THE EYES OF *IPNOPS MURRAYI* GÜNTHER, 1878

By O. MUNK
Institute for Comparative Anatomy and Zoological Technique, Copenhagen

INTRODUCTION

According to the literature *Ipnops* is the only vertebrate in which both the eyes and the optic nerves are completely missing. The present investigation has however shown, beyond doubt, that the peculiar organs on the head of *Ipnops*, which are generally held to be phosphorescent organs, are in reality modified eyes.

Like REGAN (1911), PARR (1928) places the genus *Ipnops* in the family Sudidae (Ordo Iniomi), by PARR divided into 4 subfamilies: Chlorophthalmini, Notosudini, Bathypterini and Paralepidini. Bathypterini, which is characterized i. a. by having very small eyes or no eyes at all, comprises the genera *Benthosaurus* GOODE and BEAN, 1886, *Bathypterois* GÜNTHER, 1878, *Bathymicrops* KOEFOED, 1927, and *Ipnops* GÜNTHER, 1878. PARR writes about Sudidae that "...in the series: *Chlorophthalmus – Bathysauropsis – Benthosaurus – Bathypterois – Ipnops* we recognize a continuous series of differentiations characterized by a gradual reduction of the eyes, depression of the head and elongation of the tail." BERG's classification of the iniomous fishes is in accordance with that of PARR (BERG 1940).

PREVIOUS INVESTIGATIONS

The first specimens of *Ipnops (I. murrayi)* were caught by the "Challenger"-Expedition, and from the very beginning much uncertainty has prevailed as to the function of the peculiar cephalic organs. In his description of the genus GÜNTHER (1878) writes among other things: "Head depressed, with broad, long, spatulate snout, the whole upper surface of which is occupied by a most peculiar organ of vision (or luminosity), longitudinally divided into two symmetrical halves." Later on the same author (GÜNTHER 1880) writes about the same organs: "The eye seems to have lost its function of vision and assumed that of producing light." In 1885 GÜNTHER described the cephalic organs of *Ipnops* as modified eyes and in the same place there is a description of the eyes by MOSELEY (pp. 239-240); according by MOSELEY each eye is covered by a transparent membrane, most likely representing the cornea. Under the membrane and separated from this by a shallow chamber filled with liquid, is the retina, which solely contains rods. Between the rods and the chamber is a very thin layer of nerve fibres. The chorioidea is subdivided into hexagonal areas which are concave towards the eye, and the rods seem to be aggregated in corresponding bundles, the rods resting on the concave inside of the hexagonal areas. About the function of the organ MOSELEY writes: "It is not improbable that these curious expansions of the recipient surface of the eye and its retina are a device for detecting the presence of very small quantities of light, at the expense of all apparatus for forming an image." Later, however, MOSELEY forms the opinion that the organs must be regarded as phosphorescent organs, and that any trace of eyes and optic nerves is missing (Appendix A in GÜNTHER 1887), and as this opinion is prevailing in most of the recent literature, MOSELEY's paper will be briefly recorded.

The symmetrical organs extend from an area a little behind the nasal capsules to an area dorsally of the hindmost part of the brain, and are situated in a pair of oblong cavities dorsally of the cranial cavity; the cavities are separated by a median septum, in front consisting of hyaline cartilage (a median crista on the cartilaginous plate which is situated in the roof of the mouth; cf. GÜNTHER 1887, pl. LXVIII) which is dorsally completed by connective tissue. According to MOSELEY the organs are covered by the dorsal cranial wall, which, corresponding to the deepest part of the cavities, has a pair of convex cornea-like prominences, while the cranial wall in front and laterally of these is flat and provided with concentric striae (cf. text-fig. 1). Where the cranial wall covers the organs it is very thin and completely transparent. On the medial part of the organs a closed canal is situated. It contains partly a mucous canal, partly a nerve running to the nasal capsule, according to MOSELEY probably the nasal branch of the fifth cranial nerve. Corresponding to the anterior part of the brain the canal slants laterally. MOSELEY is of the opinion that the deepest part of the cavities, which is in the centre of the organ, corresponds to the place where previously the orbits were situated, just as the median septum should correspond to the interorbital septum. Seen from the dorsal side in reflected light the organs seem to be composed of a mosaic of light, hexagonal areas, each being about 40 microns in diameter.

Histologically the organs are of a quite uniform structure in their whole extent (cf. text-fig. 2); they are said to consist of hexagonal columns resting on a pigmented layer of connective tissue. Each hexagonal column, which is about 40 microns high, is composed of 30-40 transparent, hexagonal rods, the bases of which rest on the concave inside of a large, bowl-shaped hexagonal pigment cell containing a clearly marked nucleus. Distally each rod carries a hexagonal, nucleated cell. A few of the transparent rods, the longitudinal axis of which is at right angles to the surface of the organ, contain, according to MOSELEY, a small nucleus near the basis. The hexagonal columns are entangled in a reticulum of pigmented strings, the ramifications of which also traverse in between the rods. Furthermore, the organs contain capillaries. The hexagonal columns correspond to the light, hexagonal areas which are seen on the intact animal in reflected light. Moreover, MOSELEY states that both the pigmented reticulum and the capillaries can be seen on the intact animal in transparent light (optic section). Under the organs there is connective tissue with pigment cells, blood-vessels, and nerves. The organs get ample blood supply through a pair of vertical branches from the carotids.

