

33. *Lacerta Simonyi.* (Turned.)
34. *Egernia Cunninghami.* (Turned.)
35. *Macroscincus cocteaui.* (Turned.)
36. *Tiliqua nigroluteus.* (Turned.)
37. *Pygopus lepidopus.*
38. *Chalcides ocellatus.* (Turned.)
39. *Chamæleon vulgaris.*
40. *Naja tripudians.*

PLATE 25.

41. *Boa constrictor.* (Turned.)
42. *Coluber guttatus.* (Turned.)
43. *Heterodon madagascariensis.* (Turned.)
44. *Python molurus.*
45. *Tropidonotus piscator.*
46. *T. fasciatus.*

Note.—Where the natural orientation had to be changed, to suit the page, this is indicated. All such figures have been turned 90° to the left (counter-clockwise).



20. *Pachydactylus.* 21. *Hemidactylus.* 23. *Anolis.* 25. *Metopoceros.*
26. *Conolophus.* 27. *Ophisaurus.* 30. *Lygosoma.* 33. *Lacerta.*
34. *Egernia.* 35. *Macroscincus.* 37. *Pygopus.* 39. *Chamæleon.*

Side views of pecten in various genera—numbered to agree with figures on Plates 20 to 25.

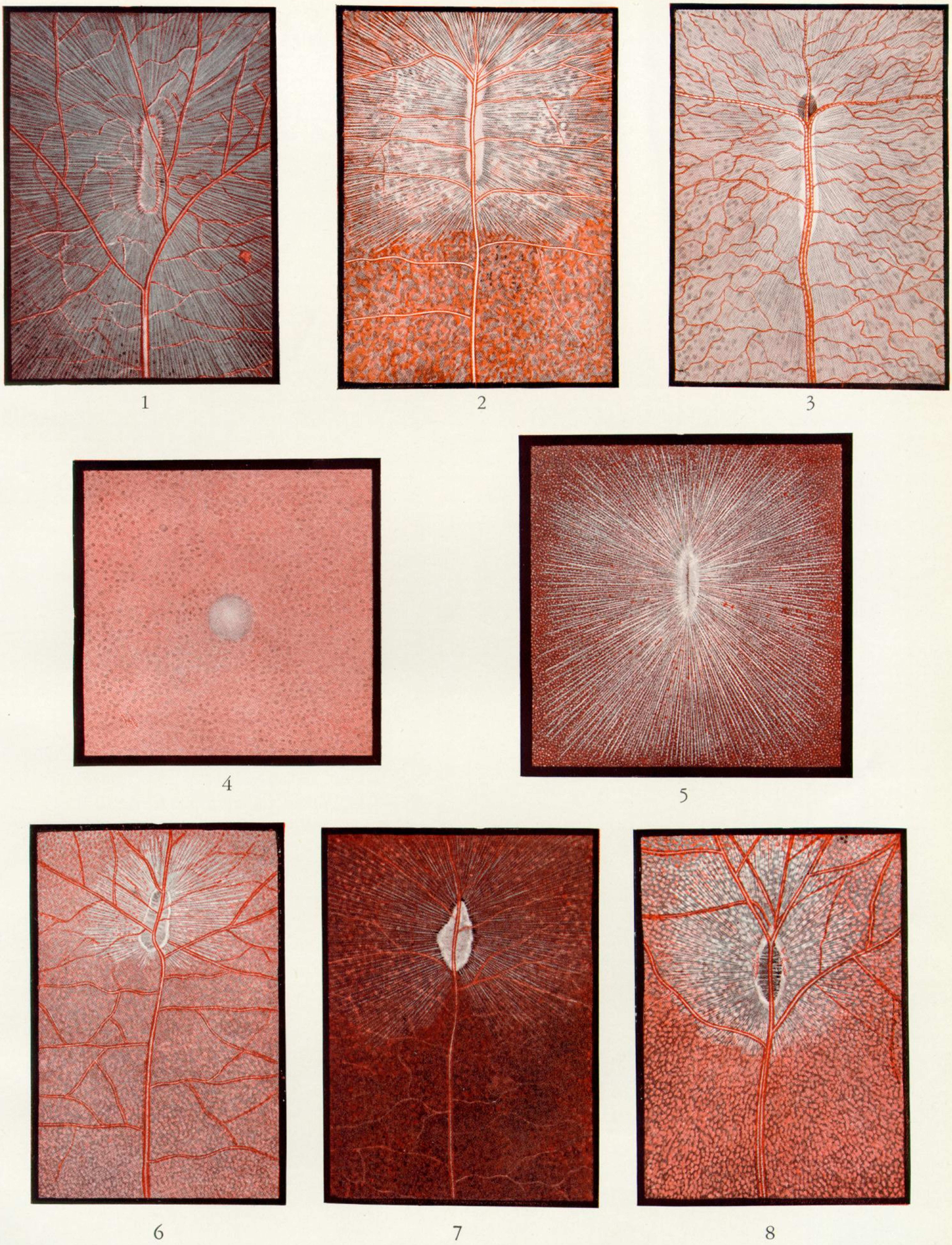
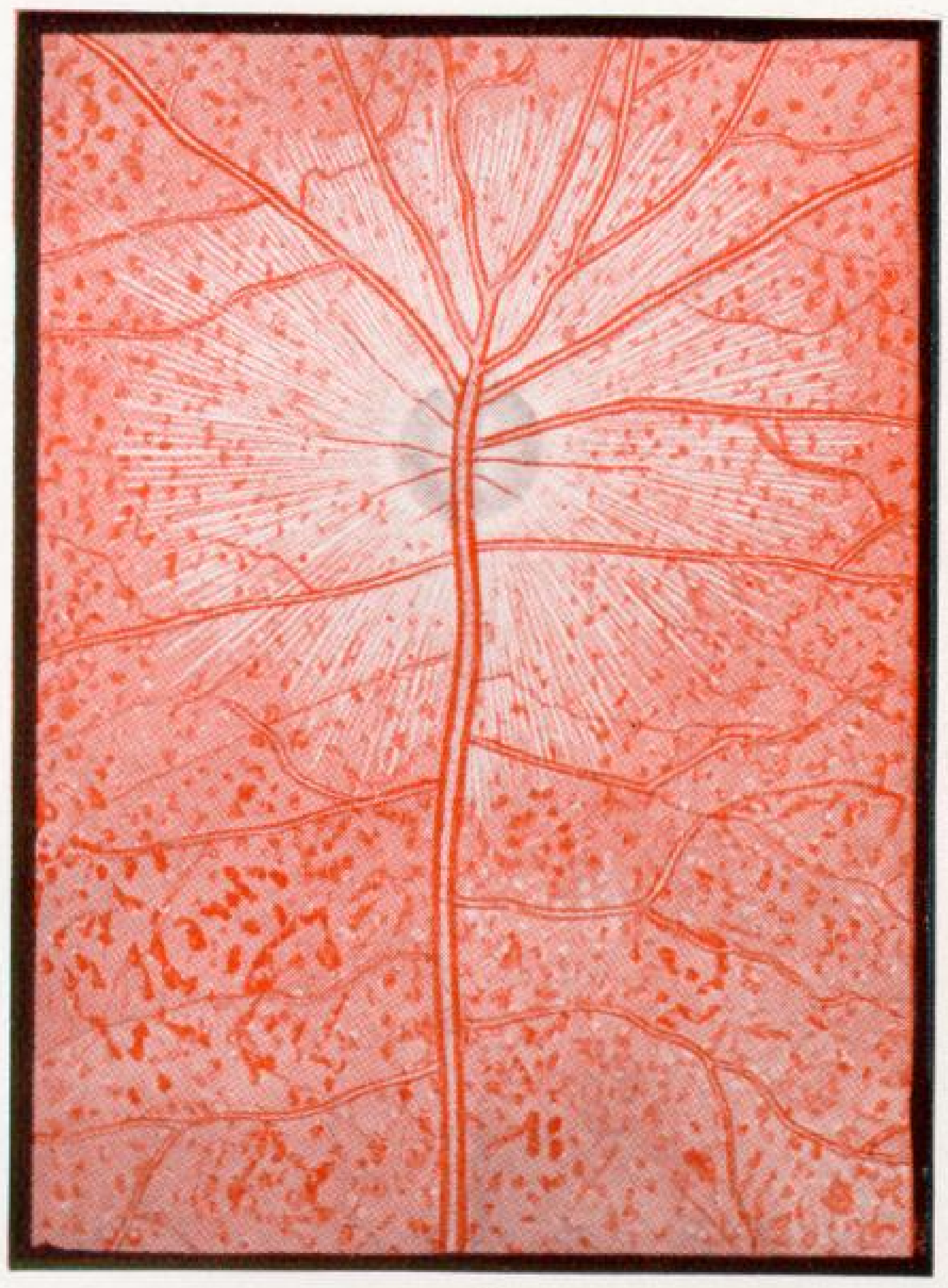


PLATE 20.

1. *Rana clamata.*
2. *R. tigrina.*
3. *R. catesbiana.*
4. *Salamandra maculosa.*
5. *Sphenodon* (for comparison).
6. *Bufo boreas.*
7. *B. melanostictus.*
8. *B. marinus.*



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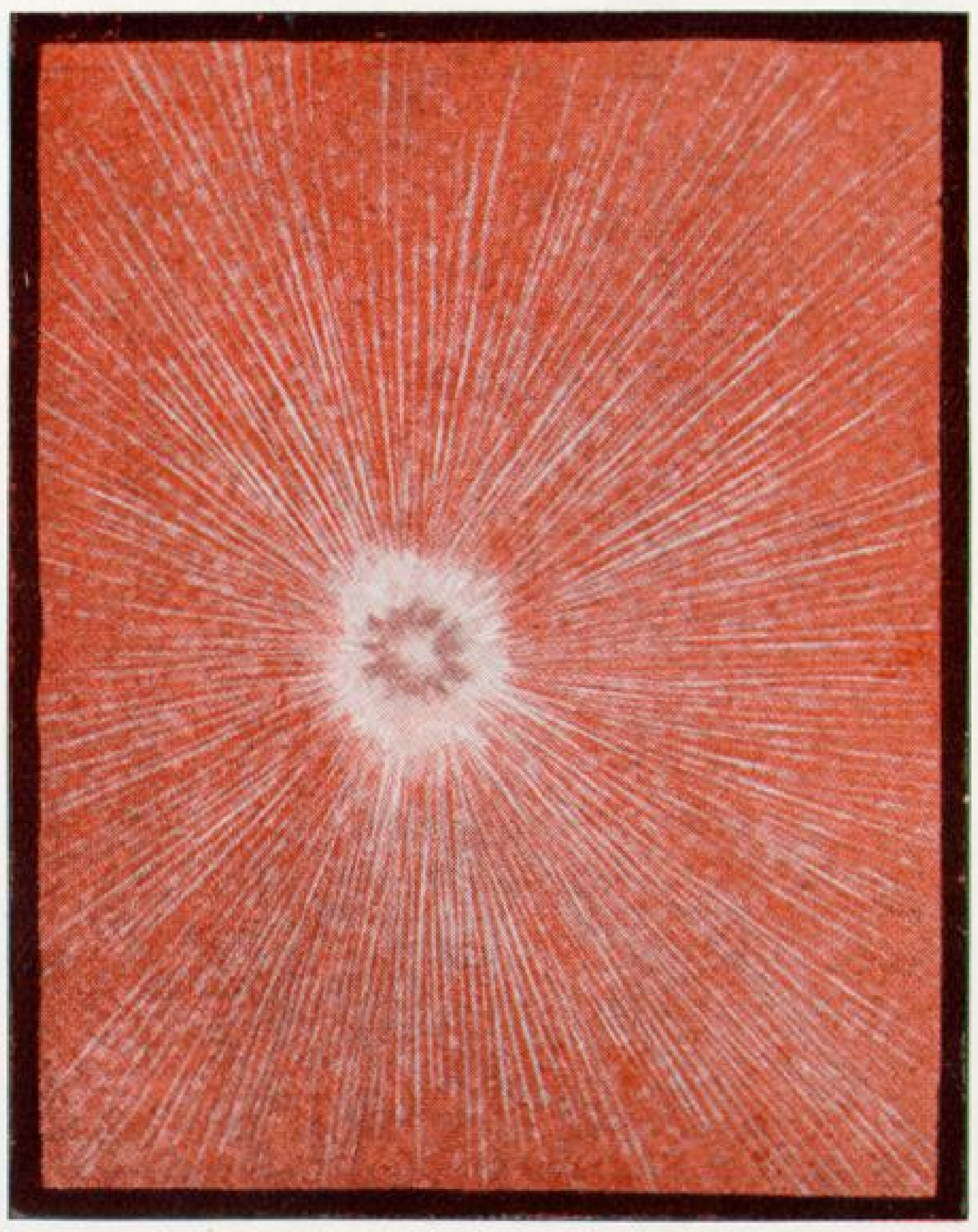

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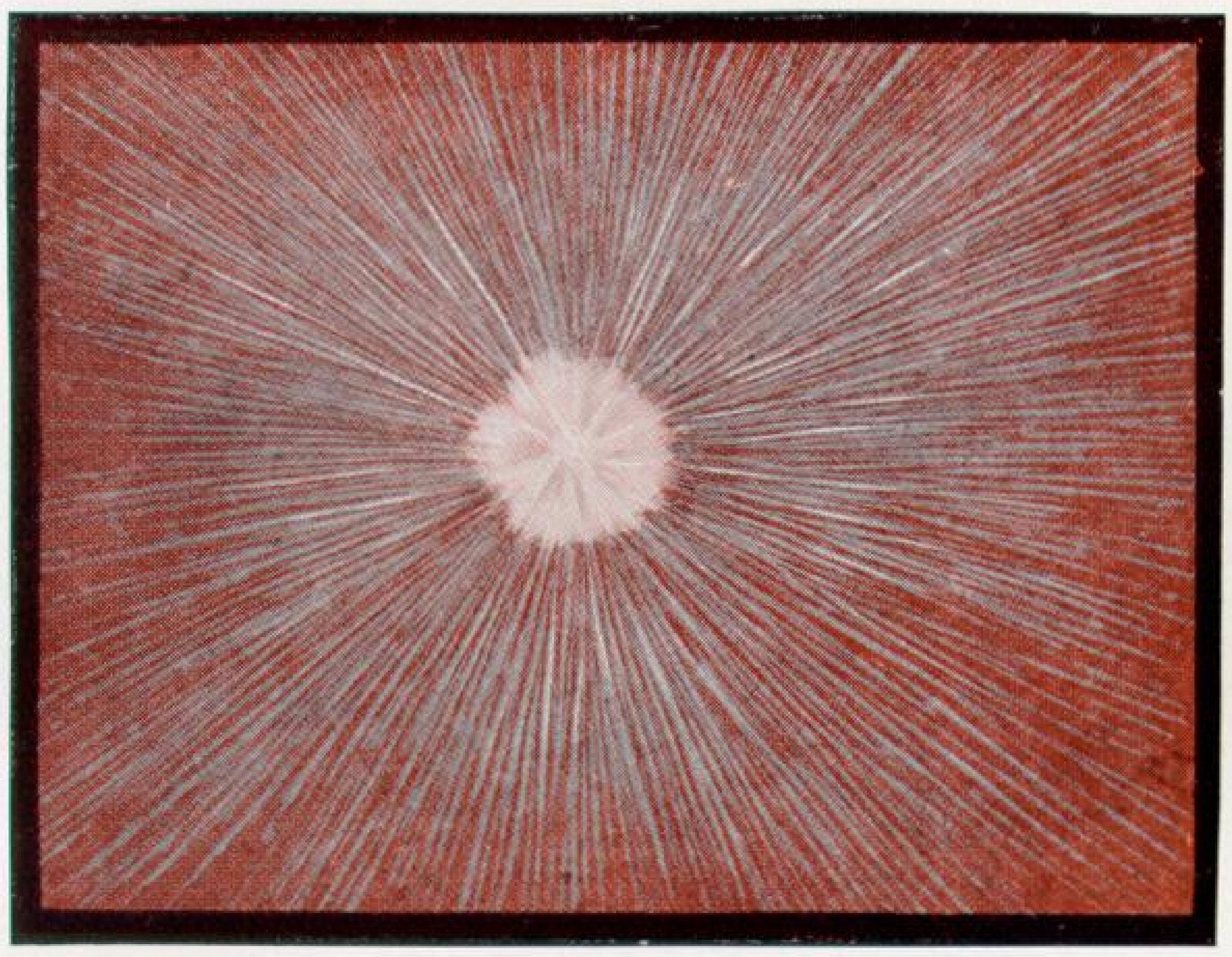

