ON THE CRANIAL MORPHOLOGY
OF *IPNOPS MURRAYI* GÜNTHER, 1878
WITH SPECIAL REFERENCE TO
THE RELATIONS BETWEEN THE EYES AND THE SKULL

By BIRGIT THEISEN

Zoological Laboratory, University of Copenhagen

INTRODUCTION

No investigations have, until now, been made on the skull of *Ipnops* (Ordo Iniomi). A few osteological observations are found in GÜNTHER's descriptions (1878 and 1887), but he writes that further specimens could not be sacrificed for the purpose of investigating the osteology of the skull.

The head of *Ipnops murrayi* is broad and depressed with two large dorsal cephalic organs, which MOSELEY (1887) described as phosphorescent organs, while MUNK (1959) showed them to be modified eyes. The eyes are flattened and directed upwards; they extend anteriorly over part of the ethmoid region and posteriorly over part of the otic region. The present investigation deals particularly with the relations between these eyes and the bones and cartilage of the head. As the skull is found to be very specialized, a comparison has been made between *Ipnops* and another genus of the Iniomi, *Chlorophthalmus*.

MATERIAL AND METHODS

The material is from the collection of the *Galathea* Deep-Sea Expedition.

Ipnops murrayi Günther, 1878. Four specimens. Standard length of specimen A (St. 314, Bay of Bengal, 2600 m) was 105 mm. The head of this formalin-fixed specimen was decalcified, embedded in paraffin, and cut into 10 μ serial transverse sections. Every second slide was then stained with hematoxylin-eosin and the other slides according to Bodian's protargol method. The length of specimen B (St. 238, W. Indian Ocean, 3960 m) was about 90 mm and the length of specimen C (St. 234, W. Indian Ocean, 4820 m) was also about 90 mm. These two specimens were placed at my disposal by Mr. O. MUNK. The head of specimen B, Bouin-fixed, had been decalcified, embedded in paraffin, cut into 8 μ serial transverse sections, and stained with hematoxylin-eosin, while the head of specimen C, formalin-fixed, had been decalcified, embedded in celloidin, cut into 50 μ serial transverse sections, and stained with the phosphotungstic acid hematoxylin of Mallory. The fourth specimen was stained with alizarin, but unfortunately with poor results, as the skull disintegrated during the treatment with H_2O_2.

A graphical reconstruction of *Ipnops* has been made from specimen A, but as the surface of the head is rather broken in several places, some details of the fronto-parietal have been drawn from the alizarin-stained bone.

Chlorophthalmus agassizi Bonaparte, 1840. One specimen, 70 mm in standard length (St. 197, off Durban, 495 m). The head of this formalin-fixed specimen was decalcified, embedded in paraffin, and cut into 10 μ serial transverse sections. Every second slide was then stained with hematoxylin-eosin and the other slides according to Bodian's protargol method.

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DESCRIPTION

The ethmoid region is rather short and shows an extreme dorso-ventral flattening. Rather a large amount of cartilage is preserved in this region, forming in the main a broad, flat ethmoid plate with a well developed rostrum (RO, Fig. 1), a somewhat slightly developed mesethmoid cartilage (septum nasi) (MEC, Pl. I 2), and on each side a preethmoid cornu (PEC, Fig. 1), and a parethmoid cornu (PAC, Fig. 1, Pl. I 2) (SWINNERTON 1902). A planum antorbitale is not present. From the posterior border of the ethmoid plate the trabecula communis (TCO, Pl. I 3) projects into the orbital region.

The unpaired *ethmoid* (ET, Fig. 1, Pl. I 1-2) is ossified on the median part of the ethmoid plate, and consists of two thin perichondral lamellae, a dorsal and a ventral. The ventral lamella extends to the anterior border of the rostrum, while the dorsal is shorter. Posteriorly the dorsal lamella is overlapped by the fronto-parietal (FRP).

The cartilage between the two lamellae is not hyaline but seems to be calcified, and there is clear indication of a beginning endochondral ossification, especially in specimen A; a trait common to nearly all the cartilage-bones.

Fused to the dorsal lamella on each side there is a thin postero-lateral intramembranous extension. This extension probably represents the *supraethmoid* (SE, Fig. 1, Pl. I 1).

The *lateral ethmoid*[1] (LET, Fig. 1, Pl. I 2) is ossified around the postero-lateral part of the ethmoid plate with the parethmoid cornu. It consists of a perichondral lamella. In addition, there is clear indication of a beginning endochondral ossification, and postero-laterally there is an area where the cartilage is fully replaced by bone. The lateral ethmoid is ligamentously attached to the palatine (PAL). The two lateral ethmoids are separated by the ethmoid and are almost overlain by the fronto-parietal.

The lateral ethmoid and the fronto-parietal are connected by connective tissue laterally, and diverge medially. A similar condition is found between the ethmoid and the fronto-parietal, the two bones being connected by connective tissue in a median zone (where the ethmoid is ossified on the mesethmoid cartilage), and diverging laterally. The cavity, found between these bones, limited dorsally by the fronto-parietal, medio-ventrally by the ethmoid, and latero-ventrally by the lateral ethmoid, lodges the anterior part of the eye. Thus, anteriorly, the eyes are separated by the ethmoid, and more exactly, by that part of the ethmoid which is ossified on the mesethmoid cartilage. This means that the eyes have extended forwards and now also occupy the normal sites of the olfactory organs. The eyes extend almost to the anterior border of the fronto-parietal. In this region the mesethmoid cartilage is slightly developed, and the fronto-parietal is connected with the ethmoid by connective tissue.