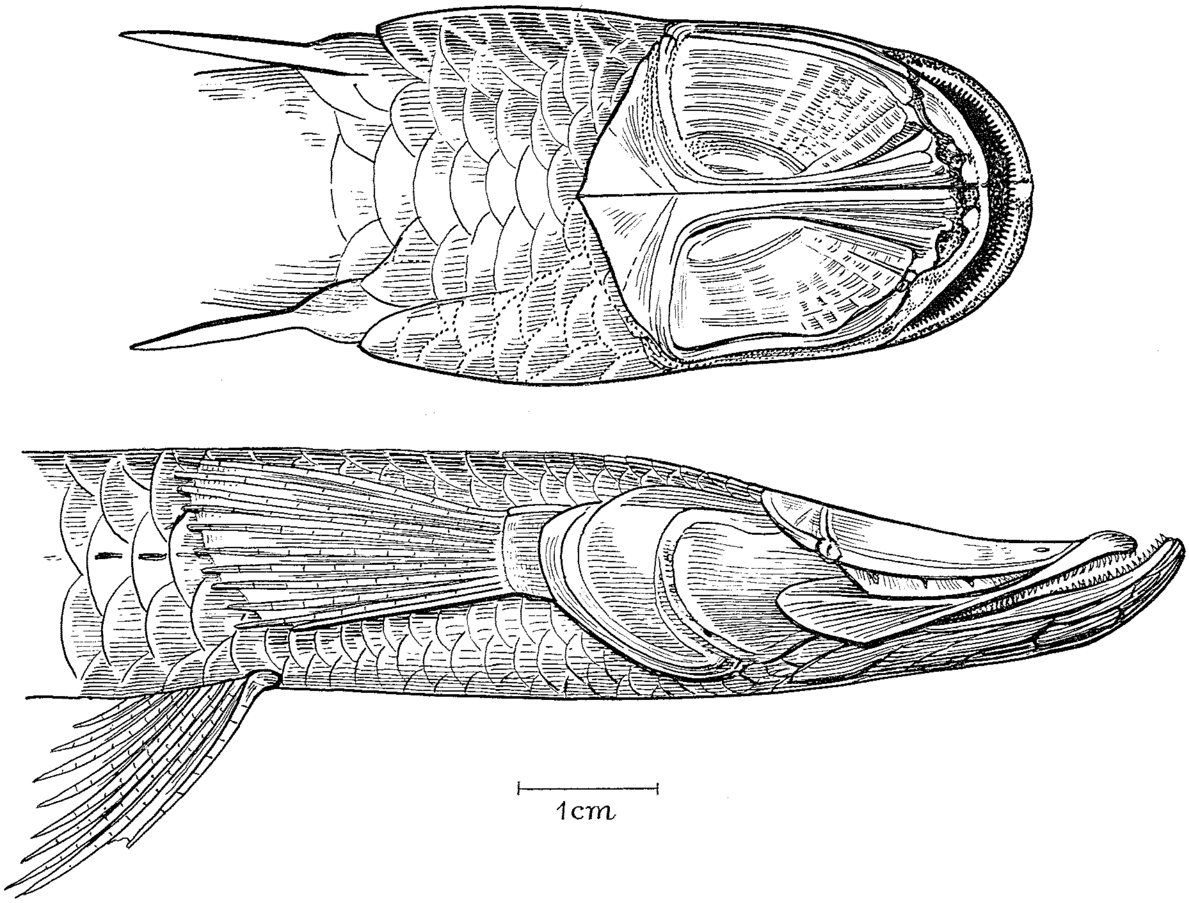
MOSELEY states that he has traced nerve fibres from the layer of connective tissue under the organ to the area with the pigmented hexagonal cells, but that it has been impossible to ascertain any actual connection between the nerve fibres and the elements of the organ. According to MOSELEY the nerve fibres no doubt originate from the fifth cranial nerve. MOSELEY concludes: "The phosphorescent organs can hardly be sense-organs, since they appear to be supplied with no special nerves but only by ordinary nerves. They are certainly not modified eyes. The richness of their blood supply is in favour of their being phosphorescent organs, as is also the extreme transparency of the portion of the roof of the skull covering them." He supposes that the phosphorescent organs in *Ipnops* are homologous with the phosphorescent organs on the head of other Scopelidae, being formed by fusion of their supranasal and subocular phosphorescent organs on either side of the head, resulting in complete obliteration of the eyes (by GÜNTHER *Ipnops* was placed in the family Scopelidae, cf. GÜNTHER 1878, 1880, and 1887). As in the Scopelidae the organs are internally delimited by pigmented connective tissue made of the corium.

