CHAPTER XX

RUDIMENTARY EYES

THE adoption of peculiar habits by a species of animal frequently stimulates the development of structural alterations suited to the unusual environment ; in a previous chapter we have discussed the many striking modifications adopted by the vertebrate eye to meet different conditions—aquatic or aerial vision, for example. Changes in the opposite sense may also occur when vision is no longer required, in which case the eyes may become rudimentary or vestigial or even disappear. The adoption of a sessile or sedentary habit involving sluggishness or quiescence so complete that light stimuli are valueless may lead to the development of a state of quasi or complete eyelessness in this way, but the more usual stimulus is a lightless habitat as in abyssal depths of the sea, dark caves, muddy rivers, burrows under the ground, or within the body of another animal.

A sharp distinction should be noted here between the permanent adoption of an environment wherein light is absent and the periodic adoption of *nocturnal habits* by many species for purposes of concealment or hunting—the daily use of caves by bats, for example, as opposed to permanent residence in a cave by cavernicolous fishes, or the use of a burrow as a home by the tuatara as opposed to the subterranean life of the mole. As a rule these nocturnal animals show the opposite tendency ; their eyes are elaborately developed to take every advantage of the dim illumination available, being often provided with a large lens, a wide pupil and a rod-retina.

This tendency for the structural recession and loss of function of an organ which is no longer biologically useful is not, of course, confined to the eye: the fate of the human appendix and coccyx are well-known examples of the regression of an organ, while the loss of its alimentary canal by the tapeworm or the possible reduction of a micro-organism to the bare bones of its nucleo-protein on the adoption of the habit of intracellular parasitism as a virus may be cited as examples of the complete disappearance of unnecessary characters. The biological mechanism of the transmission of such a disappearance, however, is not clear ; it is as if development has become arrested from lack of use. It is generally accepted that biologically useful characteristics tend to be retained in so far as they have survival value, but that those which are no longer useful should be purposely discarded as excess baggage is an expression of Lamarckian regression more positive than many would accept. Regression, however, does not necessarily imply degeneration as the term is generally understood. Darwin (1859) in his *Origin of Species* pointed out that both the use or disuse of an organ might equally lead to inherited changes both in plants and animals, and that parasites and " degenerate " creatures are as much a product of evolution as higher organisms ; they are as perfectly adapted to their restricted environment.[1]

[1] The opposing argument used by August Weismann in his *Essay on Inheritance and Related Biological Questions* (1892) that successive generations of rats the tails of which had been cut off persisted in breeding rats with normal tails is inapposite since an artificial mutilation bears no biological relation to a purposive evolutionary regression. See Ray Lankester, *Degeneration, a Chapter in Darwinism* (1895) ; Demoor and others, *Evolution by Atrophy in Biology and Sociology* (1894) ; Vandervelde, *Parasitism, Organic and Social* (1895).

An alternative explanation is to suppose that there is an innate tendency for the eye to disappear which is normally opposed by natural selection because of its biological utility. It is doubtless true that a loss-mutation may become effective and the organ may disappear if its utility has ceased. It is to be remembered, however, that individuals may show a capacity for the eye to retrogress or develop according to its usefulness. Thus on the one hand, the eyes of larval cave-salamanders (*Proteus*, *Typhlotriton*) usually regress at metamorphosis, but will develop if the larvæ are grown artificially in the light (Kammerer, 1912) ; these sightless Amphibians thus appear to become blind in each successive generation. On the other hand, Ogneff (1911) found that if goldfish were kept in the dark for 3 years their eyes became degenerate and functionless while the eyes of many species of open-water fish become reduced if their biological value is lessened by increasing their food and eliminating predators from their environment.

We have already seen that ocular regression of this type may occur in most Invertebrates, particularly worms, Molluscs and Arthropods ; the phenomenon is also encountered in all classes of Vertebrates with the exception of Birds. It is interesting that in most cases there is a corresponding increase in the development of other senses, such as the chemical, olfactory or tactile sense, which are of greater use than vision in dark surroundings.

THE SEDENTARY HABIT

A SEDENTARY HABIT may lead to the eyelessness in sessile forms. Thus among actively swimming Lamellibranchs such as the common scallop, *Pecten*, eyes of an extremely elaborate type are found, but in sluggish and quiescent forms they may be primitive, as in the bivalve, *Lima*, or absent as in the mussel, *Anodonta*. Among Crustaceans, those species of the Amphipod, *Gammarus*, which live in pools, or the Isopod, *Asellus*, which lives in holes is completely blind. In other species eyes may be present in the actively swimming nauplius stage, but when the adult becomes sessile these may become vestigial (the acorn-shell, *Balanus*, which encrusts rocks ; the ship-barnacle, *Lepas*). We have already seen [1] that in insects the degree of ocular development is generally correlated with that of the wings (Kalmus, 1945).