On each side there is a small olfactory organ lying antero-lateral to the eye. The olfactory organ partly overlies the gap between the antero-lateral edge of the fronto-parietal and the postero-medial edge of the supraethmoid, and partly lies dorsal to the postero-medial part of the supraethmoid. The nervus olfactorius (I) passes down between these bones from the olfactory organ to a position lateral to the eye and dorsal to the lateral ethmoid, and then takes a postero-medial course between the eye and the ethmoid. The ramus ophthalmicus superficialis V (O V), the ramus ophthalmicus superficialis VII (O VII), and the nervus oculomotorius pass here, together with the nervus olfactorius (Pl. I 2).

MOSELEY (1887) has erroneously taken the premaxillary cartilages for the nasal capsules (on his Pl. LXVII); he writes that two nerves are seen passing to the nasal capsules, but they go towards the premaxillary cartilages and not to the olfactory organs, which lie more laterally and are also seen on the plate. MUNK (1959) made the same mistake (on his Pl. 1, Fig. 1).

The *nasal* (NA, Fig. 1, Pl. I 1) is a small and oblong bone lying dorsal to the supraethmoid and dorsal to the anterior part of the fronto-parietal. The nasal is firmly attached to, but not fused with the osseous supraorbital canal of the fronto-parietal, while it is just loosely attached to the ethmoid. In transverse section the bone is nearly tubular, but straightens out anteriorly. It lodges the anterior part of the supraorbital lateral line canal, and a branch of the ramus ophthalmicus superficialis VII is seen piercing the wall of the nasal to innervate an organ of the lateral line.

The *prevomer* (PV, Pl. I 1-2-3) is an unpaired, thin, almost flat bone; the anterior part is very broad, while the posterior part forms a narrow

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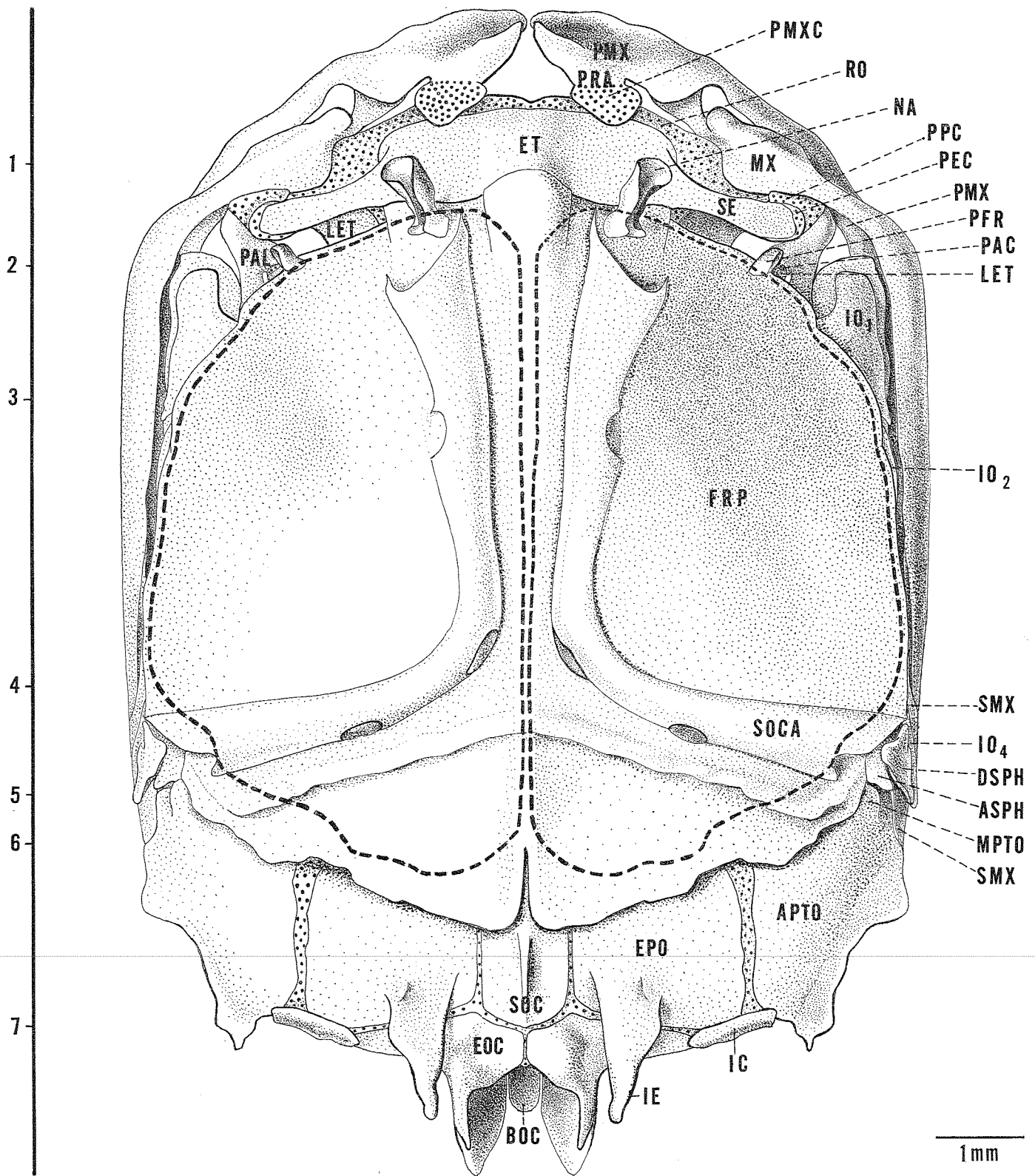. The bones are paired unless otherwise mentioned.

