On the Presence and Structure of the Pineal Eye in Lacertilia.

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With Plates XIV, XV, XVI, XVII, XVIII, XIX and XX.

The following work has been carried on in the morphological laboratory of the University of Oxford. It has been made possible solely through the kindness of Professor Moseley, whose invaluable assistance in various ways, especially in procuring from different sources the necessary specimens, I here desire to acknowledge with sincere thanks.

Historical Account.—Though it was impossible for the external indication of the important organ which forms the subject of the following pages to escape the notice of naturalists and more especially of those dealing with the classification of the group, consisting as it does in the modification of a median scale upon the dorsal surface of the head, yet it is strange that only within a very recent period has there been any thorough investigation of the structures lying beneath. This is perhaps chiefly to be accounted for by the fact that the structure in question lies usually within the parietal foramen, enclosed tightly by bone and connective tissue, and is thus left intact within the skull on removal either of the skin from the external or the brain from the internal surface.

Brandt,[1] writing in 1829, uses the following words when describing the skull of Lacerta agilis. "Hinterhaupts-

[1] 'Medizinisch Zoologie,' 1829, Bd. i, p. 160.

schilder 4; selten nur 3; die beiden mittelsten hintereinander stehenden, die kleinsten, das obere, grössere regelmässig 5-eckig, meist mitten, mit einer runden, vertieften stelle," and he adds in a foot-note, "Eine eigne Drüsenstelle bezeichnend." The external marking on the surface of the head is not represented in the drawing of L. agilis (fig. A, Tf. xix), but his description shows that he recognised the presence of an internal modification corresponding to the specialised scale.

Milne Edwards[1] and Dugès[2] both figure the external modification in certain lizards, but neither, strangely, make the slightest mention of it in their descriptions of the animals.

Leydig,[3] writing more than forty years later, is apparently the first to point out with any clearness the presence of the organ, and to give some account of its structure and of the development of the epiphysis, though he entirely failed to discover the relationship existing between the two. Under a high power, he says, the body in question which lies "above the thalamencephalon or the region of the third ventricle," is seen to consist of long cells similar to those of a cylindrical epithelium, so arranged that they form altogether a shallow pit with a circular outline; the rim of the pit is turned upward, and has a thick black girdle of pigment; "welcher schon für das freie Auge das Organ sehr bemerklich macht." After stating that it has a special blood supply, he goes on to say: "Das Organ ist keineswegs, woran Man zunächst denken könnte, die embryonale Zirbel, dem diese folgt erst darunter und ist von ganz anderer Beschaffenheit."

"Fragliches Gebilde entspricht ferner der Stelle, wo sich am skeletirten Schädel des fertigen Thieres im späteren scheitelbeine, das oben schon erwähnte kreis runde Loch befindet."

He examined the organ in Lacerta agilis, L. muralis, L. vivipara, and Anguis fragilis. On pl. xii (fig. 159) he

[1] "Recherches Zoologiques pour servir à l'histoire des Lèzards," 'An. Sci. Nat.,' 1829, tom. xvi, p. 50.

[2] "Mémoire sur les espèces indigènes du genre Lacerta," 'An. Sci. Nat.,' 1829, tom. xvi, p. 337.

[3] 'Die Arten der Saurier,' 1872, p. 72, Taf. 12.

draws a section at right angles to the long axis of the head in L. agilis, passing through the organ in question, which he calls the "Stirn Organ," and the pineal gland. Speaking of this section he says: "Man gewinnt dadurch die Ueberzeugung das es sich um eine innerhalb der Epidermis besonders abgegrenzte Partie handelt; und zwar einer solchen, welche von kugeligen Umriss und zelliger Zusammensetzung über der Oeffnung im Scheitelbein ruht. Unmittelbar unter dem Knochen in der gleichen senkrechten Linie steht die Zirbeldrüse. Sollen etwa die Lagen des Schnittes genauer aufgezählt werden, so folgt von aussen nach innen zuerst die Hornschicht der Epidermis; dan die Schleimschicht und das kugelige zellige, Organ in ihr; darauf die nicht ossificirte, stark schwarz pigmentirte Theil der Lederhaut; alsdann der Knochen mit seinen Markraümen, welche gegen die Oberfläche geöffnet sind. Unterhalb des Knochens kommt die wieder stark gefärbte harte Hirnhaut, und unter dieser, ihr angeheftet die Zirbel; sie verbindet sich durch zwei nervöse Schenkel mit dem Gehirn."

He describes also the presence of the organ in Anguis frigelis; it is present as a small dark spot on the thalamencephalon of very young embryos (cf. Tf. xii, fig. 160), whilst in somewhat older embryos (fig. 162), in addition to the spot, a dark streak is present lying above the unpigmented part, which he recognises as the true pineal gland as well as "ein kleiner unpigmentirter Körper, wie ein winziger Hügel bemerkbar" (fig. 163, c).

These three parts are distinct from the epiphysis itself, and can be seen on removal of the skin from the head. Further, it is evident that the black spot and the black streak are of a similar structure, the walls of each are composed of long cylindrical cells so arranged in the streak as to bound a clear space (see fig. 163), whilst at the black spot they enclose a pit "die vielleicht als Ausgang jener Lichtung zu deuten ist." The cells of both structures have pigment at their inner ends bounding the cavities, the pigment in those of the "spot" being much deeper than in those of the "streak." With regard to the epiphysis, he says: "Die Zirbel deren Stiel aus zwei Schenkeln besteht, liegt unterhalb des 'Punctes' und 'Streifens,' und zeigt sich als etwas von beiden wohl verschiedenes. Ihre Oberfläche hat das schon gedachte, fältige Aussehen, das ich auf eine Zusammensetzung aus gewundenen Schlaüchen bezog. Doch erhielt ich auch den Eindruck, als ob es sich um eine blasige Bildung mit Faltung der Oberfläche handle. Die Zirbel ist vollig unpigmentirt." As to the nature and function of the structure, he says: "Wie das Organ zu deuten sie, wird im Augenblick wohl Niemand zu sagen sich im Stande fühlen. Doch kann ich nicht umhin, einstweilen an die 'Stirndrüse' der Batrachier zu denken und etwas dieser Bildung verwandter zu vermuthen."

In 1882 Rabl Rückhard,[1] dealing with the development of the epiphysis in the Trout, stated that the pineal gland appears early in the median line on the dorsal surface of the brain, between the first and second brain vesicles, as an outgrowth which admits of close comparison with that of the primary optic vesicles. This resemblance led him to the idea of the possibility, supposing certain secondary developments of epiblast (to form a lens) and of mesoblast took place, that the pineal gland might become transformed into an eye just as are the optic vesicles. This result—the formation of an eye more or less closely similar to the paired eyes—is of course precisely that which does not obtain in Lacertilia, where no such secondary development from epiblast and mesoblast takes place.

He says: "Allein während diese unter Mitmirkung des sich zur Linse einstülpenden Ectoderms und des Mesoderms complicirte Veränderungen eingehen, die schliesslich zur Entwickelung des höchst entwickelten Sinnesorganes, des Auges, führen, sehen wir an der Zirbeldrüse trotz der günstigen Lage ihres distalen Endes dicht unter dem Ectoderm nichts dergleichen. Mann denke sich eine ähnliche Wucherung und ihre Folgen, wie an dem die Augenblasen bedeckenden Ectoderm, das Auftreten von Pigment im sich betheiligenden Mesoderm und nichts steht der Vorstellung im Wege, dass

[1] "Zur Deutung und Entwickelung des Gehirns der Knockenfische," 'Arch. f. Nat. und Phys.,' 1882, p. 111.

sich aus der Zirbel ein den Augen ähnliches unpaares Sinnesorgan entwickelt. Interessant ist, dass diese Gegend in einen bestimmten embryonstadium bei Reptilien (Lacerta, Anguis) eine ähnliche Entwickelung wenigstens andeutungsweise zeigt und dass hier am Scheitelbeine des fertigen Thieres sich ein kreisrundes Loch befindet."

In a subsequent paper, which I have not had the opportunity of seeing, but a quotation from which is given by the author in a recent note to the 'Zoologischer Anzeiger,'[1] he apparently makes a further suggestion with regard to the pineal gland, and says "Das Schädeldach der riesigen fossilen enaliosaurier des Lias des Ichthyosaurus und Plesiosaurus besitzt ein unpaares Loch, welches seiner Lage nach mit dem Loch in Scheitelbein der Saurier übereinzustimmen scheint. Vielleicht lag auch hier das viel entwickeltere Zirbelorgan mit seinem distalen Endtheil zu Tage, und man könnte sich vorstellen, das seine Leistung nicht sowohl die eines Sehorgans als die eines Organs des Wärmesinnes war, dazu bestimmt, seine Träger vor der zu ntensiven Einwirkung der tropischen Sonnenstrahlen zu warnen, wenn sie in träger Ruh, nach Art ihrer noch lebenden Vettern der Crocodile, sich am Strande und auf den Sandbänken der Liassee sonnten."

Ahlborn[2] has described carefully the structure of the epiphysis in Petromyzon, giving a series of drawings to illustrate the histology of the part and its attachment to the brain.

He follows Scott in saying that it arises as a glove-finger-shaped outgrowth on the hinder part of the roof of the thalamencephalon in front of the posterior commissure and behind the ganglion habenulæ.

In the adult, according to Ahlborn, the basal proximal part is reduced to a mere rudiment, whilst the most distal portion of the pineal gland has acquired a secondary fusion with the

[1] 'Zool. Anzeig.,' 21st June, 1886, "Zur Deutung der Zirbeldrüse." The paper referred to here was, of course, published subsequently to Ahlborn's paper, "Ueber die Bedeutung der Zirbeldrüse," published in 1884.

[2] "Untersuchungen über das Gehirn der Petromyzon," 'Zeit. f. Wiss.,' 1883, p. 230, Tf. 13 and 16.

terminal division of the left ganglion habenulæ, whereby is simulated the existence of a primitive genetic connection of the epiphysis with the anterior roof of the thalamencephalon.

In the epiphysis Ahlborn states that three parts can be distinguished clearly separated off from each other.

(1) A hinder thread-like stalk.

(2) Two anterior vesicles lying upon one another (Taf. xiii, fig. 2, and Taf. xvi, figs. 43, 44, 46, and 47). The latter form, the "Weisse kuchenartige Masse," which Wiedersheim recognised as the primitive pineal gland, and lie above the point of the beak-shaped roof of the thalamencephalon. The thread-like stalk is attached to the upper vesicle, and corresponds to the proximal and median part of the epiphysis of Selachians and Amphibians (and we may now add to the stalk connecting the "eye" with the dorsal surface of the thalamencephalon of Lacertilia).

The distal portion of the epiphysis consists of two vesicles, of which the upper is the larger; their cavities, save in rare cases, do not communicate with each other. Ahlborn describes the upper vesicle as being a delicate hollow structure, flattened out dorso-ventrally, and placed close to the skeletogenous roof of the cranial cavity. The cells of the lower wall are always much thicker and deeper than those of the upper, and in his figures (Taf. xvi, figs. 44, 46, and 47), though he does not describe them minutely, are seen to have their long rod-like ends free from nuclei, and turned towards the cavity, whilst the nuclei are all placed close to their external extremities. These rod-like structures, however, are quite devoid of pigment, and, moreover, have a thin but well-marked layer of nervous matter present between them and the cavity of the vesicle, which is itself apparently occupied by strands of nervous tissue passing from the posterior to the thin anterior wall. There is nothing comparable to a lens.

The under vesicle is attached on its ventral surface to the left ganglion habenulæ (the whole organ is placed asymmetrically, and lies on the left side), whilst its upper wall is fused with the larger upper vesicle. This secondary fusion with the brain roof necessitating the closure of the epiphysis within the cranial cavity.

Ahlborn[1] has also, in a separate article, discussed the nature of the pineal gland. He does not agree with Van Wijhe, who, following Goette's work on Amphibia, had regarded the pineal gland as "Ein Umbildungsprodukt einer letzten Verbindungs des Hirns mit der Oberhaut" (a mistake corrected later by Van Wijhe (see *infra*). He agrees, on the other hand, with Balfour,[2] who stated that the epiphysis arose as an outgrowth from the dorsal surface of the thalamencephalon, and says, himself: "Das Neuralrohr is relativ lange vor dem Auftreten der ersten epiphysenanlage vollständig geschlossen, der Porus ist nicht mehr vorhanden." He states, further, that the cavity of the primitive pineal gland is a new structure formed as an outgrowth of the neural canal, and "ist also nicht ein Rest der vorderen Verschlussöffnung des Gehirns;" hence it cannot be compared with the anterior neuropore of Ascidians and Amphioxus; but he says: "Durch den Vergleich der Epiphysis cerebri mit einer primitiven Augenblase glaube ich nun eine Reihe sehr gewichtiger Gründe für eine neue und wie es scheint richtige Deutung der Zirbeldrüse gefunden zu haben." He then draws attention to the fact that both the pineal gland and the optic vesicles agree in origin as hollow outgrowths, the only difference between the two being that the optic vesicles are large and laterally placed, whilst the pineal vesicle is small, dorsal, and median. After giving in detail other reasons, he says, Alles zusammengenommen komme ich nun aus folgenden gründen:

(1) Nach mit dem Augenblasen übereinstimmenden Entstehung der Epiphysis durch eine hohle Austülpung der Hirnwand;

(2) nach dem Ursprung und der Verknüpfung der Epiphysis mit der optischen Hirnregion, speciell mit dem Thalamus opticus;

[1] "Ueber die Bedeutung der Zirbeldrüse," 'Zeit. f. Wiss.,' 1884, Bd. xl, p. 331.

[2] 'Elasm. Fishes,' p. 177.

(3) nach der morphologischen Aehnlichkeit des Organs mit einer primitiven Augenblase (Bläschen und Stiel);

(4) nach der angenähert peripherischen Lage des Bläschens bei den Selachiern, Ganoiden und Petromyzonten und nach einer volkommen peripherischen Lage bei den Amphibien (ausserhalb des Schädels auf gleicher höhe mit den Augen;

(5) nach dem ursprunglichen zusammenhang der Epiphysis mit der Nervenleiste (van Wijhe); zu der Vermuthung, das die glandula pinealis als das Rudiment einer unpaaren Augenanlage anzusehen ist. Wenn dieser Schluss richtig ist, so besitzt die Epiphysis als Rudimentäres Stirnauge, wie mir scheint, noch jetzt ein funktionirendes Analogon in dem unpaaren Auge der Tunicaten und vielleicht auch des Amphioxus."

Van Wijhe, dealing with the development of Selachians, stated first that the anterior neuropore (the spot at which the brain remained last in connection with the epidermis during closure of the neural canal) corresponded to the pineal gland as was stated by Goette to hold true for Amphibia. In his more recent paper,[1] wherein he describes the results arrived at by working with duck embryos, he corrects his first mistake, and states that in birds, though the neuropore exists till the stage with twenty-eight somites, it then completely disappears, whilst when twenty-nine somites are present, the earliest rudiment of the epiphysis appears.

Hoffmann[2] states that in representatives of nearly all classes of Vertebrates it has been proved that the epiphysis arises as an evagination of the roof of the thalamencephalon, and figures its earliest stages in various reptilian embryos (Tropidonatus natrix and Lacerta); showing also that it is perfectly distinct from, though present at the same time as, the anterior neuropore. The latter, he says, indicates the position where the "Vorderhirn" joins the "Zwichenhirn" whilst the epiphysial

[1] "Ueber den vorderen Neuroporus und die phylogenetische Function des Canalis Neurenterious der Wirbelthiere," 'Zool. Anzeig.,' 1884, p. 683.

[2] "Weitere Untersuchungen zur Entwickelungsgeschichte der Reptilien,' 'Morph. Jahr.,' Bd. xi, 1885, p. 192.

rudiment is situated where the "Zwichenhirn" and the "Mittelhirn" unite. He states further: "Die vordere Ausbruchtung der Epiphysis schnürt sich volständinge von den Hirndach ab; sie bildet eine kleine, runde, selbstandige Blase von plattgedruckter Form und stellt die Anlage des sogenannten Leydigschen Organes von Strahl hat dieses zuerst erkannt und ich kann seinen Befund bestatigen."

The most recent, as well as most interesting work upon the pineal gland is that of de Graaf,[1] to whom is certainly due the merit of having first clearly shown that in one particular animal (Anguis fragilis) the pineal gland actually is modified into a structure comparable to an Invertebrate eye. He says: "Dem zufolge gleicht bei Anguis fragilis das ganze abgeschnürte Stück etwa dem Auge eines höher entwickelten wirbellosen Thieres, wie uns z. B. Cephalopoden, Pteropoden und Heteropoden bekannt ist."