THE ABYSSAL HABIT

An ABYSSAL HABITAT renders eyes useless ; for in the deep seas there is perpetual night. The transparency of the different seas varies greatly, a factor which depends largely on the concentration of plankton organisms, but at 370 metres in the Mediterranean and at 1,500 metres in mid-Atlantic there is not sufficient light to affect a photographic plate unless it is exposed for 2 hours ; while the pelagic zone (down to 200 metres) is illuminated, the bathypelagic zone (200 to 2,000 metres) is thus very dark, and on the deep-sea floor (the benthonic zone), which may be several miles in depth, darkness is complete.

[1] p. 224.

It would seem, indeed, that all the inhabitants of this still, cold, dark world should tend to lose their eyes ; possibly they would were it not for the development of luminous organs, a common acquisition by the inhabitants of the benthos.[1]

Thus among abyssal Molluscs (*Chiton*, etc.) the eyes tend to degenerate even in Cephalopods wherein these organs are usually well marked ; the only known blind Cephalopod, however, is *Cirrothauma murrayi*, an octopod which inhabits the N. Atlantic at depths of approximately 3,000 metres (Chun, 1911). Similarly among Crustaceans living at moderate depths, the arrangement of the pigment surrounding the ommatidia of the compound eyes remains permanently in the dark-adapted position, while in bathy-

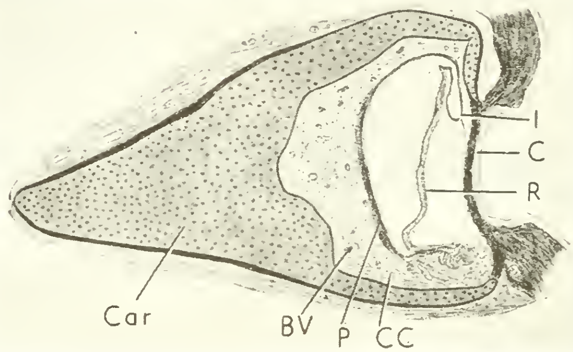

FIG. 866.—THE EYE OF A BLIND SELACHIAN FISH, *BENTHOBATIS*.

The ocular structures are of the most rudimentary type. *BV*, blood vessel ; *C*, cornea ; *Car*, cartilage ; *CC*, connective tissue ; *I*, iris ; *P*, retinal pigment ; *R*, retina (after Brauer).

pelagic types various stages of degeneration appear wherein all pigment is absent (*Cyclodorippe*)[2] or the ommatidia entirely disappear and the eye-stalks become fused with the carapace or are converted into tactile organs (*Cymonomus*, etc.) (Doflein, 1904). Paradoxically, side-by-side with species with degenerate eyes dwell other Crustaceans (shrimps, etc.) with fully developed and pigmented eyes, frequently, however, in creatures of a roving habit (Edwards and Bouvier, 1892).[3] In general among bathypelagic fishes, species which penetrate to lower and lower depths develop progressively better eyes, adopting all possible expedients to improve their vision in dim illumination—a telescopic shape, an immense lens, a huge pupil, a brilliant tapetum, and a multiplication of the rods—until these organs become relatively larger than in any other Vertebrate. But below 500 metres in many instances the struggle is given up and the eyes shrink so that among the deeply benthonic fishes they are often vestigial and functionless or

[1] p. 736. [2] p. 166.

[3] Compare the " wondrous-eyed hopper " (Fig. 203), an inhabitant of the deep seas.

absent ; in this event it is interesting that some species maintain projicience by developing long filamentous " feelers " (the " feeler fish," *Bathypterois*). It is true that most of the inhabitants of the sea-bottom retain their eyes and that in some families these are neither unusually large nor small (such as the grenadiers, Coryphænoididæ) ; it is also true that the only biological value of these visual organs is to catch the fitful gleams of luminescence ; but it is also true that many lose them (Alcock, 1902).

Thus among Selachians the eyes are vestigial in several families of the rays—*Typhlonarke*, *Bengalichthys* and *Benthobatis*. The eye of the last, for example, has a crude cornea, a rudimentary iris, an undifferentiated retina, and no lens (Fig. 866) (Brauer, 1908). Among Teleosts in some deeply bathypelagic forms such as *Saccopharynx* and *Cetomimus* the eye is vestigial. In the latter the oval globe is only 0·7 mm. in diameter, the lens and retina are rudimentary and the pigment epithelium unusually thick (Brauer, 1908). Among some benthonic Teleosts the eyes may be still more rudimentary and covered with opaque skin—*Barathronus*, *Typhlonus*, *Aphyonus*, and

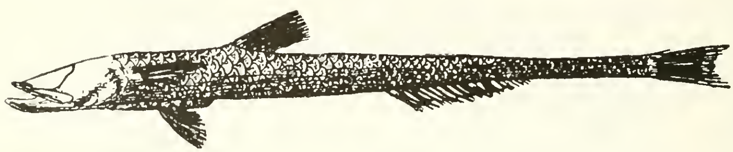

Fig. 867.—The Blind Deep-sea Teleost, *Ipnops agassizi*.
Found at 2,000 m. (½ natural size) (after Garman, *Albatross* Report, 1899).

