On the Skull of Holocephali

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Phil. Trans. R. Soc. Lond. B 1935 **224**, 287-312
doi: 10.1098/rstb.1935.0001

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(Communicated by E. S. GOODRICH, F.R.S.—Received June 8, Read November 1, 1934)

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I—INTRODUCTION

Of all groups of living fishes, the Holocephali are the least well known, owing to the difficulty of obtaining embryonic material. As regards the morphology and embryology of the skull in these animals, we owe what little knowledge we possess to papers by HUBRECHT (1877), SCHAUINSLAND (1903), FÜRBRINGER (1904), DEAN (1906), LUTHER (1909), and ALLIS (1915, 1917, 1919, and 1926). Of these, only SCHAUINSLAND and DEAN are concerned with embryonic stages, and what little they have to say serves to stimulate further enquiry.

Among the morphological problems presented by the Holocephalian skull, three stand out as particularly demanding solution. These are :—

1. What is the real nature of the attachment of the pterygo-quadrate to the brain-case ; is a true otic process present ; does the hyomandibula in any way contribute to the attachment.
2. What is the true nature of the skeleton of the hyoid arch ; are both epihyal and pharyngohyal cartilages present.
3. What is the nature of the so-called ethmoidal canal ; what do its floor and roof represent.

To these questions we have been able to provide answers, which we trust are satisfactory. We have also been led as a short digression to consider the general morphology of the trabecular horns in fishes and Tetrapods. Other problems, such as those presented by the rostro-labial cartilages, we have not ventured to attack, lacking the necessary material to add anything of value to our existing knowledge. We have, however, thought it worth while to attempt a comparison between the skull of Holocephali, so far as we know its structure, and that of Selachians, with a view to defining the phylogenetic relationship between these groups in the light of the skull. The conclusions to which this comparison has driven us seem to be so far-reaching and important that, following the suggestion of Professor GOODRICH, we have re-investigated the fossil Holocephali in order to see whether our embryological results receive support from palæontology.

Briefly, our conclusion is that the Holocephali represent the most primitive living Gnathostomes known, and we may anticipate by saying that taking all the evidence into consideration we believe this opinion to be justified.

The embryological portion of this paper is the work of G. R. DE BEER, the palæontological is that of J. A. MOY-THOMAS, but we have each of us checked the work of the other and are jointly responsible for the opinions here expressed.

Our thanks are due to Professor GOODRICH who first suggested the importance of attacking these problems, and in whose Department the work was done; to Mr. J. R. NORMAN by whose kindness we have been able to study young and adult specimens of *Callorhynchus*, and to Dr. WHITE and the authorities of the British Museum (Natural History) and of the Royal Scottish Museum, by whose helpful courtesy we have had the opportunity of examining the specimens of *Squaloraja* under their charge. We are deeply grateful to Professor STENSIÖ and Dr. SÄVE-SÖDERBERGH, for their kindness in enabling us to see proofs of some of their as yet unpublished work.

II—EMBRYOLOGICAL INVESTIGATIONS

These investigations are based on the study of a 95 mm embryo of *Callorhynchus antarcticus*, cut into serial transverse sections.

i—*The Attachment of the Jaws to the Brain-case*

It is well known that the pterygo-quadrate of Holocephali is firmly fused on to the cartilage of the brain-case by its own processes, in a manner which HUXLEY (1876) imagined as approximating to his "autostylic" type. It is now, however, clear that this attachment differs from the autostyly found in Dipnoi and Amphibia (GOODRICH, 1909), and the expression "holostylic" may be used to denote the Holocephalian condition (GREGORY, 1904).

The essential feature of the attachment in these animals is its completeness. The front part of the pterygo-quadrate is fused with the nasal capsule and ethmoidal region of the skull; the hind part is fused with the otic capsule, and the intermediate part of the pterygo-quadrate is fused with the lateral edge of the trabecular plate of the skull, leaving only three gaps or foramina, through which certain nerve-roots and blood-vessels pass.