According to de Graaf the Epiphysis, in Amphibia and Reptiles (Lacertilia), arises as a hollow outgrowth of the thalamencephalon,[2] never passing much beyond this stage in Urodeles (Pl. 2, figs. 13—18), but in Anura and Lacertilia becoming divided into two parts. In the former, growth results in the formation of a distal bladder-shaped portion and a solid stalk connecting this with the brain-roof (Pl. 2, figs. 22—29); the distal part is gradually constricted off from the stalk and comes to lie excerebrally and finally without the cranium and close beneath the skin; the stalk, on the other hand, lies permanently within the brain membranes and thus enclosed in the skull cavity.

In the adult, he says, the cut-off portion of the epiphysis ("Stieda's gland") lies embedded in the cutis close beneath the epidermis, is surrounded by a specially close-woven case,

[1] (*a*) "Zur Anatomie und Entwickelung der Epiphyse bei Amphibien und Reptilien," 'Zool. Anzeig.,' 29th March, 1886. (*b*) 'Bijdrage tot de kennis van den bouw en de ontwickkeling der epiphyse bij Amphibiën en Reptiliën,' van Henri W. de Graaf, Leiden, 1886.

[2] He thus differs from Goette in regarding the epiphysis as a secondary outgrowth, having nothing to do with the neuropore.

and shows retrogressive metamorphosis, undergoing fatty degeneration. What Goette regarded as the epiphysial stalk is, according to Graaf, nothing more than a branch of the Ramus supra-maxillaris of the fifth nerve, and always terminates in the connective-tissue case, never in the organ itself. The extra-cranial part, though present in the adult Rana esculenta, R. temporaria, Alytes obstetricans, Bombinator ingens, and Bufo cinerea, is completely wanting in the full-grown Hyla arborea. In Reptilia the development of the epiphysis takes place as in Amphibia, the distal portion being, according to de Graaf, completely cut off from the proximal stalk; it lies between the brain membranes and has the form of a small, roundish, more or less flattened out vesicle, and shows cellular structure. The wall lying in contact with the parietal foramen is thickened and lens shaped, whilst the hinder wall is pigmented on its inner side.

De Graaf describes in some detail and figures (Pl. 4, figs. 32—34) the organ in Anguis fragilis. Reference to this description will be made later on.

Results of the present investigation.

I desire in the first place to acknowledge the kindness of Dr. Günther, to whom I am indebted for the gift of examples of different genera (indicated by an asterisk in the list below) from the duplicate specimens of the British Museum; my thanks are also due to Professor Stewart for the opportunity of examining specimens of Iguana and Varanus from the collection of the Royal College of Surgeons.

To E. B. Poulton, Esq., of Keble College, and to F. Beddard, Esq., of the Zoological Society, I am indebted for specimens of Hatteria.

My thanks also are due to Professor Westwood for the gift of a fine Chameleo vulgaris, and for the opportunity of examining C. bifurcatus; and to G. C. Bourne, Esq., of New College, for a specimen of Gecko mauritanicus.

I have also to acknowledge gratefully the gift of various species of Lacertilia, prepared especially and sent to me from the Bahamas by J. Gardiner, Esq.; they arrived too late for the results of their examination to be included in the present article, but I hope to be able to publish an account of the structure of the organ in these forms in a short time.

The forms investigated have been the following:

Hatteria punctata.	Lyriocephalus scutatus.
*Varanus giganteus.	*Calotes versicola.
„ bengalensis.	* „ ophiomaca.
Monitor (sp.?).	*Agama hispida.
Ameiva corvina.	*Stellio cordylina.
Chameleo vulgaris.	*Grammatophora barbata.
„ bifurcatus.	*Moloch horridus.
Gecko verus.	Leiodera nitida.
„ mauritanicus.	Anguis fragilis.
Anolis (various species).	Cyclodus gigas.
Leiolœmus tenuis.	Lacerta ocellata.
*Uraniscodon (Plica) umbra.	„ viridis.
*Iguana tuberculata.	„ (Zootoca) vivipara.
Draco volans.	Seps chalcidica.
*Ceratophora aspera.	

The material has, in the great majority of cases, consisted of spirit specimens in a better or worse state of preservation so far as histological structure was concerned, so that in many instances it has been impossible to do much more than ascertain the presence or absence of the organ, its connection or separation from the proximal part of the epiphysis, and perhaps a few details with regard to its histological structure. Even in fresh specimens the organ lies so deeply embedded in connective tissue and so closely shut in by bone, which must be removed along with it to prevent injury to the structure, that there is great difficulty in rapidly reaching it with reagents. Of two of the most important forms—Hatteria punctata and Varanus giganteus—I have had the great advantage, through Professor Moseley's kindness, of examining fresh specimens, and have thus been able to investigate more carefully the structure of the retina.

In the account which follows the structure of the organ is described separately in the different forms examined; this structure, as might have been expected to be the case in an organ of this kind (which must be regarded as in a more or less rudimentary condition), shows considerable variation, even amongst species of the same genus. I hope on a future occasion to describe the organ in other forms of Lacertilia.

Hatteria punctata, Pl. XIV, figs. 2, 3, 4, and 5; Pl. XV, figs. 7 and 8; Pl. XX, fig. 7.

(1) External Appearance.—There is in Hatteria but very little external trace of the eye, no special scale being modified into a "cornea;" an absence of pigment, however, in the skin of the median line, slightly posterior to the level of the paired eyes, indicates the position of the parietal foramen; this external indication being more evident in some than in others.

(2) Position of the Eye.—The foramen itself is filled up by a plug of connective tissue, which, notwithstanding the absence of pigment, must effectually prevent the organ lying beneath from functioning as an eye in the ordinary sense of the word; light would more easily penetrate the skin at this than at any other portion of the surface of the head, but yet it is perfectly impossible for an image to be formed upon the retina. The fibres of the connective tissue in the foramen may be divided into two sets—(1) an outer set (Pl. XV, fig. 7, *Ct*[1]) arranged on the whole at right angles to the surface of the head, and which on the inner side of the foramen are connected with (2) an inner set lying immediately in front of the eye, and arranged so as practically to form a hemisphere, part of the internal surface of which forms the anterior boundary of a capsule enclosing the eye (figs. 2, 7, and 8, *Ct*[2]). The hinder half of the capsule which thus lies in the lower part of the foramen is formed of somewhat loosely aggregated fibres with well-marked nuclei scattered irregularly amongst them, and is drawn out in the direction of the optic stalk, which, together with a blood-vessel, pierces the capsule wall at its

most posterior point (fig. 2); the extreme length of the capsule is 1·4 mm. Special fibres cross from the capsule wall to the edge of the lens, and, being connected with the tissue immediately surrounding the retina, may serve the purpose of keeping the eye in position, and thus represent the rudiment of a structure of importance when the eye was fully functional. The capsule in its hinder part contains much irregularly scattered connective tissue with nuclei, its anterior part, however, being free from them. Within the capsule breaks up an artery (figs. 2 and 7, *B.v.*) whose branches ramify amongst the fibres behind the eye; this special blood supply is a prominent feature in connection with the organ in all the forms examined.

The eye lies with its long axis directed upwards and forwards in the most anterior part of the capsule; figs. 7 and 8 show the relative position of the eye in its capsule with regard to the brain and the parietal foramen.

Structure of the Eye.—Through the kindness of Prof. Moseley I have been able to examine the structure in a fresh specimen, and, notwithstanding the fact that the organ cannot now be fully functional, the retina is fairly well developed.

The eye has, roughly speaking, the shape in section (Pl. XIV, fig. 2) of a cone, the base of which lies turned towards the surface, whilst the pineal stalk is connected with the apex. The walls of the optic vesicle are divided into two parts, (1) an anterior; (2) a posterior; of which the former forms the lens, and the latter the sensitive structures.

(1) Lens.—The lens of the pineal thus differs markedly from that of the paired eyes, where it originates as a secondary structure by invagination of the epiblast, whilst in the former it is apparently directly the product of the brain wall itself, and equivalent in position to that part of the paired optic vesicles which after invagination forms the retinal elements.

De Graaf has likened the eye to that of such Invertebrates as Cephalopods and Pteropods; but, apart from other differences which exist between the two in regard to both development and structure, the lens is not in the least degree comparable in the two cases, being in the Invertebrates mentioned formed as a cuticular secretion.

In Hatteria as in all forms examined it is distinctly cellular, the nuclei being prominent and numerous (fig. 2). The median cells are elongate so as to give the lens a curious cone shape, the base corresponding to the front of the eye and the apex lying in the optic axis; the cells are further arranged in a definite manner as shown in fig. 2, and are, as the latter indicates, directly continuous with those of the retina.

(2) Retina.—The retinal elements are arranged in the manner typical of Invertebrates, i. e. the rods lie on the inner side bounding the cavity of the optic vesicle, the nerve entering posteriorly and not spreading out in front of the rods.

Within the same vertebrate animal we thus find eyes developed on both vertebrate and invertebrate types, both being also formed from the modification of the walls of hollow outgrowths of the brain.

The retina consists of the following elements (Pl. XIV, figs. 2, 3, 4, and 5):

(1) A layer of rod-like bodies (*R*) enveloped in deep pigment, which when the rods are separated (fig. 5) is seen to be so deposited upon them as to produce a striated appearance. The pigment is specially densely deposited around the margin of the retina in contact with the lens, extending here through the whole thickness of the wall. A curious specialisation takes place in connection with the rods lying in the optic axis, which also obtains in the pineal eye of many other forms. The rods in this portion are elongated (R^1) to at least twice the length of the ordinary ones, and are in connection at their outer ends with a special group of nucleated cells (n^3) which lie enclosed by a somewhat definite membrane in the pineal stalk, with the fibres of which they are directly connected (fig. 4).

(2) A double and, in parts, triple row of spherical nucleated elements (n^1), which appear to be connected by processes, on the one hand with the rods, and on the other with the layers external to them. They surround posteriorly the elongate rods,

and their processes in this region run in many cases (n^4) directly into connection with the fibres of the optic stalk. The layer gradually thins out anteriorly until that part is reached where, in the neighbourhood of the lens, the pigment is present through the whole breadth of the wall. In its thickest part the whole layer (consisting of the double or triple row of elements) is about the same breadth as the layer of rods.

(3) External to the spherical elements lies a thin layer consisting of a fine punctated material, which takes the stain (hæmatoxylin) with difficulty but contains numerous scattered fine pigment granules. Into this, which may be called the Molecular layer,[1] pass processes from the retinal elements on either side (fig. 2, *mo.*). The layer in question is a very thin one in Hatteria punctata, but forms, when seen in section (fig. 2), a definite boundary line separating the retinal elements into an internal and an external division. Posteriorly the layer spreads out and surrounds the specially elongated rods in the optic axis, anteriorly it reaches as far forwards as the ring of pigment surrounding the lens. It is possible that this layer and many of the processes passing into it may be of the nature of supporting structures.

(4) A layer of nucleated spherical elements (fig. 3, n^2) lying close to the molecular layer, and distinguished from those on the inner side by their greater size; they are arranged so as to alternate (the alternate arrangement is, however, by no means perfectly constant) with

(5) A layer of cone-shaped bodies (*Co.*) in which no nuclei can be detected. They lie with their broad ends externally, and gradually taper internally till their pointed ends are closely in contact with the molecular layer into which processses from them run (fig. 3).

(6) Between the bases of the above are a series of spindle-shaped elements with nuclei, from which processes pass off internally, which may either run directly into the molecular layer or into the spherical bodies on its external side. At the

[1] Cf. de Graaf, Pl. 4, fig. 34, *gl.*

posterior part (i. e. near the pineal stalk) the cone-shaped elements seem to be absent, and their place to be taken by large nucleated spindles (*Co*[1]), which, as it were, bend round internally (fig. 5) and give off processes running directly into the fibres of the stalk.

Connection with the Brain.—It has hitherto been stated by all writers that the distal part of the epiphysis becomes separated from the proximal which forms the pineal gland of the adult, and that the former comes to lie (as shown by de Graaf in Anguis fragilis) external to the cranial cavity in the parietal foramen. De Graaf[1] figures in Anguis the eye as fitted closely into the parietal foramen encased by connective tissue, but separated by a considerable interval from the proximal hollow epiphysial stalk from which in development it has been cut off.

In Hatteria, as also in several other forms to be described below, longitudinal vertical sections show clearly that the highly developed eye is connected with the epiphysis by a solid and well-marked stalk, which may be called the pineal stalk.

This runs in the median line backwards and slightly downwards; it enters the eye at the posterior end, the walls of the optic vesicle being here (fig. 2) drawn out somewhat backwards. The relationship of the elongated rods to the stalk has been already described; passing backwards from the eye the stalk makes a decided bend upwards, then pierces the wall of the eye capsule at its most posterior point and runs straight back to the epiphysis; its fibres enter the latter, being apparently connected with the cells of the apex and the under surface. The pineal stalk contains elements which have much the appearance of those found at an early stage in the developing nerve of the paired eyes, that is, they much resemble cells which are undergoing a process of elongation so as to form long fibres (figs. 2 and 4); some having undergone considerable elongation, others being yet spindle shaped.

There can be little doubt that this median, azygos, nerve

[1] Pl. 4, figs. 31, 32, 33, and 34.

represents the originally hollow process uniting the proximal with the distal portion of the epiphysis, and which, losing its connection with the optic vesicle in some forms (e.g. Anguis), is in others (e.g. Hatteria) transformed into a solid stalk serving as the nerve of the pineal eye. It has been sufficiently demonstrated that the latter is the distal portion of the epiphysis, and we are thus presented with a new sensory structure —the pineal eye—agreeing precisely with the paired eyes in (1) its development as an outgrowth from the walls of the neural canal, and (2) the formation of its nerve by the gradual solidification of the primitively hollow tube connecting the distal vesicle with the proximal portion of the outgrowth. In the case of the paired eyes the whole of the outgrowth save the vesicle is transformed into a nerve; in the pineal eye only the median part of the outgrowth is thus metamorphosed, the proximal part retaining its originally hollow nature.

Varanus giganteus, Pl. XIV, fig. 1, fig. 6; Pl. XV, fig. 10; Pl. XIX, fig. 34.

External Appearance.—In a large specimen of this animal, measuring six feet one inch from the snout to the tip of the tail, which I was enabled to examine in the fresh state through Professor Moseley's kindness, the external indication of the eye is so clear that it is remarkable that no one has hitherto examined the organ lying beneath. The head is covered with small, deeply-pigmented tubercle-like scales, save in the median line, where, somewhat posterior to the paired eyes, a single large scale is present, standing out prominently by reason of its creamy whiteness (fig. 10).

The scale is roughly hexagonal in shape, measuring 5 mm. across, and has upon it a slightly-raised circular rim, the area within which has the appearance of a transparent membrane drawn tensely over a cavity beneath. A dark circular spot in the middle, visible in the living animal, indicates the position of the eye, and is, as will subsequently be shown, due to the presence of a mass of pigment in the lens. In the matter of external indication of the structure Varanus thus differs much from Hatteria in the possession of this scale, modified to form a cornea.

Position of the Eye.—The cornea thus formed lies immemediately above the parietal foramen, the space in which is tightly filled by connective tissue, in the midst of which again lies the pineal eye. There is thus no real cavity beneath the cornea, but the pigment, which elsewhere is abundantly present in the skin, is here entirely absent, so that by this means the passage of light to the organ is much facilitated. Beneath the epidermis and the rete mucosum the connective-tissue fibres of the cutis vera are arranged in two definite sets, as in Hatteria: (1) a series running parallel to the anterior surface of the eye from side to side of the foramen (Pl. XIV, fig. 1, Ct^2), interlacing with each other, and thus forming a dome-shaped structure above the eye; and (2) a series of bundles (Ct^1) at right angles to the former, upon which they spread out at their internal ends, whilst externally they run outwards to the rete mucosum. Obliquely directed strands pass from one bundle to another, and the irregular spaces thus left are filled up by a meshwork of indefinitely arranged fibres.

Immediately below the level of the first series of fibres is placed the eye itself, but, instead of lying, as in Hatteria, in a capsule, the connective tissue closely invests it. The tissue within the parietal foramen may be divided into three parts: (1) a series (Ct^3) bounding the sides of the parietal foramen, and continuous with the upper series (Ct^1); these follow in their course the outline of the bone; (2) irregularly arranged fibres (Ct^4), filling up the greater part of the foramen; (3) a series forming a special encasement for the eye, to the sides of which their long axes are parallel (Ct^5, the arrangement of these is scarcely made sufficiently prominent in the figure).

In Hatteria is found a special capsule in the space within which the eye is situate. Even in this form a certain amount of connective tissue lies within the capsule, whilst a still greater development of the tissue would lead to the condition which obtains in Varanus giganteus.