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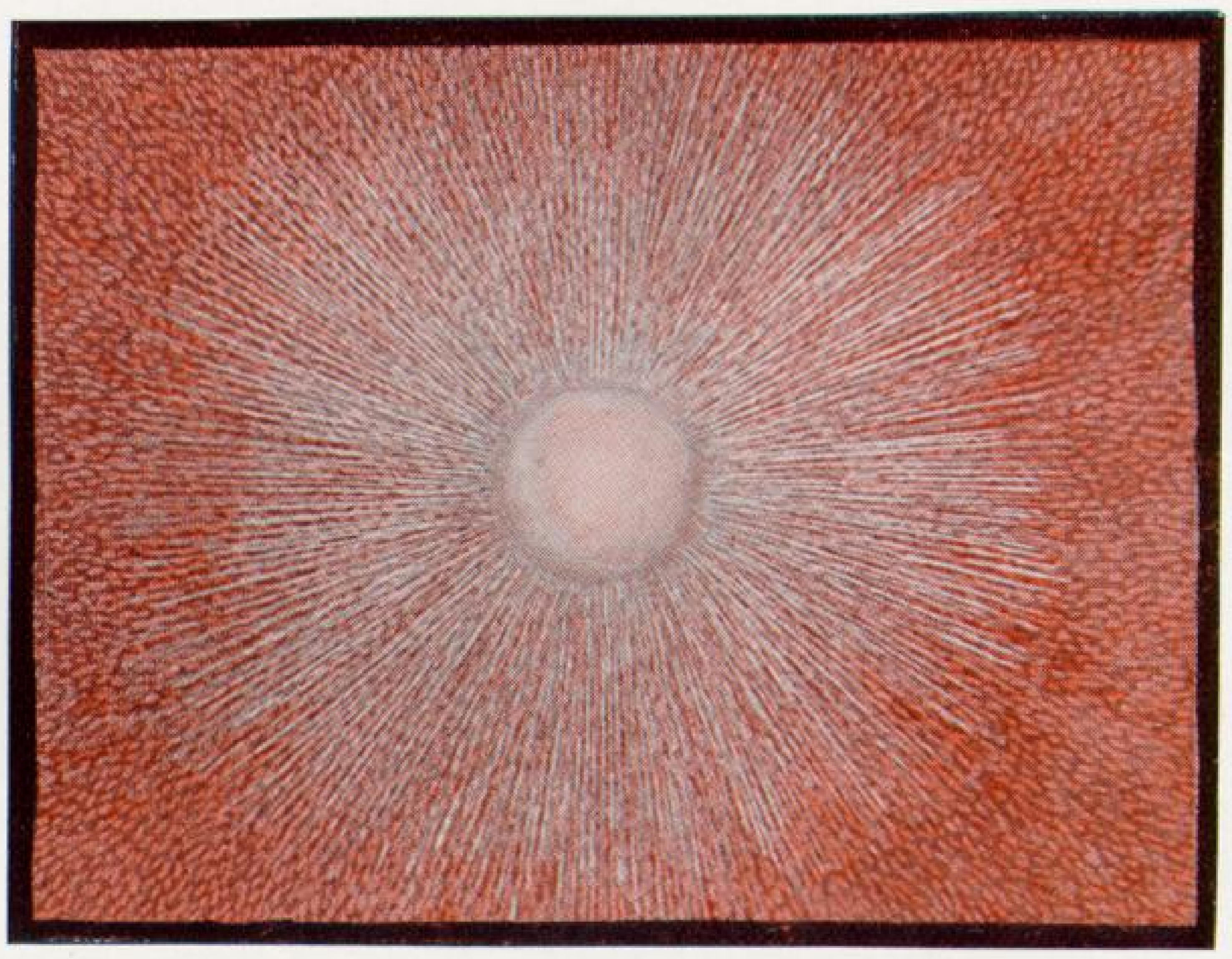

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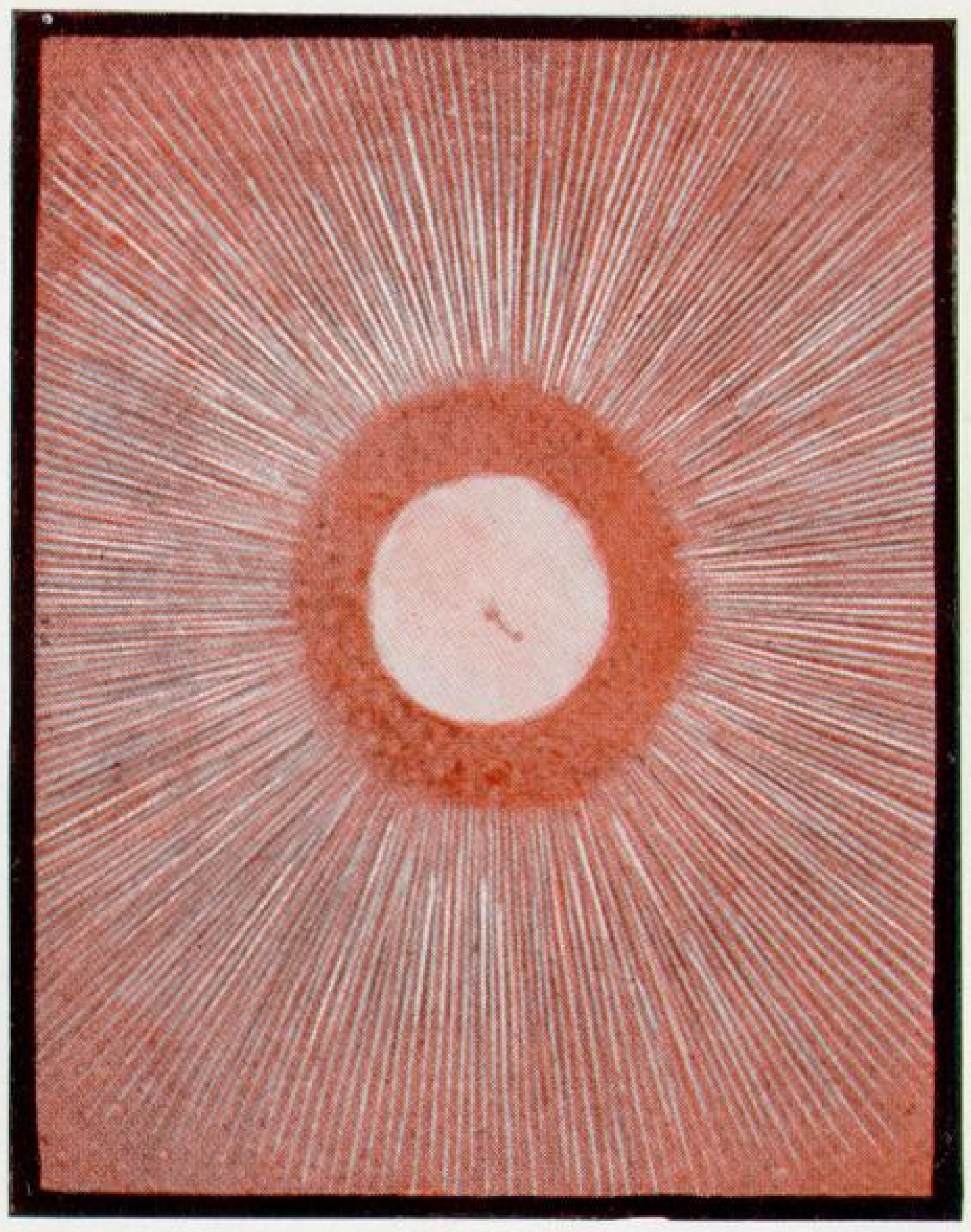

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PLATE 21.

9. *Hyla cœrulea.*
10. *Chelodina longicollis.* (Turned.)
11. *Chelydra serpentina.* (Turned.)
12. *Chrysemys scripta rugosa.*
13. *Testudo radiata.*
14. *Cinyxis erosa.* (Turned.)
15. *Emyda granosa.* (Turned.)
16. *Alligator mississippiensis.* (Turned.)

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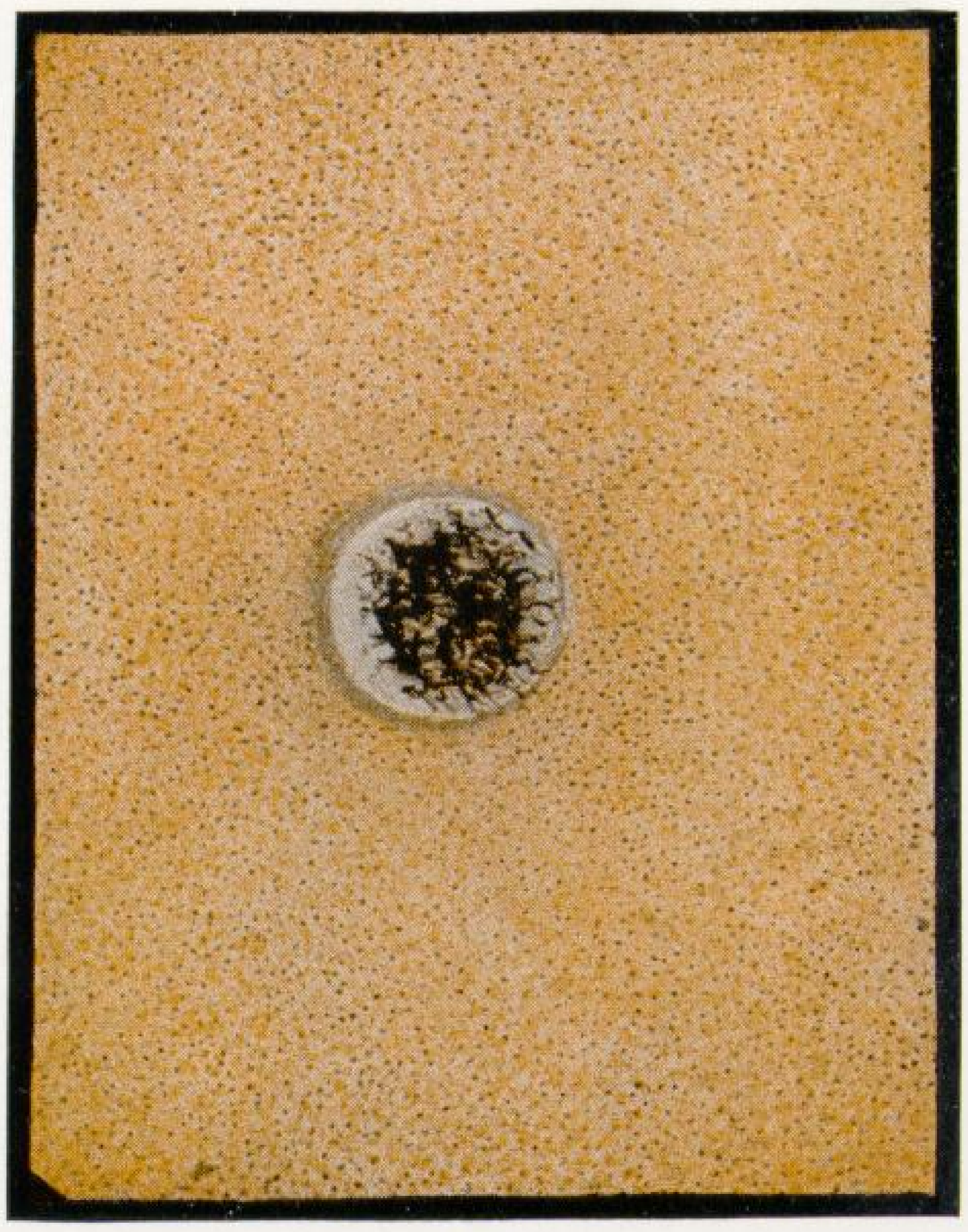

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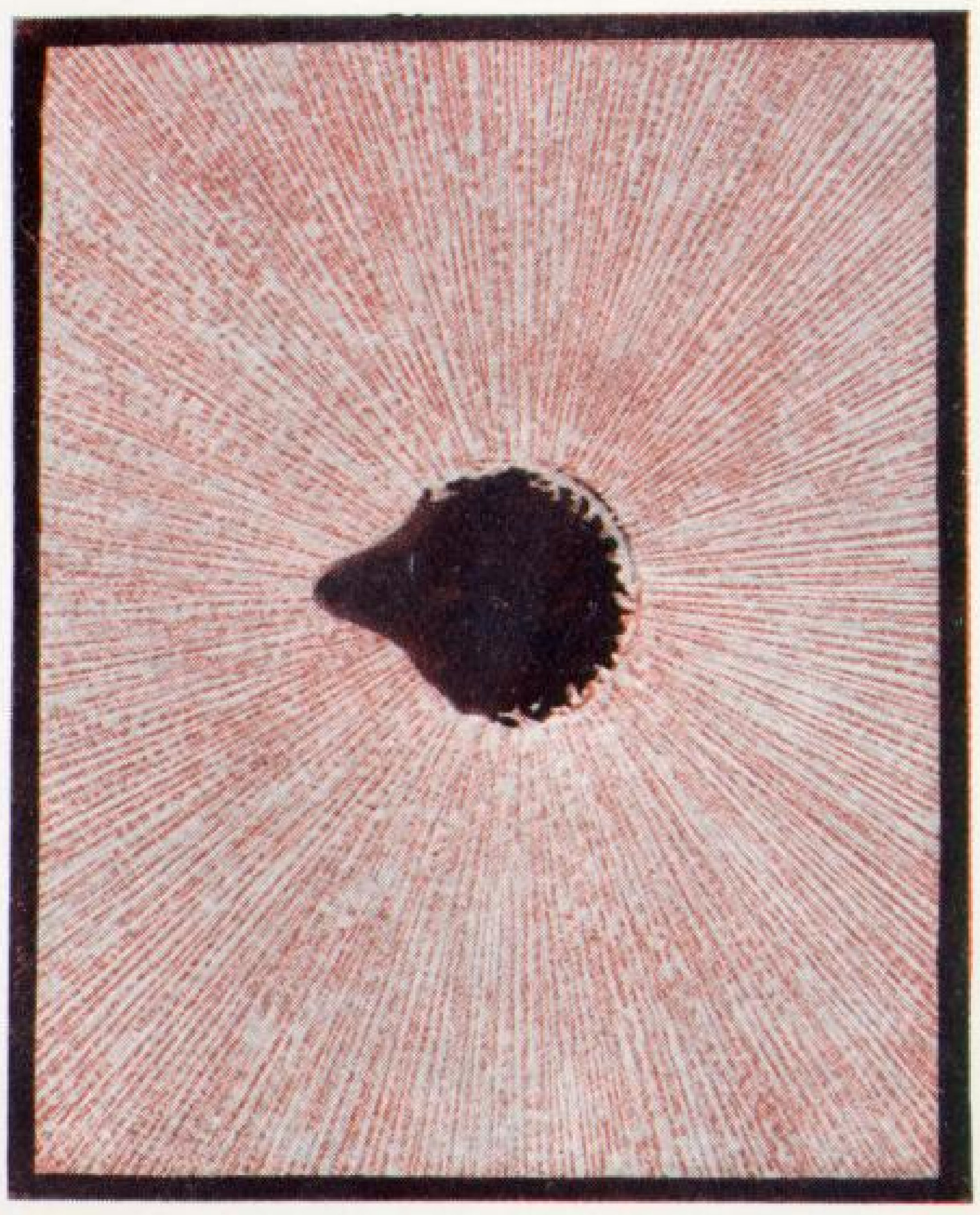