Apparently, no later histological examination of the cephalic organs of *Ipnops* has been made, and MOSELEY's view is adopted in most of the later literature (e. g. GOODE and BEAN 1895, GOODRICH 1909, REGAN 1911, BARNARD 1925, PARR 1928, NORMAN 1939, WALLS 1942, FOWLER 1943, MARSHALL 1954, THINES 1955, and BERTIN 1958). Certain authors, however, have regarded the organs as eyes (JORDAN and EVERMANN 1896, JORDAN 1925). For the sake of completeness it ought to be mentioned that two authors have held the opinion that the organs function both as visual organs and as phosphorescent organs. Thus AGASSIZ (1888) writes about the modifications of the eyes of deep sea fishes: "In some cases the eyes have not been specially modified, but in others there have been modifications on the one hand to phosphorescent organs more or less specialized, or on the other to such remarkable structures as the eyes of *Ipnops*, intermediate between true eyes and specialized phosphorescent plates." GARMAN (1899) expresses a similar opinion: "Eyes (of *I. agassizii)* excessively differentiated, as visual organs, reflectors, and flash lights, occupying nearly half of the top of the head...".

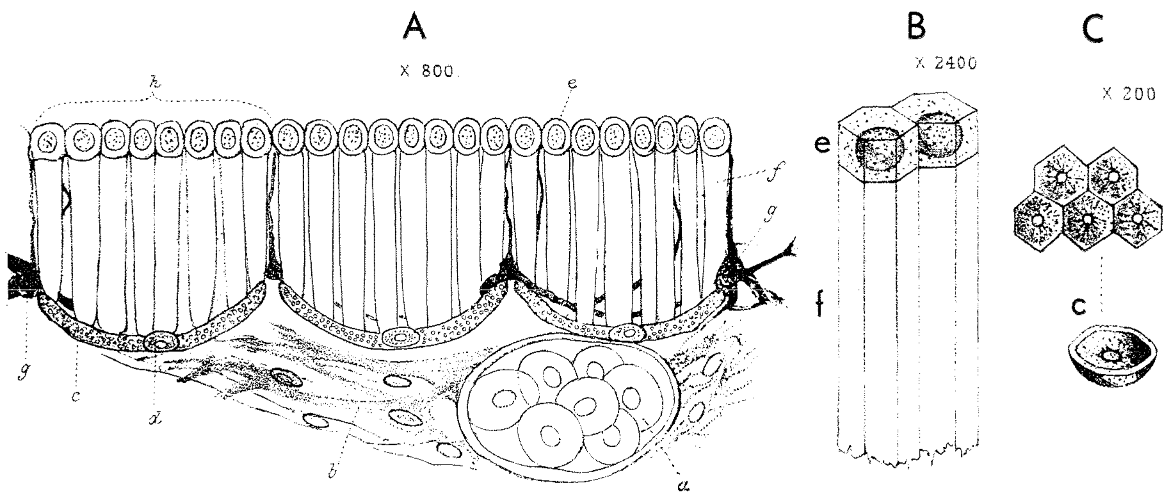
THE PRESENT INVESTIGATION

Material and Methods. Dr. A. F. BRUUN, of the Zoological Museum of Copenhagen, has been so kind as to place 3 specimens of *I. murrayi* GÜNTHER, 1878 from the collection of the "Galathea"-Expedition at the present author's disposal. The length of the fishes was about 9 cm. One specimen was fixed in Bouin's fluid; the head was embedded in paraffin, cut into 8 micron sections (transverse sections) and stained with hematoxylin-eosin. The two other specimens were fixed in formalin; the head of one of those was embedded in celloidin, cut into 50 micron sections (transverse sections) and stained with the phosphotungstic acid hematoxylin of MALLORY, while the other specimen was stained with alizarin.

The investigation clearly showed that the cephalic organs of *Ipnops* are modified eyes, the structure of which in the main is in accordance with MOSELEY's first description (MOSELEY in GÜNTHER 1885). This result follows partly from the fact that positively