In addition to the connective tissue within the foramen a large blood-vessel is present, which, accompanying the optic stalk till the foramen is reached, breaks up in this into numerous branches ramifying in the connective tissue (*B.v.*), a branch finally passing from either side in front of the eye (fig. 1), whilst one pierces the connective-tissue dome.

Structure of the Eye.—The eye is, though the size of the two specimens of Hatteria and Varanus are so different (Hatteria under 2 ft., Varanus 6 ft.), as nearly as possible precisely the same size in both, measuring, in the line of the optic axis, ·4 mm., but in Varanus the eye is compressed somewhat in this direction, so that it is broader from side to side slightly than in Hatteria (cf. figs. 1 and 2).

Lens.—The lens is distinctly cellular in structure, the cells being elongated in the direction of the optic axis, and having the appearance of stretching the whole breadth of the lens, their nuclei, which are very prominent, being situated so that in section (fig. 1) they form a well-marked line across the lens from side to side somewhat nearer to the inner than the outer surface. The whole lens has the appearance represented in fig. 1, being thickest in the median line and thinning away rapidly at each side where it joins the retina.

Right in its very middle is present a large, more or less globular mass of small spherical cells, deeply pigmented (fig. 1, *pig.*), and lying directly in the optic axis. The presence of these must of necessity interfere with the action of the organ as an eye, in fact, the whole structure is characterised by the presence of a great amount of pigment deposited in every part. It is this pigment in the lens which causes the eye seen through the transparent cornea to appear like a black spot, and its presence, which must be regarded as due to degeneracy in the tissues, indicates that the organ is now in a rudimentary condition.

Structure of Retina.—The rods line the cavity of the vesicle and form a very definite layer, being deeply embedded in pigment, which renders it difficult to distinguish their outlines. Processes pass from them, often accompanied by pigment granules, into the external-lying layers. As in Hatteria certain of the rods become elongated; this lengthening is con fined in the former to those lying in the optic axis, but in Varanus takes place at two points, one of which, the most prominent, lies in the optic axis, whilst the other lies to the anterior side, each being connected with the entrance of a separate nervous strand into the eye.

Amongst the rods are scattered numerous spherical masses of pigment. There is not the slightest indication of any structures lying internal to the rods embedded in pigment, such as are described by de Graaf in Anguis; on the other hand, the internal limit of the layer of rods is so well marked as to present the appearance of a definite membrane lining the cavity. The latter was most probably filled during life by a fluid, the coagulated remains of which are seen attached as an irregular structureless coagulum to the inner ends of the rods. External to the rods is a layer of finely punctated material (*Mo*) apparently corresponding to the much narrower layer in Hatteria. This layer, together with the rods, occupies as nearly as possible one half of the breadth of the retina. In this layer are situated spherical elements (n^1), which in some cases can be traced into connection with the rods; no arrangement in two or more rows, as in Hatteria, can be detected, but they appear to be placed somewhat irregularly. External to the molecular layer, the outer limit of which is somewhat sharply defined, lie a series of spherical-shaped elements (n^2). The appearance of these as seen in section is given in fig. 6. Some of the elements resemble those lying within the molecular layer (n^1), others have processes passing straight through to the rods on the internal and the nerve-fibres on the external side, whilst others again are connected with one another and with the layers on either side by irregularly branching processes.

Certain of the nerve-fibres pass round behind the vesicle and then enter the retinal elements, but apparently the greater number are directly connected with the two above-described bundles of elongated rods.

Within the external layers of the retina are many large spherical masses of deep brown pigment (*pig.*[1]), connected in some cases with the pigment enclosing the rods; beyond this, again, a certain amount of pigment in minute granules is scattered irregularly amongst the external spherical elements, and completely external to the optic vesicle posteriorly is massed around the entrance of the nerve a great amount of pigment deposited in branchial cells (*pig.*[2]).

Nerve.—The pineal stalk is well marked in Varanus giganteus and differs moreover from anything met with amongst other forms (even other genera of Varanus).[1] Instead of being single there are three distinct nervous strands entering the vesicle posteriorly; two of these are more prominent than the third, which appears to be in connection with the anterior of the former; the single posteriorly placed nerve entering very nearly but not quite in the line of the optic axis. The larger and smaller anterior strands join together, and then, after a marked curve, shared in by the posterior one, they join the latter and run back as the solid pineal stalk to the proximal part of the epiphysis.

At first it seemed possible that the appearance described might be due to the cutting in longitudinal section of the walls of a hollow stalk distorted somewhat by reagents, but an examination of a continuous series soon showed that this was not the case, and that the pineal stalk, single proximally, broke up distally into two, and finally into three separate nerves entering the optic vesicle.

The most noticeable features in the eye of Varanus are:

(1) The great development of pigment in all parts, and more especially in the lens.

(2) The curious nature of the retina, which has really the form of a cellular network; the cells being in connection with one another by branched processes, the nuclei being scattered somewhat irregularly and giving rise, together with the protoplasm around them, to the spherical elements of the retina.

[1] The only other lizard as yet examined, in which anything comparable to this is found, is Lacerta ocellata, to be described later on.

Reference to this structure of the retina will be made again when dealing with the epiphysis in Cyclodus.

(3) The triple nature of the pineal stalk.

Varanus bengalensis, Pl. XV, fig. 12; Pl. XVI, fig. 17; Pl. XIX, figs. 37 and 41.

External Indication.—In the several specimens of Varanus examined (in addition to V. giganteus) the external indication of the eye was very clear indeed, consisting of a large, modified, median scale (Pl. XIX, fig. 37), lying somewhat posterior to the level of the paired eyes, and having at its centre a circular dark space, surrounded at a short distance by a dark circular line. The central part, which is to a certain extent transparent, acts as a cornea for the eye placed beneath.

Position of the Eye.—In small specimens of Varanus, when the skin is removed from the head, the pineal eye is removed with it and may be examined whole. Fig. 12 represents a portion of the skull roof of a very young specimen of V. bengalensis viewed from the under surface, the bone being very thin indeed. The portion surrounding the parietal foramen is represented in the figure, together with the pineal eye, lying in the latter and viewed as a solid object. The foramen has a somewhat oval shape and backwards from it leads a groove in the median line. The specimen from which this is taken was not in good histological preservation, and no connection with the brain can be traced. The eye is circular in outline and depressed from above downwards, and shows, when viewed by transmitted light, the rods embedded in pigment and forming a very definite layer. Since they line a space within the vesicle, circular in outline, those at the sides, when the object is viewed from above or below, form a circle (*R*), external to which lie the other elements of the retina. In the optic axis posteriorly lies a prominent mass of rods more deeply pigmented than elsewhere, and which indicate most probably a series of elongated rods connected with the union of the pineal stalk; the latter may have been pulled away along with the brain membranes when the surface of the skull was removed from above the brain.

The connective tissue lying external to the eye is quite transparent, and being placed as it is immediately beneath the skin, the entrance of light is thus made possible; in fact, it is impossible to prevent the light from entering, not only in this but in the case of the pineal eyes of all other Lacertilia, when they are placed so near to the skin.

In section, the eye of a somewhat larger V. bengalensis shows the following structure differing much from that of V. giganteus, a difference the more noticeable since it exists between members of the same genus.

Fig. 41 represents a longitudinal section along the median line of the head passing through the parietal foramen; the results are represented somewhat diagrammatically. The eye lies within the foramen tightly enclosed again within connective tissue, no special capsule being present. A very noticeable feature is the entire absence of pigment above the eye, though this is present in abundance in the skin elsewhere (*Ct, pig.*) in the connective tissue of the cutis vera. The eye itself is depressed dorso-ventrally, so that but comparatively little space remains within the vesicle; the latter lies directly above the anterior extremity of the proximal part of the epiphysis, which runs right up into the foramen from the dorsal wall of the thalamencephalon lying some distance posteriorly.

Fig. 17 gives a more detailed representation of the foramen with its contents. Beneath the cuticle (*cu.*) the epidermis is seen (*ep.*), then the rete mucosum, the nucleated cells of which are in this part somewhat longer than those elsewhere; beneath this lies the connective tissue of the cutis vera (*Ct*). On either side of the foramen are numerous pigment cells (*Ct, pig.*), and the fibres as before may be divided into two series—(1) a set running at right angles to the long axis of the head, and (2) others forming a roof for the foramen, and connected with those lying within the latter, which form a close investment for the eye (Ct^5).

Within the foramen also is a much branched blood-vessel which enters along with the epiphysial stalk; a small branch passes forward on either side in front of the eye just as in V. giganteus. The figure shows the specialisation in the connective tissue above the eye, and the entire absence of pigment-bearing cells in the same position, though they are present on both sides in the section.

Lens.—The lens has very much the same structure as in V. giganteus, being distinctly cellular with well-marked nuclei, forming in section a double or triple row from side to side, the cells appearing to run the whole breadth, whilst in the middle of the lens a great mass of pigment is deposited in the line of the optic axis. The pigment masses are spherical on the external, and more rod-like on the internal surface.

Structure of Retina.—The specimen being preserved in spirits without special reference to histological work, it was somewhat difficult to make out many points with regard to the structure of the retina. The rods are well developed and prominent, lining the cavity of the vesicle, and having their long axes arranged as indicated in the figure, those in the optic axis being at right angles to the external surface, the eye itself being immovably fixed, so as to look directly upwards. They are embedded in pigment, and none amongst them appear to be specially elongated (associated, doubtless, with the absence of connection with any nerve, such as is present in V. giganteus or Hatteria). No trace of any definite structure internal to the rods can be seen.

External to the rods lie a series of spherical-shaped elements (*n'*), corresponding, presumably, to the same in Hatteria and V. giganteus, and at intervals amongst these can be detected spindle-shaped bodies, which, together with the former, stain easily (with hæmatoxylin and borax-carmine). Both these lie within a layer, consisting, as in V. giganteus, of finely-punctated material, whose external limit is well defined. It is difficult to ascertain precisely the structure of this particular layer, which in these two (as well as in other forms) has the appearance of a ground substance, in which lie the external ends of the rods and the spherical elements, but its constant presence and character renders it unlikely that it is the result simply of reagents; it is here called the molecular layer, but may, perhaps, differ in nature from the layer to which the same name is applied in Hatteria.

External to this lies a series of cone-shaped bodies (*Co.*), the pointed internal ends of which abut against the molecular layer, their broader external extremities being placed against the limiting membrane of the eye, where a certain amount of pigment (*pig.*[1]) is deposited in the form of fine granules.

In some cases a connection (not well drawn in the figure) can be traced between the cones and the rods, or, in other cases, the spherical elements. This connection is best developed in the optic axis.

Epiphysis.—In a preliminary communication to the Royal Society[1] the eye of one specimen of V. bengalensis was described as connected with the brain by a hollow epiphysial stalk. Further investigations have shown that this statement must be modified. It is by no means easy to determine the point, and possibly with a fresh specimen a connection between the eye and the proximal portion of the epiphysis may be shown to exist. The two come very close together (closer than is represented in fig. 17), and there is a decided appearance of a connection between them. Further study of my sections has failed to establish the point, and fig. 17 represents, as far as can at present be ascertained, the actual state.

The epiphysis (fig. 41) may be divided into three parts: (1) the distal, separated off as the pineal eye; (2) a short, hollow, proximal portion, arising from the roof of the thalamencephalon, and running at right angles to this; and (3) a median portion running forward from the end of the latter along the roof of the cranial cavity enclosed in the brain membranes. This part also is hollow, and its walls consist of a single layer of distinctly nucleated columnar cells. Its distal extremity lies immediately beneath the pineal eye, and is swollen out and filled with blood-corpuscles, the cells in the wall of this part being somewhat cubical in shape. Passing backward the walls approach one another until they come into contact, and for a short distance a solid stalk is formed; further back, again, the walls part from each other, and in this region the cells lengthen out very much until they pass into the proximal part (fig. 41).

[1] 'Proc. R. S.,' "Preliminary Communication on the Structure and Presence in Sphenodon and other Lizards of the Median Eye, described by de Graaf in Anguis fragilis," June 10th, 1886.

Monitor (sp. ?).—In the Monitor examined there was no external trace of the organ to be discerned, though when the skin was removed from the dorsal surface of the head and viewed by transmitted light, an absence of pigment and general transparency in the spot overlying the parietal foramen indicated the position of the eye. The latter could be easily distinguished as a small black spot lying within the foramen, which was itself, in the form examined, extremely small. Unfortunately the specimen was in a bad state of preservation histologically, and the tissues very dry, so that it was again impossible to make out the details of the structure. The eye, which is deeply pigmented save anteriorly, where is the lens, appears to be placed at the distal extremity of a pineal stalk which, as in Varanus giganteus, runs up vertically through the foramen, accompanied as usual by a large artery.

Chameleo vulgaris, Pl. XVI, fig. 21; Pl. XIX, fig. 40; Pl. XX, fig. 6.

In this form a curious modification takes place, an optic vesicle being formed but not reaching any high degree of development. In the short account written in 'Nature,'[1] it was stated in a note that the organ was present in Chameleo vulgaris—a statement of which de Graaf has subsequently denied the truth. He says that though the parietal foramen is open in the young form it becomes closed as the adult state is reached, and that there can be thus no organ remaining in connection with the proximal part of the epiphysis. Before reading his note, and subsequently to the publication in 'Nature,' three more adult specimens were cut in section (the first note was based upon a dissection), with the result that each one has fully confirmed the statement that the organ is present in Chameleo, and moreover remains in connection with the proximal part of the epiphysis, though it certainly is in a comparatively low state of development.

External Indication.—The presence of the organ is indicated in both Chameleo vulgaris and Chameleo

[1] 'Nature,' May 13th, 1886.

bifurcatus by a tubercle slightly depressed below the level of the surrounding ones, and having a very transparent appearance;[1] it lies in the median line just in front of the anterior end of the strongly marked ridge, which occupies the dorsal surface of the head posteriorly.

Fig. 40 gives a diagrammatic view of the relationship of the different parts; the parietal foramen is not large but is still clearly present, and very easily distinguishable in sections. Within it and lying immediately beneath the modified tubercle is the optic vesicle; elsewhere as usual the skin is deeply pigmented, but the pigment cells are entirely wanting above the vesicle, a fact which is especially noticeable in sections of this animal, the cells having long processes and being closely packed together (fig. 21). It is this absence of pigment which produces the transparent effect in the tubercle. The surface of the latter is very convex, and beneath it the layers of the skin are arranged as usual, a series of special connective-tissue fibres forming an encasement for the vesicle. Within the foramen there is the customary well-marked and branching blood-vessel (*b.v.*), which accompanies the pineal stalk.

Structure of Vesicle.—In Chameleo the structure of the vesicle is very simple. It has the form of a hollow sphere whose walls have been compressed dorso-ventrally, so that its greatest length lies in the line of the long axis of the head. Its walls are formed of elongated distinctly nucleated cells, those facing into the cavity bearing long cilia; no pigment is present and there is no differentiation into lens and retina, the cells of the anterior and posterior walls of the vesicle being alike. Posteriorly the inner wall of the vesicle is, as it were, drawn downwards (fig. 21), a small horn-like space being thus formed, turned somewhat towards the pineal stalk; its general appearance conveys the idea of the vesicle having at first had the relationship to the then open pineal stalk which is at present shown by the swollen distal extremity to the epiphysial tube in Cyclodus. By the meeting of the walls of the epiphysial tube the vesicle would become closed, and the solid

[1] The external indication is much clearer in some than in other specimens.

pineal stalk formed; this would be attached primitively to the posterior end, and the bending of the cells of the vesicle wall (fig. 21) make it appear as if a subsequent drawing down of the stalk to the ventral surface had taken place. In the specimens examined the stalk is seen to end anteriorly somewhat sharply against the under surface of the vesicle, at any rate, in this part none of its fibres could be traced into the cells above, though, as the specimens examined were not specially preserved for histological purposes, it is quite possible that with fresh ones a connection might be demonstrated. Posteriorly, however, where the drawing down of the wall occurs the fibres and cells are in connection with each other.

The pineal stalk itself is a very definite structure, running from the under surface of the vesicle downwards and slightly backwards, till just without the parietal foramen, where it joins the hollow epiyhysial stalk running backward to the roof of the thalamencephalon. In structure it resembles closely that of Hatteria.

Gecko verus.

Neither in the adult nor in the embryo is there the slightest external trace of the organ, the skin being tuberculated and capable of being lifted up from the head without remaining attached in the position of the parietal foramen. There is no discernible trace of the latter: in lizards in which it is present the skin cannot be removed wholly from the surface of the head.

Sections show that the epiphysis is a well-marked structure in Platydactylus arising from the roof of the thalamencephalon and running straight upwards till it comes into contact with the roof of the cranial cavity. This portion corresponds to the proximal part of the structure in other forms, and apparently the pineal stalk, which usually runs forward from this along the dura mater, as well as the distal portion modified into the pineal eye, are both absent in Gecko. The epiphysis is hollow and its cavity gradually increases in size as it passes further from the roof of the brain and approaches the skull, against which it ends blindly; there is no differentiation in its walls, so far as could be discerned, to form an optic vesicle.