With regard to the anterior region of this extensive attachment, fig. 6, there is little difficulty in recognizing a fusion between the ethmoid process of the pterygo-quadrate and the ethmoid region of the skull. The Selachii (*Scymnus*, *Clamydoselache*, ALLIS, 1923b, DE BEER, 1931), present evidence of contact between these elements, as do also the Teleostomi (*Polypterus*, BUDGETT, 1902, LEHN, 1918, MOY-THOMAS, 1933; *Amia*, PEHRSON, 1922, DE BEER, 1924b; *Lepidosteus*, VEIT, 1911; *Salmo*, DE BEER, 1927). In some species, the articular joint which arises is preceded by temporary cartilaginous fusion (*Gasterosteus*, SWINNERTON, 1902). In Amphibia, it is common to find persistent cartilaginous fusion between the ethmoid process of the pterygo-quadrate and the ethmoid region of the skull (*Rana*, GAUPP, 1893; several *Urodela*, EDGEWORTH, 1923 and 1925). In all these cases there is no doubt that a cartilaginous fusion between the ethmoid process of the pterygo-quadrate (visceral skeleton) and the ethmoid region of the skull (neurocranium), whether temporary or permanent, is a secondary and modified phylogenetic condition (DE BEER, 1931), and such we must consider it to be in the Holocephali.

Turning now to the hindmost region of the attachment in Holocephali, figs. 11, 12, the question arises whether it represents an otic process, either alone or in combination with other elements.

A study of the morphological relations of the otic process with surrounding structures throughout the vertebrate series (DE BEER, 1926, *a*) has made it possible to establish the following definition: the otic process is a part of the pterygo-quadrate which articulates or fuses with (or shows evidence of having previously articulated or fused with) the auditory capsule, in such a manner as to be morphologically anterior to the spiracular visceral cleft, lateral to the vena capitis lateralis, anterior, lateral, or latero-dorsal to all the branches of the facial nerve, and to the mandibular blood-vessel as represented by the efferent pseudobranchial artery, and posterior to the branches of the trigeminal nerve.

Now, a glance at fig. 1, which is a graphic reconstruction as seen from the left side of the skull of a 95 mm specimen of *Callorhynchus*, shows that despite the fact that the region of the pterygo-quadrate in question is stretched backwards horizontally (*op*), it bears all the prescribed relations of an otic process to the vena capitis lateralis, and to the trigeminal and facial nerves. There can be little doubt, therefore, that this structure represents an otic process, slightly displaced topographically so as to assume the horizontal position, as a result of the extreme anterior position of the articulation of the upper with the lower jaw.

The question now arises whether the otic process is accompanied by and fused with some part of the hyomandibula: a possibility which has been envisaged (GOODRICH, 1909), and which it is all the more necessary to decide since in such a form as *Acipenser* (DE BEER, 1925) the hyomandibula bears the same relations to surrounding structures as does the otic process, *except* that it is posterior instead of anterior to the spiracle. It should be noted, however, that the hyomandibula of *Acipenser* is dorsal to the vena capitis lateralis, instead of ventral to it as in *all* Selachians. If the hyomandibula in Holocephali were fused with the otic process, its relations to the vena capitis lateralis would be unique in Elasmobranchs.

Unfortunately, in the Holocephali, the spiracle becomes closed and disappears at an early stage; there is nothing left of it at the stage here studied, nor in those stages in which the chondrocranium has appeared, described by SCHAUINSLAND (1903) and DEAN (1906); and the figures of earlier stages shown by these authors are insufficient to give any clue as to the position which the spiracle would have occupied in later stages, had it persisted.