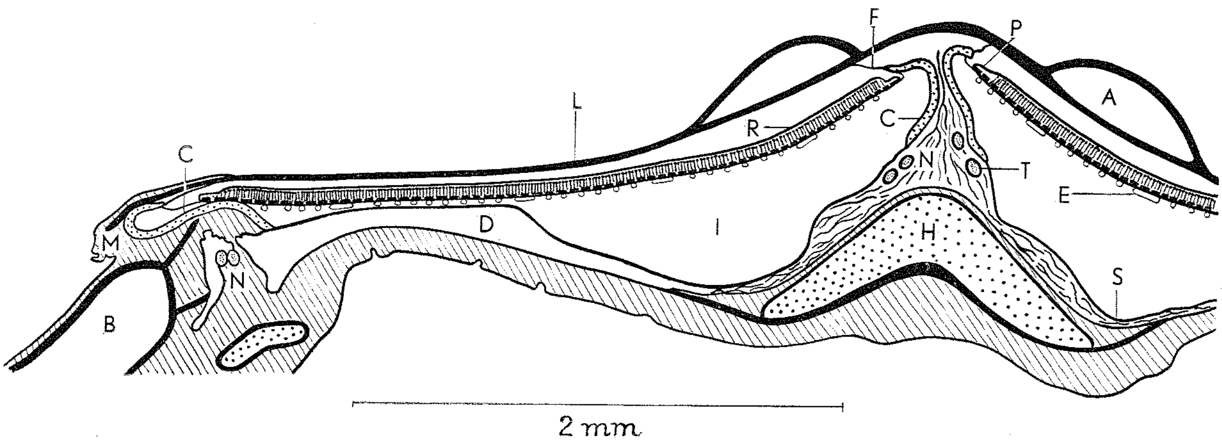


Text figure 1. Dorsal and lateral view of the head of *Ipnops murrayi*. Re-drawn from fig. 97, p. 239 in GÜNTHER 1885.



Text figure 2. The histological structure of the cephalic organs of *Ipnops murrayi*, as regarded by MOSELEY (from GÜNTHER 1887, pl. LXVIII, fig. 6, 7 and 10; H. N. MOSELEY del.). Fig. 2A shows a transverse section of the organ, fig. 2B shows the rods highly magnified, and fig. 2C shows the pigment cells. The letters on fig. 2B and C are added by the present author.

a: erythrocytes
b: pigment cell in the connective tissue under the organ
c: hexagonal pigment cell
d: nucleus of hexagonal pigment cell
e: hexagonal, nucleated cell
f: hexagonal rod
g: pigmented strings
h: a group of rods forming together a hexagonal column



Text figure 3. Diagram based on a photo showing a transverse section of the head of *Ipnops murrayi*, corresponding to the foremost half of the eyes (cf. pl. 1, fig. 2).

A: supraorbital canal
B: infraorbital canal
C: the sclera (cartilaginous part)
D: subbulbar fissure
E: choriocapillaris
F: peripheral part of scleral cornea (?)
H: hyalin cartilage
I: intraocular blood sinus
L: transparent membrane (the frontals ?)
M: lateral edge of transparent membrane
N: nerve(s)
P: pars coeca retinae
R: pars optica retinae
S: sclera (fibrous part)
T: olfactory tract

identified optic nerves, running to the organs, are present, partly from the structure of the organs, which have a retina with typical rods. The lense and its suspensory apparatus (including the retractor muscle) is missing. The iris (in the shape of a transverse diaphragm) is missing. The eyes are flattened and directed upwards. Since the optic nerves and the retina are of decisive importance for the understanding of the function of the organs, they will be dealt with first in the following.

The Optic Nerves. The papilla of the optic nerve (pl. 2, fig. 1) is situated a little behind and somewhat medially to the centre of the eyes The optic nerve is directed medio-caudally and perforates the sclera medially to the papilla of the optic nerve, so that a greater part than usual of the optic nerve is situated in the chorioidea. After the perforation of the sclera the direction of the two optic nerves is medio-caudal and dorsal, till they meet in the median plane, and for the rest of their course to shortly before the entrance into the mesencephalon they lie in contact with each other. The two optic nerves run parallel caudally, and in the chiasma, which is situated ventrally to the olfactory tracts, one of the optic nerves crosses the other (pl. 1, fig. 3-4). In the one specimen the left optic nerve, in the other the right optic nerve was lying on the top of the other in the chiasma. The optic tracts can be followed to the tectum opticum.

The Retina. The eyes of *Ipnops* may quite hypothetically be derived from typical laterally situated eyes by a turn of the bulbus of about 90°, so that the anatomical axis has been directed dorsally, while at the same time it must be imagined that the curvature of the retina has been straightened out and the iris reduced (text-fig. 3. Pl. 1, fig. 1-2). How the ontogenetic development really takes place is of course impossible to decide on the basis of the present material. Yet it seems reasonable to suppose that the region around the papilla of the optic nerve of *Ipnops* corresponds to the fundus.

According to BRAUER (1908) the retina of deep sea fishes is characterized partly by the lack of cones, partly by the fact that the pigment is in constant dark position; the processes of the cells of the pigment epithelium have been retracted into the cell body and cannot be re-formed. As regards these two features the retina of *Ipnops* makes no exception.

It is possible to distinguish between a pars optica and a pars coeca retinae. The latter is very narrow. The thickness of the retina in the anterior and posterior parts of the eye is about 35 microns, gradually tapering towards the ora terminalis retinae. In the central part of the retina the thickness is about 45 microns, and the thickness only diminishes close to the ora terminalis. Hyaloid vessels are not to be found.