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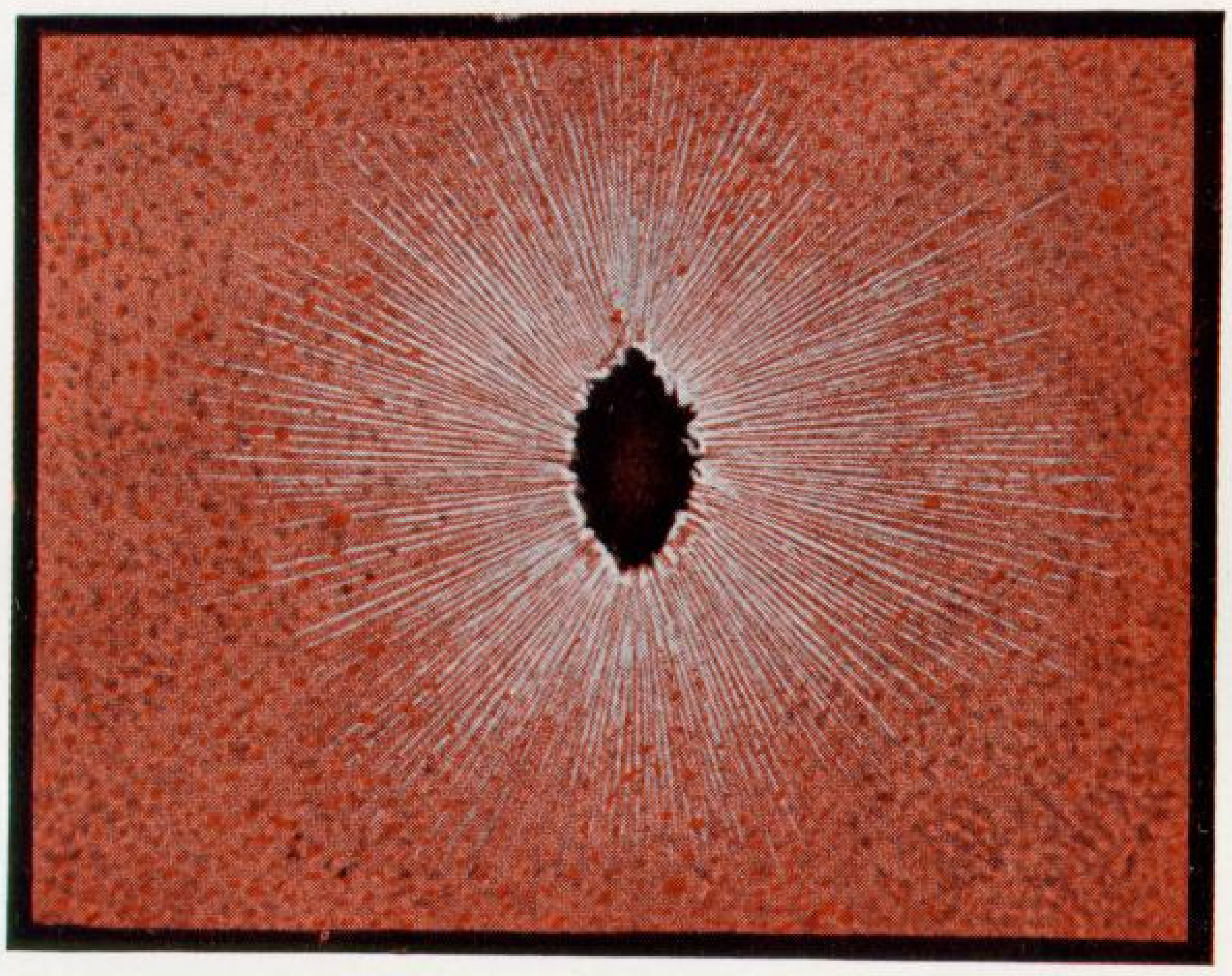

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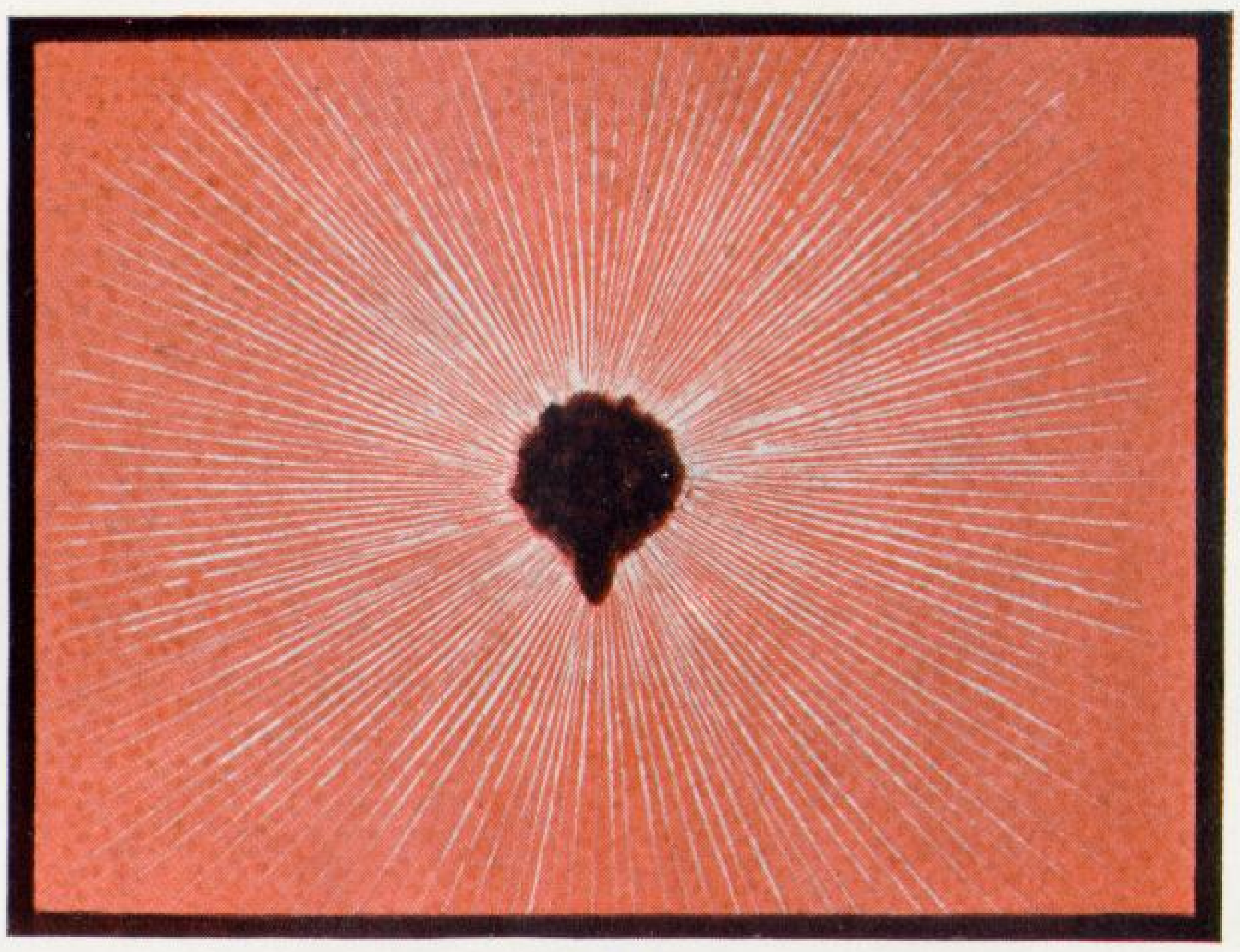

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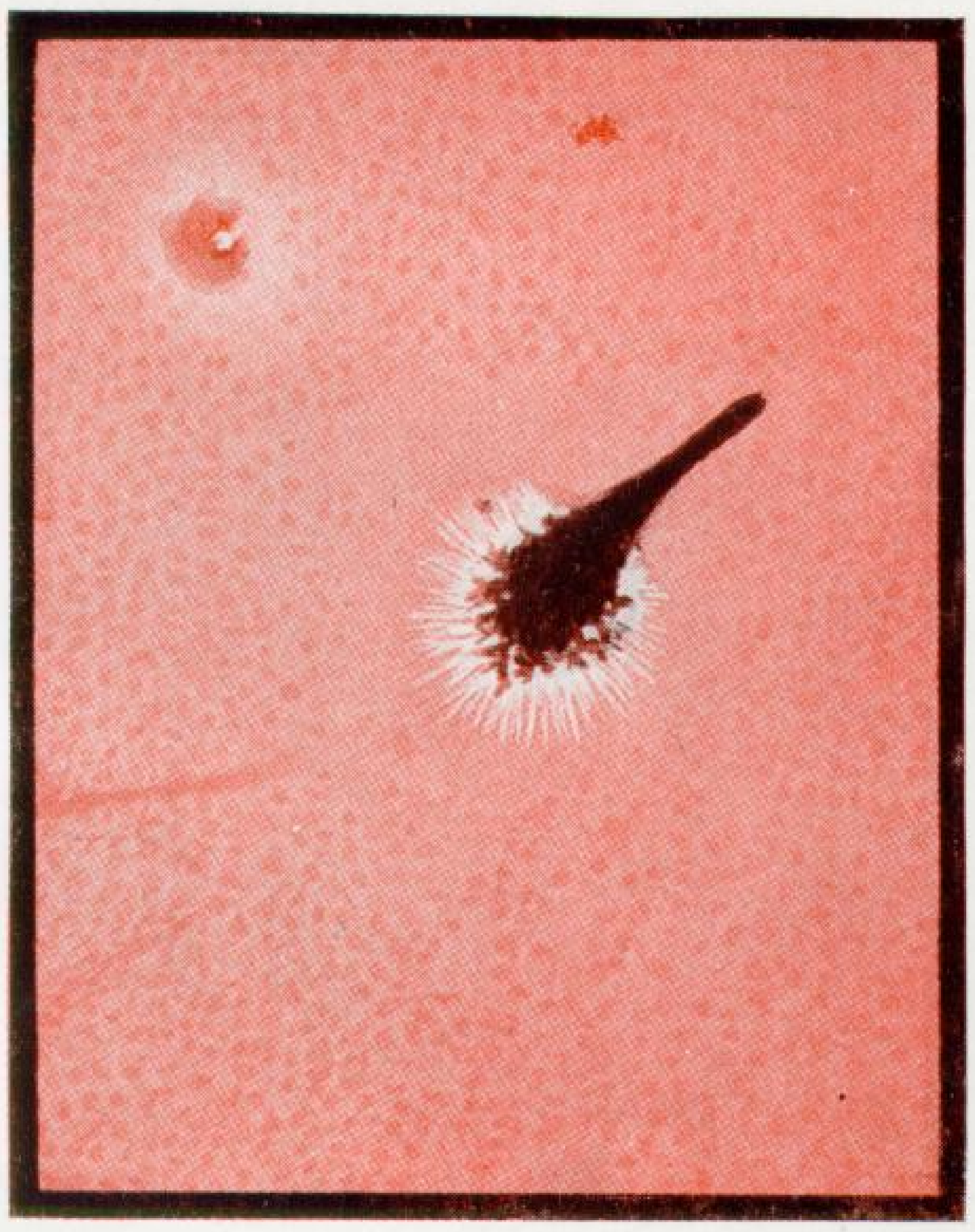

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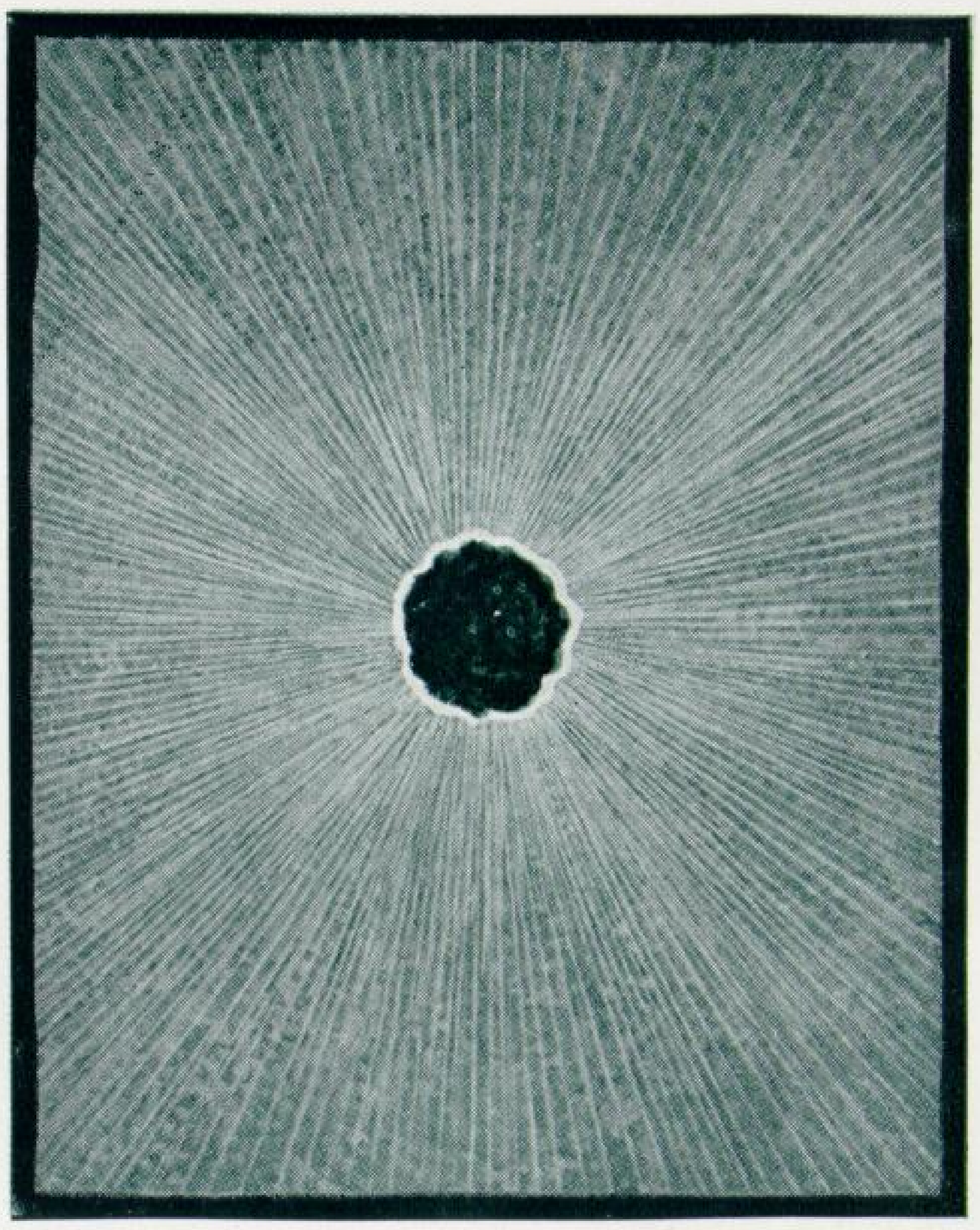

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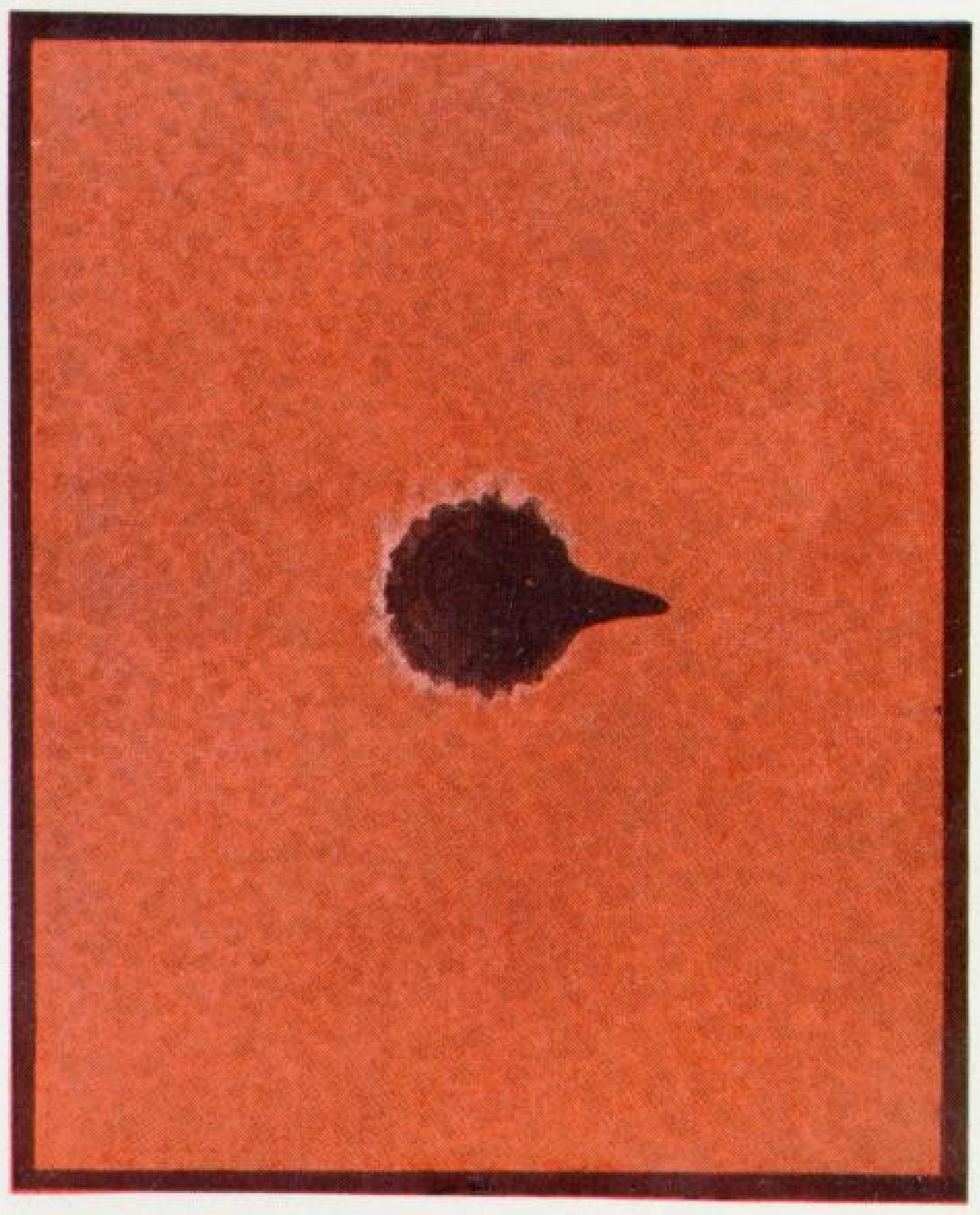