Tauredophidium. An inhabitant of the ocean floor, *Ipnops*,[1] is the only Vertebrate known to have no trace of eyes (Eigenmann, 1909) ; this is a small black fish with two luminous areas (resembling lanterns) in its head under the translucent bones of the skull where the eyes might be expected, possibly adaptations of these organs (Fig. 867).

THE CAVERNICOLOUS OR LIMICOLINE HABIT

A cavernicolous or limicoline habit, whereby life is spent in the darkness of caves or crevices or in a similarly lightless environment in mud or beneath stones, also leads to a tendency for ocular regression. This is seen among cave-dwelling worms such as the planarian Kenkiidæ, or among Arthropods inhabiting a similar environment. In the latter phylum typical examples are seen in two species of Onychophores, *Peripatopsis alba* which lives in lightless caves, and *Typhloperipatus*, found under rocks ; in the cavernicolous beetle, *Anophthalmus*, which is possessed only of a dermal light sense (Marchal, 1910) ; the eyeless white cave-crayfish, *Cambarus ayersii*, which retains some light-sensitivity in its cerebral ganglion (Wells, 1952) ; and the cave-spiders (*Anthrobia*) which are entirely sightless ; but the phenomenon is most markedly seen in cave-dwelling Fishes and Amphibians.

[1] ἰπνός, a lantern ; ὤψ, eye.

Among Invertebrates with such degenerate eyes the Isopod *Typhlocirolana*—a small Crustacean found in a cave in the island of Majorca—may be taken as an example. The compound eyes are minute degenerate bodies $\frac{1}{3}$ mm. in diameter, without pigment in the ommatidia, while the crystalline cone and the proximal part of the retina are grossly atrophied (Menacho, 1913).

CAVE-FISHES [1] are all Teleosteans and it would seem probable that the ancestors of most of them can be traced from species in which a pre-adaptation to ocular regression had already been present owing to a previous existence in deep seas or muddy bottoms[2]; few of them (*e.g.*, catfishes of the genus, *Rhamdia*) have well-formed eyes ; and some types (*e.g.*, the Mexican catfish, *Anoptichthys jordani*) show all grades of reduction of the eye from normal organs to rudimentary remnants. The latter are hatched with small but complete eyes, lacking, however, a circulation, and as the fish matures these gradually degenerate until all that is left in the adult is a most rudimentary organ lying deeply buried in a recognizable orbit associated with hypoplasia of the optic lobes (Gresser and Breder, 1940–41 ; Breder, 1942 ; Lüling, 1953–55 ; Kuhn and Kähling, 1954 ; Stefanilli, 1954). Some of the cave-fishes derive from deep-sea types such as the Brotulidæ which emigrated to the surface and there sought the darkness of crevices in reefs or caves. Three species have made the still more remarkable transition to fresh water—*Lucifuga* and *Stygicola* which are found in caves in Cuba, and *Typhlias* in Yucatan. Eigenmann (1909) concluded that these Cuban fishes initially inhabited caves in the coral beaches where they remained as these caves were elevated and became filled with and enlarged by fresh water ; in his view the fishes are older than the island of Cuba. The eyes, which lie under the skin, are best developed before birth; thereafter they progressively degenerate until in old age they are represented by a shrivelled, pigmented vesicle, lying deeply in the large orbit, a process perhaps determined by a disturbance of the circulation. The bottom-grubbing catfishes which habitually shun the light are the ancestors of other types. These Siluroids which encyst themselves in the mud often have rudimentary eyes (Cope, 1864) ; thus the eye of the bull-head catfish, *Ameiurus*, has an ill-formed lens and a retina wherein the rods are large, the cones few and small, while the outer nuclear layer is represented by only two rows of nuclei, the inner by one, and the ganglion cells by a few widely-scattered elements.

The Amblyopsidæ, the North American group of cave-fishes characteristic of the caves of the Mississippi basin, are of considerable interest (Telkampf, 1844 ; Wyman, 1850–54 ; Kohl, 1892–93 ; Eigenmann, 1899–1909 ; Hubbs, 1938). They are

[1] A monograph by Carl H. Eigenmann, the Professor of Zoology of Indiana University gives a good account of the *Cave-Vertebrates of America* (Carnegie Inst., Washington, 1909), including a particularly illuminating and interesting study of the cave-fishes of the Mississippi Valley and Cuba. A subsequent monograph by Hubbs, *Fishes from the Caves of Yucatan* (*Carnegie Inst. Wash.*, Pub. No. 491, pp. 261–295, 1938), lists all known blind fishes apart from deep-sea types.