The Pigment Epithelium. The cells are low, without processes (pl. 2, fig. 1-4). Pigment is only to be found in the outer part of the cell (i. e. towards the chorioidea) where also the nucleus is placed (pl. 2, fig. 2 and 3). The outer part of the cell is frequently convex (pl. 2, fig. 3-4) and since only this part is pigmented, the pigment of each cell stands out as a crescent-shaped figure in the sections. No doubt these correspond to the bowl-shaped, hexagonal pigment cells, described by MOSELEY. According to MOSELEY the hexagonal rods rest on the inside of the bowl-shaped pigment cells. However, the pigment cells are not bowl-shaped, and the rods do not reach farther out than to the inner, unpigmented part of the cells. Now and then fragments of the rods are seen in the pigment cells, but this is obviously an artefact (pl. 2, fig. 3-4). The convex form of the outer part of the pigment cells, however, seems to be an artefact too. In the specimen fixed in Bouin the convex form was most frequently found in the fundus, where the bulbus is deepest. In the peripheral regions of the retina the outer part of the cells is plane (pl. 2, fig. 2). In the specimen fixed in formalin the pigment of all the cells in the pigment epithelium stands out as crescent-shaped figures, and the unpigmented part of the cells cannot be seen at all or only with difficulty. Supposing that MOSELEY had only a specimen fixed in formalin at his disposal, this may be the reason why he did not notice the inner, unpigmented part of the pigment cells. Thus the convex form of the outer part of the cells is probably due to a shrinking of the entire retina. In the specimen fixed in Bouin's fluid the shrinking is less marked; it is more pronounced in the fundus, the deeper part of the bulbus, as might be expected.

Thus the pigment cells are certainly not bowl-shaped, pigmented connective tissue cells, as described by MOSELEY, but retinal pigment epithelium cells without processes.

The retina s. str. contains only rods that are not hexagonal (pl. 2, fig. 1-4). Not the slightest trace of the hexagonal columns described by MOSELEY is to be found. The pigmented reticulum which, according to MOSELEY, is found in the layer of rods is an artefact.

The outer segments of the rods show the cross-lamination which is characteristic of visual cells. The inner segment is very short and contains no ellipsoid. The outer nuclear layer contains only a single layer of nuclei. In his first description (in GÜNTHER 1885), MOSELEY states that the retina "... is composed of a layer of remarkably long rods". The length of the visual cells in the eyes of teleosts is, as a rule, between 60 and 80 microns (ROCHON-DUVIGNEAUD 1943). DETWILER (1943) states that the length of the rods in the light-adapted eye of *Ameiurus* is 92-93 microns, in the dark-adapted eye 33,8 micron. BRAUER's survey of the length of the rods of some deep sea fishes (BRAUER 1908, p. 222) comprises several species the rods of which have about the same small length as those of *Ipnops*.

Immediately inside the outer nuclear layer there is a layer consisting of nerve fibres. The layers of nuclei, the inner nuclear layer and the ganglion cell layer, which are normally found inside the outer nuclear layer, are apparently lacking in *Ipnops*. However, some scattered nuclei are to be found inside the outer nuclear layer; they can be distinguished from the nuclei of the rods partly by their position, partly by means of their greater nuclear diameter. The nuclei of the rods are oval; the nuclei which are situated inside the outer nuclear layer possibly comprise three different nuclear types, two of which are shown on pl. 2, fig. 3 (X and Y). One of these (X) is almost spherical, the other type (Y) is oval. It is possible, however, that these two nuclear types represent a transverse section (X) and a longitudinal section (Y) of the same oval nuclear type, partly because the diameter of the spherical type corresponds to the width of the oval type, partly because the chromatin granules show the same arrangement in the two nuclear types. Besides these two (?) types, there is an oval nuclear type which is more flattened than type Y. The number of the nuclei, which certainly do not belong to the rods, is of the magnitude of 5-6000 in each retina. The number of optic fibres is about 500 (538 axons were counted in the right optic nerve, 496 axons in the left optic nerve in the specimen fixed in Bouin's fluid). None of the above mentioned nuclear types exists in a number corresponding to the number of nerve fibres in the optic nerves. The count, however, clearly shows that other cells than ganglion cells exist inside the outer nuclear layer, but neither these nor the ganglion cells can be identified. Yet it seems reasonable that the nerve fibres of the optic nerves represent the third neuron of the visual pathway, as in other vertebrates.

The membrana limitans externa could not be established conclusively. The membrana limitans interna exists. The falciform process is missing.

The thickness of the retina showe greater variation among the bony fishes than within other groups of vertebrates, from less than 100 to more than 500 microns (WALLS 1942). Its small thickness in *Ipnops*

(35-45 microns) is of course partly due to the shortness of the rods and partly to the reduction of the layers inside the outer nuclear layer. The number of rods in each retina is of the magnitude of 250000. Consequently, there is a very considerable summation (about 500 rods per optic nerve fibre). The total number of rods per retina is amazingly small compared with the numbers given by BRAUER (1908, p. 222). According to BRAUER the number of rods *per sq. mm* ranges from 115600 *(Cyclothone microdon)* to 20 millions *(Macrurus pumiliceps)* in the species examined by him. BRAUER calls attention to the fact that the numbers are not accurate, the varying thicknesses of the sections and the varying diameters of the nuclei not having been taken into account; nevertheless there are considerably more rods than in *Ipnops.*

The pars coeca retinae is quite narrow, 25-30 microns, and consists of two layers of cells in which only the cells belonging to the outer layer are pigmented. Unlike the pigment epithelium cells in the pars optica the whole cell body is pigmented. In some sections only one cell is seen in the outer layer. An accurate description of the morphology of these cells, however, cannot be given, as the cell limits are not visible on account of the pigment. The inner layer of cells consists of low, unpigmented cells. Evidently, no epithelial muscle cells exist in the pars coeca.