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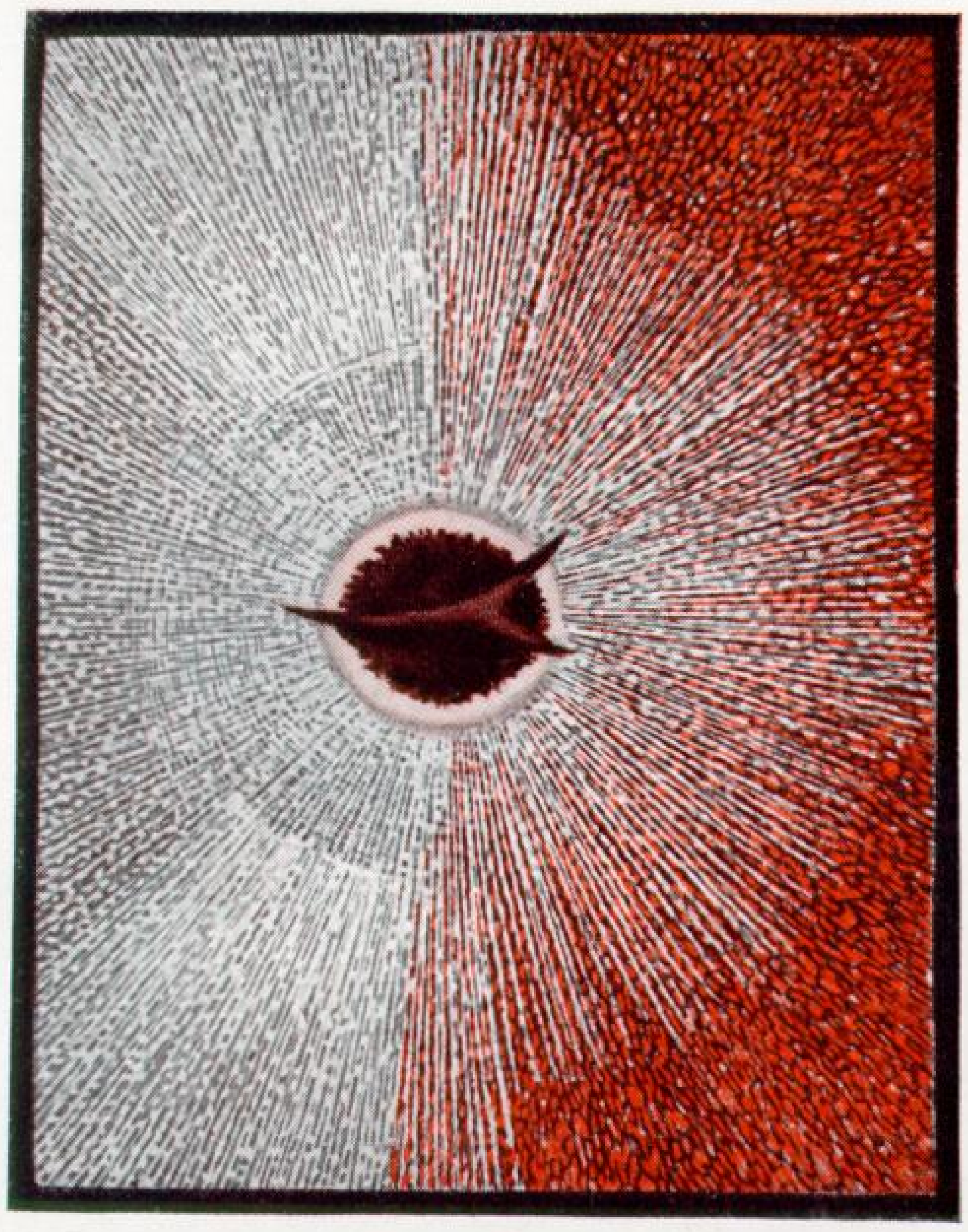
PLATE 22.

17. *Alligator chinensis.* (Turned.)
18. *Crocodilus frontatus.* (Turned.)
19. *Phleuma madagascariense.* (Turned.)
20. *Pachydactylus maculatus.*
21. *Hemidactylus turcicus.*
22. *Apteryx* (for comparison). (Turned.)
23. *Anolis alligator.* (Turned.)
24. *Uroplates fimbriatus.* (Turned.)



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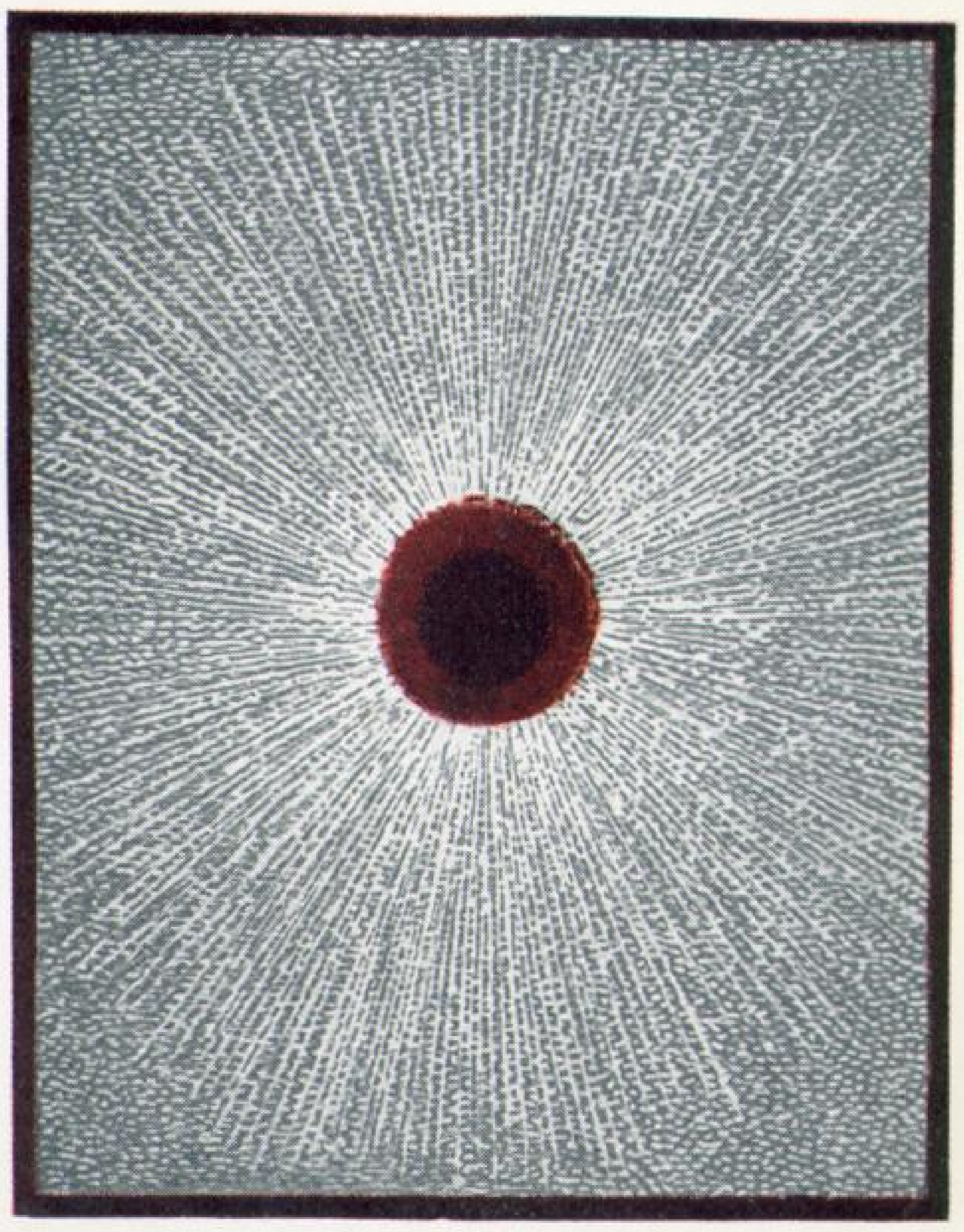

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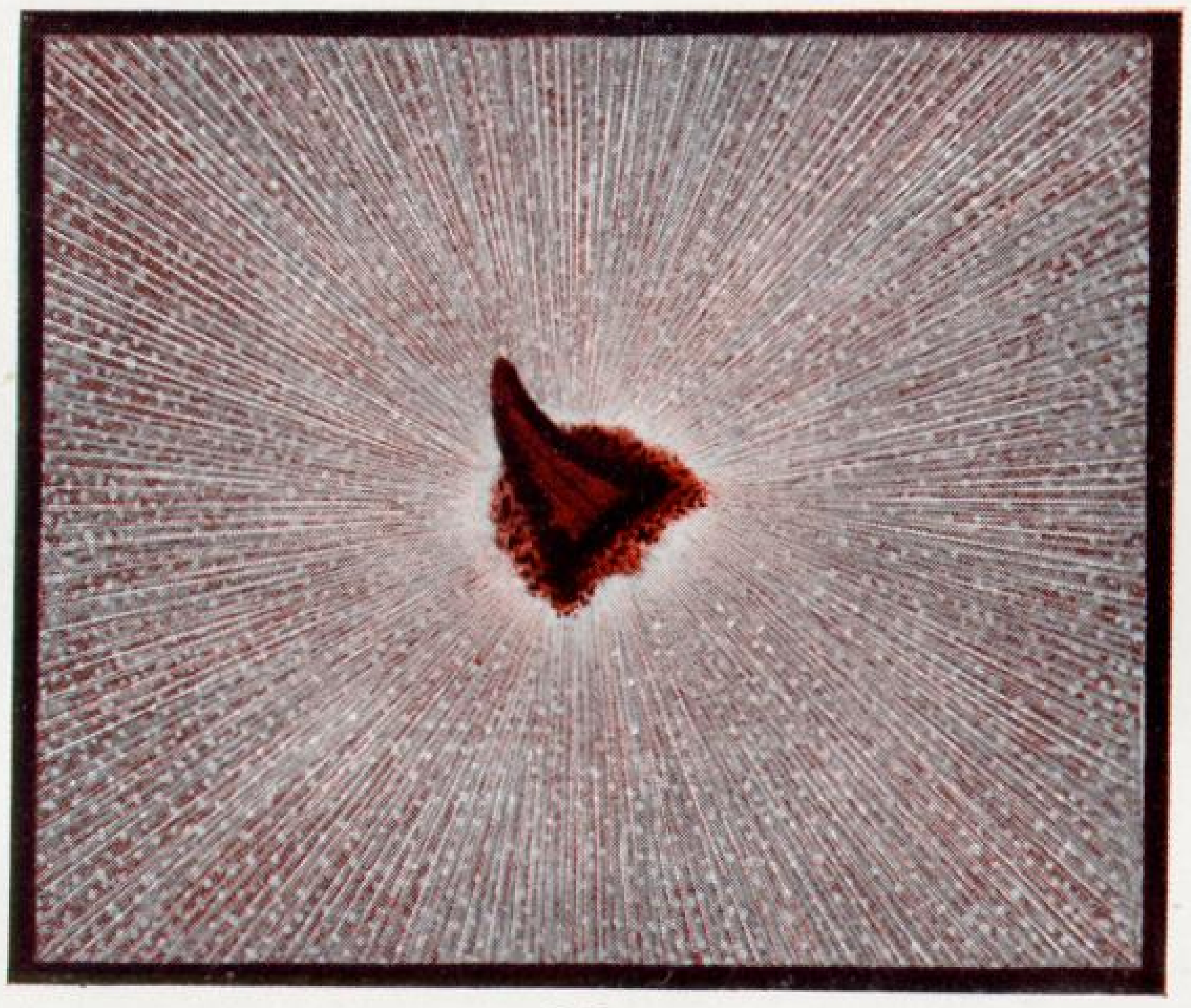

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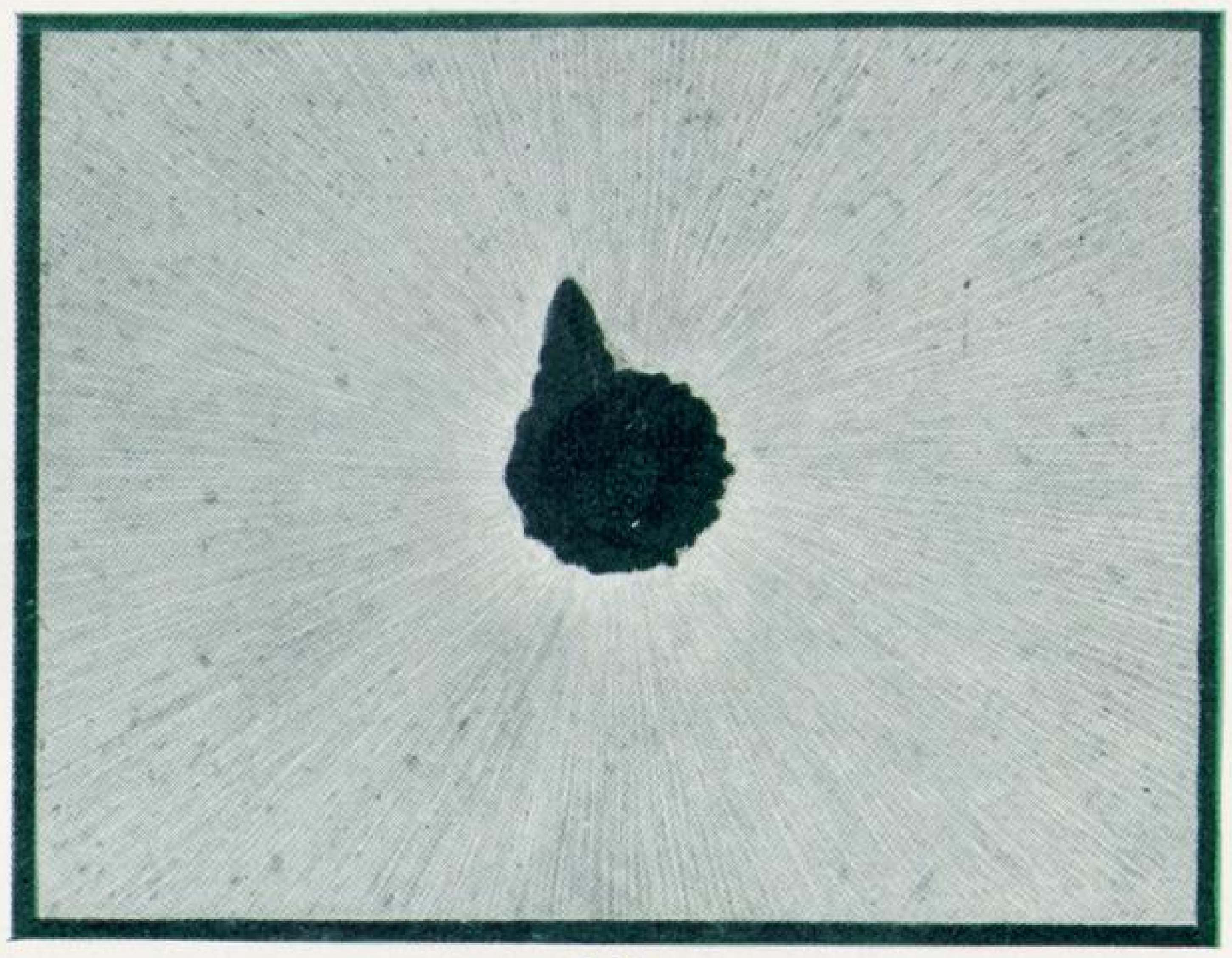