[2] *Anoptichthys* is an exception in that it probably entered cave life as a stray and on losing its vision was constrained to remain.

negatively phototactic and if exposed in a well-lit pool will immediately seek refuge and hide under rocks. In *Amblyopsis* the eye lies deeply under the surface, the lens is vestigial or absent, the iris is represented by a pigment-free membrane and the retina contains only a few ill-formed cones. Similar rudimentary eyes are found in the two other related genera, *Typhlichthys* and *Troglichthys* ; and in the only non-cavernicolous representative of this family, *Chologaster*, which inhabits the swamps of Kentucky and Tennessee, the eyes which lie under a patch of pigment-free epidermis are reduced rather than degenerate ; the fish does not depend on its eyes, however, for detecting or securing its prey or for avoiding obstacles. Although possessed of ears, experiments have shown that the sense of hearing of the Amblyopsidæ is limited ; the tactile sense is the one on which they rely to find and locate their food for which purpose they are provided with numerous tactile ridges principally in the region of the head (Eigenmann, 1909).

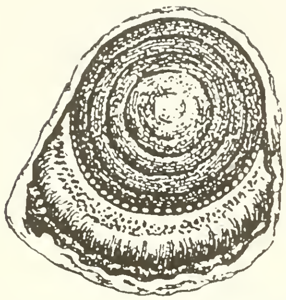

FIG. 868.—THE EYE OF THE GOBY FISH, *TRYPAUCHEN WAKÆ*.

The eye is rudimentary and functionless (after Franz).

Some goby fishes (Gobiidæ), particularly the "sleepers" living on muddy bottoms or in crevices, also have degenerate eyes. *Typhlogobius californiensis*, a blind fish which co-habits rocky crevices on the Californian coast with a blind species of shrimp on which it depends for food, has relatively normal eyes in the larval stage which become small, functionless and rudimentary in the adult, lying under the thick skin (Ritter, 1893) ; they lack tapetum, cones and vitreous, while, curiously, the lens may be either very large indeed or absent. It is as if a brave struggle were made to collect what light there is or, alternatively, the attempt has been abandoned. *Trypauchen* and *Trypauchenophrys*, littoral crevice-dwellers in Japan, and other limicoline gobies as *Austrolethops*, and the sole, *Typhlachirus*, have similarly minute or rudimentary eyes (Fig. 868) (Franz, 1910–34). Undersized eyes are also usual in the fresh-water fishes which inhabit silty rivers such as are common in the great plains of America ; only occasionally, as in Lake Balaton in Western Hungary, an immense shallow lake the waters of which are so turbid as to be virtually opaque, is an effort made to increase the sensitivity of the eye by the liberal deposition of guanine in an unusually well-developed tapetum (Wunder, 1926–30).

AMPHIBIANS. Amongst the Urodeles, the salamanders which live a secretive existence in shallow water, in caves, in mud and under flat stones, have little use for eyes. These organs are well differentiated in the larvæ but regress at metamorphosis (Zeller, 1888) (Fig. 869) ; as we have already

FIG. 869.—THE OLM, *PROTEUS ANGUINUS* (Zool. Soc., London).

FIGS. 870 AND 871.—THE EYE OF *PROTEUS ANGUINUS*.

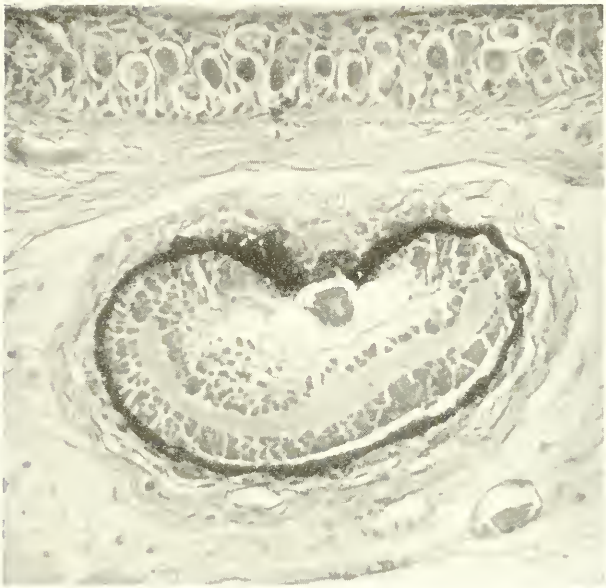

FIG. 870.—A vertical section through a rudimentary lateral eye in an animal of normal cavernicolous habit. The eye is seen to be a simple vesicle containing vitreous-like material centrally. It is surrounded by pigmentary epithelium and, owing to the absence of the lens, the lips of the optic cup meet at the distal aspect of the vesicle. The retina is unusually thick and relatively undifferentiated. The entire organ lies underneath the skin (E. F. Fincham).