The pars coeca retinae is connected with the inside of the scleral cartilage near the upper edge of this by means of connective tissue cells in the inner layer of the chorioidea.

The Chorioidea. Immediately outside the retinal pigment epithelium the choriocapillaris follows, which consists of relatively few, rather wide capillaries (pl. 2, fig. 1-2). In this inner layer of the chorioidea there are locally many pigmented cells. The rest of the chorioidea is constituted by a very large, blood-filled sinus (text-fig. 3. Pl. 1, fig. 2) the extent of which corresponds to that of the retina, and which has its greatest depth in the region of the fundus. The argentea is missing. The corpus vascularis chorioideae is missing. As it is now and then claimed in the literature that the corpus vascularis is only to be found in species with pseudobranchs (e.g. WALLS 1942), it should be pointed out that *Ipnops* lacks pseudobranchs. There is no tensor chorioideae. WALLS (1942) maintains that this muscle is found only in fishes which are able to accomodate.

The Sclera. Corresponding to the peripheral parts of the eye the sclera consists of cartilage, while the remaining part is fibrous and very thin (text-fig. 3. Pl. 1, fig. 2-3), thus agreeing with the structure of the sclera of most other bony fishes, in which the sclerotic coat as a rule is fibrous and thin in the fundus, while in the anterior segment of the eye it is cartilaginous to a greater or smaller extent; in most of the species this cartilage forms an unbroken cartilaginous ring in the anterior segment of the eye. No ossicles have been found in the sclera of Ipnops. The cartilage of the sclera is connected with the transparent membrane that covers the eyes by means of a thin, fibrous membrane, which unites with the inside of the transparent membrane. Most likely this fibrous membrane represents the peripheral part of the scleral cornea (text-fig. 3. Pl. 1, fig. 2).

Under the lateral part of the sclera a subbulbar fissure is seen in the sections (text-fig. 3. Pl. 1, fig. 2). Below the anterior and the posterior part of the eye it is quite narrow and situated under the scleral cartilage, while below the central part of the eye its extent fairly corresponds to the breadth of the lateral half of the eye. As regards position this cavity corresponds to the lower of the two retrobulbar sinuses found in many bony fishes.

The transparent membrane (text-fig. 3. Pl. 1, figs. 1-2) which covers the eyes lies in the corium and appears in the sections as a uniform, non-cellular lamina. The membrane is unpaired and in extention slightly greater than that of the bulbus. The specimen stained with alizarin shows that the membrane consists of lamelliform bone. Corresponding to the hindmost part of the eyes, the membrane is on the inside provided with a short, low, median bony crista. The cornea-like prominences and the concentric striae described by MOSELEY (cf. text-fig. 1) were not found in any of the specimens which the present author had at his disposal; probably they are artefacts.

The two canals on the transparent membrane, one on either side of the median line, contain partly a nerve, partly lateral line organs; no doubt they are supraorbital canals. Under the lateral edge of the transparent membrane there is on either side another canal (text-fig. 3. Pl. 1, fig. 2) of which the delimitation, with the exception of the lateral wall, is osseous. Probably, they are infraorbital canals. The supraorbital as well as the infraorbital canals communicate with the surface in several places and they are both of them open in front and behind. As the supraorbital canals are situated on the transparent membrane, it is probable that this represents the frontals, as also suggested by PARR (1928) in his characterization of the genus *Ipnops*.

Rudimentary Eye Muscles. Several rudimentary eye muscles were found, partly under the fundus region of the eye, partly antero-laterally and antero-medially. The muscles of the fundus region originate from a thin osseous lamina, which is situated ventrally to the sclera; they insert in the fibrous part of the sclera. That they are eye muscles is shown by the fact that they are innervated by the nervus oculomotorius. Since the muscle rudiments were found at intervals in many of the 8 micron sections, it is probable that there are several muscles (they may be m. rectus inferior, superior and anterior). Unfortunately, it was impossible to verify the number of muscle rudiments in the fundus region on the celloidin sections, because in these thick sections the pigment of the surrounding connective tissue concealed them completely. The m. rectus posterior is probably missing, since all the muscles of the fundus region seem to be attached to the n. oculomotorius, and since it has been impossible to find the n. abducens.

Antero-laterally there is a rudimentary muscle which inserts in the cartilage of the sclera, probably the m. obliquus inferior; it is innervated by the n. oculomotorius.

Antero-medially there is a muscle rudiment as well, inserting in the scleral cartilage, probably the m. obliquus superior. It has been impossible to follow the nerve of the muscle, and the present author has not been able to find the n. trochlearis in the isthmus region of the mesencephalon; the nerve is probably lacking.

All the rudimentary muscles are rather small; the muscle rudiments of the fundus region are about 30 microns wide, the m. obliquus superior and inferior are only about 18 microns wide.