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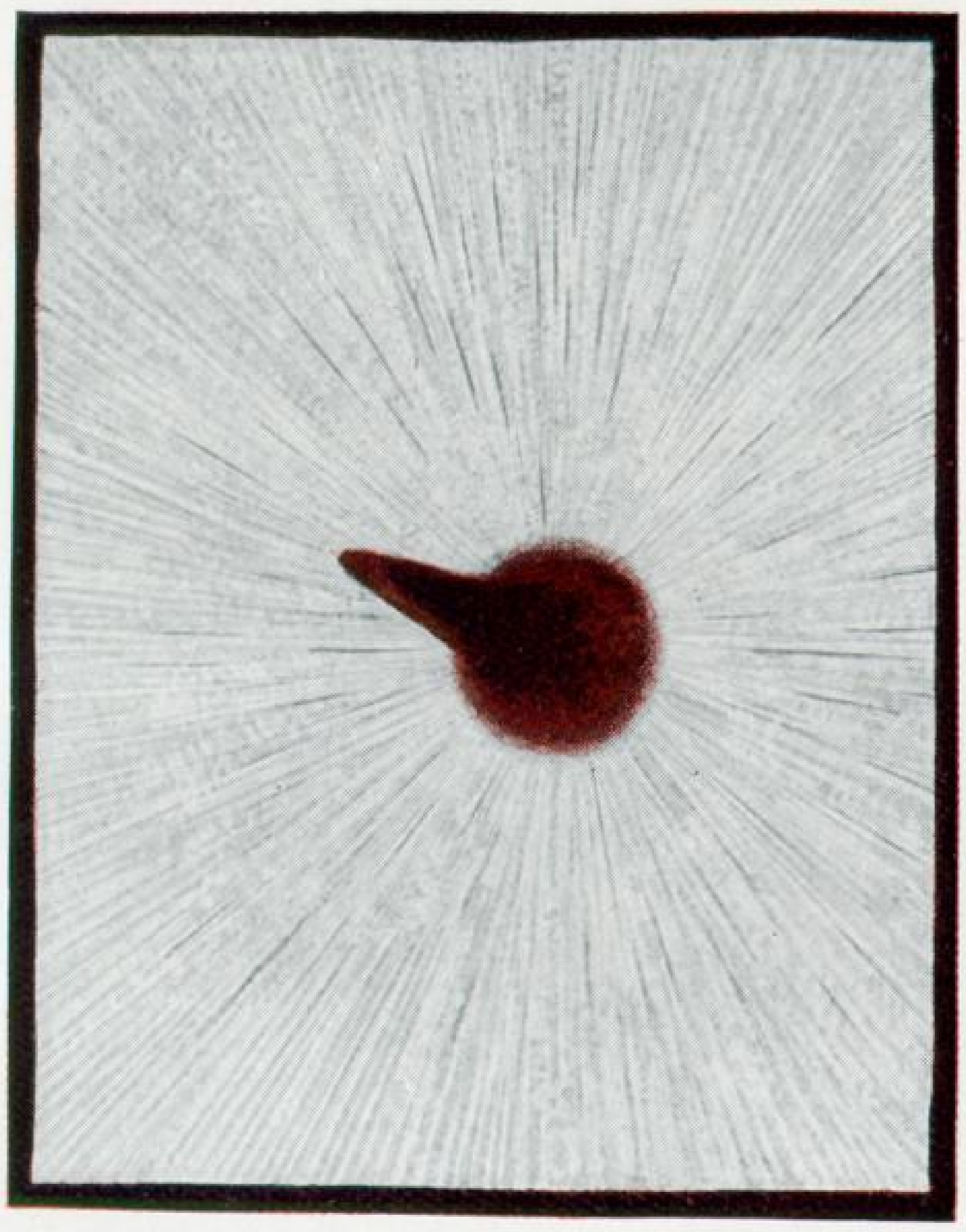

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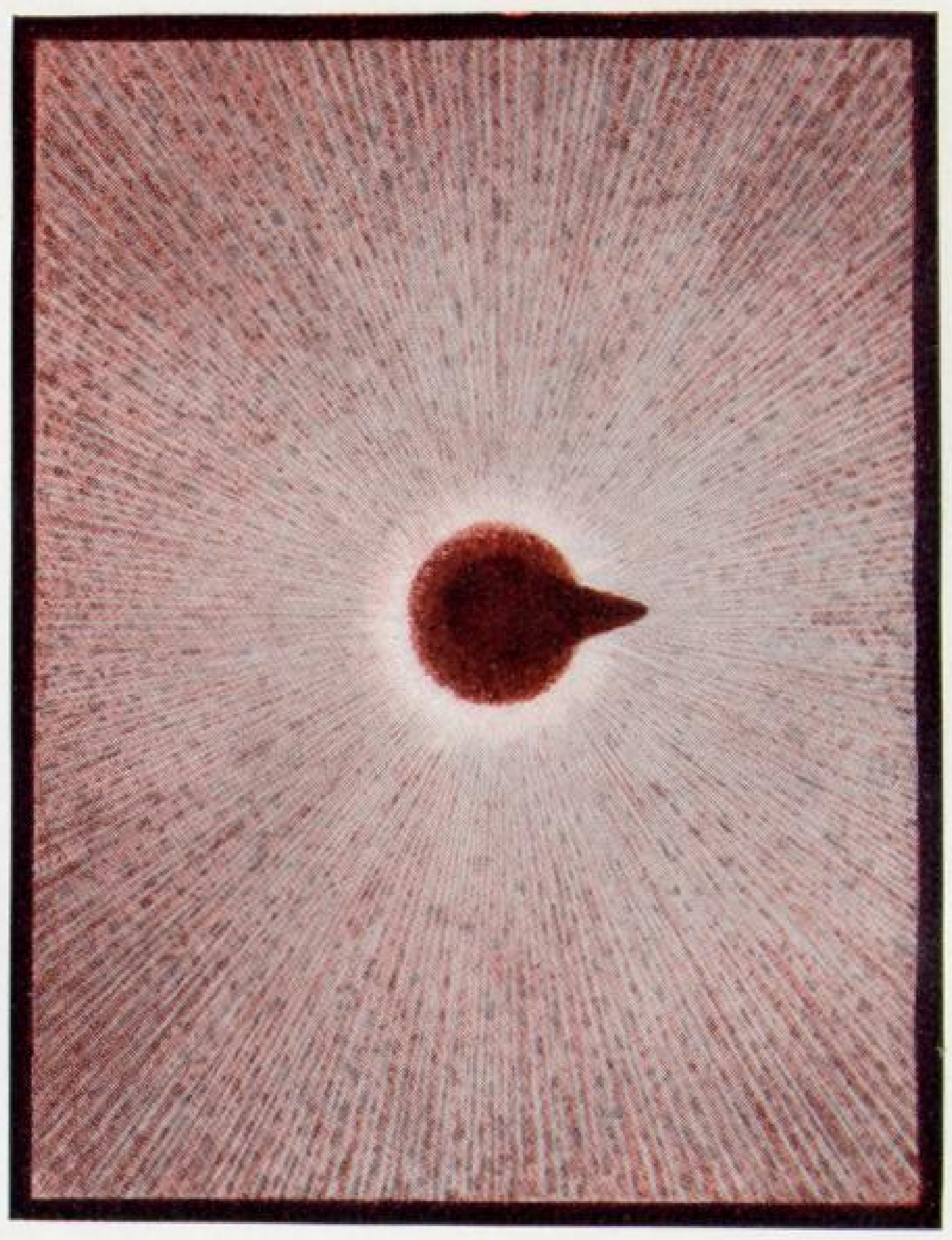

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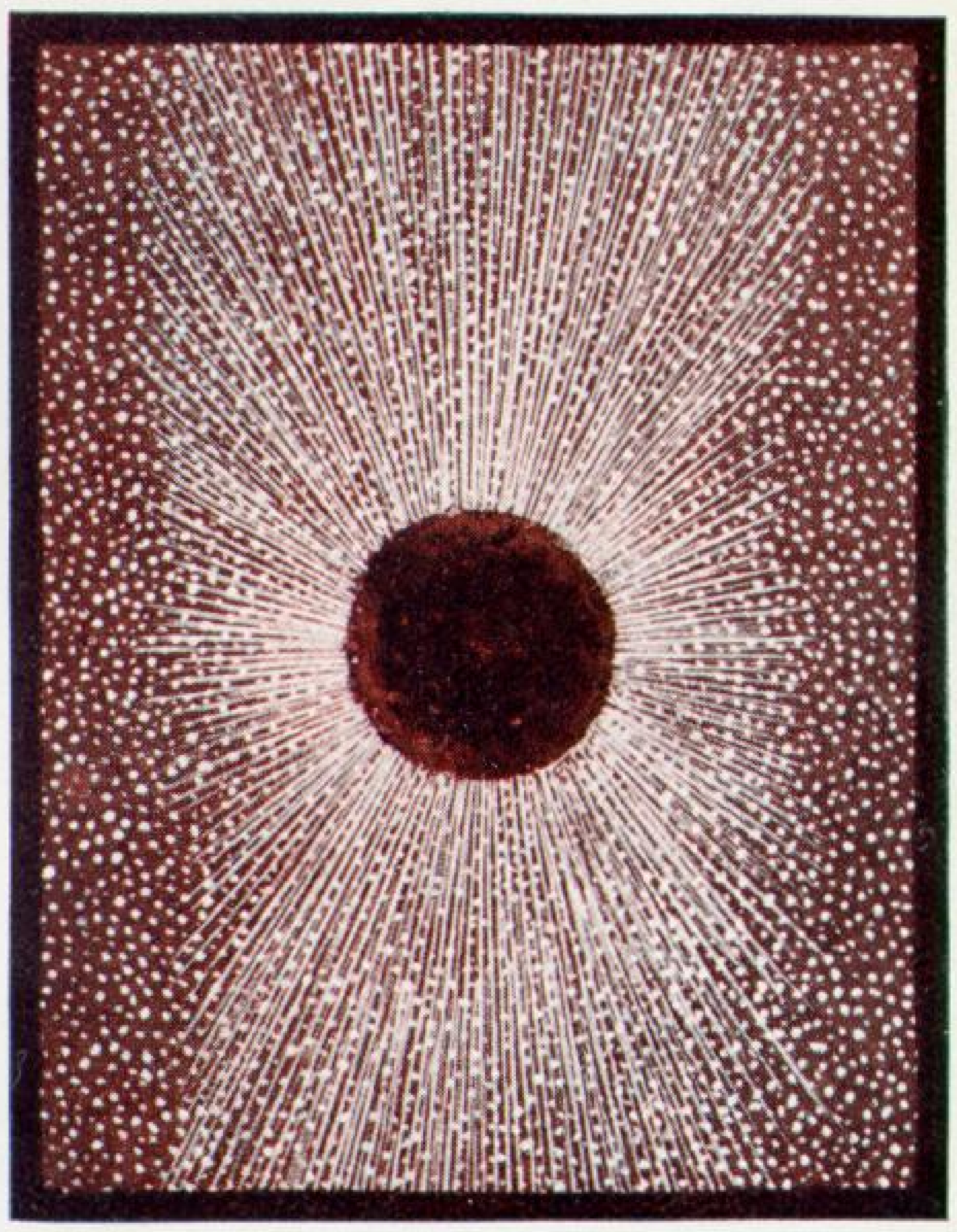

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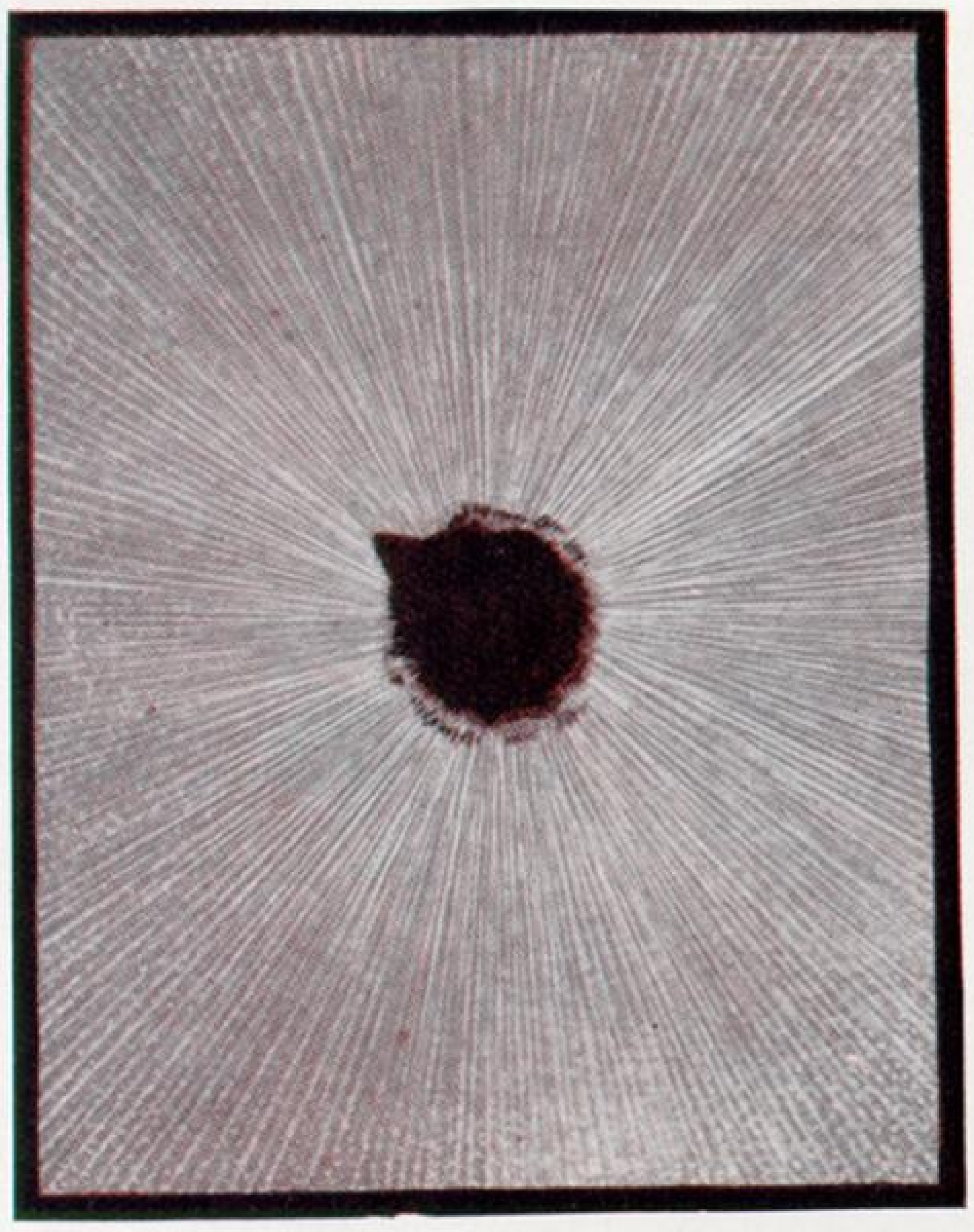
PLATE 23.

25. *Metopoceros cornutus.* (Turned.)
26. *Conolophus subcristatus.* (Turned.)
27. *Ophisaurus apus.* (Turned.)
28. *Varanus bengalensis.* (Turned.)
29. *Varanus Gouldi.*
30. *Lygosoma Quoyi.* (Turned.)
31. *Tupinambis nigropunctatus.* (Turned.)
32. *Lacerta Galloti.* (Turned.)