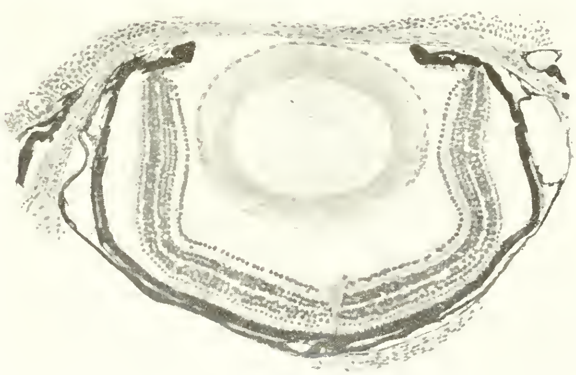

FIG. 871.—Meridional section through the eye of an animal kept in daylight. Note the presence of the ill-formed cornea, the well-formed lens and uveal tract, the hyaloid type of vascularization and the highly differentiated retina (after Kammerer).

noted, however, they may remain large and relatively well formed if development from the larval to the adult stage is artificially conducted in bright illumination (Kammerer, 1912) (Figs. 870–1). In natural conditions, however, they are concealed under the skin, microscopic and either capable merely of a directional light sense, as in limicoline types, or functionless, as in cave-living types. Other Urodeles, on the other hand, such as the newt (*Triturus*) or the North American axolotl, *Ambystoma*, have relatively simple but effective eyes, lacking iris folds and with a spherical lens, while in terrestrial salamanders the eyes, though small, are well formed.[1]

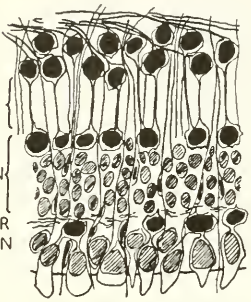

Fig. 872.—The Retina of *Proteus anguinus*.

G, ganglion cells; IN, inner nuclear layer; IR, inner reticular layer; ON, outer nuclear layer; OR, outer reticular layer; V, visual elements (after Kohl).

Among the cave forms the olm, *Proteus* may be taken as a typical example, several species of which inhabit the caves of Carinthia and Dalmatia (Fig. 869.) The eyes of the adult *Proteus anguinus* are minute spheres less than 0·5 mm. in diameter seen as shadows deep underneath the skin. They form simple vesicles without cornea or lens; originally a mere accumulation of epidermal cells within a capsule, the capsule disintegrates and the cells of the lens are replaced by connective tissue (Fig. 870). The ocular cavity is almost entirely taken up by a retina of a most rudimentary type and between it and the external epithelium lie the open remains of the optic vesicle. The visual cells are globular and bear no resemblance to rods or cones; there is an elementary nuclear layer and a reticular layer while the optic nerve is vestigial and largely neuroglial (Fig. 872) (Configliachi and Rusconi, 1819; Desfosses, 1882; von Hess, 1889; Kohl, 1889–92; Benedetti, 1922; Stadtmüller, 1929).

Similarly rudimentary eyes, even more degenerate than those of their cavernicolous European relatives, are found in related types such as the American blind salamanders, *Typhlomolge*, inhabiting the underground streams of Texas, and *Haideotriton*; such eyes are functionless. The eyes of *Typhlotriton*, however, a salamander found in the caves of the Mississippi Valley, normal in the larva but degenerate in the adult, are more fully formed with a lens and a considerable degree of retinal differentiation although the rods and cones disappear in the fully grown animal; these constitute a link between the degenerate eyes of the Proteidæ and the normal urodelan eye (Eigenmann, 1909).

THE FOSSORIAL HABIT

The FOSSORIAL OR BURROWING HABIT has led to the regression of the eyes of many types of Invertebrates and Vertebrates.

Thus among worms which burrow on the land (*Lumbricus terrestris*) we have already seen that the visual organs are of a very primitive type,[2] while

[1] p. 346. [2] p. 190.

those Polychætes which burrow in the sand or mud of the sea-shore may be without visual organs (the lob-worm, *Arenicola marina*)[1]; sometimes the larval forms have eyes which disappear on reaching adulthood (Tampi, 1949). Similarly, sand-burrowing Molluscs may be unprovided with eyes (elephant's tooth shell, *Dentalium*).[2] Among Arthropods, those Myriapods which burrow in moist forest debris may lack eyes (*Pauropus*),[3] as well as certain burrowing types of woodlice (Arcangeli, 1933). Among Insects the primitive minute Protura which burrow in moist soils impregnated with organic debris and are widely found in Europe, America and India, are without eyes, antennæ and wings ; but the most interesting eyeless insects are termites and ants.

Termites (Isoptera), often mistakenly called " white ants," are widely found in Europe, Asia and Africa but are unrepresented in Great Britain ;

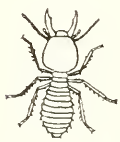

Fig. 873.—Termite Soldier.

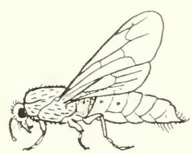

Fig. 874.—Male Driver Ant.