The same structure is present in Gecko verus and Gecko mauritanicus.

Ameiva corvina.

Ameiva externally agrees with Platydactylus in the absence of a modified scale to function as a cornea; the skin of the head is also easily removable, not being attached in the position of the foramen, which is also wanting in this species. I have not yet examined it by means of sections, but as far as can be told it agrees with Gecko.

Anolis, Pl. XV, fig. 11; Pl. XVII, fig. 24.

It is not my intention in this paper to describe the structure of the eye of Anolis in any great detail, as before long I hope, by the kindness of Mr. J. Gardiner, to be enabled to describe, by means of specimens prepared carefully by him, the eyes of several species of Anolis from the Bahamas. The eye of one specimen has, however, been figured viewed as a solid object from beneath (fig. 11). The brain membranes are represented, the dura mater having branched pigment-cells scattered over it, and having a specially dark ring around the margin of the parietal foramen in which lies the eye. The latter is somewhat elliptical in shape, its long axis lying in the same line with that of the head: the eye is compressed dorso-ventrally, and when compared with the organ in Varanus bengalensis (fig. 12), placed by its side, the rods are seen to be much larger than in the latter; the cavity within the optic vesicle, whose size is indicated by the circular space bounded by the inner ends of the rods, being hence considerably less in Anolis than in Varanus.

Fig. 24 (Pl. XVII) is a drawing of the eye of another species of Anolis from the West Indies. The organ lies in the foramen with its upper surface close beneath the surface of the head. Its shape is unlike that of any form described hitherto, being elongated in a dorso-ventral direction. The lens is cellular and its hinder border is deeply convex towards the cavity of the vesicle, calling to mind somewhat the shape of the structure in Hatteria; in the optic axis certain of the cells are apparently undergoing degeneration, pigment being deposited in them.

Retina.—The hinder wall of the vesicle forming the retina is thinnest where it joins the lens and thickest posteriorly. The whole is noticeable by reason of a great development of pigment, which appears to surround all the elements. The rods (*R.*) are very well marked and in some cases, especially in the line of the optic axis, present the appearance of being striated; in the latter position also they are especially elongated. At their external ends they seem to be connected with spherical elements (*n*), also embedded in pigment; these are united by means of processes, rendered evident again by pigment deposited upon them, with a layer of elements apparently corresponding to the cone-shaped bodies of other retinas (*Co.*). In its most posterior region the elements seem to be in connection with the fibres of the optic stalk (*Op. s.*), which runs downwards and backwards within the vacuolate tissue filling up the parietal foramen.

Leiolœmus tenuis.

The external indication of the eye is very clear in the specimen; the scale is in the usual position and surrounded by a series arranged in a circular manner around it as a centre, the two posterior ones being larger than the other four. In the middle of the eye-scale itself lies the circular cornea, white and dome-shaped. Sections show that the eye is present beneath, the walls of the vesicle being differentiated into a transparent cellular lens anteriorly and a retina posteriorly; the rods are enveloped in pigment, and the latter is deposited also through the whole thickness of the retina. The whole organ had shrunk so much that it was impossible again to do more than recognise the presence of the structure, and the fact that it was differentiated into an eye; the proximal part of the epiphysis stretches, in the dura mater, very nearly to the eye, but whether there is or is not any connection between the two could not be determined. In this form also pigment is present in great abundance in the skin, and its absence above the eye is a marked feature in sections.

Plica (Uraniscodon) umbra.

In this the external indication is particularly clear. The scales on the dorsal surface of the head are small, save one whose great size renders it prominent; in the centre of this a small, white, slightly dome-shaped structure indicates the position of the eye beneath.

Position of the eye.—The organ lies very far forward on the dorsal surface, being placed (Pl. XIX, fig. 35) over the anterior region of the cerebral hemispheres; it is situated within the parietal foramen, the size of which is far greater than that of the eye itself, which lies embedded in connective tissue. The usual absence of pigment immediately above it is to be noted.

Structure.—The organ was not in a good enough state of preservation histologically to render any detailed examination of its structure possible. So far as could be discerned the connection of the eye with the epiphysis is retained, the solid pineal stalk (*Op. s.*) running backward immediately within the skull cavity. Attention may be drawn to one curious point—close to the eye is a small secondary and deeply pigmented vesicle (*op*[1].). It may be possible that in the specimen examined this is merely due to a shrinkage of the walls of the whole optic vesicle, whereby the anterior and posterior have come into close contact, and thus simulated the appearance of two vesicles, but, as far as could be ascertained, this was not the case. The deep pigmentation of the anterior as well as the posterior wall is strong evidence against this view.

Iguana tuberculata, Pl. XV, figs. 15 and 16; Pl. XXVII, fig. 23.

The full description of the organ, which is present highly developed in Iguana is not given in this paper. I hope before long to have the opportunity of examining its structure in a living specimen.

External Indication.—The usual modified scale is present and in large specimens is very conspicuous. In smaller ones (Pl. XV, fig. 16) a slightly raised central portion is present, which is devoid of pigment, and transparent enough to allow of the eye beneath being seen as a dark spot. In larger specimens (fig. 15) the central part is still more raised, and forms a dome-shaped structure. In the figure, which is twice the size of the original, the scales from the dorsal surface of the head are represented, and the prominence of the scale with its modification to form a cornea can be seen. The only wonder again is that long before this a careful examination of the structure has not been made.

Structure.—The eye lies within the parietal foramen, which is well developed in Iguana, surrounded closely by connective tissue, there being no capsule present. The eye is so placed that its optic axis is as nearly as possible in the vertical line. In shape it simply resembles an inverted cup with the lens, which has a flattened external surface, occupying the anterior end. The organ is usually more cup-shaped and symmetrical than the one figured (Pl. XVII, fig. 23); but this, which is drawn without any of its surroundings, will serve to demonstrate the structure as far as it will be described in the present communication.

Lens.—The lens is convex posteriorly, and almost—due to its anterior surface being flattened—plano-convex in shape; it is distinctly cellular, with well-marked nuclei scattered irregularly in section. On either side it thins out to join the walls of the posterior part, in which, at the line of union, a specially deep circular ring of pigment is deposited.

Retina.—The rods (*R*) are well marked and embedded in deep pigment. In the line of the optic axis is a bundle of specially elongated ones (R^1); externally they are in contact with spherical elements (n^1), which are as usual of, roughly speaking, the same size as the nuclei of the lens cells. These elements, together with the external ends of the rods, appear to be surrounded by a molecular layer of punctated material, clearly distinguishable, but yet not so well marked as in Varanus giganteus. Most externally is a layer of cone-shaped bodies (*Co.*), the internal ends of which taper off into processes connecting them either with the spherical elements or with the rods. Their flattened bases rest upon the connective-tissue investment of the eye.

At its posterior extremity enters the pineal stalk. The appearance of this in one form examined is given in fig. 23, where it had the form of a simple nervous strand, much as in Hatteria, the specialised rods running down into it, though there was no group of nucleated bodies to be seen at their external ends.

Draco volans.

The eye is present in Draco volans, though the specimens examined did not make it possible to investigate the structure in detail, the vesicle walls having apparently shrunk and come to lie close together, so as to obliterate the internal cavity. The whole is in a condition, as far as could be ascertained, which resembles that seen in Chameleo or Lyriocephalus.

The vesicle is ovoid in shape, and placed with its long axis in the median line of the head within the parietal foramen; its walls are composed of cells with very distinct nuclei, but no further differentiation to form retina or lens could be distinguished, and the vesicle itself was remarkable for the absence of pigment in its walls, a feature already noticed in Chameleo and Lyriocephalus. The only pigment present lay in the dura mater, and surrounded the very posterior extremity of the vesicle in the position in which the pineal stalk would enter, though it was not possible to determine the existence of this.

Externally specimens of Draco differed somewhat in their indication of the organ, its position being in most cases easily determined by the presence of a specially modified scale in the usual position, and bearing a cornea-like space.

Ceratophora aspera.

The organ is indicated externally in the usual manner by a scale modified to form a cornea. The structure of the epiphysis is interesting, being unlike that met with before. In the specimen examined, though the external indication was present, the parietal foramen was seen, when sections through the head were cut, to be closed. Its position is indicated by a large blood-vessel which branches on the internal surface of the skull as it enters the bone exactly as the vessel accompanying the pineal stalk branches on entering the parietal foramen, the two branches thus formed pass through to the external surface. The parietal foramen appears simply to have closed up, the blood-vessel remaining and piercing the bone.

In many forms such as Leiolœmus the optic vesicle is placed quite on the internal side of the foramen; in such a form as this were the bone to grow and close up the foramen the vesicle would be left on the internal surface; this is exactly what appears to have taken place in Ceratophora aspera. The epiphysis has the usual form, being well developed and consisting of a proximal portion at right angles to the roof of the thalamencephalon, whilst, from the further end, the distal portion runs forward along the under surface of the dura mater as the pineal stalk until it ends in a slightly swollen portion immediately beneath the parietal foramen. This corresponds to the optic vesicle of other forms; in structure it appears to be solid and to consist of rounded elements, resembling very closely those present and figured by de Graaf in Rana esculenta.

There is this important difference, however, between Amphibia and Lacertilia, that in the former the distal portion of the epiphysis becomes completely cut off from the proximal and is placed externally to the skull, whilst in Lacertilia, on the other hand, the distal part not only remains in connection with the proximal but is permanently closed within the skull cavity after closure of the parietal foramen.

Lyriocephalus scutatus.

The usual external indication is present though not so prominent as in many other forms, the scale being somewhat smaller than those by which it is enclosed posteriorly, which form a V-shaped ridge behind it, the point of the V being directed backward; on the scale a circular, slightly raised, transparent part is modified to form a cornea.

Internally the structure of the optic vesicle resembles more that of Chameleo than any other, there being no differentiation of the walls to form a lens and retina. The shape of the vesicle is, however, unlike that of Chameleo, being elongated dorso-ventrally. Its walls consist of nucleated columnar cells, and are thicker anteriorly than posteriorly, where there is present a small amount of pigment on the external surface of the cells.

The whole structure lies in the parietal foramen, and has the form, viewed as a solid object, of a small ovoid body whose anterior end is closely apposed to the connective-tissue, forming a roof to the parietal foramen, between which and the cuticle no pigment is present. The pineal stalk is a prominent structure, entering the posterior end of the vesicle where it unites with the cells; unfortunately, in the specimen examined the part with the optic vesicle and portion of the pineal stalk attached to it was torn away from the underlying structures, but their can be little doubt from the similarity between this form and such as Chameleo, that the stalk simply passes back to join the proximal portion of the epiphysis, the upper part of which is seen running forward in the dura mater directly towards the optic vesicle.

Calotes, Pl. XV, figs. 13 and 14; Pl. XVIII, figs. 31 and 33; Pl. XX, fig. 8.

In smaller species of Calotes the external indication of the eye is most clear. A large median scale is so modified (fig. 13) as to present precisely the appearance of an eye. In its centre is a circular black space, within which lies a white ring enclosing a dark space resembling exactly the pupil. This effect is produced by reason of the central part of the scale being transparent and slightly raised into a dome-shaped cornea, while beneath it lies the pineal eye which, on removal of the scale, is seen to have a globular form. The external surface is covered with a glistening white substance, save anteriorly, where the transparent lens is placed; the internal cavity is lined by the rods embedded in deep pigment, and hence appears intensely dark when seen through the lens, the whole eye having thus the appearance, viewed from above, of a white rim surrounding a dark circular space, and lying immediately beneath the scale, is easily visible on the dorsal surface of the head.

Calotes ophiomaca and C. versicola.—In both these species the external indication is very clear, the modified scale with its corneal, central part forming a prominent object on the surface of the head: internally the structure is practically the same in both forms, and the description which follows is that of the first mentioned of the two species.

Position of the Eye.—The organ is considerably smaller than the foramen in which it lies, and is enclosed in connective tissue; the inner fibres of the cutis vera are so arranged as to form a dome-shaped structure above the eye (*Ct.*[2]) whilst there is the usual marked absence of pigment between the latter and the external surface, which is also dome-shaped. The cells of the rete mucosum are noticeably elongated and columnar immediately above the eye (*R.M.*).

Structure.—The whole organ is considerably compressed, in the dorso-ventral line, its longest axis (Pl. XVIII, fig. 33) lying in the same line with that of the head.

Lens.—The lens is distinctly cellular though the nuclei of the component cells are not clearly visible (fig. 33, *Le.*) as in other form such as Seps (fig. 32). The structure is concavo-convex in shape, its anterior surface being convex outwards, whilst certain of the cells on the inner side have become pigmented (*pig.*) and thereby assumed a striking similarity to the rods.

Retina.—The rods (*R.*) are very well developed, facing into the cavity of the optic vesicle; from their external ends prominently marked processes pass to an outer layer of cone-shaped bodies (*Co.*), the broad bases of which lie upon the external limiting structure of the eye. There is an absence of any spherical elements such as are seen in other forms. As before said, no nuclei can be recognised in the lens, and the failure to detect both may very probably be due to the fact that the specimen was not in a very good state of histological preservation rather than to their being absent.

In connection with the eye a large blood-vessel (*B. v.*) is developed which runs up by the side of the epiphysial process to the foramen.

Epiphysis.—The eye is, as far as could be told, completely separated off from the brain; the proximal part of the epiphysis runs, as usual, at right angles to the dorsal surface of the brain, whilst the median part corresponding to the pineal stalk of other forms runs forward from the former along the upper surface of the cranial cavity, ending blindly before the foramen is reached (fig. 31, *Ep*[1]., *Op. s.*).

Agama hispida, Pl. XIX, fig. 39.

The external indication of the eye is very clear in this form, consisting, in a specially large scale placed medianly on the head posteriorly to the paired eyes, in a slight depression and surrounded by small tubercle-like scales. A raised white rim encloses a circular space marked by a curious hour-glass shaped, dark looking patch.

Sections show that the organ lies within the parietal foramen and is almost spherical in shape; above it the connective tissue of the cutis vera is modified as in other forms (e. g. Varanus bengalensis), and is entirely free from pigment, the cells of the rete mucosum being also somewhat elongated above the eye; the latter is surrounded immediately by vacuolate tissue as in Cyclodus or Anolis (figs. 18 and 24). It is difficult to determine the structure of the eye owing to the fact that not only the rods, which are long and well marked, but also the external part of the retina is deeply pigmented; it appears as if nearly all the elements lying external to the rods had degenerated into pigment-bearing cells, amongst which at intervals spherical elements corresponding to those of other forms can with difficulty be distinguished. In many cases processes, also pigmented, pass from the rods to the pigment masses lying external to them.

The lens is distinctly cellular and forms the transparent anterior boundary to the optic vesicle, though as the walls of the latter are comparatively thick the cavity is small; even in some of the cells of the lens pigment is deposited. It is difficult to determine whether the organ is or is not yet connected with the proximal part of the epiphysis, owing to the great development of pigment in the dura mater surrounding the upper part of the epiphysis, and leading from this to the eye; it was not possible to say definitely whether in the specimen examined this did or did not contain a process from the proximal part of the epiphysis.

Grammatophora barbata.

The scale modified to act as a cornea is present and prominent on the surface of the head.

The eye is present beneath and has apparently (having been only examined as a solid object) the form of a bulb, very similar indeed to that already described in Calotes; in fact, the figures of this as a solid object (fig. 14) would serve also for that of Grammatophora. Externally the bulb is covered with a glistening white substance, whilst internally it is lined by deep pigment in which the rods are embedded. Above the eye, which does not appear to be connected with the epiphysial stalk, pigment is, as usual, entirely wanting in the skin.

Moloch horridus, Pl. XIX, fig. 36.

External Appearance.—In the specimen examined the external indication was very well marked, consisting of a circular dark space, surrounded again at a short distance by a dark circular line, and lying upon a small smooth space in the median line dorsally amongst the stiff horn-like processes covering the head.

Position of Eye.—Longitudinal sections at once showed (Pl. XIX, fig. 36) that this space corresponded roughly in extent to that of the parietal foramen, and that within this and close beneath the surface lay the eye. Unfortunately like many others this specimen was in too bad a state of preservation to do more than enable me to ascertain with certainty the presence and general outline of the organ. It is remarkable for its spherical shape, deep pigment, and comparative size. These points are indicated in fig. 36 where the eye is drawn as a solid object. It will be seen that it lies close beneath the surface, the skin being here completely devoid of pigment and quite smooth, forming in fact a cornea (*Cor.*). As far as could be ascertained, though the point could not be determined with certainty owing to the state of preservation of the specimen, the eye is connected, as represented diagrammatically with the proximal part of the epiphysis by the solid pineal stalk (*Op. s.* ?).