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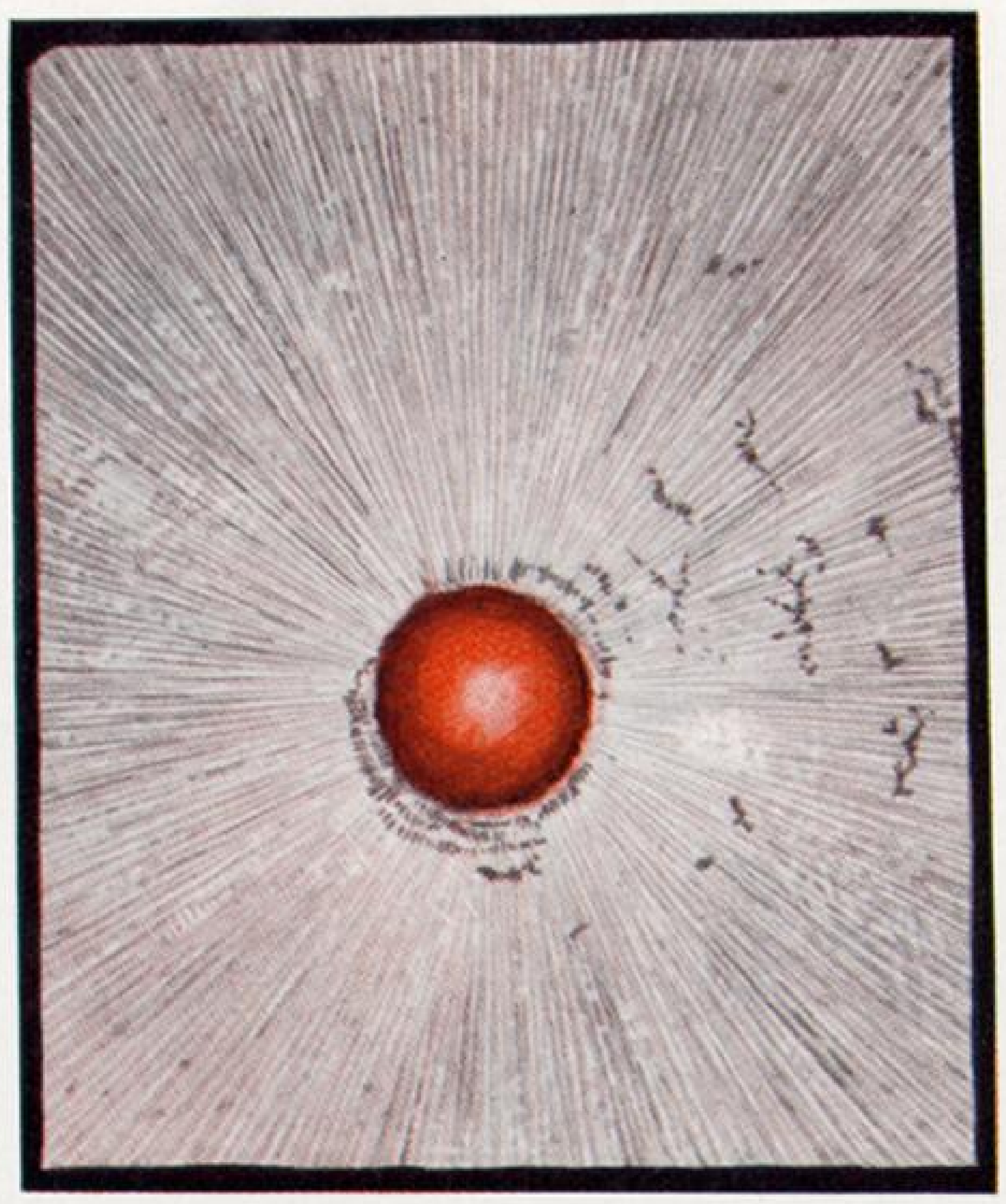

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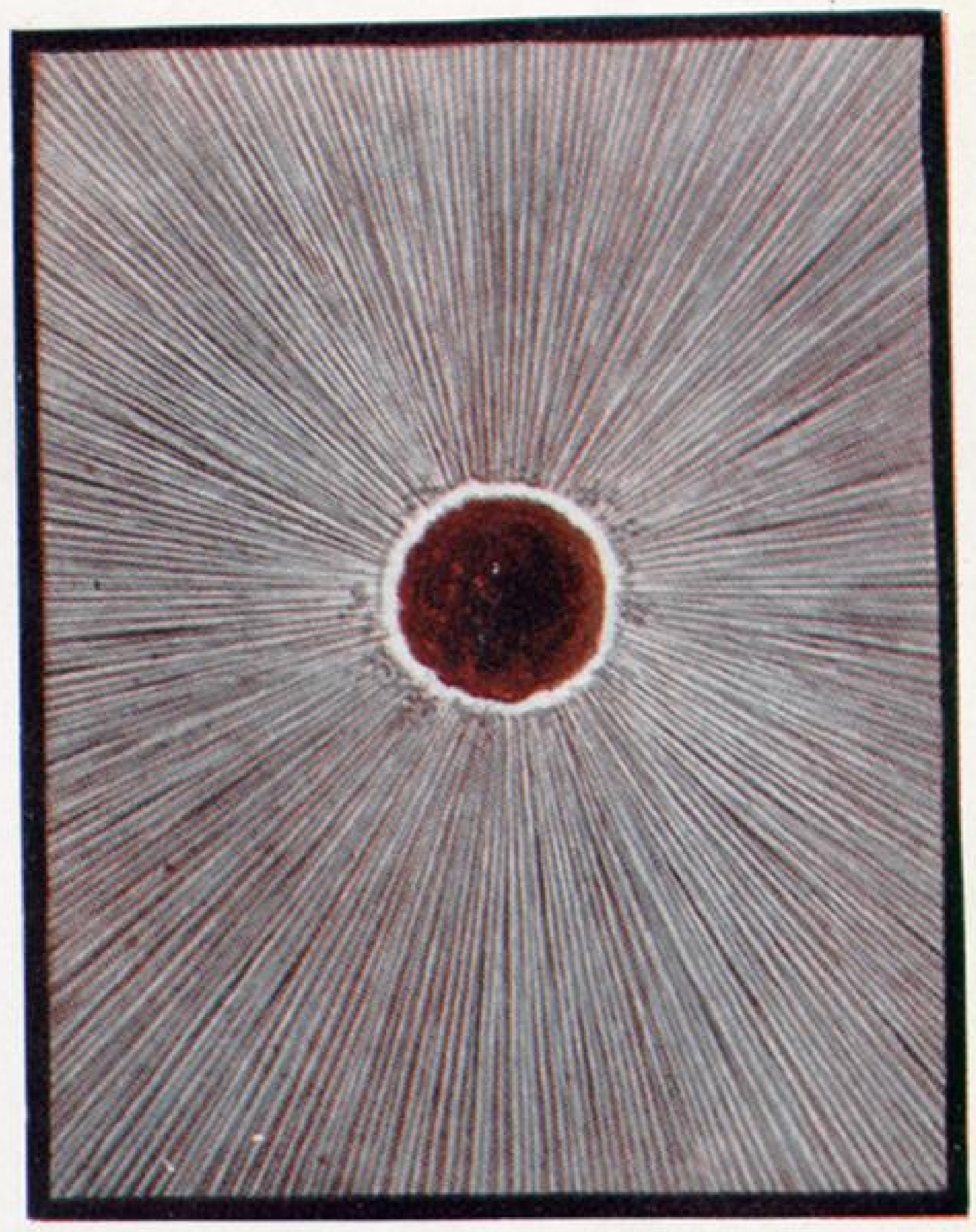

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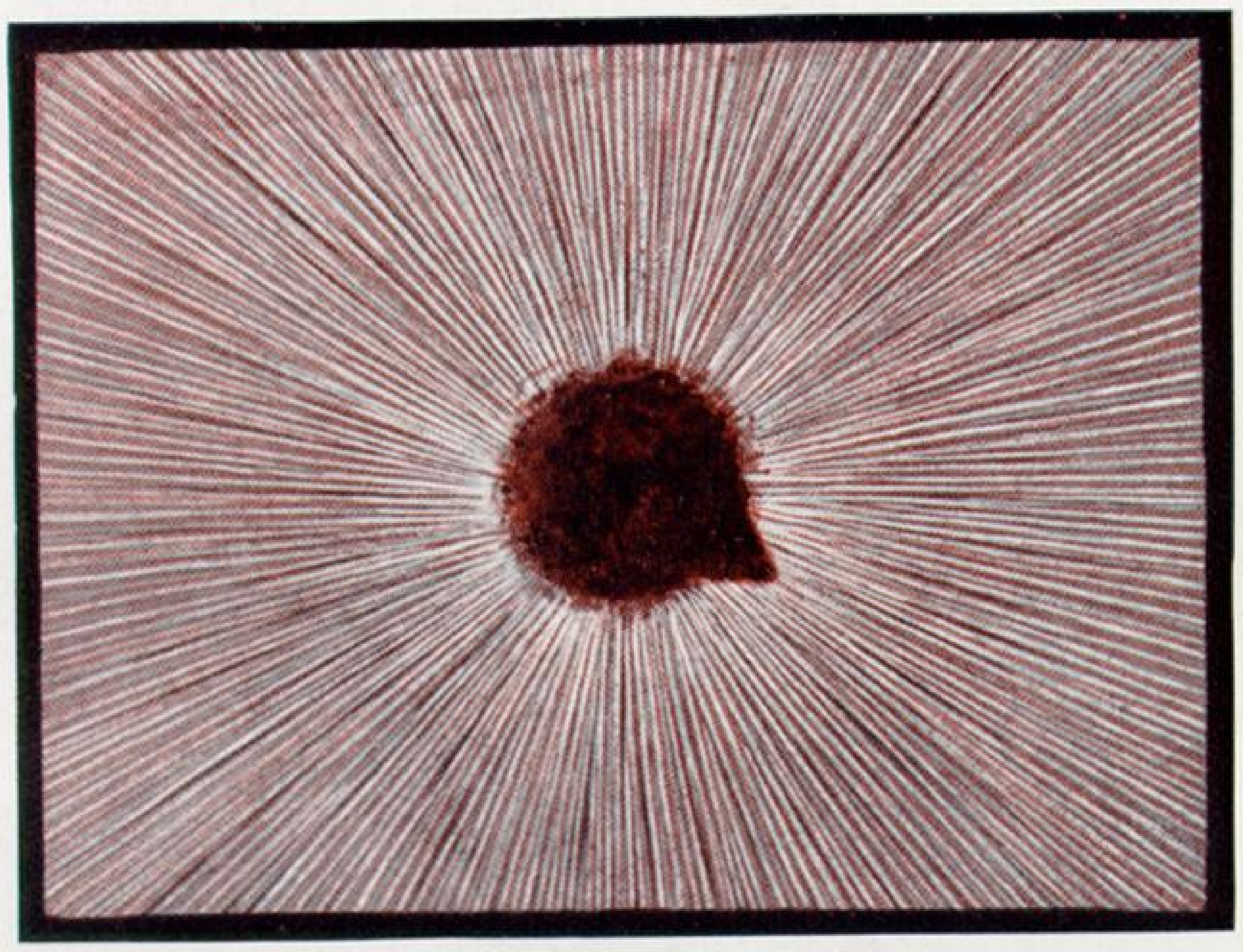

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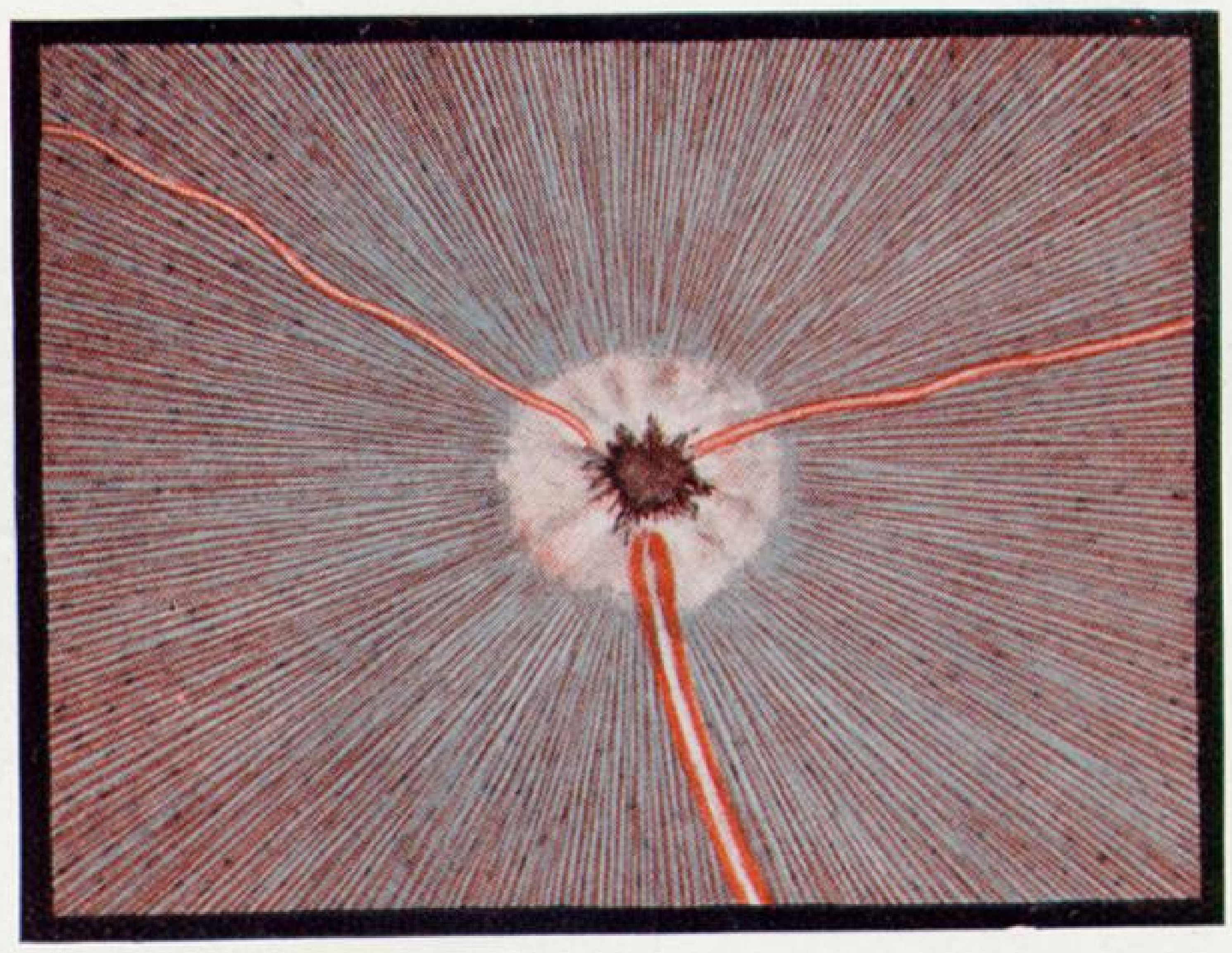