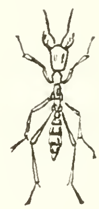

Fig. 875.—Female Driver Ant.

while they are extremely sensitive to light, most are blind and are completely without eyes (Fig. 873). They live in teeming millions in vast underground communities governed by a complex and efficient social system and alive with an immense and ordered business ; nevertheless, blind and eyeless though they are, they conduct long regimented marches overland to seek and convey back the wood they eat, and the young alates temporarily develop wings in a frequently disastrous nuptial flight in the air.

Most ants (Formicidæ) have large and well-developed compound eyes but in some forms of Dorylinæ which dwell under the ground, eyes are lacking. The wandering ants (*Eciton*) of Central and South America show eyes in various stages of disappearance—small eyes without an optic nerve, orbital sockets without an eye, and so on—while the female driver ant (*Dorylus*) of Africa has no evidence of ocular or orbital remnants whatever. It is interesting and perhaps significant that in the latter species the winged male is possessed of eyes surpassing those of most insects, while all females, whether queen, fighter or worker, are blind (Figs. 874–5) (Maeterlinck, 1927–30 ; Marais, 1937).

It would seem probable that like all other members of the Hymenoptera (wasps, bees, etc.) all ants were originally sighted and it might seem logical that the underground types might tend to lose their eyes ; but why the eyeless female should continue

[1] p. 191. [2] p. 197. [3] p. 211.

to produce the fully-eyed male is not clear. Moreover, although their nest is underground, these ants are nomadic on the surface and their armies, the members of which are completely blind, are forever on the move. It is to be remembered that the big-eyed, innocuous male driver ant is a gentle and relatively useless creature—merely a stud animal with a momentary function as likely as not never to be fulfilled ; while the monstrous regiment of his sisters ranks among the most ferocious and bloodthirsty creatures the world knows. It has been suggested that these unsexed females which march ahead against any obstacle and into any danger, which attack and devour anything alive in their line of march, would find difficulty in maintaining the iron discipline of their ranks if they were distracted by vision, and that blindness is therefore an asset of evolutionary value to the ferocious and purposive female but not to the idle and harmless male (Crompton, 1954). The suppression of eyes in this view (which many would not accept) is positive, differing entirely from the mechanism which usually induces eyelessness.

On the other hand, it may be that some other system of inter-communication exists of which we have no knowledge, outside the visible limits of the electromagnetic spectrum. It is indeed difficult to conceive how otherwise the extraordinarily complex activities within these underground cities could be conducted, not only as an ordered routine but with coordinated variations to meet unexpected emergencies of construction or war with equal facility, in which each member of the community—queen, king, soldier, policeman or worker—finds an appointed place. It may, indeed, be that eyes have become useless owing to the development of senses other, and perhaps more efficient, than our own.

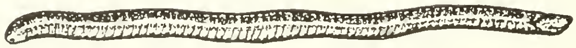

FIG. 876.—*Ichthyophis.*

A subterranean burrowing Amphibian, limbless, somewhat resembling an earthworm ; the eyes are small, functionless and covered by skin (head on right).

Among Vertebrates, fossorial Amphibians, Reptiles and Mammals are encountered ; in a sense some limicoline fishes (catfishes, etc.) which we have already discussed might be brought into this category.

Among Amphibians, the Cæcilians (Apoda) form a peculiar archaic group highly specialized for burrowing (Fig. 876)—*Cæcilia* of South America, *Ichthyophis* of Southern Asia, *Hypogeophis* of East Africa, *Siphonops* of America ; with the exception of the aquatic *Typhlonectes*, all spend most of their lives underground. Their most efficient sensory organ is a retractile sensory tentacle situated at the anterior border of the orbit, while the eyes are very small (less than 1 mm.) and can be useful only in light-detection.

The minute eyes of the Cæcilians are attached to the skin and lie in a roomy orbit, largely filled by a Harderian gland which, however, is used to lubricate the sensory tentacle ; the levator bulbi muscle of Amphibians is used as a compressor of this gland to assist in its evacuation. Two of the other extra-ocular muscles are commandeered to move the tentacle and have no action on the immobile eye, the retractor bulbi acting as a retractor of the tentacle and the internal rectus as a retractor of its sheath. The cornea is fused with the skin, there is no ciliary body or mesodermal iris, the lens is large, spherical and usually cloudy, while the retina is provided only with simple but massive rods, and the two nuclear layers and the ganglion cells are represented by a few rows of sparse cells (Kohl, 1892; Hanke, 1912; Engelhardt, 1924).

Among Reptiles, burrowing snakes and lizards come into the same category. Within the group of snakes (Ophidia) the lowest types are the Typhlopidæ, blind subterranean burrowers usually smaller than earthworms which occur in most of the warmer parts of the earth. The eyes are tiny and vestigial. It would seem that when the snakes originally went

FIG. 877.—THE EYE AND ORBIT OF THE BLIND SNAKE, *TYPHLOPS*.