Leiodera nitida, Pl. XVII, fig. 22; Pl. XIX, fig. 38.

External Appearance.—The specialised scale (Pl. XIX, fig. 38) forms a prominent feature in the median dorsal line of the head, bearing in its centre a small dome-shaped structure perfectly white, and hence standing out in clear contrast to the deeply-pigmented scale, of which it is a specialised portion.

Position of the Eye.—The organ lies closely embedded in connective tissue, and not really filling up the parietal foramen, than which it is considerably smaller. The layers of the skin above it are so modified as to form the external dome-shaped structure already noticed, whilst pigment is markedly absent from this part, though present on either side (fig. 22, *Ct. pig.*). A very striking feature in section is the peculiar elongation of the cells of the rete mucosum (*R. M.*), whose internal ends appear in many cases to be prolonged downwards, each cell being so placed that its long axis is at right angles to the surface at that particular spot. The connective tissue, further, very closely invests the eye, whilst no such well-developed blood-vessel is to be recognised as is met with in most cases.

Structure.—The organ has a very definite shape shown in fig. 22, being depressed dorso-ventrally, as a result of which the cavity of the vesicle is very small.

Lens.—The lens is well developed, and, as usual, cellular, the nuclei of its cells being prominent in section, and so arranged that they form in the main a line from side to side.

It is thickest in the line of the optic axis, and thins off to each side, where it joins the retina. The lens is, in fact, doubly convex, its anterior surface being in close contact with the investing connective tissue, and parallel to the surface of the dome-shaped cornea above.

Retina.—The retina, owing to the compression of the eye, may be likened in shape to the walls of an oblong box, the lid of which is formed by the lens. The rods line the internal surface, and are very clearly marked; none appear to be especially elongated; their external ends are in connection with a layer of spherical-shaped elements (n^1), as in other forms these elements being also of the same size as the nuclei of the lens. Most externally lie a layer of cone-shaped bodies (*Co.*), whose inner ends taper off into processes passing to the spherical or rod elements, whilst their broad bases lie upon the external limiting membrane of the eye.

Epiphysis.—The eye appears to be completely separated off from the proximal part of the epiphysis, which consists of (1) a proximal part with walls of distinctly nucleated cells, which extends vertically from the thalamencephalon to the roof of the brain cavity; and (2) of a solid thin part running forward along the brain roof from the proximal part towards, but not reaching as far as, the parietal foramen; it is enveloped in pigment, and, being very thin, is somewhat difficult to trace.

Anguis fragilis, Pl. XVII, fig. 25.

This form has been described and figured in detail by de Graaf,[1] but in certain important points I am unable to agree with him.

Fig. 25 represents, somewhat diagrammatically, a longitudinal vertical section through the foramen, the eye, and the epiphysis. The eye in the specimen figured was considerably smaller than the foramen, and the epiphysis was remarkable for running forward until very close to the eye, whilst its distal rounded extremity was invested by pigment cells (*Ep. pig.*).

[1] Op. cit., pl. 4, fig. 34.

As described by de Graaf, the eye is separated off from the epiphysis. In his figure the lens is shown completely separated off from the retina, which overlaps it anteriorly. This does not appear to be the case; but, on the contrary, the eye, as far as could be told, agreed with all other forms examined in having the lens directly continuous with the posterior walls of the vesicle.[1]

The most important point of difference, however, is concerned with the retina. De Graaf figures this (Pl. 4, fig. 34) as having a layer of unpigmented rods (*sl.*)—his "Staafjeslaag"—together with a layer of unpigmented cells (*cep.*)—his "Cyllindercellenlaag"—lying internal to the pigmented rods. Of neither of these two layers can I succeed in finding any trace, either in Anguis fragilis, or in any of the forms yet examined. In every instance all that can be discerned within the rods is merely the remains of what may be supposed to have been during life the fluid contents of the vesicle. In coagulating this does in some instances appear to attach itself to the parts of the rods facing into the cavity, but never forms, in any specimen examined hitherto, any structures so definite as to be interpreted into the "Staafjeslaag" or "Cyllindercellenlaag" of de Graaf.

Cyclodus gigas, Pl. XV, fig. 9; Pl. XVI, figs. 18, 19, and 20; Pl. XVIII, fig. 29; Pl. XX, fig. 5.

In Cyclodus the epiphysis is not developed into an eye, but the structure is nevertheless in an interesting state, showing most probably a stage passed through during the development of the eye in other forms.

External Appearance.—In fig. 9 is represented a portion of the scale specially modified in connection with the organ. It lies, as in all other forms, in the median line posterior to

[1] In my first communication to 'Nature,' the lens of Hatteria was described as separated from the retina, but examination of a fresh specimen showed at once this was a result due to slight post-mortem degeneration of the tissues, and that in reality the two were perfectly continuous, a result which subsequent investigations of many forms has fully confirmed.

the paired eyes, and is easily discernible in the living animal, one of which I was enabled to examine. It consists of a dark patch, having again the appearance of a membrane stretched tensely over a cavity, surrounded by an irregular, slightly-raised, white border, represented in the figure, in which is drawn only the central part of the scale.

Thus the modification to form a "cornea" is, as reference to the figure will show, in a rudimentary state, and foreshadows the similarly rudimentary condition of the organ beneath. In fig. 29 is represented a solid side view of the brain, showing the position of the pineal gland; it lies enclosed in the brain membranes, and fitting closely into the parietal foramen, out of which it is easily removed along with the dura mater. The epiphysis is very long, and stretches far forward beyond the roof of the thalamencephalon, almost to the anterior extremity of the cerebral hemispheres, its distal extremity being deeply embedded in pigment in the dura mater, and having the appearance, as in fig. 29, of a dark, swollen mass.

In section it is seen that the epiphysis is hollow throughout its whole course, the cavity being in direct communication with the third ventricle; the cells composing its walls are all columnar in nature and distinctly nucleated, cilia also being easily distinguished in most parts.

The whole may be divided into two parts: (1) a proximal portion, stretching from the roof of the thalamencephalon in the form of a tube to the parietal foramen; and (2) a swollen distal extremity lying in the latter, and closely invested by vacuolate tissue. In other words, the epiphysis in Cyclodus has the form of a vesicle attached to the brain by a hollow stalk. The vesicle may be regarded as homologous with the eye of other lizards in a rudimentary state,[1] and the hollow connecting process with the solid pineal stalk and proximal part of the epiphysis of such a form as Hatteria.

In figs. 19 and 20 is represented, on a larger scale, the structure of the anterior and posterior walls of the vesicle (by the anterior wall is meant that nearest the external surface).

[1] It may also be closely compared with the condition in adult Elasmobranchs.

In both, the cells are seen to be much elongated with very distinct nuclei; in the case of the anterior ones, save for the presence of well-marked cilia, they differ but little from those of a lens. An elongation of those lying in the middle would, in fact, transform this into the lens of such a form as Lacerta ocellata (Pl. XVIII, fig. 30).

Passing to the posterior surface, however, a curious but interesting modification takes place (cf. figs. 19 and 20), the nuclei all pass to the external surface, whilst the ends of the cells, which are left facing into the cavity of the vesicle, bear a close resemblance to the rod-like structures of the retina of other forms.

It is possible that we have here a stage in the development of the retina. The internal portion of the cell forms the "rod," the nucleus passes to the external end, and with the protoplasm lying around it forms the spherical-shaped element of the retina, still retaining its connection with the rod. Other cells, lying on the opposite side (supposing the wall of the vesicle, as in Cyclodus, to be more than one cell thick), become transformed into the external-lying elements of the retina, their protoplasm becoming in part drawn out into processes, which enter into connection with those of other cells, in part remaining around the nuclei, forming thus the external spherical elements and the processes connecting these with each other. This development would give exactly such a structure as has been already described in Varanus giganteus. In this form it is noticeable that the spherical elements of the retina consist of nuclei with a small amount of protoplasm around them, the nuclei being identical in size with those of the lens, the greater part of the protoplasm of the cells seeming to be developed into processes connecting the various elements. By this means is developed a network of branched cells, connected on the one hand with rods, and on the other with nerve-fibres.

In Cyclodus the stage is reached and retained in which the rods have begun to be formed by a removal of the nuclei to the outer ends of the cells, where they form, together with those of the external-lying cells, a prominent layer (figs. 18 and 20, *n.*).

Lacerta.

Two species of this genus have been examined.

(1) Lacerta viridis, Pl. XVII, fig. 26.

In this form the external indication, though recognisable, is not at all prominent, consisting merely in a dark circular space upon a median scale.

The organ lies immediately beneath this within the foramen; it is flattened out dorso-ventrally and embedded in deep pigment, as represented in fig. 26, where it is drawn as a solid object. Its smallness and the great deposition of pigment rendered it very difficult to examine the structure in detail, and the backward extension of the pigment towards the epiphysis made it also difficult to distinguish any pineal stalk, though in parts there were indications of its existence (*Ep.*[1] ?); this pigment may, however, be a deposition in the brain membranes which must once have surrounded the stalk connecting the vesicle with the epiphysis, and which persist after the separation of the two has taken place.

(2) Lacerta ocellata, Pl. XVIII, figs. 27, 28, and 30.

In this the external indication of the organ is far more conspicuous than in L. viridis; the scale with its dark central circular space, surrounded by a slightly raised light-coloured rim, forming a well-marked feature on the dorsal surface of the head.

Position of the Eye.—This differs somewhat from that of other forms inasmuch as it lies closer to the external surface; the connective tissue in which it lies completely fills up the foramen, and when the brain, together with its membranes, are pulled away internally from the skull, the eye is brought away with them (Pl. XVIII, fig. 28). The position within the foramen is represented in fig. 27, where the eye is drawn as a solid object surrounded by a great number of branched pigment cells. The foramen is supposed to be cut in half longitudinally and vertically, one side being removed to show the eye; the connective tissue enclosing it being omitted for the sake of clearness.

Structure.—In shape the eye resembles more than anything else a hemisphere, the equatorial plane being occupied by the lens, which is, in shape, almost concavo-convex, its outer, anterior surface being flattened. The bulb is encased closely by the connective tissue of the dura mater (*D. M.*), a thin layer passing in front of the lens, whilst all the posterior surface is surrounded by branched pigment cells (*pig.*^{3}).

Lens.—The lens has the usual cellular structure, being thinnest round the margin where it is continuous with the retina; the nuclei of its component cells form a well-marked layer running across it in section from side to side.

Retina.—Within the retina a considerable deposition of pigment in various parts indicates, to a certain extent, degeneracy, and at the same time renders the examination of its structure difficult.

The rods (*R*) are well marked, and in places present the appearance of being striated. Two bundles of rods are slightly elongated (R^1), being in connection with two distinct nervous strands entering the retina posteriorly. External to the rods lie spherical nucleated elements arranged in two layers, an inner (n^1) and an outer (n^2), whilst amongst them much pigment is scattered in small granules, rendering their detection difficult; in parts still larger masses of pigment are present, which may perhaps be due to the degeneracy of the spherical elements into pigment-bearing cells.

Epiphysis.—As before said, two distinct nervous strands may be seen entering the retina posteriorly and close together (*ne*), one being larger than the other; back from these two, which soon unite, may be traced a single nervous strand which it is extremely difficult to follow, owing to its close investment by connective tissue of the dura mater, but which I believe runs downwards and backwards until it joins the proximal part of the epiphysis (*Ep.*), which is considerably swollen and has a curious development of pigment in its walls.

Along with the pineal stalk runs the usual blood-vessel, which on nearing the eye bulb breaks up into numerous branches which ramify (figs. 27 and 30, *B. v.*) amongst the pigment cells encasing the eye.

Zootoca vivipara.

The presence and structure of the eye in this form has been described to a certain extent by Leydig, though he failed to recognise its connection with the epiphysis, and did not apply to it the name of eye. The presence of deep pigment in the specimen examined makes it impossible to describe in detail the structure of the retina. Pigment is also thickly deposited in the skin, but it is seen in section to end abruptly on each side of the parietal foramen; so thick is the layer of pigment that no light, save for this provision, could possibly reach the pineal eye.

The eye has the usual form of a hollow vesicle with the lens anteriorly, lying immediately beneath the specialised scale. Pigment runs from the proximal part of the epiphysis to the eye, but, as far as could be told, the latter is separated from the brain.

The eye is present in early stages, before any definite indication of the parietals can be distinguished; in an embryo whose head measured 6 mm. in length, the eye is a prominent object on the dorsal surface of the head, immediately beneath the skin. It is flattened in the dorso-ventral line so that the cavity is small; anteriorly the lens is differentiated and its cells are perfectly continuous with those of the vesicle behind, which are being transformed into the retinal elements, though the fine pigment granules already deposited throughout their substance (and absent from those of the lens) render it difficult to distinguish the different elements; facing into the vesicle, however, the rods can be seen around which the pigment granules are thickest; external to these lie spherical elements massed closely together and not yet separated into definite layers. These may very probably be regarded as the nuclei of the cells whose internal parts are becoming transformed into rods. The eye appears to be connected with the proximal portion of the epiphysis by a fibrous strand, such as is represented by De Graaf as connecting the distal with the proximal portion of the epiphysis in Bufo cinerea.

Seps chalcidica, Pl. XVIII, fig. 32; Pl. XX, fig. 5.

External Appearance.—The external modification is not so evident in this form as in some others. If one of the median scales posterior to the paired eyes on the dorsal surface of the head be examined it will be found to have upon it a dark-coloured oval patch (hence distinguishable from the yellow-brown surface of the scale); this, which has the characteristic appearance of a membrane stretched over a space beneath, indicates the position of the eye lying beneath it.

Position of the Eye.—The eye lies somewhat on the inner side of the foramen (Pl. XVIII, fig. 32), there being as usual no pigment between it and the external surface. It is remarkable in being the only one in the forms yet examined, which is larger than the foramen; its relation to this is shown in the figure, where it is seen that the parietal bones overlap it on each side to a small extent; if by any reason the foramen became closed then the eye would be situated intracranially, whilst in Amphibia the position is always extracranial, when the distal vesicle of the epiphysis becomes, as in Anura, separated off from the proximal. The eye is surrounded immediately by a great development of pigment bearing tissue which fills up what part of the foramen is not occupied by the organ itself.

Structure.—The whole eye is, in longitudinal vertical section, seen to be elliptical in shape, the long axis corresponding in position with that of the head and hence forming a strong contrast to such an eye as that of Anolis (Pl. XVIII, fig. 24).

Lens.—The lens is distinctly cellular, the nuclei of the constituent cells forming a line prominent in section across from side to side, slightly nearer to the inner than to the outer surface; the whole is doubly convex in shape, thickest in the line of the optic axis, and thinnest where it is continuous with the retina.

Retina.—The specimen not being in very good order histologically, the structure of the retina could not be determined with any great amount of accuracy. The rods as usual formed the most prominent feature; at their external ends in certain parts spherical elements could be distinguished (n^1), whilst, most externally, elements corresponding doubtless to the cone-shaped ones of other eyes were present (Co.). In many parts external to the rods masses of pigment (*pig.*^{2}), indicating doubtless degeneracy in the tissues of the retina, were present.

Connection with the brain.—The eye is apparently completely separated off from the brain, no pineal stalk being recognisable.

General Account of the Structure in Lacertilia.

The above account reveals the epiphysis within the group Lacertilia as a structure of very varied development, in some forms presenting merely the appearance of a hollow process from the roof of the thalamencephalon, in others being modified into a well-marked eye, whilst between these two extremes various intermediate forms are found. In taking a short general review of the results detailed above we may deal with them under the four following heads:

(1) General Form of the Epiphysis.[1]—The simplest form seen is in Platydactylus, where it has merely the structure of a hollow outgrowth running at right angles to the surface of the thalamencephalon until it reaches the dura mater lining the cranial cavity. In Hatteria, on the other hand, we have a form in which specialisation is carried to its furthest extent, with the result that the epiphysis becomes modified into three parts—(1) a proximal part, still hollow, and connected with the brain roof, (2) a median, solid pineal stalk, serving to connect the former with (3) the distal portion differentiated into an optic organ. These forms may be taken as two extremes, the gap between which is filled up by various modifications: thus in Cyclodus the epiphysis instead of running straight upwards turns forwards, and at the distal end swells out into a vesicle whose walls show a trace

[1] Compare the diagram showing the development of the epiphysis in various forms on Pl. XX.

of differentiation into lens anteriorly and retina posteriorly; the hollow connection with the brain persisting through life. In such forms again as Calotes, Seps, or Leiodera the same differentiation into an optic organ with retinal elements takes place as in Hatteria, but the connection with the brain is lost. In a few forms further, such as Chameleo vulgaris and Lyriocephalus scutatus, the development of the epiphysis is carried to a great extent, resulting in a division into three parts, as in Hatteria, but the distal vesicle is not differentiated into an eye, its walls retaining their primitive structure.