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Fig. 1. Dorsal view of the skull of *Ipnops murrayi*. Graphical reconstruction. The figures on the vertical line indicate the positions of the transverse sections shown on Pl. I. The hatched lines indicate the positions of the eyes.
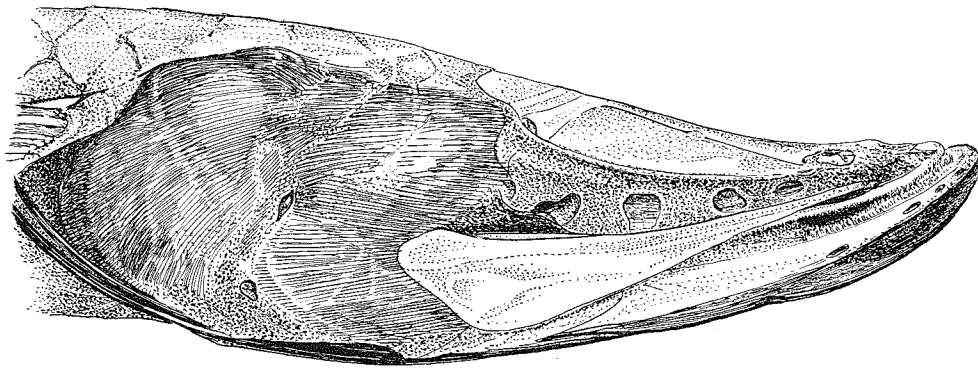For explanation of lettering see p. 20.

Fig. 2. Lateral view of *Ipnops murrayi* (anterior part).

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median shaft. It is superficial to the parasphenoid (PSP) and the ethmoid. The shaft has a median longitudinal ridge, which fits in a corresponding groove on the ventral surface of the parasphenoid. The anterior limitation of the prevomer, the ethmoid, and the rostrum of the ethmoid plate almost coincide, but the parasphenoid does not extend so far forwards. Additionally, the lateral edge of the prevomer and the rostrum of the ethmoid plate almost coincide, and there is close contact between the bone and the perichondrium of the ethmoid plate. The prevomer is attached by ligaments to the palatines. On the broad portion of the bone there is an area on each side with small uniform teeth.

At the transition between the ethmoid plate and the anterior part of the preethmoid cornu, and dorsal to the postero-lateral corner of the broad part of the prevomer there is a small ossification which is only seen in specimen A. It probably is a *preethmoid* (PE, Pl. I 1), which is also present e. g., in *Esox* and *Belone* (SWINNERTON 1902) and in some genera belonging to the family Cyprinidae (SAGEMEHL 1891, HARRINGTON 1955). SAGEMEHL, ALLIS (1898) and other authors apply the name septomaxillary to this bone, but SWINNERTON (1902) suggests the name preethmoid. Both SWINNERTON and DE BEER (1937) have discussed the problems concerning the name, and DE BEER writes, "as it remains to be proved that this perichondral and endochondral ossification is homologous with the dermal septomaxillary of Tetrapods, it appears to be safer to call it the pre-ethmoid".

The preethmoid consists of a ventral perichondral lamella and the obvious beginnings of endochondral ossification which almost reaches through the ethmoid plate. However, a dorsal perichondral lamella is not present; in its place cartilage articulates with the maxillary by a submaxillary cartilage.

The mouth is wide and the lower jaw projects beyond the upper jaw. The *premaxillaries* (PMX, Fig. 1, Pl. I 1-2-3-4) exclude the maxillaries (MX) from the border of the mouth; a feature common to all the Iniomi (REGAN 1911). Where the rami of the lower jaw meet there is an edentulous symphyseal knob which fits into a small notch in the border of the upper jaw. Antero-medianly, the premaxillaries are separated. The premaxillary is a long and slender bone, the antero-median part being edentulous while the rest of the ventral surface is covered with a band of small, uniform teeth; the band is narrower posteriorly. Anteriorly, the premaxillary has a processus ascendens (PRA, Fig. 1), and closely connected with this there is a cartilage which articulates with the rostrum of the ethmoid plate. This must be the *premaxillary cartilage* (PMXC, Fig. 1), described in various Teleostean fishes. Fishes with paired premaxillary cartilages as in *Ipnops* are e. g., *Salmo* (GAUPP 1906, BRUCH 1861), *Anguilla* and *Galaxias* (NORMAN 1926), *Gasterosteus* (SWINNERTON 1902). These cartilages are considered to be homologous with the small, median and generally independent cartilage, often called rostrale (SAGEMEHL 1885), which in various Teleostean fishes connects the premaxillaries and the ethmoid region (NORMAN 1926).

At the transition between that part of the premaxillary which forms the margin of the jaw, and the processus ascendens, there is a small process which has ventrally an articular surface articulating with the anterior extremity of the maxillary. The

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articular surfaces are covered with fibrous cartilage, and between the two articular surfaces there is a very thin plate (probably also consisting of fibrous cartilage).

The *maxillary* (MX, Fig. 1, Pl. I 1-2-3-4-5-6) is a long and well developed bone which dilates posteriorly. It lacks teeth. The anterior extremity of the bone lies ventral to the premaxillary and articulates, as earlier mentioned, with this bone. Behind this, the maxillary lies, at first dorso-medial, and later, dorsal to the premaxillary. The maxillary projects a little more posteriorly than the premaxillary.

In addition to the articulation with the premaxillary, the maxillary also articulates with the cartilaginous ethmoid plate and with the palatine part of the palatoquadrate bar. Between the articular surfaces of the maxillary and the ethmoid plate there is a small double-concave disc consisting of fibrous cartilage. This disc is probably the *submaxillary cartilage* (SMXC, Pl. I 1), described by SAGEMEHL (1885) as 1-3 small skeletal fragments, consisting of cartilage or bone. DE BEER (1937) uses the term maxillary cartilage. Just behind the surface of articulation against the ethmoid plate follows dorso-medially on the maxillary the surface of articulation against the palatine part of the palatoquadrate bar.