The Innervation of the Eye. Ventro-laterally of the optic nerves and slightly in front of the chiasma there is on each side a ciliary ganglion. The ganglion lies in contact with the n. oculomotorius. The ganglion receives a branch from the ganglion Gasseri (there is no separate profundus ganglion). No separate radix sympathica is to be found. From the ganglion two ciliary nerves lead to the bulbus. Where they leave the ganglion both of them lie slightly laterally of the n. oculomotorius. One ciliary nerve runs rostro-dorsally and medially, crossing over the n. oculomotorius, and perforates the sclera medially on the boundary between its chondral and fibrous part; then it crosses the intraocular sinus and runs dorsally along the choriocapillaris to the region immediately medially of the pars coeca retinae; here it is divided into two branches, one leading forward, one backward. The nerve innervates the vessels of the choriocapillaris.

The second ciliary nerve runs medially too, crossing over the n. oculomotorius. It perforates the sclera together with the optic nerve and can be followed for a short distance on the inside of the sclera, where it runs laterally. There are also nerve fibres in the innermost layer of the chorioidea, immediately laterally of the pars coeca retinae at the lateral edge of the eye. These nerve fibres innervate the vessels of the choriocapillaris and are probably branches of the ciliary nerve which perforates the sclera together with the optic nerve, but it has not been possible to follow the intraocular course of this nerve. No separate long ciliary nerve has been found.

The n. oculomotorius runs forward ventrally of the bulbus and innervates the muscle rudiments which insert in the fibrous part of the sclera corresponding to the fundus region of the eye. Then it turns medially and runs forward along the scleral cartilage. Medially of the foremost part of the eye it joins a branch of the n. trigeminus for a short distance before it turns laterally and runs under the scleral cartilage to the antero-lateral edge of the bulbus; then the n. oculomotorius turns caudally and runs to the m. obliquus inferior.

DISCUSSION

The present investigation clearly shows that the cephalic organs of *Ipnops murrayi* are modified eyes. MOSELEY's first short description of the organs (in GÜNTHER 1885) is on all essential points correct. MOSELEY's second description of the histological structure of the organs (in GÜNTHER 1887), however, is erroneous and in the main seems to be based on artefacts. The most amazing discrepancy between his first and second description is that the layer with nerve fibres inside the layer of rods is completely neglected in his second description. This layer does not appear in any of MOSELEY's figures (GÜNTHER 1887, pl. LXVIII. Text-fig. 2). The only basis for the opinion that the rods consist of two separate components (transparent, hexagonal, non-nucleated rods and hexagonal, nucleated cells) seems to be MOSELEY's statement that an artificial fissure was often found in the layer of rods, separating the nucleated cells from the transparent rods. That MOSELEY was unable to see the cross-lamination of the outer segments of the rods, may either be due to the poor fixation of his material, or to the fact that his sections were too thick, probably both. In his second description MOSELEY states that an artificial fissure is to be found between the pigmented connective tissue under the rods (i.e. the innermost part of the chorioidea) and the bottom of the cavity in which the cephalic organs are situated. This fissure, however, is not artificial, it is the intraocular blood sinus.

That the cephalic organs of *Ipnops* are modified eyes is primarily shown by the positively identified optic nerves and by the structure of the organs, because they have a retina with typical rods. Furthermore, it has been emphasized that certain structural features, which are characteristic of the eyes of the teleosts, are present also in *Ipnops:* the structure of the sclera and the subbulbar sinus (?). The retina is in accordance with that of other deep sea fishes in lacking cones and in having a constant dark position of the retinal pigment. The eyes are directed upwards, which is to be expected in a benthonic fish. The reduction of the eye muscles is naturally connected with the form and position of the entire eye. No doubt the eye is immobile and thus the eye muscles have hardly any function in the adult animal.

The eyes of *Ipnops* must be regarded as specialized visual organs. The reduction of the retinal layers which are situated inside the outer nuclear layer is a natural consequence of the great summation. There is nothing at all in the structure of the organs to suggest that they should function both as visual organs and as phosphorescent organs as supposed by AGASSIZ (1888) and GARMAN (1899). As so clearly expressed by MOSELEY, it must be supposed that the structure of the organs with the flat retina is "... a device for detecting the presence of very small quantities of light, at the expense of all apparatus for forming an image."

SUMMARY

The paper deals with the peculiar cephalic organs of *Ipnops murrayi* GÜNTHER, 1878, which have been described as phosphorescent organs (MOSELEY 1887). In the literature *Ipnops* is ordinarily said to be the only vertebrate in which every trace of eyes as well as optic nerves is lacking. On the basis of the present investigation it can be positively stated that the cephalic organs of *Ipnops* are modified eyes. Positively identified optic nerves are to be found, and the organ has a retina with typical rods. The lens and its suspensory apparatus are lacking. The iris is reduced. The processus falciformis and hyaloid vessels are missing. Several rudimentary eye muscles exist, some of which are innervated by the n. oculomotorius. Nervus trochlearis and n. abducens are apparently missing. There is a ciliary ganglion, lying in contact with n. oculomotorius, and from where two ciliary nerves lead to the bulbus, where they innervate the chorioidea (choriocapillaris). The flattened and upwards directed eyes are covered by a transparent, unpaired bony membrane, which is supposed to represent the frontals, because two canals, probably supraorbital canals, are lying on the membrane, one on either side of the median line. Under the lateral edges of the membrane there are two more canals, supposed to be infraorbital canals.