In Varanus giganteus a peculiar modification takes place, seen in no other form examined; the pineal stalk, which is well developed, breaking up into three divisions before the eye is reached, whilst in V. bengalensis the eye is apparently separated from the proximal portion of the epiphysis, and the part equivalent to the pineal stalk of the other species is hollow and ends beneath the optic vesicle in a slight swelling.

(2) State of Retinal Elements.—Dealing with the state of development of the retinal elements, the eyes are found to differ to no little extent in this respect; thus in Hatteria it is better developed than in any other form examined: in Varanus, on the other hand, while the elements can be distinguished the whole eye is marked by a great deposition of pigment; even in the centre of the lens a large globular mass is present which must effectually prevent the entrance of light to the vesicle in the line of the optic axis, whilst, in addition to this, many of the retinal elements degenerate into pigment-bearing cells. In others, such as Anolis, almost all the elements are enveloped in pigment, whilst in others, as Agama hispida, so great is the deposition that it is not possible to distinguish any elements save the rods. In contrast to this we find in some genera, such as Chameleo and Lyriocephalus that no pigment is present at all, and, accompanying this absence of pigment, it is found that the vesicle is not developed into an eye, its walls retaining their

primitive structure of columnar cells, ciliated internally. In Cyclodus again we find another modification present, the epiphysis having apparently reached a stage passed through in the development of the eye of other Lacertilia; a vesicle is formed distally, but the pineal stalk remains widely open, very little pigment is present amongst the cells, and no true eye is found. In Ceratophora, lastly, the distal extremity of the epiphysis is placed within the cranial cavity beneath the spot, corresponding in position to the parietal foramen of other forms; the portion equivalent to the optic vesicle is present, forming a slightly swollen mass at the distal extremity of the pineal stalk (?), consisting of rounded elements very similar to those present in the extracranial part of the epiphysis of Bufo cinerea.

(3) External Modification.—When we come to deal with the external modification it is very remarkable to notice that a high development in this is by no means necessarily accompanied by, or the index of, a highly-developed sense-organ beneath. In Varanus giganteus the external indication is extremely well marked, whilst the eye beneath is also well developed, and connected with the pineal stalk; in Hatteria, on the other hand, the eye is still better developed, the retinal elements being more clearly differentiated, whilst there is quite absent that great development of pigment which must indicate to a certain extent degeneracy in the eye of Varanus. Despite this there is in Hatteria no external modification, or, at all events, only a very slight one present indicating the position of the eye beneath; the latter also lies deeply embedded in connective tissue—deeper still than in the case of Varanus—though, as in every other form, there is a marked absence of pigment between the eye and the surface of the head. Thus, in the one of these two forms in which the organ is most highly developed, we find that the external modification is much the least evident. If, again, such genera as Calotes, Seps, Leiodera, and Anolis be taken, in these the modified scale is so prominent as to form the most noticeable feature on the dorsal surface of the head, and to resemble a cornea; below it

the eye is in a more or less highly developed state, its elements often obscured by deposition of pigment, but revealing in all cases, even when best developed, its rudimentary nature by the absence of any nervous connection with the brain.

(4) Position of the Eye.—With regard to the position of the eye considerable variation is seen. In such forms as Calotes, Leiodera, Anolis, or Agama, for example, the eye is close beneath the external surface, lying in the upper part of the well-marked parietal foramen. In Varanus the eye lies somewhat deeper, whilst in Hatteria it is placed deeper still on the inner side of the foramen, and in both forms a great development of connective tissue takes place, the latter being in every instance arranged in a definite manner. In Lacerta ocellata and Cyclodus the eye is placed within the parietal foramen, fitting it closely, the foramen having the form (see Pl. XVIII, fig. 27) of a truncated cone, whose apex lies externally. In Ceratophora aspera finally, the parietal foramen is closed, and the modified distal portion of the epiphysis lies quite within the skull cavity. The connective-tissue encasements of the eye also show some variations. In Hatteria is seen the highest development in this respect, the eye lying in a definite capsule, and having special supporting fibres stretching across to it from the walls in the anterior part. In Varanus the arrangement of the connective-tissue fibres appear to indicate the fact that a capsule formerly enclosing the eye, as in Hatteria, has become filled up with fibres, so that the eye is now immovably fixed. In other forms, again, such as Cyclodus, Anolis, or Anguis, it lies surrounded by vacuolate tissue, whilst in others, as Chameleo, Lacerta ocellata, Leiodera, Monitor, Uraniscodon, Calotes, and various other genera, the connective tissue, without any trace of capsule, closely invests the eye, no space being left within the parietal foramen.

If now we take typical examples from amongst the Lacertilia, and consider the state of development in each with regard to the above four points, it is seen that no one form shows a high state in all, some being well developed in one and some in another respect, but each being degenerate in at least one of the four features.

Referring to the latter under the numbers (1), (2), (3), and (4), and taking first Hatteria, we find that it shows in (1) and (2) a high, in (3) a low, and in (4) a somewhat low state.

Varanus giganteus shows in (1) a high, in (2) a considerably degenerate, in (3) a high, and in (4) a somewhat low state.

Calotes shows in (1) a degenerate (i.e. connection with brain lost), in (2) a somewhat degenerate, in (3) a very high, and in (4) a high state of development.

Chameleo vulgaris shows in (1) a high, in (2) a low, in (3) a fairly high, and in (4) a somewhat low state.

The same result exactly is obtained when each form is tested in the same way, showing that the organ is never present in a perfectly functional state, but always presents some one feature, at least, in which it is more or less imperfect.

We are thus brought to the conclusion that the pineal eye in Lacertilia is a rudimentary structure—that at the present time it is not so highly developed as it must have been at some previous period when fully functional.

It is, indeed, difficult to ascertain whether the structure is now functional at all. In lizards, whose paired eyes are closed, no result is obtained by rapidly focussing a strong beam of light on to the modified eye scale, and thus on to the pineal eye; in fact, strong light suddenly focussed into one of the paired eyes merely causes the lid to be drawn down without any further apparent result, whilst in the pineal eye there is no protecting lid, and no movement whatever takes place to remove the eye from the direction in which the light is coming.

Wiedersheim has, since the greater part of this paper was written and the preliminary communication to the Royal Society published, attempted to show that the organ is functional and not rudimentary; he bases his conclusions upon the study of several forms such as Varanus, in which, as previously described by myself, a most noticeable feature is the absence of pigment between the eye and the exterior. This is certainly very clearly marked and, further, is perfectly constant; but there can be no doubt, in face of the descriptions given above, that, if we use the term "rudimentary organs" to include such as are now from change in their structure less capable of fulfilling their function than they have been at some previous time, then within this category must certainly be included the pineal eye of Lacertilia. Such features as the great development of pigment in, for example, Varanus, or the loss of connection with the brain in many, such as Calotes, are surely only capable of explanation on the supposition that the organ is rudimentary.

One of the most prominent features in connection with the organ is its Invertebrate structure. This was pointed out by de Graaf in Angius fragilis, but in none of the forms examined have any structures equivalent to the rod-like bodies placed internally to those embedded in deep pigment, described and figured by him as present in the above-mentioned species, been found. There is often, however, a structureless substance resembling a coagulum present within the vesicle, which doubtless represents the remains of a humour which was fluid during life; in certain cases it appears to have attached itself to the inner ends of the rods and thus simulates to a certain extent elements lying internal to and connected with them. Further, there seems to be but little ground for likening the eye to that of Cephalopods and Pteropods, as is done by de Graaf; the structure of the retina is different, and that of the lens essentially so, being formed as a cuticular secretion in Mollusca, whilst in Lacertilia it is distinctly cellular and formed directly from the cells of the neural canal.

As before[1] pointed out the development and structure ot this organ is extremely interesting, as showing that out of the walls of a vesicle originating as a hollow outgrowth from the neural canal, may be formed an optic

[1] 'Nature,' May, 1886.

organ of the Invertebrate type, whilst from the walls of a precisely similar vesicle, and within the same animal, may be formed an eye of the Vertebrate type.

In both cases the nerve-fibres enter into connection with the retinal elements lying on the side remote from the rods; in one case, however, important secondary developments take place which are wanting in the other, and to which are further entirely due the differences existing between the two types of eyes.

In the case of the pineal eye, first, we have a vesicle, the anterior portion of the walls of which are transformed into the lens; of the cells forming the walls of the posterior half, those facing into the cavity give rise to the rods, whilst external to these are formed the other retinal elements, into connection with which enter the fibres of the pineal stalk; the primary optic vesicle persists, and there is thus formed an eye on what is usually spoken of as "the Invertebrate type," i. e. the rods facing directly into the cavity of the vesicle, and the nerve entering into connection with the external lying elements.

In the case of the paired eye, however, we find that, whilst up to a certain point it agrees in development precisely with the pineal eye, after that point is reached secondary structures appear which have an important influence on its final form. The retinal elements are formed out of the cells of the vesicle wall; the lens, however, is not, but arises as an invagination which pushes before it the external wall; whilst there is this difference between the lenses of the two forms, we see at once, when dealing with the retinal elements, that they are formed in a similar position to that in which they are present in the pineal eye—that is, the cells facing into the optic vesicle give rise to the rod-elements, whilst the external lying cells give rise to what are really the outer layers of the retina (nuclear and molecular layers, &c.). It is simply the formation of the lens as an invagination which causes the rods to assume what appears to be an external position, but is external only when regarded in connection with a secondarily formed cavity, the primary optic cavity which persists in the pineal eye entirely disappearing in the paired eyes.

There is, however, this difference, that in the pineal eye the posterior portion of the vesicle wall forms the retina, in the paired eyes the anterior; the lens of the pineal eye being a structure totally distinct from that of the paired eyes.

In the pineal eye both light transmitting and light receiving structures are formed out of the walls of the neural canal; the absence of this in the paired eye does not perhaps constitute so great a difference as appears at first sight, for though the lens is not formed out of the neural wall it is formed out of epiblast cells exactly as this is, and in such forms as the Amphibia, where the epiblast is divided into two layers, nervous and epidermic, then the lens is formed solely by the cells of the nervous layer.

In both cases, finally, the nerve-fibres are in connection with the external lying elements and retain this connection throughout life, to do which, after invagination has taken place in the paired eyes, they must pierce the walls of the secondary vesicle; there is thus produced the phenomenon of the nerve-fibres spreading out "in front of" (as it is called), and internal to, the retinal elements, though, morphologically speaking, they are behind and external to them, exactly as in the pineal eye.

Significance of the Organ.

In all forms of Vertebrates the epiphysis arises at an early stage as a hollow outgrowth from the roof of the thalamencephalon. Goette stated that the epiphysis was identical in position with the anterior neuropore—the part at which the walls of the neural canal remained longest in connection with the epiblast—but there seems to be no doubt whatever that this is not the case and that the rudiment of the epiphysis is formed at an early period in a position some little way posterior to that of the anterior neuropore. There can thus be no connection between the persistent anterior neuropore of Amphioxus and the epiphysis of other animals, supposing the former to be equivalent to the neuropore of remaining Chordata, which cannot be regarded as perfectly certain when its relationship to the anterior end of the notochord is considered.

In Petromyzon, according to Ahlborn,[1] the epiphysis arises as a hollow outgrowth from the roof of the thalamencephalon, which in subsequent development becomes divided into three parts, (*a*) a proximal solid stalk, (*b*) two distal vesicles of which the larger is the uppermost, whilst the smaller acquires a secondary connection with the left ganglion habenulæ. The whole lies within the cartilages enclosing the brain, and though a certain rod-like appearance is subsequently produced in the cells, particularly those of the upper vesicle, still no pigment is developed and no differentiation into retina or lens takes place.

In Elasmobranchs[2] the epiphysis stretches forward as a hollow outgrowth with a dilated end, which may remain within the skull cavity or be enclosed in the cartilage of the roof.

In Amphibia[3] the same development takes place in early stages, the organ remaining in Urodeles as a mushroom-shaped structure, whilst in Anura it is differentiated into a vesicle distally and a solid fibrous stalk proximally, the former being afterwards cut off and occupying an extracranial position immediately beneath the skin.

In Reptilia it arises in all forms as a hollow, forwardly directed outgrowth, which becomes most highly differentiated in Lacertilia, where, in many forms, its distal vesicular portion forms an optic organ.

In Aves the structure also stretches forward, originating as a hollow outgrowth, and being subsequently divided into a distal part which becomes vascular and a proximal solid stalk.

In Mammalia, finally, the structure is much less developed, the process being shorter than in the lower forms and directed backwards.

[1] "Untersuchungen über das Gehirn der Petromyzon," 'Zeit. f. Wiss.,' Bd. xxxix, p. 230, Tf. 13 and 16.

[2] Balfour, 'Elasm. Fishes,' p. 17.

[3] Henri de Graaf, op. cit., p. 23 (Urodeles) and p. 27 (Anura).

Taking thus the animal kingdom as a whole, we see that the epiphysis presents in all forms below mammals the following two points in common with regard to its structure.

(1) It originates as a hollow vesicular outgrowth stretching forward from the roof of the thalamencephalon.

(2) It becomes divided during development into two main divisions.

(*a*) A distal vesicle.

(*b*) A stalk (hollow or solid) connecting (*a*) with the brain roof.

In Mammalia the first of these two points obtains (except that the structure stretches backwards instead of forwards), but degeneration of the tissues sets in at an early period and secretion of solid material takes place in the part corresponding to the hollow vesicle of other forms.

In Aves both points obtain, but in course of development the distal vesicle becomes solid and highly vascular. Below Aves it apparently remains vesicular throughout life save in the Anura where the distal division separates off, becomes solid, and lies extracranially.

So far as is known to us at present the distal portion becomes most highly modified in Lacertilia; further investigations into its structure in other groups is needed, but, as far as our present knowledge goes, we are justified in saying that in Lacertilia alone, amongst living forms, the distal part of the epiphysis is modified into an eye and the tissues between it and the external surface are modified so as to allow of the easy transmission of rays of light to the organ.

In Petromyzon certainly the structure of the organ as figured by Ahlborn resembles somewhat an eye, but closer examination reveals considerable differences between it and the eye of any Lacertilian.

(1) Its division into two vesicles, one above the other, is a point of some importance, indicating that in this case development takes place along another line from that pursued in Lacertilia, where the vesicle always remains single.

(2) The absence of true retinal elements or lens is remark-

able. At first sight Ahlborn's figures of the organ, especially of the walls of the upper vesicle, call to mind the rod elements of other forms, but a closer examination again reveals important points of difference; they do not, as in Lacertilia, face into the cavity, being bounded internally as well as externally by nervous matter, and, more important still, there is an entire absence of pigment, which is the prominent feature possessed in common by the rods of all Lacertilian eyes. Further, again, the cavity of the optic vesicle is traversed by strands of nervous matter passing from the anterior to the posterior wall, a feature entirely wanting in any pineal eye, however degenerate, amongst Lacertilia.

On the other hand, these rod-like structures occupy the hinder wall of the vesicle, the proper position, supposing them to be true but degenerate retinal elements; and it may be remembered that amongst Lacertilia, which must be regarded as descended from ancestors possessed of pineal eyes, we do know of one form (Cyclodus) in which the eye now stops at a stage of development in which the cells of the posterior wall much resemble those of Petromyzon, and are devoid of pigment. The absence of lens also is paralleled in the case of Cyclodus.

(3) The organ is completely enclosed within the cartilaginous cranium, and acquires a secondary connection with the brain (its lower vesicle fusing with the left ganglion habenulæ) which is quite unknown amongst any Lacertilian.

The conclusion to be drawn from these facts[1] is that at the present time the epiphysis of Petromyzon certainly does not become modified into a pineal eye at all comparable to that of

[1] For our knowledge of the structure of the epiphysis of Petromyzon we must rely on Ahlborn's description here quoted; it is, of course, possible that, viewed in the light of recent work, the structures described by him might be found to bear another interpretation. I have not at present been able to study the structure, but would suggest the possibility of what Ahlborn figures as nervous material lying internal to the rod-like structures, and as strands of tissue crossing from the anterior to the posterior wall of the vesicle, being in reality only the coagulated remains of the fluid contents of the vesicle.

Lacertilia, in which its double nature and secondary fusion with the brain are quite unparalleled. At the same time it is of course possible, though we have no direct evidence of the fact, that the epiphysis is in a rudimentary state, and may be the degenerate representative of a once well-developed pineal eye. The general structure of the organ—a distal vesicular part with a solid proximal stalk—being in favour of this view, as is also the resemblance—upon which, however, too much stress must not be laid, between the walls of the upper vesicle and those of the swollen extremity of the epiphysis in Cyclodus.