A short ligament connecting the premaxillary cartilage and the maxillary is attached to the maxillary between the articular surfaces against the premaxillary and the ethmoid plate respectively.

The posterior one-third of the maxillary is surmounted by a *supramaxillary* (SMX, Fig. 1, Pl. I 4-5-6), which can hardly be seen from the lateral side, as it is almost horizontal and, thus, nearly at right angles to the maxillary.

Of the *palatoquadrate cartilage* there is preserved an anterior part around which an autopalatine is ossified, and a posterior part around which a quadrate and a metapterygoid are ossified.

The *autopalatine* (PAL, Fig. 1, Pl. I 2-3) is a tube of bone around most of the palatine part of the palatoquadrate cartilage (PPC, Fig. 1, Pl. I 2-3), the ossification extending almost from the posterior end of the cartilage to a point between the preethmoid cornu and the parethmoid cornu of the ethmoid plate. From here the ossification extends a little more forwards, and now mainly lies ventro-laterally on the cartilage.

As earlier mentioned, the palatine part articulates with the maxillary, and it is ligamentously attached to the ethmoid region (one ligament going between the cartilaginous palatine part and the supra-ethmoid, and the other between the palatine and the lateral ethmoid). The palatine too is ligamentously attached to the prevomer.

Fused with the autopalatine there is a *dermopalatine,* a bony ridge with a single or two rows of teeth found ventrally on the autopalatine. The teeth are very small, and they cover only a small area. GÜNTHER (1878 and 1887) writes that the palate is toothless, but as is shown here, there are small teeth on both the prevomer and the palatines.

The large, flat *metapterygoid* (MPT, Pl. I 6-7) is ossified postero-dorsally around the quadrate part of the palatoquadrate cartilage. It is mainly a perichondral ossification, only the dorsal part being fully ossified.

The *quadrate* (QU, Pl. I 5-6) is ossified ventrally around the quadrate part of the palatoquadrate cartilage, and this bone, too, is large and flat. Ventrally, there is a well developed surface of articulation for the articular. In front of the jaw articulation the quadrate consists of perichondral lamellae, but from the jaw articulation, the ventral part of the bone is fully ossified. This part has ventrally two prongs, between which the anterior end of the preopercular bone occurs. The symplectic is dorso-medial to these prongs.

The two parts of the palatoquadrate bar are connected by two dermal bones, an ectopterygoid and an endopterygoid. The *ectopterygoid* (ECPT, Pl. I 3-4-5) is, in transverse section, somewhat Y-shaped. The anterior end of the bone lies ventro-lateral to the palatine, and in such a way that the two dorsal prongs of the Y surround the palatine. It is a rather long bone which gradually dilates as the lower prong in the Y is lengthened dorso-ventrally. This occurs simultaneously with the whole skull increasing in height. Posteriorly, the ectopterygoid again decreases, lying close to the medial surface of the quadrate.

The *endopterygoid* (ENPT, Pl. I 4-5-6) is long and slender. The anterior end lies ventro-medial to the palatine and medial to the ectopterygoid. Between these bones there is dense connective tissue.

Anteriorly, the quadrate part of the palatoqudrate cartilage is, in transverse section, seen as a small circular piece of cartilage completely surrounded by the endopterygoid and the ectopterygoid. Posteriorly the cartilage (QPC, Pl. I 4-5-6-7) remains very narrow medio-laterally while it increases in size dorso-ventrally, and separates the ectopterygoid from the endopterygoid. Posteriorly, the endoptery-

goid is attached to the medial surface of the metapterygoid.

As in the ethmoid region a rather large amount of cartilage is preserved in *the otic region,* and the flattening of the skull is also seen here, the auditory capsules being depressed and slightly tapering laterally. The auditory capsules are postero-dorsally connected by the tectum synoticum, which has a median process representing part of the *taenia tecti medialis* (TM, Pl. I 5-6). On each auditory capsule there is a postorbital process. Of the cartilaginous semicircular septa only the lateral, vertical one is present. The cartilage-bones consist of thin perichondral lamellae on the inner and outer surfaces of the auditory capsules, and at the same time, clear indications of a beginning endochondral ossification are often seen. Relatively broad, unossified areas are often found between these bones. The large eyes extend posteriorly over the otic region, lying dorso-medial to the auditory capsules.

The *autosphenotic* (ASPH, Fig. 1) is ossified around the anterior end of the auditory capsule, and around the processus postorbitalis. This is a perichondral ossification, but has an anterior intramembranous extension from the processus postorbitalis (IP, Pl. I 4). This extension, to which a muscle is attached, is overlapped by the fronto-parietal. The greater part of the dorsal surface of the autosphenotic is also overlapped by the fronto-parietal. Laterally, dense connective tissue is seen between these bones, while medially the eye is wedged between them. The posterior edge of the bone is overlain by an extension from the membranopterotic (MPTO) which extends between the autosphenotic and the fronto-parietal, and here the lateral part of the eye lies between the membranopterotic and the fronto-parietal. The autosphenotic has, ventro-laterally, a groove for the anterior articular head of the hyomandibular, while the posterior part of the hyomandibular (HM, Pl. I 5-6) articulates with the autopterotic.

Dorso-lateral to the autosphenotic there is a dermal bone, which connects the supraorbital canal and the infraorbital canal. The bone is not in close contact with the autosphenotic and is probably a *dermosphenotic* (DSPH, Fig. 1, Pl. I 5).

The *autopterotic* (APTO, Fig. 1, Pl. I 5-6) is ossified as perichondral lamellae around the lateral wall of the auditory capsule and on the vertical, lateral septum bounding the canalis semicircularis lateralis of the membranous labyrinth. Posteriorly the autopterotic has an intramembranous extension for muscle-attachment (IA, Pl. I 7).