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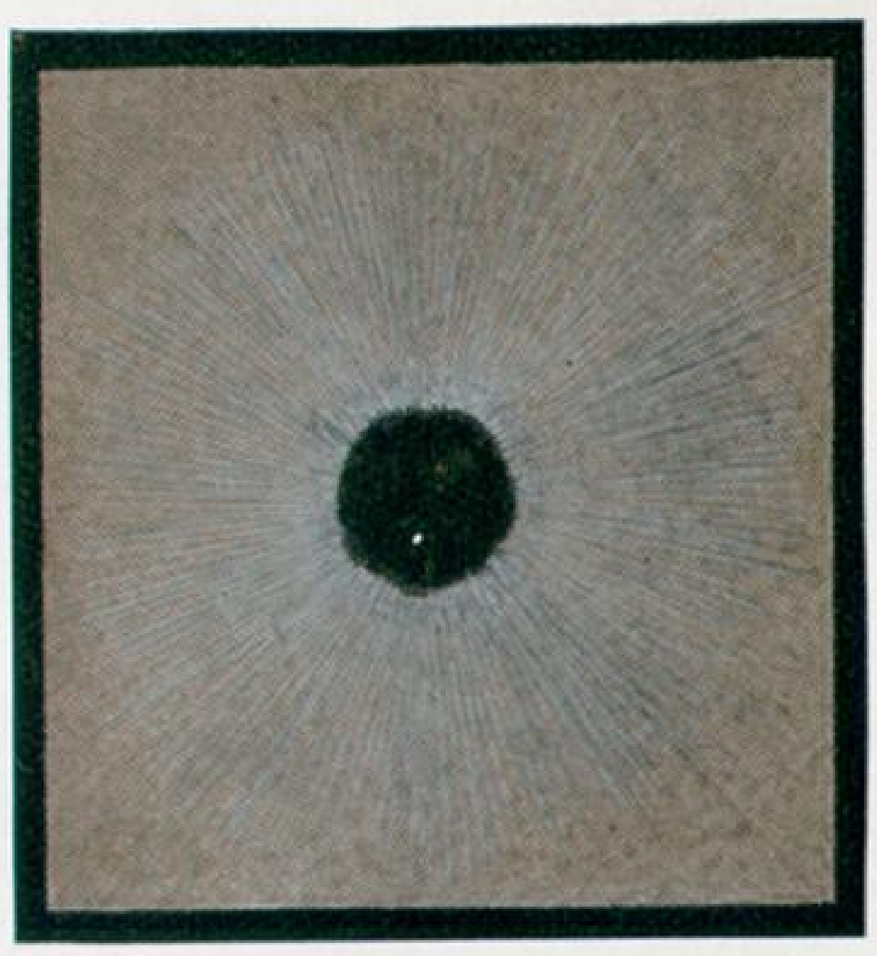

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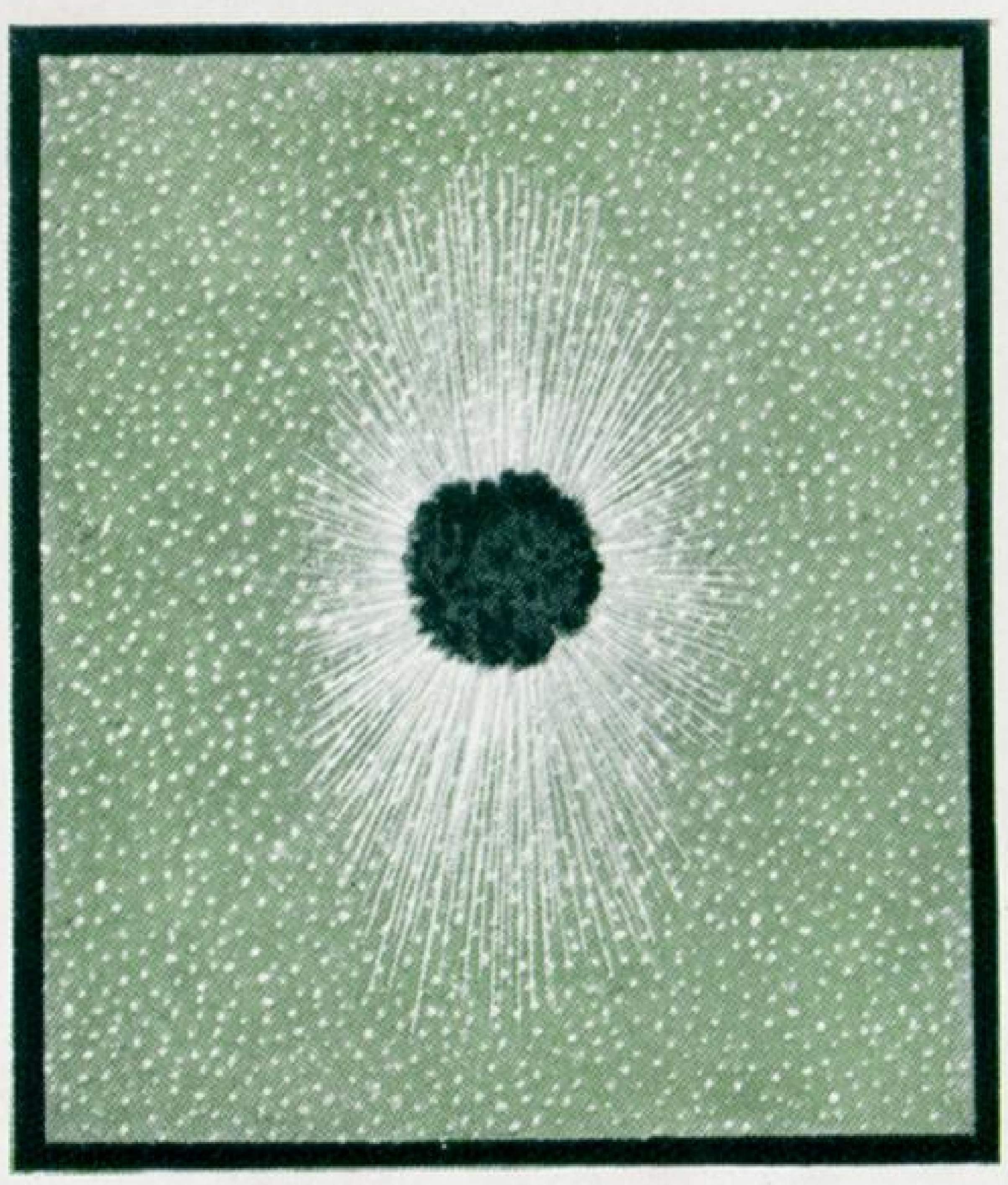

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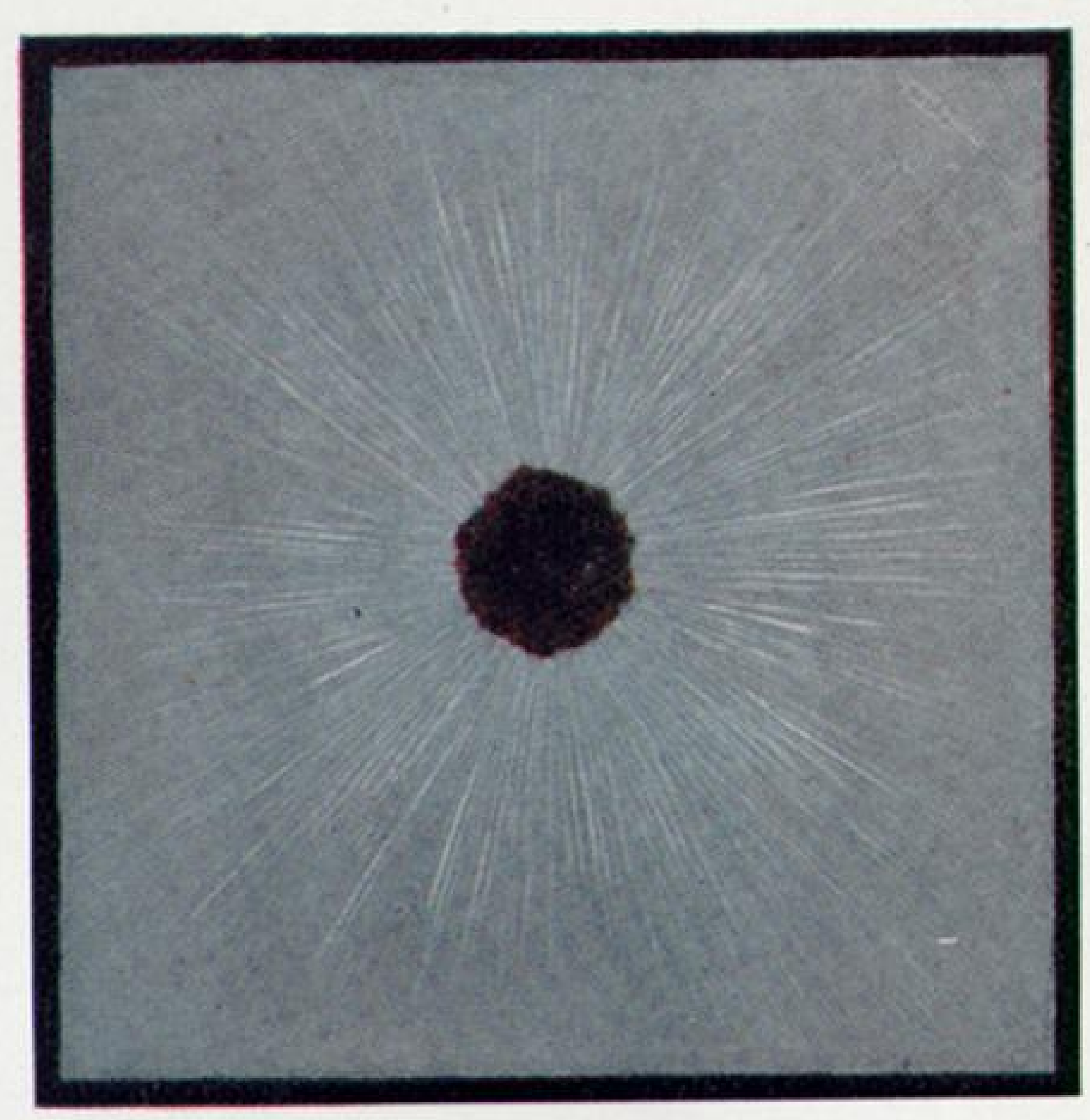

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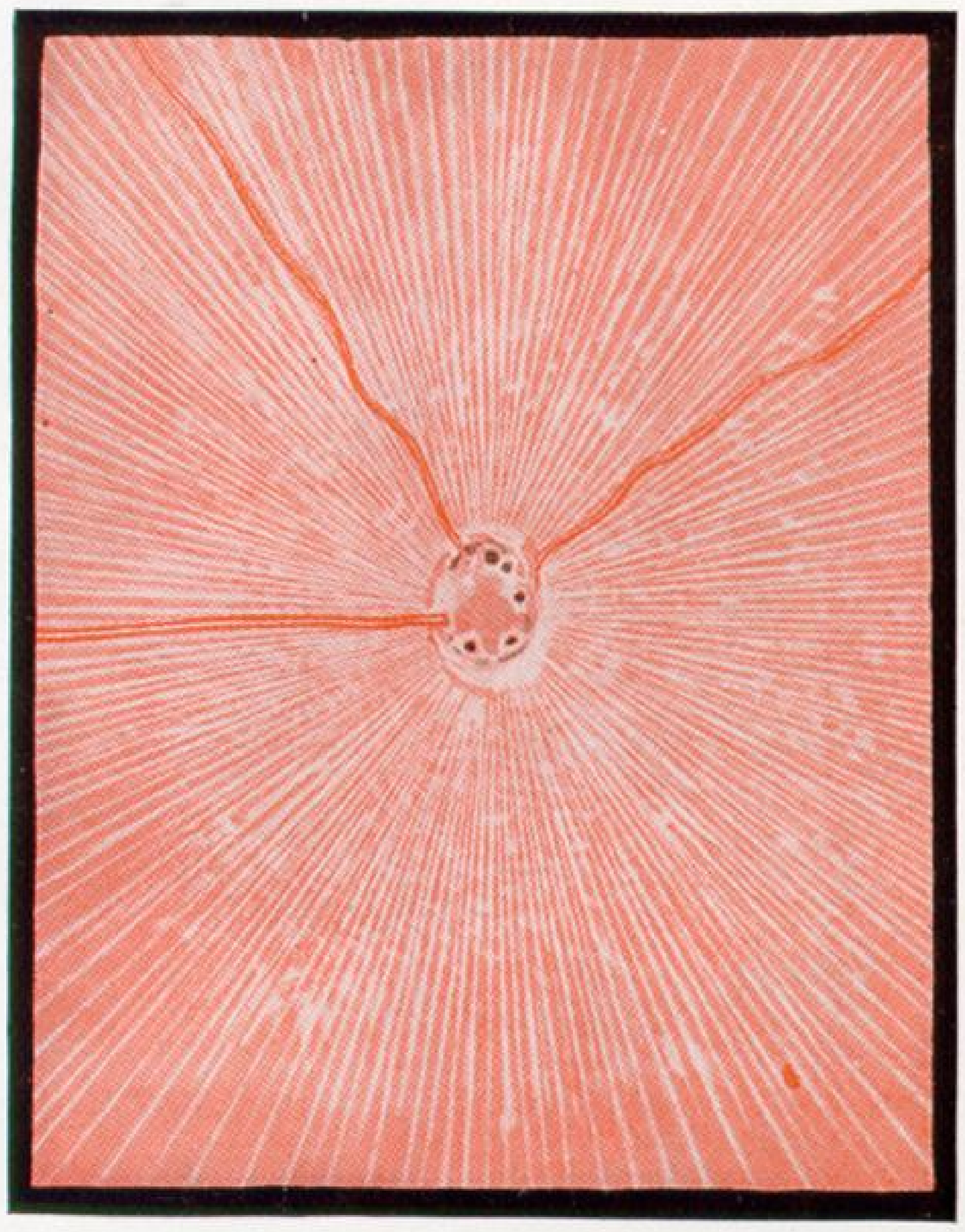
PLATE 24.

33. *Lacerta Simonyi.* (Turned.)
34. *Egernia Cunninghami.* (Turned.)
35. *Macroscincus cocteaui.* (Turned.)
36. *Tiliqua nigroluteus.* (Turned.)
37. *Pygopus lepidopus.*
38. *Chalcides ocellatus.* (Turned.)
39. *Chamæleon vulgaris.*
40. *Naja tripudians.*



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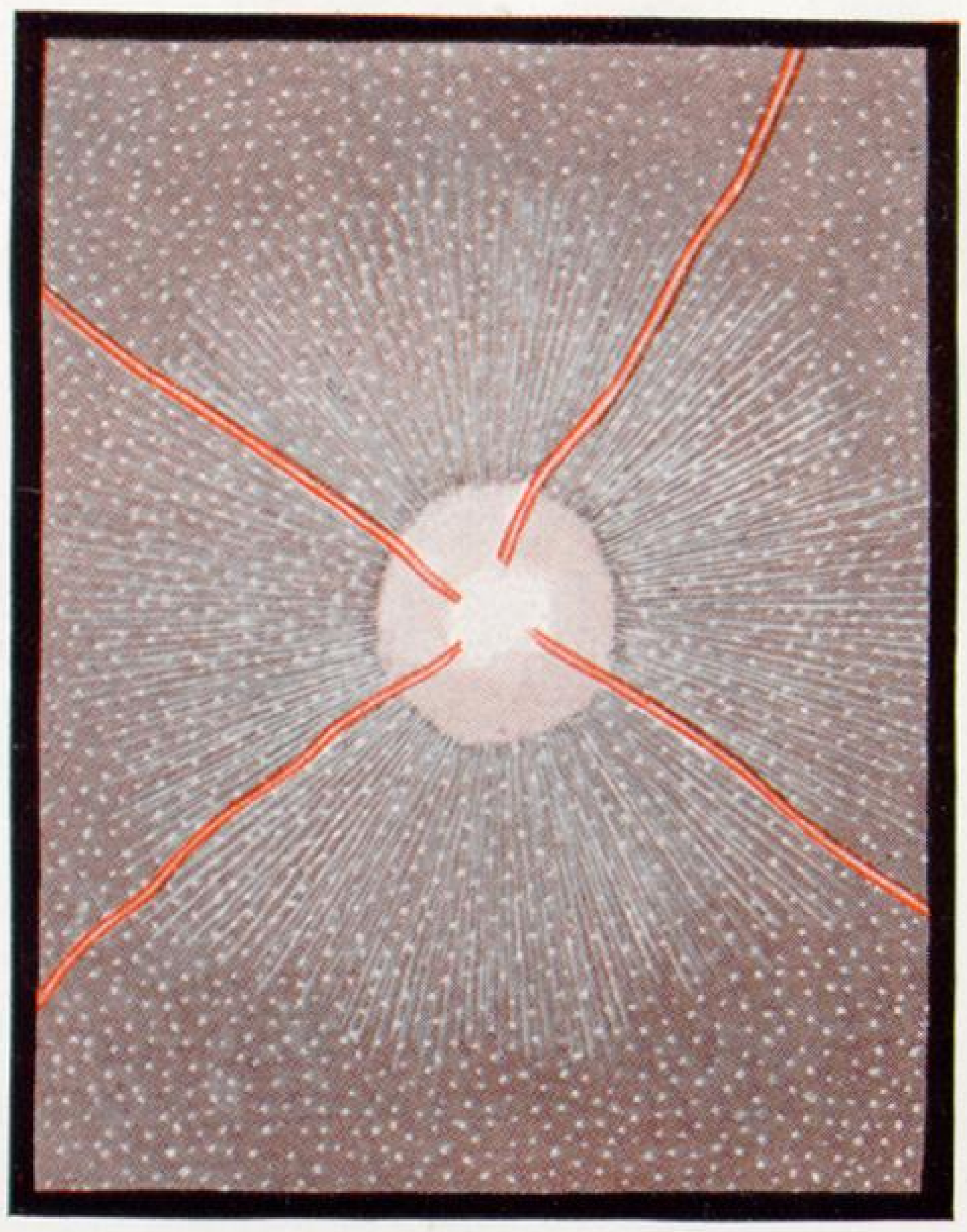