Further investigations into the structure of the epiphysis are much needed amongst Pisces. At present it is known that amongst Elasmobranchs the structure developes as a hollow outgrowth from the roof of the thalamencephalon. This, as figured by Balfour in Scyllium,[1] stretches forward right over the cerebral hemisphere, and comes finally to consist of (1) a swollen distal extremity, and (2) a hollow stalk connecting (1) with the brain roof. The swollen extremity may further remain, as in Raja, external to the cranium, or become embedded within the cartilage, as in Acanthias. There is thus a striking similarity between this and the epiphysis at a certain stage of development in Lacertilia and the final stage persistent in Cyclodus.

When, however, we come to the Amphibia we find that amongst these the epiphysis passes through precisely the same forms in development, but (1) remains very rudimentary indeed in Urodela, and (2) after reaching a considerably higher stage of development in Anura undergoes great degeneration. The structure in the latter becomes differentiated into a distal vesicle, connected by a solid pineal stalk with the brain; the stalk soon, however, disappears, and the distal portion lies completely separated extracranially, its constituent cells undergoing degeneration. Never at any period does it become developed in any living Amphibian into an eye.

The word living is used and emphasised, because it is by no means certain that the same remark can be applied to all

[1] 'Comp. Embryology,' vol. ii, p. 355.

the extensive group of extinct forms classed together as Labyrinthodonta, and usually regarded as the extinct representatives of the class Amphibia. On the contrary, one of the most interesting features in the cranial skeleton of these is the possession of an extremely well-marked and prominent parietal foramen,[1] which is proportionately quite as large, and in many cases larger, in comparison to the size of the skull than in living Lacertilia.

There is no doubt that the presence of a parietal foramen is intimately associated with a high state of development of the epiphysis, and we are thus brought without hesitation to the conclusion that, whilst amongst living Amphibians the epiphysis is present only in a rudimentary and degenerate condition, in extinct Amphibia (Labyrinthodonta) the epiphysis was in a high state of specialisation. Further, the only group of living animals in which, as before said, a parietal foramen is present, is Lacertilia. Within this group, though various degenerate forms are seen, yet, inasmuch as

The organ is found in genera of every family, ancient and recent alike (in Hatteria, in Calotes, in Agama, in Moloch, in Anolis, in Iguana, in Anguis, in Varanus, in Seps, in Lacerta), in which a foramen is developed; whilst again, in such as Gecko, Ameiva, and Ceratophora, where no foramen persists, the organ is absent,

It may be further said that the presence of a parietal foramen, as a structure typical of the skulls of a group of animals indicates the presence of a pineal eye within that group.

It is quite true that in three forms described—Cyclodus, Chameleo, and Lyriocephalus—the foramen is present, and though the epiphysis is, in certain respects, highly developed in each case, the distal portion retaining its connection with the brain roof, yet no true eye is formed. This, however, need present no difficulty in the way of acceptance of the above statement. Regarding the present families of Lacer-

[1] See especially the drawings of Fritsch in 'Fauna der Gaskohle und der Kalkstein,' Prag., 1885.

tilia as descendants of some common ancestor, we can come to no other conclusion, inasmuch as the more primitive and specialised forms agree at the present time in the possession of a parietal foramen occupied by a pineal eye, and that this is, further, a characteristic of the nearest allies of the forms mentioned, than that the ancestral form possessed both these structures, and that the condition seen in Chameleo, Cyclodus, and Lyriocephalus is not typical but secondary; they possess a parietal foramen simply because their ancestors possessed a pineal eye, which in them is in a rudimentary condition, as indeed the external modification in Cyclodus (Pl. XV, fig. 9) seems to show in the case of this form in particular.

When, therefore, we find the parietal foramen exceedingly well developed throughout all the group Labyrinthodonta, we are justified in concluding that in them a pineal eye was in all probability present, even though we may grant the possibility (an unlikely one under the circumstances) of its occasional presence, as in Lacertilia, in a low state of development.

In living Reptilia the presence of the foramen is confined to one group, but amongst the extinct forms, which may be regarded as the ancestors of the Reptilia now living, whilst some, at all events, may further be regarded as intimately connected with the ancestors of living birds, we find that the foramen is a well-developed structure. Judging from its present condition in the relatively small Lacertilia of the present day, we may imagine that in the huge extinct forms of Mesozoic periods—in such as Ichthyosaurus and Plesiosaurus, the walls of whose foramina even present rugosities as if for the insertion of muscles—the pineal eye attained a development and importance quite disproportionate to that with which we are now acquainted in any living form.[1]

[1] I am indebted to Professor Moseley for calling my attention to the paper upon "The Brain of a Theromorphous Reptile of the Permian Epoch," by Cope, in which is figured a cast of the brain of one of the Diadectidæ. Perhaps the most remarkable feature is the huge comparative size of the cavity within

The walls of the foramina are lifted above the level of the parietal bones, and it is perfectly possible, if not certain, that the organ itself, enclosed in the eye capsule, projected considerably beyond the surface.

With the gradual extinction of these forms and of the Deinosauria (i. e. Iguanodon, &c.), after the Cretaceous period was passed, the organ, we may suppose, began with the rapidly dwindling size of the specialised tertiary and later Reptilia and Aves to lose its importance, until, degenerating in various degrees in different groups, it retained traces of its original eye-like structure in the only groups in which, amongst living reptiles, the parietal foramen persists; its preservation being intimately connected with and dependent upon the presence of this structure. The foramen is preserved amongst no group whatever of existing Aves, and hence in these the epiphysis undergoes considerable degeneration, though in its development it still reaches a stage when, as in Reptilia, it consists of a distal vesicle connected with the brain roof by a solid stalk.

In Mammalia the degeneration is far more complete, and all trace of the ancestral importance is completely lost.

There now remains for consideration the two classes, Urochorda and Cephalochorda; with regard to the latter it is very difficult, if not impossible, to homologise any part of its nervous system with the epiphysis of higher forms; the persistent anterior neuropore described by Hatscheck may perhaps be homologous with that of other forms of Chordata which closes during development, though even this must be regarded as extremely doubtful owing to its position considerably posterior to the anterior end of the notochord; neither can it for the same region be considered the homologue of the epiphysis, which again lies posterior to the neuropore. The azygos pigment spot described as an "eye" has no apparent

the parietal foramen, presumably filled during life by the epiphysis. In addition to this, Professor Cope points out a large posterior process leading back towards the optic lobes and roof of the thalamencephalon, and which recent work on living forms can scarcely leave room to doubt represents the flattened pineal stalk.

resemblance in position or structure to the pineal eye of Lacertilia.

As figured by Langerhans[1] and Nüsslin,[2] it is a pigment spot within the walls of the neural canal, and lies anterior to the part shown subsequently by Hatschek to be the anterior neuropore; whereas if it were the homologue of the azygos eye of Tunicata it must lie posteriorly to this.

Turning to the Urochorda a structure is at once met with which naturally suggests comparison with the pineal eye. Yet, however tempting it may be to homologise the azygos Tunicate eye with the latter, it cannot be too clearly pointed out that the two organs differ fundamentally in structure and position, and we have not the slightest reason for supposing that the pineal eye is the direct representative of the Tunicate eye. In the first place, the internal position of the latter clearly distinguishes it from the pineal eye; even supposing the tunicate organ to, in some way, undergo evagination there still remains the difficulty that the retina corresponds in position to the part which after evagination would give rise to the lens, whilst the latter structure is perfectly distinct in nature and formation from that of the pineal eye.

The curious formation of the lens in Tunicates from the union of two or more separate parts, differing in shape and quite distinct from that of Lacertilia in their relationship to the retina, is an important point of difference, and renders it quite impossible, whatever may be the case with the retina, to homologise the lens in the two forms. At the same time there is considerable analogy between the two lenses, inasmuch as each is formed directly out of the walls of the neural canal, a point in which they at once agree with one another, and differ from every other Vertebrate. Notwithstanding this it must, I think, be admitted that the vesicular nature of the eye in Lacertilia and the formation of the lens out of a portion of the vesicle, constitutes a difference of fundamental importance between the two eyes in their fully-developed condition.

[1] 'Arch. f. Mikr. Anat.,' Bd. xii, Tf. 12, fig. 17.

[2] 'Zur Kritik des Amphioxusauges,' Otto Nüsslin, Tübingen, 1877.

Whilst it must be admitted that we are without evidence sufficient to warrant us in regarding the pineal as the direct representative of the azygos Tunicate eye, it is, perhaps, worth suggesting that there may be some connection between the larval eye of Tunicata and the epiphysis of higher forms. It may be pointed out, first of all, that the position of the eye and that of the rudiment of the epiphysis is the same with regard to the anterior end of the notochord, both, further, being situated on the dorsal surface of the "brain," applying this term to the anterior vesicle of the neural canal in Tunicata. It must, however, be also noticed that the eye of the latter is placed not exactly medianly, but slightly to the right side.[1] There still remains the great difficulty of the transformation of the internally placed eye into an external hollow process of the brain roof.

According to Kowalewsky,[2] the Tunicate eye first appears as a thickening of the dorsal wall of the brain cavity, in one particular portion the cells becoming cylindrical and much elongated, and pigment appearing at their internal ends. The refractive structures forming the lens are produced subsequently, so that at first the eye is merely a specially thickened part of the roof of the brain cavity, and only at a later period appears to assume its distinctly internal position, bulging out into the cavity (cf. figs. 32, 34).

Turning now to the epiphysis, we find that it arises as a hollow outgrowth from the brain roof, presenting, as a rule, nothing comparable to the structure of the Tunicate eye. In one form, however, amongst Amphibia, it is just possible that we meet with an indication of a connection existing between the two. A further examination in other forms, particularly those of Pisces, might possibly reveal a similar

[1] Ahlborn draws attention to the slightly asymmetrical position of the epiphysis in Petromyzon, where it becomes, by secondary growth, united to the left ganglion habenulæ; but since the eye of Tunicates is on the right side, it is difficult to imagine any connection between the two.

[2] 'Arch. f. Mikr. Anat.,' Bd. vii, 1871, pl. xii, figs. 32 and 34.

method of development; at any rate, without laying undue stress upon the example to be quoted, it is worth while drawing attention to it, inasmuch as it reveals to us the possible path by which the epiphysis of higher forms has been developed out of a structure similar to the larval Tunicate eye at an early stage. De Graaf, in his recent memoir,[1] figures and describes the development of the epiphysis in Bufo cinerea. His figures are, unfortunately, not drawn with such regard to histological detail as could be desired in the present instance, but, so far as they go, they indicate the possible existence of a connection between the epiphysis of Bufo and the azygos eye of the embryo Tunicate. He shows the epiphysis as arising at first as a thickening of the roof of the thalamencephalon, which soon assumes the form of a slight hollow outgrowth. On the inner surface of the cells, sharing in the thickening and subsequent outgrowth, is a small but well-defined mass of pigment. This pigment very soon entirely disappears, and a hollow process—the epiphysis—is formed, which gradually increases in size, and becomes differentiated into a vesicular distal portion and a solid stalk, the former gradually becoming constricted off. Is it not possible that in these phenomena we have an indication of the change from the internally situated Tunicate eye into an externally placed hollow process? As before said, the Tunicate eye arises as a distinct thickening of the brain-roof, the cells forming the thickened portion bearing pigment on their internal ends. Just the same phenomena are witnessed in the case of the epiphysis of Bufo cinerea, but, instead of developing into an eye internally placed, the cells, whose external ends already form a bulging on the outer surface, form into a well-defined evagination, the internally placed pigment disappears, and the epiphysis, as present in all the higher groups of the Chordata, is developed.

Whether we are here presented with an epitome of the steps passed through during transformation of the internally-placed eye of a transparent organism into the externally-lying evagina-

[1] Op. cit., pl. iii, figs. 22 and 23, p. 27.

tion of a creature whose skin has become opaque, and to whom an eye within the brain has become useless, it would be extremely difficult to say with certainty;[1] it is, however, worth while calling attention to the fact that the epiphysis in very early stages in its development in Bufo cinerea resembles the Tunicate eye before the appearance of refractive elements, whilst subsequent loss of pigment and evagination transforms it into the epiphysis of the adult.

If there be any truth in the above hypothesis it follows that we must start with a form which may be regarded as the common ancestor of present Tunicata and the higher Chordata; in this, which closely resembles an embryonic Tunicate, certain cells of the dorsal wall of the neural cavity are specially elongated and bear pigment at their internal ends, just as in the embryo Tunicate eye and Anuran epiphysis. From this point development leads in two directions—(1) to the highly developed internal eye of present Tunicata with its secondarily developed refractive structures, and (2) by evagination and loss of pigment to the epiphysis of higher Chordata. Subsequent differentiation in the latter results in the formation of a distal vesicle united to the brain roof by a stalk, at first hollow and afterwards solid, whilst finally the distal vesicle becomes modified into the pineal eye.

The evolution of the epiphysis is represented diagrammatically

[1] It will be seen that this differs from the suggestion of Professor Lankester that the internal eye of Tunicates by evagination forms the Vertebrate eye. In the first place I suppose the evagination to give rise to the epiphysis, subsequent differentiation of the distal vesicle of which gives origin to the pineal eye. Secondly, I assume the development of the Tunicate eye and the epiphysis out of an ancestral form common to Tunicata and the higher Chordata, development taking place along two different lines and being possibly connected with the transparency of the one and the opacity of the other form. At the same time it may be pointed out that it is possible that the paired eyes may be formed by evagination of paired internal eyes similar to the one which becomes transformed into the epiphysis. The vesicles giving rise to the paired and pineal eyes are precisely similar to each other, and may have originated in the same way, the two types of eyes being entirely the result of the development of secondary structures.

in the figures on Pl. XX, which show the various stages passed through before the highest form of development is reached, and also the various forms as the result of degeneration. Each stage save the earliest ones (1, 2, and 3) which are found in the development of Tunicata and Bufo cinerea, represent the permanent condition of the epiphysis in some living form.

The question now arises, is it possible to determine at what period or rather within what group of animals the distal vesicle first became differentiated into a pineal eye. There must clearly have been a period during which the hollow epiphysial evagination was not functioning as an eye, precisely in the same way in which the primary optic vesicles must have existed as hollow outgrowths of the brain before they, in like manner, were differentiated into optic organs; in fact, the three distinct stages of (1), a hollow bladder-like evagination (fig. 4); of (2), a distal vesicle connected by a hollow stalk (fig. 5) to the brain; of (3), a vesicle connected with a solid stalk (fig. 6), must necessarily all have intervened before the final stage (fig. 7) was reached. When in any particular form we find one of these three stages are we to assume that in that given form, and hence in the closely allied members of the same group, the epiphysis has never in its philogenetic history reached a higher stage of development than the one in which it is now present? Suppose, for example, that we find an animal in which the epiphysis has the form represented in fig. 5, must we take it for granted that in that animal and its ancestors no higher stage of differentiation has ever been reached. Taking the animals in which this particular stage is permanent, we find that they include certain Elasmobranchs together with Cyclodus gigas amongst Lacertilia. Now we have clear evidence that, in the forms from which we must suppose Cyclodus in common with all other lizards to be descended, as well as in its nearest living allies, the epiphysis is developed into a pineal eye. To what conclusion must we come in the case of Elasmobranchs; certainly the non-development of a pineal eye in living examples is no proof whatever that such a structure was not present in its ancestors. It must at once be granted that an Elasmobranch, such as Raja or Acanthias, differs from Cyclodus inasmuch as none of its living allies have the organ more highly developed, whilst in forms allied to Cyclodus it is in a high state of development; yet even this is by no means of so great importance, as to make us conclude that living forms present us with the highest stage yet reached in Elasmobranchs. If we turn to the Amphibia we find a group of animals amongst whom in no living form is there a pineal eye present, and yet we may feel perfectly sure that in the great group of extinct Amphibia (Labyrinthodonta) one was not only present but most probably developed to its highest point. It must be admitted that we have at present no direct evidence of the existence of pineal eye within the group Pisces : until our knowledge is far greater with regard to the development of the structure in, more especially Dipnoi and Ganoidei, it will be impossible to determine the question of the presence or absence of the structure within the group. Meanwhile, the varied state of development seen in such forms as Petromyzon on the one hand, and Acanthias, Raja, and Scyllium on the other, may perhaps be taken as evidence tending in favour of the view that in its present form the organ is rudimentary. All that may now be rightly insisted upon is that the absence of the eye in living forms, either of this or of any other class, is no proof that one has not been present at some period in the phylogenetic history of the group.

The conclusions, finally, to which we are brought are the following :

(1) Our present knowledge is not great enough to allow us, in Amphioxus, to homologise any structure either with the Tunicate azygos eye or with the epiphysis.

(2) The epiphysis of higher Chordata is the homologue of the larval Tunicate eye.