Dorsal to, and at several places fused with the anterior part of the autopterotic, there is a bony lamella which does not lodge any portion of the lateral line canal. This is probably a *membranopterotic* (MPTO, Fig. 1, Pl. I 5-6). The medial edge of this bone extends over the prootic (PRO), while the anterior edge, as earlier mentioned, extends over the autosphenotic. The fronto-parietal overlaps the bone, and dense connective tissue is present between these bones posteriorly (Pl. I 6). Further forwards the bones are still attached laterally, while medially, they are separated by the eye (Pl. I 5).

The *epiotic* (EPO, Fig. 1) is ossified around the dorso-medial part of the auditory capsule, dorsal to the canalis semicircularis posterior and part of the canalis semicircularis anterior. The antero-medial part of the bone is overlapped by the fronto-parietal. On the postero-dorsal surface of the epiotic there is a rather broad, posteriorly projecting intramembranous extension (IE, Fig. 1, Pl. I 7) to which muscles are attached and to the base of which the dorsal prong of the *posttemporal* (PT, Pl. I 7) is attached by ligament.

The *prootic* (PRO, Fig. 1, Pl. I 5-6) is ossified on the inner and outer surfaces of the medial wall of the auditory capsule. The inner lamella partly encloses the ampulla anterior and the anterior part of the canalis semicircularis anterior. The membranopterotic overlaps the bone dorso-laterally. The fronto-parietal overlaps the prootic, the bones being connected postero-laterally by dense connective tissue, while the eye is postero-medially wedged between them (Pl. I 6). Anteriorly the eye increases and extends laterally between the fronto-parietal and the membranopterotic, so that the fronto-parietal and the prootic are fully separated (Pl. I 5).

The prootic is also ossified around the antero-lateral part of the cartilaginous basal plate (BP, Pl. I 5-6). The pharyngobranchial I is loosely attached to the ventral surface of the bone. A prootic bridge is not present. The large eyes have only minute rudiments of eye muscles (MUNK 1959). It is very difficult to identify these rudiments. No myodome is present, and the parasphenoid lies close to the ventral surface of the prootic.

The prootic forms the lateral wall of the trigeminofacialis chamber, and posteriorly, probably divides this chamber for a short distance. Here the prootic is probably ossified in relation to the commissura lateralis, of which no cartilage is pre-

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served. Finally, the prootic connects the cartilaginous auditory capsule and the basal plate posterior to the trigeminofacialis chamber.

The Geniculate ganglion (GG, Pl. I 5) does not lie in the trigeminofacialis chamber but inside the ectomeninx, and here the truncus hyomandibularis VII and the ramus palatinus VII are emitted from the ganglion. The truncus hyomandibularis (H VII, Pl. I 5-6-7) immediately passes in lateral direction to the trigeminofacialis chamber and further out through the posterior aperture of this chamber, while the ramus palatinus (P VII, Pl. I 2-3-4) first runs forward inside the ectomeninx, and then passes through this wall to the medial part of the trigeminofacialis chamber. From here the nerve runs forwards, first lying dorsal to the basal plate, and anterior to this plate lying dorsal to the parasphenoid. Under the anterior portion of the eye the nerve turns laterally over the edge of the parasphenoid and divides into two branches, proceeding to the roof of the buccal cavity.

As the eye extends such a long distance posteriorly, the membranous wall of the orbit dorsally limits the trigeminofacialis chamber. The medial and latero-ventral walls of this chamber are formed by the ectomeninx and by the prootic respectively, in agreement with the standard condition in fishes.

A nerve, interpreted as the ramus communicans, leaves the posterior part of the Gasserion-lateralis complex and passes to the truncus hyomandibularis VII. Antero-laterally the truncus infraorbitalis, containing the ramus mandibularis V, the ramus maxillaris V, and the ramus buccalis VII, leaves the Gasserion-lateralis complex. It passes under the processus postorbitalis, where the ramus mandibularis V (M V, Pl. I 5-6) is separated from the truncus in order to reach the lower jaw, while the ramus maxillaris V and the ramus buccalis VII (MX V+B VII, Pl. I 4) run forward ventro-lateral to the eye. Medially, the ramus ophthalmicus superficialis V and the ramus ophthalmicus superficialis VII (O V+VII, Pl. I 2-3-4-5) leave the Gasserion-lateralis complex (GL, Pl. I 5) and run dorso-medially to a position medial to the eye. From here they continue forwards, running between the interorbital septum (SI) and the eye, and dorsal to the nervus olfactorius (I) and the nervus opticus (II). Medially, on the Gasserion-lateralis complex a small branch separates and leads to the ciliary ganglion. This probably represents the radix longa, as separate profundus ganglion and separate ramus sympathica are not present (MUNK 1959).

In *the occipital region* the unpaired *basioccipital* (BOC, Fig. 1, Pl. I 7) is ossified around the posterior part of the cartilaginous basal plate. The parasphenoid lies ventral to the anterior surface of the bone. Posteriorly, the basioccipital resembles the centrum of a vertebra. On the postero-ventral surface of the bone there is on either side a low ridge, and between them is found the dorsal aorta (DA, Pl. I 7).

The *exoccipitals* (EOC, Fig. 1, Pl. I 7), which are ossified on the inner and outer surfaces of the occipital arch, meet dorsal to the foramen magnum, while ventrally they form a suture with the basioccipital. The ossification extends anteriorly in the ventral wall of the auditory capsule, here consisting partly of perichondral lamellae around the wall of the auditory capsule and partly of a ventro-medially directed extension which meets a corresponding extension from the basioccipital. The exoccipital here underlies the posterior end of the canalis semicircularis lateralis, the ampulla posterior, and part of the sacculus. Behind the autopterotic the outer ventro-lateral lamella of the exoccipital is overlapped by the intercalary (IC). The exoccipital also extends behind the foramen magnum, consisting partly of perichondral lamellae and partly of a dorso-medial extension. On the postero-ventral surface of the exoccipital are found the two foramina for the nervus glossopharyngeus and the nervus vagus.