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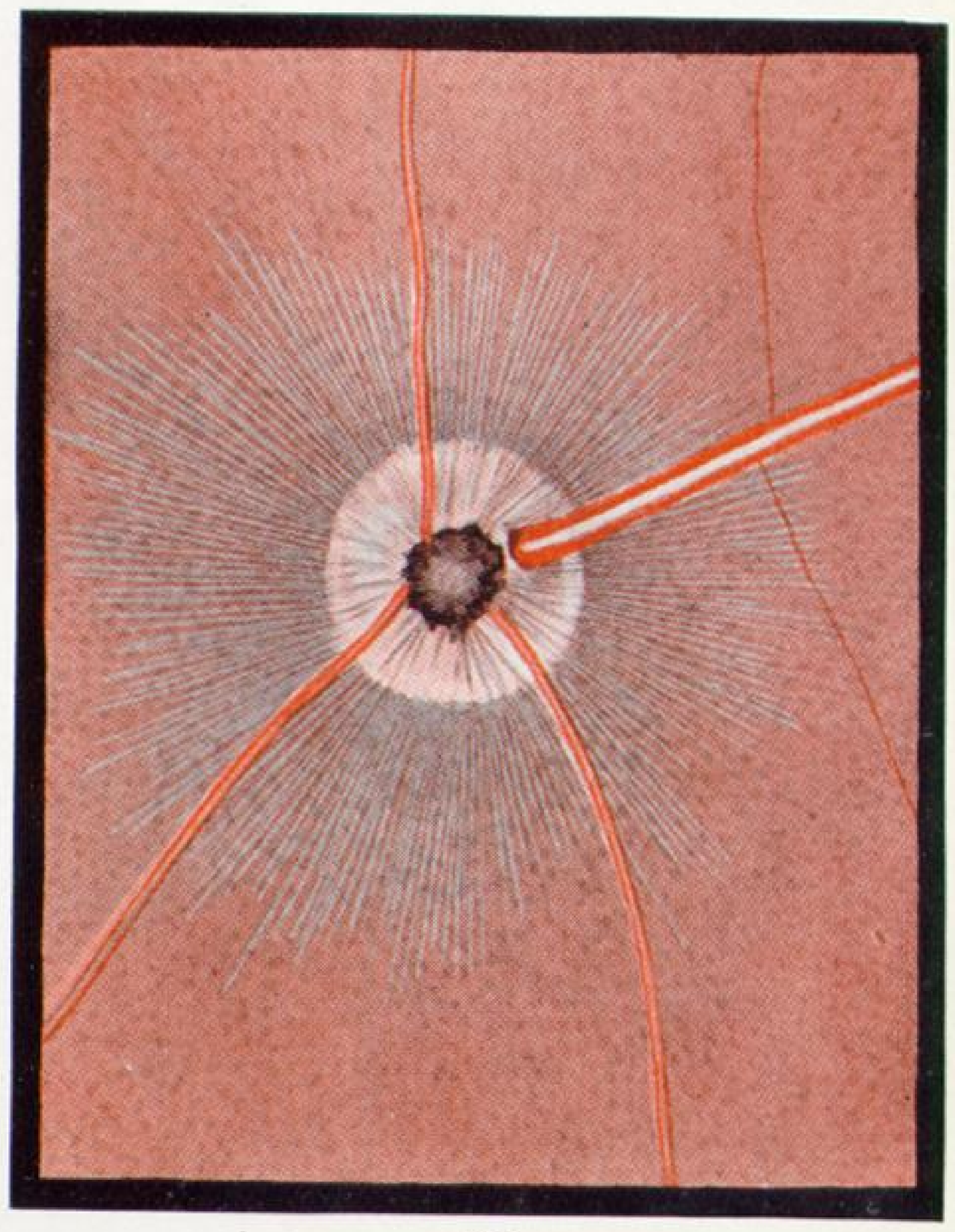

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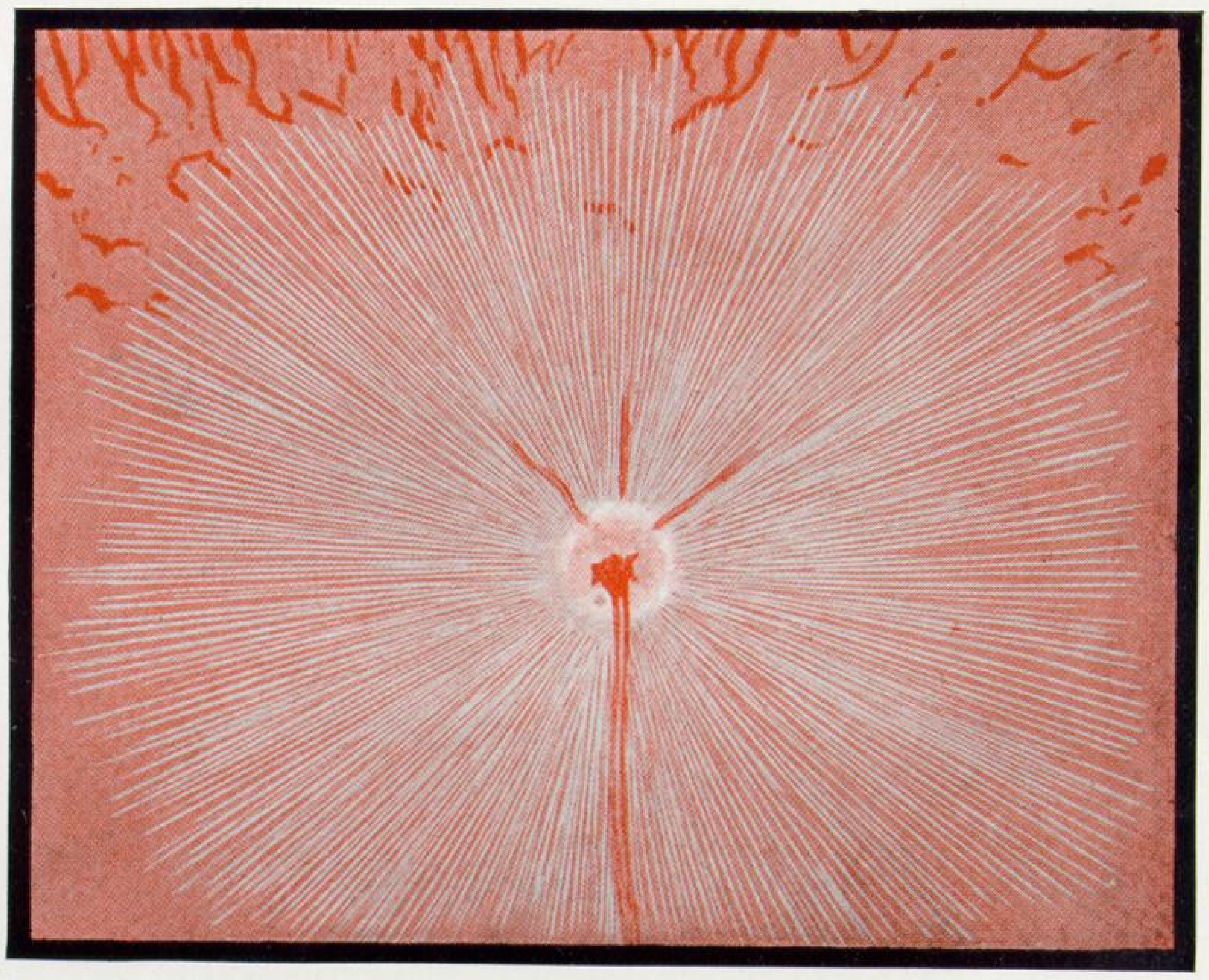

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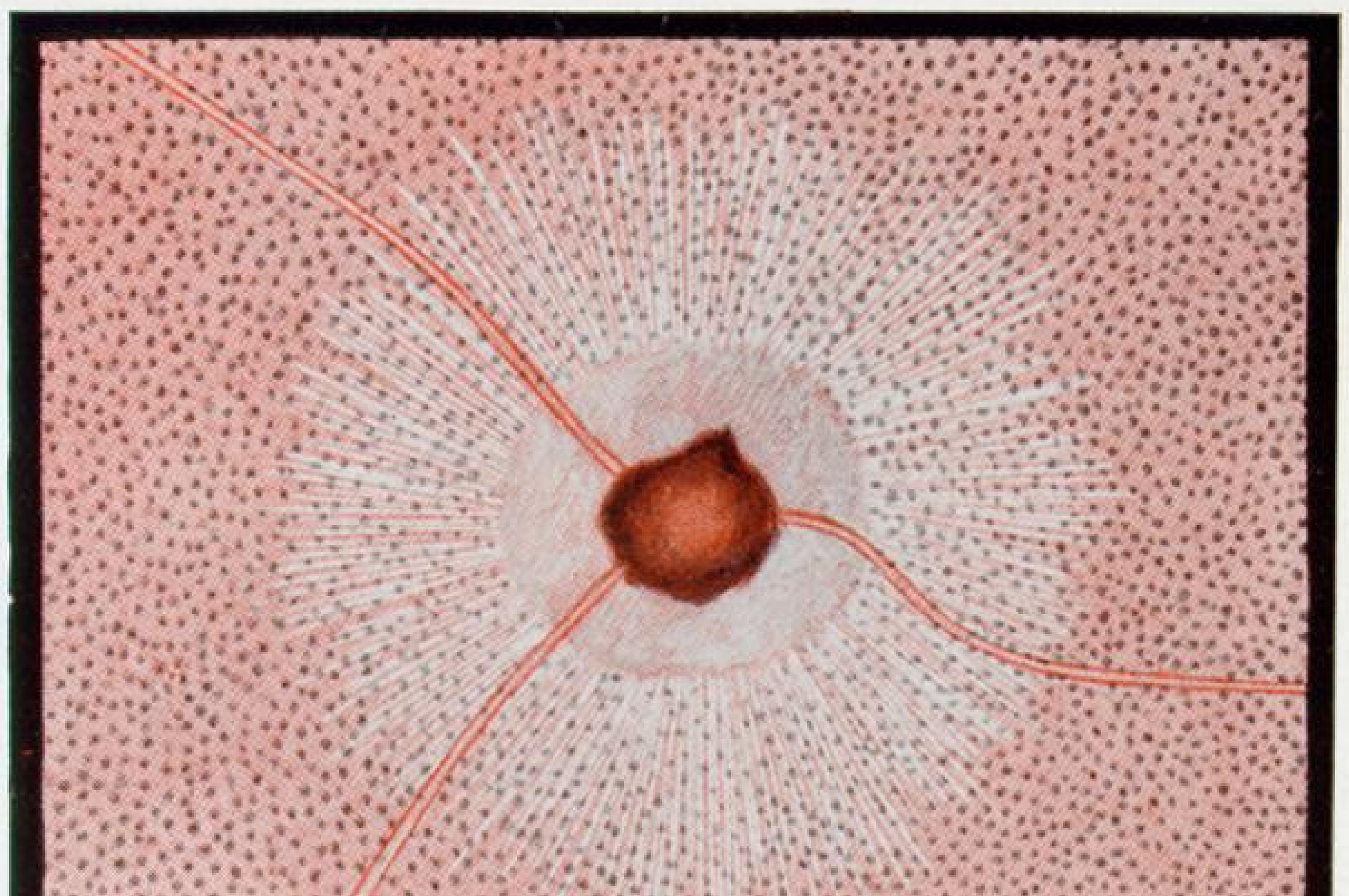

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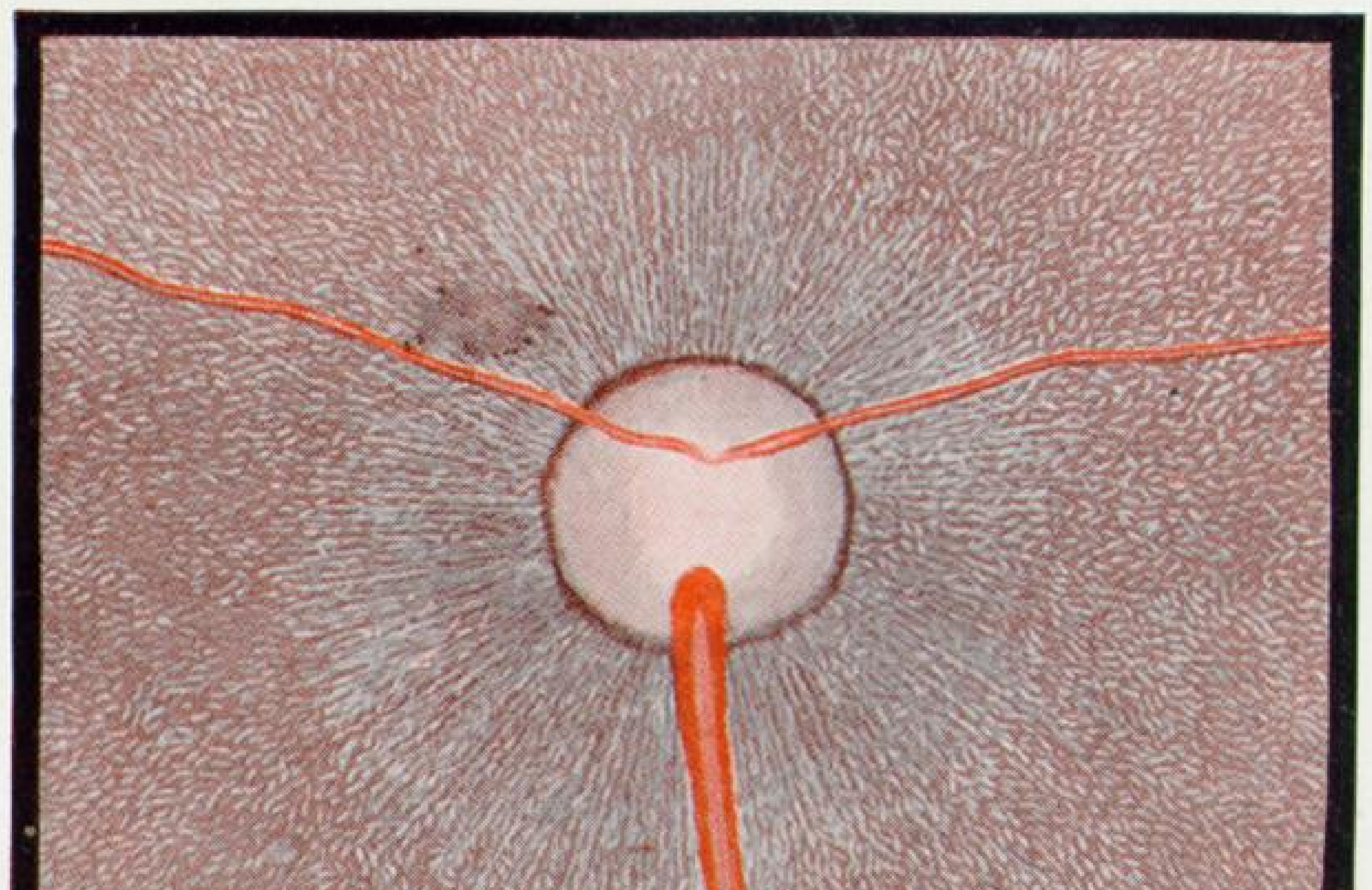

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PLATE 25.

41. *Boa constrictor*. (Turned.)
42. *Coluber guttatus*. (Turned.)
43. *Heterodon madagascariensis*. (Turned.)
44. *Python molurus*.
45. *Tropidonotus piscator*.
46. *T. fasciatus*.