The globe is minute, less than 1 mm. in diameter. The heavily pigmented uvea, *u*, and the ill-formed retina, *r*, are well seen. Most of the cavity of the eye is taken up by the large lens. Anterior to this is the tenuous cornea, the enclosed conjunctival sac and the dermal "spectacle." *m* is a tenuous extra-ocular muscle (O'Day).

underground the eyes became vestigial, and when they again emerged from the ground the eye had to be reconstructed, but those of this primitive species retained their simple form (Walls, 1942)[1].

The eye of *Typhlops*, a blind snake widely distributed in the Southern Hemisphere and South East Europe, which lives on worms and insects obtained by burrowing, has a rudimentary uvea and a small embryonic cellular lens; the retina contains few and rudimentary visual cells and insignificant nuclear and ganglion-cell layers while a central area is lacking (Kohl, 1892) (Fig. 877). A similarly primitive eye is seen in *Typhlops lumbricalis*, a blind snake seen in the West Indies and Guiana (Muhse, 1903), and in the uropeltid snake, *Rhinophis* (Baumeister, 1908).

[1] p. 383.

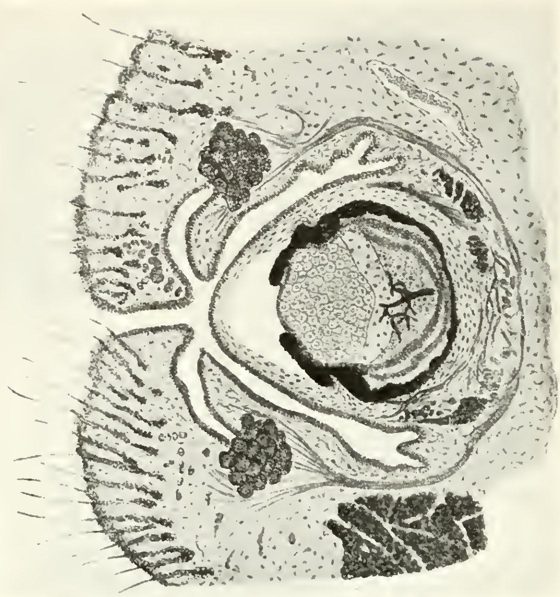

FIG. 878.—Section through the whole eye.

Note the pore-like opening in the lids, the elementary uvea, the cellular lens, and the hyaloid form of the central retinal artery (after Ciaccio).

FIG. 879.—The lens.

Showing the immature cellular state and the persistence of the vesicle (after Rabl).

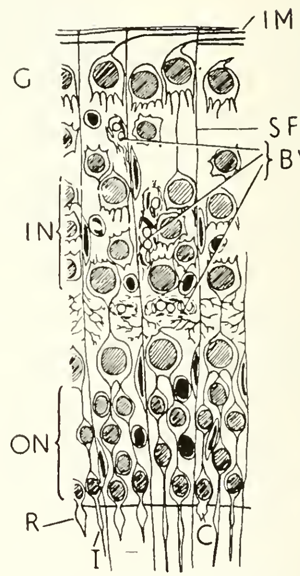

FIG. 880.—The retina.

The layering of the retina is relatively well-developed : *G*, ganglion cell layer ; *IN*, inner nuclear layer ; *ON*, outer nuclear layer. Blood vessels, *BV*, are seen in the inner layers and there is an external limiting membrane, an internal limiting membrane, *IM*, and nucleated supporting fibres, *SF*. Three types of visual cells are present : rods, *R*, cones, *C*, and " indifferent " elements, *I* (after Kohl).

Degenerate subterranean lizards (Amphisbænidæ), which are without limbs and almost without scales—such as the worm-like *Amphisbœna punctata* of Cuba or the similarly legless *Rhineura floridana* abundant in parts of Florida—have eyes equally minute buried beneath opaque skin, rarely consisting of more than a capsule of connective tissue enclosing an optic cup and a cellular lens without fibre-formation ; extra-ocular muscles and iris are lacking (Payne, 1906 ; Eigenmann, 1909). It is interesting that both in these snakes and in lizards, Harder's gland is many times larger than the eye.

Among Mammals a similar degeneration of the eye is seen in a small group of animals with burrowing habits which have led to a life of permanent darkness. These fossorial animals have little vision but an exquisitely developed sense of smell on which, indeed, most of them depend for their living ; the eyes are minute in size but relatively well differentiated, almost although not completely covered by skin to which they are adherent. In the common European mole only a minute pore, 0·1 mm. in diameter, is left in the skin through which little but the merest perception of light can be possible. In the blind mole of Southern Europe, *Talpa cœca*, this aperture is said to be usually lacking (Weber, 1904 ; Kazzander, 1921). In addition to the European moles, this group includes other Insectivores—the South African and Asian golden mole, *Chrysochloris* (Sweet, 1909), the American water-mole, *Scalops aquaticus* (Slonaker, 1902)—as well as the marsupial mole, *Notoryctes typhlops* (Sweet, 1909) and the rodent " moles " such as *Spalax*, and *Ellobius* which belong to the hamster branch of the mouse family.