A well developed *intercalary* (opistotic) (IC, Fig. 1, Pl. I 7) is present, lying posteriorly around the unossified part of the auditory capsule behind the epiotic and the autopterotic. The ventro-medial edge of the bone overlaps the exoccipital. The intercalary has an anterior prolongation which extends under the auditory capsule and lies in such a way that the medial edge still overlaps the exoccipital, while the lateral edge overlaps the autopterotic. This prolongation of the bone extends to the prootic. Posteriorly, the intercalary seems to lie close to, although outside, the perichondrium of the auditory capsule. The bone is connected by a ligament to the ventral prong of the posttemporal.

Posteriorly, the unpaired *supraoccipital* (SOC, Fig. 1, Pl. I 6-7) forms perichondral lamellae around the tectum synoticum, while anteriorly, it consists of a perichondral ossification around part of the taenia tecti medialis. Lateral extensions come from the posterior part of the ossification around the taenia tecti medialis. The supraoccipital is excluded from the foramen magnum by the exoccipitals. The bone has a median posteriorly-projecting spine.

Anteriorly, the supraoccipital is overlain by the fronto-parietal.

The eyes extend to the anterior end of the supra-occipital. Ventrally, the orbit is limited here by the membranous wall of the cranial cavity (which lies between the supraoccipital and the prootic), and by the dorso-medial part of the prootic (Pl. I 6). Further forwards, the bottom of the orbit is made up by the membranous wall of the cranial cavity (which extends between the cartilaginous taenia tecti medialis and the prootic), by the dorso-medial part of the prootic, and by the medial part of the membranopterotic (Pl. I 5). Anteriorly, in the otic region the bottom of the orbit consists of the membranous wall extending between the taenia tecti medialis and the autosphenotic, and of the dorso-medial part of the autosphenotic.

The eyes meet dorso-medianly between the fronto-parietal and the taenia tecti medialis, and in specimen A a very low membranous *interorbital septum* is found (SI, Pl. I 5). This septum increases in height anteriorly. Anterior to the taenia tecti medialis a low ventral ridge of the fronto-parietal participates in the formation of this septum, and here the septum ventrally reaches the membranous wall of the cranial cavity. In specimens B and C the taenia tecti medialis does not extend so far forwards; the ventral ridge on the fronto-parietal is higher and for a short distance forms the entire interorbital septum.

In *the orbital region* proper little cartilage is present. The trabecula communis projects posteriorly from the ethmoid plate, but is not continous with the basal plate. A short postorbital process projects from the auditory capsule. The interorbital septum is of a type which I have not seen described in any other Teleostean fish. Anteriorly in the orbital region the septum remains intact between the fronto-parietal and the trabecula communis (Pl. I 3), but after the olfactory nerves have passed through the membranous wall of the cranial cavity the septum is divided into two parts, a ventral and a dorsal (Pl. I 4). The ventral part corresponds to that normally found in Teleostean fishes; it extends from the membranous wall of the cranial cavity to the trabecula communis and further back towards the parasphenoid, while the dorsal part connects the membranous wall of the cranial cavity and the fronto-parietal. As mentioned earlier, the dorsal part continues in the otic region.

Corresponding to the anterior third of the eye

the nervus olfactorius runs between the interorbital septum and the eye (Pl. I 3), and anterior to this it runs ventral to the eye (Pl. I 2). The connection with the olfactory organ was described earlier. As no swelling corresponding to the bulbus olfactorius is found near the olfactory organ, and as no ganglion cells could be observed, I am of the opinion that this must be the nervus olfactorius and not the tractus olfactorius, (which according to MUNK (1959) runs between the olfactory organ and the brain).

Dorsally, the greater part of the head is covered by a large transparent membrane, which again covers the eyes. The extension of this membrane is only slightly larger than that of the eyes. The membrane consists of bone and represents the frontals and probably also the parietals, which have fused into a single, large, unpaired bone, a *fronto-parietal* (FRP, Fig. 1, Pl. I 2-3-4-5-6). No sign of independent parietals could be seen. Posteriorly, the membrane overlaps the supraoccipital and this, too, indicates that it contains the parietals. Posteriorly, there is a transverse ridge on the membrane, but this has no sign of a suture.

PARR (1928) and MUNK (1959) suggest that this membrane represents the frontals. GÜNTHER (1887) was in doubt as to the interpretation of the membrane, as MOSELEY (1887) held the opinion that the peculiar organs were not eyes but phosphorescent organs. GÜNTHER writes, "if, as Professor MOSELEY's investigations seem to prove, the luminous organ is not a modification of the eye, as Mr. MURRAY and myself supposed at first, and if the organ of vision with the optic nerve has disappeared, the luminous organ is probably the homologue of that which is found in some Scopelids between the eye and nostril, and the covering plates would be the homologues of the praeorbital membrane bones. With the abortion of the eyes the luminous organs with their praeorbitals would have moved from their usual lateral position to the top of the head".

The fronto-parietal is traversed on each side by the two *supraorbital canals* (SOCA, Fig. 1, Pl. I 2-3-4). Each canal has an antero-lateral and a postero-lateral expiring section. The two sections form an angle of about 90° with each other. Each canal has three foramina.