(3) The pineal eye is produced as a secondary differentiation of the distal part of the epiphysis.

(4) There is not sufficient evidence to prove or disprove the existence of the organ within the group Pisces; it was present in extinct Amphibia, and is found amongst living forms only in Lacertilia.

(5) In all forms at present existing it is in a rudimentary state, and though its structure is better developed in some than in others, it is perfectly functional in none.

(6) It was present most highly developed in

(1) Extinct Amphibia (Labyrinthodonta), and

(2) The large group of extinct forms (as Ichthyosaurus, Plesiosaurus, Iguanodon, &c.) which may be regarded as ancestors alike of living Reptilia and Aves.

(7) The pineal eye may probably be most rightly considered, as peculiarly a sense organ of pre-Tertiary periods.

EXPLANATION OF PLATES XIV, XV, XVI, XVII, XVIII, XIX, & XX,

Illustrating Mr. Baldwin Spencer's Paper on "The Presence and Structure of the Pineal Eye in Lacertilia."

List of Reference Letters.

Ant. (*Le*). Cells of anterior wall of distal vesicle of epiphysis. *C.* Cilia of cells lining epiphysis. *Ca.* Capsule of connective tissue enclosing the pineal eye. *Car.* Cartilage within skull in Hatteria. *Cb.* Cerebellum. *C. H.* Cerebral hemispheres. *Co.* Cone-shaped bodies of pineal eye. *Co.*[1] Modified cone-shaped bodies lying near the pineal stalk. *Cor.* Cornea. *Ct.*, *Ct.*[1], *Ct.*[2], *Ct.*[3], *Ct.*[4], *Ct.*[5], *Ct.*[6] Connective tissue in various positions in connection with the parietal foramen and pineal eye. *Ct. pig.* Pigment in the cutis vera. *Cut.* Cuticle. *De.* Dermis. *D. M.* Dura mater. *Ep.* Epidermis. *Ep.*, *Ep.*[1] Epiphysis. *Ep.* 1. Swollen distal end of epiphysis. *Ep.*[1] (*ops.*) Portion of epiphysis equivalent to the pineal stalk. *Hum.* Humour of eye. *Inf.* Infundibulum. *Le.* Lens. *Md.* Medulla oblongata. *Mes.* Mesencephalon. *Mo.* Molecular layer of eye. *N.* Nuclei of cells of epiphysis walls. *N.*[1], *n.*[1] Internal row of nuclei in retina. *n.*[2], *N.*[2] External row of nuclei in retina. *n.*[3] Specialised nucleated elements in pineal stalk of Hatteria. *ne.* Nerve-fibres. *N. ct.* Nuclei of connective tissue. *Olf.* Olfactory nerve. *Op.*, *Op. v.* Optic vesicle. *Op. S.* Pineal stalk. *Op. L.* Optic lobe of brain. *Pa. for.* Parietal foramen. *Pa.*, *Par.* Parietal bones. *Post.* (*R.*) Cells of posterior wall of swollen end of epiphysis in Cyclodus. *pig.*, *pig.*[1], *pig.*[2], *pig.*[3], *pig.*[4] Pigment developed in various positions in connection with the eye. *Proc.* Processes uniting various retinal elements in Varanus. *Re.* Retina of pineal eye. *R.*, *r.* Rods of retina. *R.*[1] Specialised rods in connection with entrance of nerve-fibres. *R. Mp.* Rete mucosum. *S.* Spindle-shaped elements of retina. *Thl.*, *Th.* 3*rd vent.* Thalamencephalon and 3rd ventricle. *Vent.*[3] 3rd ventricle.

PLATE XIV.

Fig. 1.—Longitudinal vertical section through the parietal foramen of Varanus giganteus. The right side lies posteriorly, the left anteriorly, and the parietal bone enclosing the foramen is shaded yellow. The connective tissue is seen forming a dome to the foramen and filling up the latter. The pineal eye is cut through in the median line, showing the lens with its special development of pigment in the optic axis and the retina with the elongated rods where the nerves enter the vesicle. The nerves are three in number, two

joining into one and the two main strands then uniting to form the solid pineal stalk. The large blood-vessel accompanying the stalk enters the foramen, together with the latter.

Fig. 2.—Longitudinal vertical section through the connective tissue capsule containing the pineal eye of Hatteria punctata. The right side is the anterior, the left the posterior, the external surface of the head being parallel to the breadth of the plate. The capsule is formed anteriorly by the connective tissue filling up the parietal foramen. Into the capsule passes a blood-vessel, which ramifies amongst loosely scattered connective-tissue fibres. The anterior part of the capsule is comparatively empty, but special fibres pass from the walls to the sides of the lens. The optic vesicle is cut through in the median line, showing the cone-shaped lens and the elements of the retina together with the pineal stalk entering posteriorly.

Fig. 3.—Section through the retina of Hatteria punctata. The left is the internal, the right the external surface. Internally the shade indicates the fluid within the vesicle, bounding the cavity of which are the rods lying in pigment. External to the rods lie the inner spherical-shaped elements, then the molecular layer, and external to the latter larger spherical bodies together with conical and spindle-shaped bodies, the latter two being in connection with nerve-fibres. (In the figure the nerve-layer has been drawn so as to appear more prominent than it is in reality.)

Fig. 4.—Section through the portion where the pineal stalk enters the walls of the vesicle. The specialised bundle of rods lying in the optic axis, with the nuclei in connection with them, are seen together with the retinal elements around the entrance of the nerve-fibres of the stalk. The fibres run round in front of the capsular-like structure which contains the specialised nucleated elements, sending some to these on either side, the remainder passing on and either (1) entering into connection with the elements nearest to the pineal stalk, or (2) passing farther on to form a layer of nerve-fibres on the external surface of the vesicle.

Fig. 5.—Separated rods from the retina of the pineal eye of Hatteria punctata. The pigment is so deposited as to produce the effect of striations.

Fig. 6.—Section through the retina of Varanus giganteus. The rods lie embedded in pigment on the internal surface, passing into the cavity of the vesicle; the shade on the left indicates the humour within the latter. The reticular nature of the retina external to the rods is seen, the nuclei of the spherical elements being coloured red. The internal spherical elements are situated within the molecular layer; amongst the external ones are large masses of pigment; more external still is a thin layer of nerve-fibres, and outside this the connective-tissue fibres enclosing the optic vesicle.

PLATE XV.

FIG. 7.—Longitudinal vertical section through the median line of the head in Hatteria punctata in the region of the parietal foramen. The relative positions of the epiphysis, the pineal stalk, and pineal eye, are seen together with the plug of connective tissue filling up the foramen. In front of the epiphysis is the vascular roof of the thalamencephalon.

FIG. 8.—Diagrammatic side view of the brain of Hatteria punctata. The brain is lying in its cartilaginous case. From the thalamencephalon between the cerebral hemispheres and the optic lobes arises the epiphysis, which at first running almost directly upward, turns forwards on reaching the cartilaginous roof as far as the parietal foramen, where the pineal stalk pierces the cartilage and enters the optic vesicle, which is seen lying in its capsule.

FIG. 9.—External view of the modified eye-scale of Cyclodus, showing the modification to form a cornea.

FIG. 10.—External view of the scales in the median line of the head of Varanus giganteus, showing the scale modified as a cornea.

FIG. 11.—The pineal eye of Anolis (sp.?) removed, together with the brain membranes, and viewed as a solid object by transmitted light.

FIG. 12.—The pineal eye of a small specimen of Varanus bengalensis, ying within the parietal foramen and viewed from the under surface.

FIG. 13.—The modified eye-scale of a small Calotes (sp.?), with the transparent cornea in the middle through which the eye is seen.

FIG. 14.—The pineal eye of the same Calotes, whose scale is figured in Fig. 13, removed with the dura mater and viewed as a solid object.

FIG. 15.—Scales from median line on head of a large specimen of Iguana tuberculata, showing the modified eye-scale with cornea.

FIG. 16.—Modified eye-scale of a young Iguana, showing the transparent central portion with the eye beneath as a dark spot.

PLATE XVI.

FIG. 17.—Longitudinal vertical section through the parietal foramen of Varanus bengalensis, showing the pineal eye and the hollow epiphysial stalk immediately beneath. The yellow shade indicates bone. *Ep.*[1] Hollow epiphysial stalk.

FIG. 18.—Longitudinal vertical section through the distal part of the epiphysis of Cyclodus, showing the swollen extremity and the hollow epiphysial stalk connecting this with the brain. *Ep.* 1. Swollen extremity. *Ep.*[1] Epiphysial stalk.

FIG. 19.—Section through a part of the upper wall of the swollen extremity of the epiphysis in Cyclodus. *C.* Cilia of cells bounding the cavity of the epiphysis. *Ant.* (*Le*) The elongate cells, equivalent to those forming the lens of the parietal eye in other forms. *n.* Oval nuclei of the cells.

FIG. 20.—Section through portion of the under wall of the same. *Post.* (*R.*) Ends of the cells facing into the cavity in the position of the rods of other forms. *n.* Circular nuclei of the cells.

FIG. 21.—Longitudinal vertical section through the parietal foramen of Chameleo vulgaris, showing the optic vesicle, pineal stalk, and epiphysis. The yellow shade indicates the parietal bone.

PLATE XVII.

FIG. 22.—Longitudinal vertical section through the parietal foramen and pineal eye of Leiodera nitida. The great elongation of the cells of the rete mucosum is drawn, and the entire absence of pigment from the cutis vera above the eye indicated.

FIG. 23.—Pineal eye of Iguana tuberculata, cut in section and removed from the parietal foramen. When in position the optic axis looks directly upwards.

FIG. 24.—Longitudinal vertical section through the parietal foramen of Anolis (sp.?), showing the pineal eye lying within the vacuolate tissue, together with the pineal stalk.

FIG. 25.—Longitudinal vertical section through the parietal foramen of Anguis fragilis, showing the pineal eye separated from the proximal portion of the epiphysis and the forward extension of the latter.

FIG. 26.—The eye of Lacerta viridis, viewed as a solid object lying within the parietal foramen.

PLATE XVIII.

FIG. 27.—The pineal eye of Lacerta ocellata, viewed as a solid object lying within the parietal foramen, one half of which has been cut away. The eye lies within a mass of branched pigment cells, amongst which ramify the branches of the blood-vessel which accompanies the pineal stalk.

FIG. 28.—The brain of Lacerta ocellata, with the pineal eye lying in the dura mater, viewed from the side.

FIG. 29.—The brain of Cyclodus gigas, viewed from the side, with the epiphysis stretching forwards and upwards and ending in a swollen part within the parietal foramen surrounded by pigment. (The foramen should not be closed above.)

FIG. 30.—Longitudinal vertical section through the pineal eye of Lacerta ocellata, showing the double nature of the nerve.

FIG. 31.—Diagrammatic longitudinal vertical section through the brain of Calotes ophiomaca, to show the pineal eye lying within the parietal foramen and its relationship to the epiphysis, and of this to the brain.

FIG. 32.—Longitudinal vertical section through the pineal eye of Seps chalcidica, showing its relationship to the foramen and its surrounding of deep pigment.

FIG. 33.—Longitudinal vertical section through the pineal eye of Calotes ophiomaca, showing its relationship to the parietal foramen and the blood-vessel within the latter.

PLATE XIX.

FIG. 34.—Diagrammatic longitudinal vertical section through the parietal foramen of Varanus giganteus, showing the eye within the parietal foramen and the pineal stalk.

FIG. 35.—Diagrammatic longitudinal vertical section through the median line of the brain of Plica umbra, to show the eye and its relationship to the pineal stalk and epiphysis.

FIG. 36.—Diagrammatic side view of the brain and pineal eye of Moloch horridus, viewed as a solid object, the eye lying within the parietal foramen.

FIG. 37.—Modified median eye-scale of a small Varanus bengalensis.

FIG. 38.—Modified median eye-scale of Leiodera nitida.

FIG. 39.—Modified median eye-scale of Agama hispida.

FIG. 40.—Diagrammatic longitudinal vertical section through the brain of Chameleo vulgaris, to show the distal vesicle with the pineal stalk.

FIG. 41.—Diagrammatic longitudinal vertical section through the brain of Varanus bengalensis, showing the eye lying in the parietal foramen, and the pineal stalk with its swollen extremity beneath the eye.

PLATE XX.

Diagram illustrating the development of the epiphysis from an internally placed eye in the "brain" of an ancestor common to Tunicata and higher Chordata. Figs. 1—7 illustrate the evolution of the organ till its highest stage of development is reached. Figs. 2 and 3 are diagrammatised from those of two stages in the development of the epiphysis in Bufo cinerea, as given by de Graaf. Fig. 1 represents an early stage of development, according to Kowalevsky, in Tunicates, before the formation of a lens. In higher Chordata loss of pigment and evagination produce the epiphysis, which may in various forms reach different stages shown in the figures. The cross-line shading indicates the parietal bone. Figs. 9—12 representing various stages of degeneration in forms in which the parietal foramen becomes closed. All the figures are, of course, perfectly diagrammatical.

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Fig. 15.

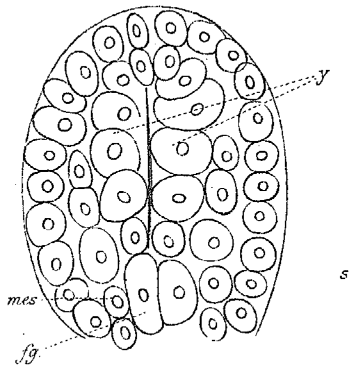


Fig. 16.

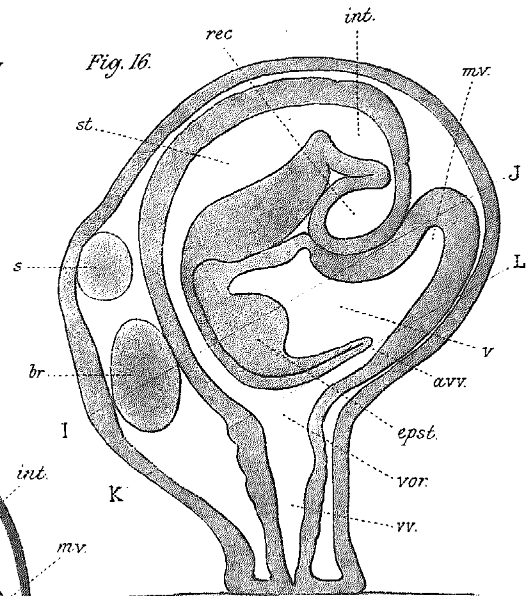


Fig. 17.

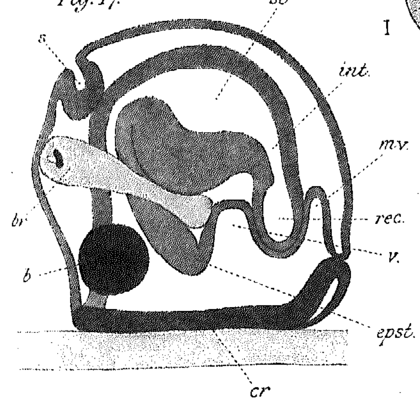


Fig. 18.

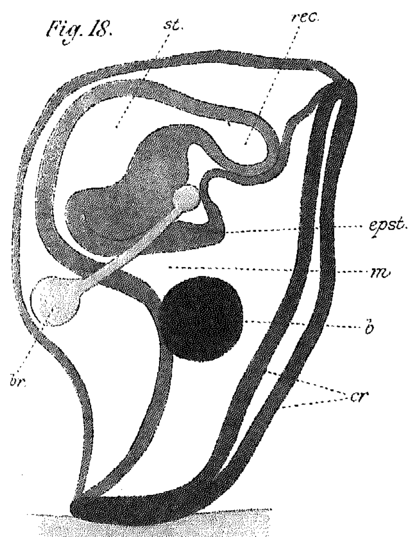
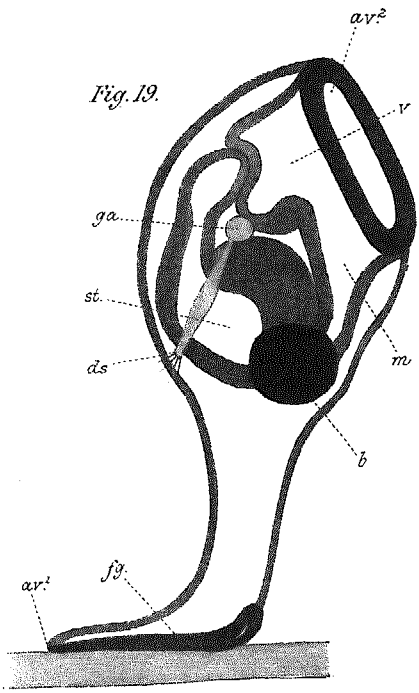


Fig. 19.



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