The eye of the mole, *Talpa*, may be taken as typical, and appears as if it had ceased to progress from an early stage of embryological development (Lee, 1870 ; Ciaccio, 1884 ; von Hess, 1889 ; Kohl, 1892–95 ; C. Ritter, 1899 ; Henderson, 1952) (Figs. 878–9). The corneal epithelium may consist of a single layer of cells, the iris is small but present, and the choroid, unlike the mammalian but like earlier vertebrate types, has a single layer of vessels ; the lens is embryonic and cellular, while the central artery of the retina retains a hyaloid form and grows into the vitreous. In the retina, rods and cones are distinguishable and intermingled with them are cells of an intermediate type, but the normal layering of the mammalian retina is evident (Fig. 880). The non-neural parts of the eye are therefore particularly retarded, and it is interesting that Tusques (1954–55) found that their relatively normal development could be stimulated by large doses of thyroxine : the globe increased in size, the lids separated, the lens developed with the production of fibres and the entire organ began to take on the appearance of the eye of sighted animals.

THE PARASITIC HABIT

In most internal parasites the eyes are rudimentary or absent for the inside of an animal is as lightless an environment as any ; moreover, the sedentary life associated with parasitism can proceed in the absence of other activities so that, in addition to the recession of the visual organs, those of locomotion and often of digestion are reduced.

In the large number of endo-parasitic Invertebrates, eyes are lacking or vestigial. Thus in the flukes (Trematodes) and in the round- or thread-worms (Nematodes) the eyes may be present in the freely-swimming larval stage but in the parasitic adult sense organs are limited to papillæ on the lips. In tape-worms (Cestodes) sense organs are lacking. Similarly eyes and other sense organs are not found in parasitic Crustaceans such as *Sacculina*, an organism parasitic on the abdomen of crabs. A similar example among Insects is provided by *Stylops* ; the winged male has many ocelli but the minute female which is parasitic within bugs and bees is eyeless.

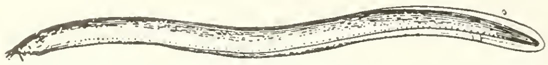

Fig. 881.—The Hag-fish, *Myxine* (after Dean).

Among the Cyclostomes, the hag-fishes have rudimentary eyes which give no response to light. These small eel-like creatures live partly in the mud at the sea bottom and are partly voraciously parasitic within larger fishes. The glutinous hag, *Myxine*, with a wide distribution in the oceans, approaches more nearly than any other Vertebrate the condition of an internal parasite (Fig. 881) ; in other species such as the slime-hag, *Eptatretus* in the Southern Hemisphere and *Bdellostoma*, found in South African and Pacific waters, the eyes are not so degenerate (see Henckel, 1944). The eyes of the ecto-parasitic lamprey, on the other hand, are well-formed.[1]

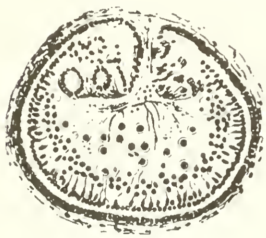

Fig. 882.—The Eye of the Hag-fish, *Myxine glutinosa*.

The eye is a simple vesicle almost entirely filled with poorly differentiated retina doubled over itself (after Dücker).

In *Myxine glutinosa*, the eyeball, about 0·5 mm. in diameter, is merely a simple vesicle lying in fat buried beneath the skin, almost entirely filled with a poorly differentiated retina doubled over upon itself (Fig. 882). Extra-ocular muscles, cornea, iris and ciliary body are unrecognizable, the sclera and choroid are undifferentiated, the lens is lacking, and there is no pigment either in the uvea or retina. The retina retains the form of the cavity of the optic vesicle, visual cells are not recognizable as such, layering of the retinal elements is crude and the optic nerve is vestigial (Kupffer, 1868 ; Kohl, 1892 ; Retzius, 1893 ; Allen, 1905 ; Eigenmann, 1909 ; and others).

It is noteworthy that although the eyes are functionless, a dermal sensitivity to light exists concentrated particularly in the head and cloacal regions and disappearing when the animal is skinned. There is a long latent period of about 20 secs. before the animal commences to swim and thereafter to burrow. The photochemical reaction is associated with vitamin A_1 and the response is mediated nervously through the spinal cord (Newth and Ross, 1955 ; Steven, 1955).

Endo-parasitic Fishes are rare, and the parasitic habit is not found among higher Vertebrates. The eel, *Simenchelys parasitica*, an inhabitant of deep seas and parasitic

[1] p. 263.

in halibut and other large fishes, has an eye covered by semi-opaque skin, but it is not rudimentary ; nor are the minute eyes of the other parasitic Teleost, the pearl-fish, *Encheliophis jordani*, which spends much of its life inside the cloacæ of sea-cucumbers.

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