MOSELEY (1887) describes a nerve passing through the supraorbital canal and considers this to be "the nasal branch of the fifth nerve". This does not aggree with my observations. Unfortunately, the surface of the head is rather broken at several

places, but as far as can be seen, a nerve does not pass through the canal. However, the ramus ophthalmicus superficialis VII passes immediately ventral to the fronto-parietal and lateral to the interorbital septum, and branches of this nerve pierce the wall of the supraorbital canal and innervate the organs of the lateral line. Moreover, another nerve, perhaps the nervus lateralis accessorius, follows the anterior section of the supraorbital canal. In some places it appears that this nerve is actually in the canal, but this may be an artefact connected with the damaged surface of the head. This nerve (NL, Pl. I 4-5-6) leaves the truncus hyomandibularis in the hyomandibular, and outside this bone the nerve is divided into an anterior and posterior branch. The anterior branch is again divided into two branches. One of these runs forward ventro-lateral to the eye together with the ramus maxillaris V and the ramus buccalis VII, and at some places it seems that this branch actually sends small branches to the skin dorsal and ventral to the infraorbital canal. The second branch runs obliquely over the eye (just ventral to the fronto-parietal), and then turns forward to run through the skin along the anterior section of the supra-orbital canal, giving off small branches to the skin. It has not been possible to find where the nerve pierces the fronto-parietal.

Antero-lateral to the supraorbital canal MOSELEY (1887) described a pair of convex cornea-like prominences and some concentric striae, which were not found by MUNK (1959), or by the present author.

Antero-lateral to the fronto-parietal there is a small dermal bone which was seen only in specimen A. As the bone does not lodge any part of the lateral line canal, and as it lies immediately dorsal to the lateral ethmoid without being fused with this bone, it is probably a *prefrontal* (PFR, Fig. 1, Pl. I 2).

Ventral to the lateral edge of the fronto-parietal,

and almost at right angles to this bone, there is a row of *infraorbital bones* (IO$_{1-4}$, Fig. 1, Pl. I 2-3-4-5). The infraorbital series consist of four dermal bones lodging the infraorbital lateral line canal. They form, in fact, a fairly large groove, open ventrally, and at some places, also laterally. Medial to the infraorbital canal the ramus buccalis VII passes, and branches of this nerve pierce the wall, proceeding to the lateral line organs.

The unpaired *parasphenoid* (PSP, Pl. I 1-2-3-4-5-6) is a long and slender dermal bone. The anterior end, which is slightly tapering, lies between the ethmoid and the prevomer, but does not extend so far forwards as these bones. Posterior to the ethmoid the bone lies close to the cartilaginous ethmoid plate and the trabecula communis. Between the trabecula communis and the cartilaginous basal plate the parasphenoid alone forms the median floor of the skull (orbitosphenoid, pleurosphenoid, and basisphenoid are not present). The median part of the parasphenoid is slightly arched dorsally, and this is most marked in the area ventral to the trabecula communis and between this and the basal plate. In the same area the arched part in specimen A is thickened, so that a dorsal ridge is seen, whereas similar thickenings are not found in specimens B and C. In front of the basal plate there is a carotid foramen on each side of the parasphenoid.

The parasphenoid lies close to the basal plate and close to the prootics, and here the bone has its maximum width. The pharyngobranchials I are here loosely attached to the ventral surface of the bone. The posterior part of the parasphenoid, which again has narrowed, is attached to the basi-occipital, and the bone is bifurcated.

There is a large distance between the median parasphenoid and the endopterygoid and the ecto-pterygoid laterally; thus for the greater part, the floor of the orbit is membranous.

COMPARISON AND DISCUSSION

The genus *Chlorophthalmus* (Fig. 3) is regarded as a comparatively undifferentiated representative of the order Iniomi, and is closely related to *Ipnops* (REGAN 1911, PARR 1928 and 1929, GREGORY & CONRAD 1936). REGAN (l. c.) made a short description of the skull of *Chlorophthalmus* based on an examination of a spirit-specimen. As *Chlorophthalmus*, like *Ipnops*, has large eyes (although they are laterally placed and directed slightly upwards), and

as it, too, has a tropibasic skull (but of a more generalized Teleostean pattern), a short comparison between the skulls of these two genera has been carried out.

The first sections to be compared are from *the transition between the ethmoid region and the orbital region.* In *Chlorophthalmus* (Pl. II 1) a planum antorbitale (PLA) separates the two regions, and the nervus olfactorius is seen piercing this wall
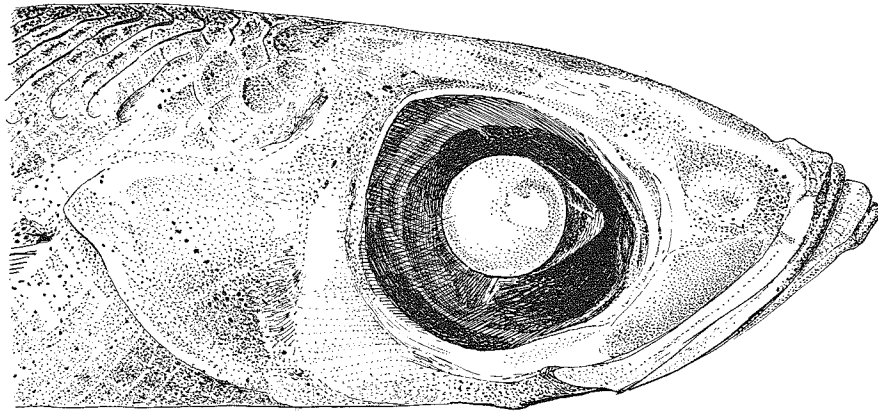
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Fig. 3. Lateral view of *Chlorophthalmus agassizi*.