LITERATURE

AGASSIZ, A., 1888: Three cruises of the U.S. coast and geodetic survey steamer "Blake". **2**. London.

BARNARD, K. H., 1925: A monograph of the marine fishes of South Africa. Ann. South Afr. Mus., **2**.

BERG, L. S., 1940: Classification of fishes, both recent and fossil. Trav. Inst. Zool. Acad. Sci. URSS, **5**, 2.

BERTIN, L., 1958: Glandes cutanées et organes lumineux. In *Grassé, P-P.:* Traité de Zoologie, **13**, 1.

BRAUER, A., 1908: Die Tiefsee-Fische. II. Anatomischer Teil. In Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898-1899, **15**. Jena.

DETWILER, S. R., 1943: Vertebrate photoreceptors. New York.

FOWLER, H. W., 1943: Descriptions and figures of new fishes obtained in Philippine seas and adjacent waters by the U.S. Bureau of Fisheries steamer "Albatross". Bull. U.S. Nat. Mus., No. 100, **14**, 2.

GARMAN, S., 1899: The fishes. Report on an exploration . . . by the U.S. Fish Commission steamer "Albatross" during 1891. Mem. Mus. Comp. Zool. Harvard Coll., **24**.

GOODE, G. B. and BEAN, T. H., 1895: Oceanic ichthyology. Special Bull. U.S. Nat. Mus.

GOODRICH, E. S., 1909: A treatise on zoology. Pt. IX. Vertebrata Craniata. 1. fasc. Cyclostomes and fishes.

GÜNTHER, A. C. L. G., 1878: Preliminary notices of deep-sea fishes collected during the voyage of HMS "Challenger". Ann. Mag. Nat. Hist., (5), **2**.

GÜNTHER, A. C. L. G., 1880: An introduction to the study of fishes. Edinburgh.

– 1885: Report on the scientific results of the voyage of HMS "Challenger" during the years 1873-1876. Narrative. **1**, Pt. 1.

– 1887: Report on the scientific results of the voyage of HMS "Challenger" during the years 1873-1876. **22**.

JORDAN, D. S., 1925: Fishes. New York, London.

JORDAN, D. S. and EVERMANN, B. W., 1896: The fishes of North and Middle America. Bull. U.S. Nat. Mus., No. 47.

MARSHALL, N. B., 1954: Aspects of deep sea biology. London.

MOSELEY, H. N., 1887: Report on the structure of the peculiar organs on the head of Ipnops. Appendix A in Günther 1887.

PARR, A. E., 1928: Deepsea fishes of the order Iniomi from the waters around the Bahama and Bermuda Islands. Bull. Bingham Ocean. Coll., **3**, 3.

REGAN, C. T., 1911: The anatomy and classification of the teleostean fishes of the order Iniomi. Ann. Mag. Nat. Hist., (8), **7**.

ROCHON-DUVIGNEAUD, A., 1943: Les yeux et la vision des vertébrés. Paris.

THINES, G., 1955: Les poissons aveugles (I). Ann. Soc. Roy. Zool. Belg., **86**, 1.

WALLS, G. L., 1942: The vertebrate eye and its adaptive radiation. Cranbrook Inst. Sci., Bull. No. 19.

10. 12. 59. 1400. 125

Pl. 1, fig. 1. Dorsal view of the head of *Ipnops murrayi.*

A: nasal capsule
B: anterior part of the supraorbital canal
C: the lateral edge of the transparent membrane
D: the lateral edge of the retina

Pl. 1, fig. 2. Transverse section of the head of *Ipnops murrayi* corresponding to the foremost half of the eyes (cf. text-figure 3). 50 micron section. MALLORY's phosphotungstic acid hematoxylin. A. Øye photo.

A: supraorbital canal
B: infraorbital canal
C: sclera (cartilaginous part)
D: subbulbar fissure
H: hyaline cartilage
I: intraocular blood sinus
L: transparent membrane (the frontals?)
M: the edge of the transparent membrane
R: the retina (pars optica)
S: the sclera (fibrous part)

Pl. 1, fig. 3. Transverse section of the head of *Ipnops murrayi* through the chiasma. 8 micron section. Hematoxylin-eosin. NA: 0,25.

C: the chiasma
D: the dura
E: the epiphysis
I: intraocular blood sinus
H: the hypophysis
R: the retina
S: the sclera (cartilaginous part)
T: olfactory tract
V: vessel

Pl. 1, fig. 4. The same section as in fig. 3 at higher magnification to show the chiasma clearly. The meaning of the letters is the same as in fig. 3. NA: 0,25.