5 mm

through foramen olfactorium advehens on its way from the olfactory organ to a position between the interorbital septum and the eye. The nerve piercing the planum antorbitale at a more dorsal position is the ramus ophthalmicus superficialis V, while the ramus ophthalmicus superficialis VII runs in the supraorbital canal. *Chlorophthalmus* has well developed eye muscles, and seen in the mesethmoid cartilage is the anterior myodome (MY) lodging the two pairs of oblique eye muscles (OM). REGAN (1911) writes that the lateral ethmoids meet in the middle line; they are far apart in my specimen.

Pl. I 2 is a section of *Ipnops* from the corresponding zone, but showing quite different conditions. No planum antorbitale is present, and it may be supposed that this was reduced when the eye extended over the posterior part of the ethmoid plate. The eyes extend to a point just medial to the olfactory organs, and they are separated by the mesethmoid cartilage with the ethmoid. The nervus olfactorius here runs downwards from the olfactory organ, and passes ventral to the eye to reach the position between the interorbital septum and the eye. The ramus ophthalmicus superficialis V and the ramus ophthalmicus superficialis VII are also seen passing ventral to the eye, but they still lie dorsal to the nervus olfactorius. No myodomes are found in *Ipnops,* the eye muscles of which are very reduced (MUNK 1959).

The following sections to be compared show the conditions in *the orbital region* after the nervus olfactorius in both genera has passed through the membranous wall of the cranial cavity. In *Chlorophthalmus* (Pl. II 2) a cartilaginous cranial roof (CR) is seen lying just under the paired frontals

(FR). In an area anterior to the section shown the cartilaginous cranial roof is missing while posteriorly, it is separated into the taenia tecti medialis and the two taeniae marginales posteriores. The interorbital septum connects the membranous wall of the cranial cavity and the parasphenoid.

In *Ipnops* (Pl. I 4) no cartilaginous cranial roof and no taeniae marginales are present, the cartilage being represented only by a short process projecting forwards from the auditory capsule. This may be correlated with the large modification of the eyes, which as MUNK (1959) writes, "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". Thus, the eyes have a rather short extension dorso-ventrally but a large extension latero-medially. As the eyes are very large, the result is that they fill up the greater part of the orbital region (especially the dorsal part), and it is to be presumed that the cartilage of this region has been reduced. The flattening out of the eyes must also give the result that the eyes meet more dorsally than is generally the case in a tropibasic skull, and this explains why the interorbital septum has a dorsal part above the cranial cavity, whereas the normal interorbital septum is present below the cranial cavity, as in other fishes. The dorsal septum extends between the fronto-parietal and the membranous wall of the cranial cavity, or the taenia tecti medialis. Further back, where the brain has increased and the eyes have decreased, only the dorsal part of the interorbital septum is present.

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This is seen in the section from the anterior end of *the otic region* (Pl. I 5). Here the eye lies dorso-lateral to the brain and dorso-medial to the auditory capsule, while the eye in the corresponding zone of *Chlorophthalmus* (Pl. II 3) lies ventral to the auditory capsule. In *Chlorophthalmus* the posterior extremity of the eye is seen, whereas in *Ipnops* the eye extends further backwards. A posterior myodome lodging the internal and external rectus eye muscles (RM) is present in *Chlorophthalmus*. It is dorsally limited by the prootic bridge (PB) and ventrally by the parasphenoid. As mentioned *Ipnops* lacks myodomes, as well as the prootic bridge. From the sections from the otic region in particular, it can be seen how broad and flattened the head of *Ipnops* is in relation to that of *Chlorophthalmus*.

Chlorophthalmus has paired parietals (PA, Pl. II 3) and paired frontals. The frontals are broad in the otic region (Pl. II 3), while they are rather narrow anteriorly, between the eyes (Pl. II 2). In *Ipnops* the frontals and the paritals are probably fused into one large unpaired fronto-parietal, which fully covers the eyes (Pl. I 2-3-4-5-6). The fusion of these bones is also found in other families of the order Iniomi: in the Scopelarchidae, the Evermannellidae, and the Cetomimidae (PARR 1929). However, in these families the fronto-parietals of the two sides are distinct from each other. In *Ipnops* a mere suggestion of a median separation, consisting of a short posterior incision, is present. PARR states, as an indication of the fusion of the frontal and the parietal in these families, that the posterior edge of the bone overlies part of the supraoccipital, as it also does in *Ipnops*.

SUMMARY

The skull of *Ipnops murrayi* is weakly ossified, and while a rather large amount of cartilage is still present in the ethmoid and otic regions, only a small amount is present in the orbital region. Nearly all the cartilage-bones consist of perichondral lamellae, but they often indicate a beginning endochondral ossification. Dorsally, the greater part of the head is covered by a large transparent, bony membrane considered to be the frontals and the parietals, which are fused into a single unpaired fronto-parietal. This bone again covers the large dorsally-directed eyes. The eyes extend over part of the ethmoid region and are here separated by the mesethmoid cartilage with the ethmoid. Planum antorbitale and myodomes are not present. The eyes fill up the greater part of the orbital region, and are separated by a special type of interobital septum. The septum is situated anteriorly between the fronto-parietal and the trabecula communis, while it is divided posteriorly by the cranial cavity into a ventral part corresponding to that normally found in Teleostean fishes, and a dorsal part situated between the membranous wall of the cranial cavity and the fronto-parietal. The dorsal part continues into the otic region. The eyes extend to the supraoccipital. In the otic region the eyes lie dorso-lateral to the brain and dorso-medial to the auditory capsule. A short comparison has been made between this specialized skull and the skull of *Chlorophthalmus*.

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ADDENDUM

According to J. G. NIELSEN's revision of the genus *Ipnops* (pp. 49-75 in the present volume) none of the specimens described in this paper is *Ipnops murrayi* Günther. The specimen A and the specimen used for Fig. 2 are *Ipnops agassizi* Garman, 1899, and the specimens B and C are *Ipnops meadi* Nielsen, 1966.