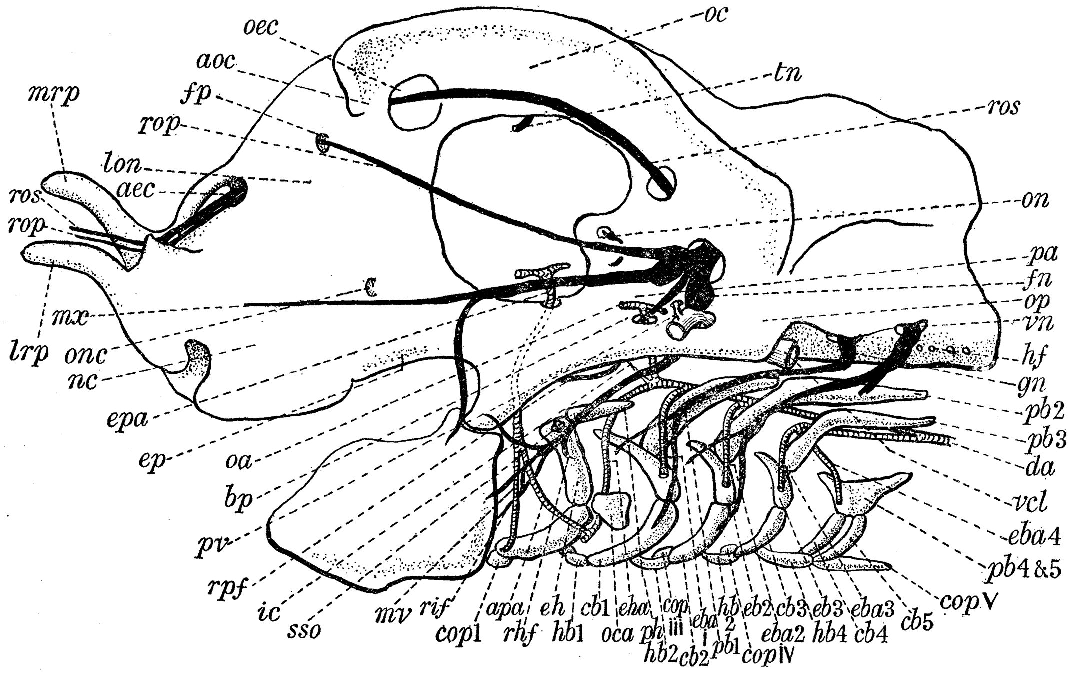


FIG. 1—Left side view of graphic reconstruction of skull of *Callorhynchus* (95 mm), showing relations of the cartilage to the chief blood-vessels and nerves.

Pending the study of the much-wanted intermediate stages, there is, however, one clue which enables the former position of the spiracle to be determined within fairly narrow limits, and this is the position of the spiracular sense-organ. Confirming COLE's (1896) description of the nerves in *Chimæra*, we have found in *Callorhynchus* what appears to be the spiracular sense-organ in the form of a clump of a few ampullæ, innervated by the facial nerve, and are able to add that it lies ventro-posteriorly to the pterygo-quadrate and otic process, fig. 10; if these observations are correctly interpreted, therefore, the otic process cannot contain any admixture of hyomandibular cartilage. This conclusion is confirmed below by the findings of the investigation of the skeleton of the hyoid arch, all the elements of which are there accounted for.

There remains now to be considered the fusion of the pterygo-quadrate with the trabecular plate in the intermediate region, between the ethmoid fusion in front and the otic fusion behind; this intermediate fusion is interrupted by three foramina, representing the space originally existing between the pterygo-quadrate and the neurocranium, and through which pass, in order from front to back, the efferent pseudobranchial artery, fig. 9, the palatine nerve and orbital artery together, fig. 10, and the hyomandibular nerve and vena capitis lateralis together, fig. 11.

Now, this is the region in which one would expect to find a representative of the basal connexion (articulation or fusion) which is one of the most constant features of the attachment of the pterygo-quadrate to the brain-case throughout the vertebrate series. Here again, it is possible to make a rigid definition: the basal connexion is formed by the contact of the basal process of the pterygo-quadrate with the basitrabecular process of the neurocranium, in such a manner as to be antero-dorsal to the palatine nerve, antero-ventral to the orbital artery, and ventral to the vena capitis lateralis and orbital sinus. In *Callorhynchus*, therefore, the fusion of the pterygo-quadrate with the brain-case immediately in front of the foramen through which the palatine nerve passes answers exactly to the definition of a basal connexion, fig. 9, and the fact that the orbital artery runs up through the same foramen as that which allows the palatine nerve to run down is exactly paralleled in *Lepidosteus* and *Salmo* (DE BEER, 1926, *a*). As to the relative participation of basal process (of the pterygo-quadrate) and basitrabecular process (of the neurocranium) little can be said. Judging from the condition in Selachii, where the basitrabecular

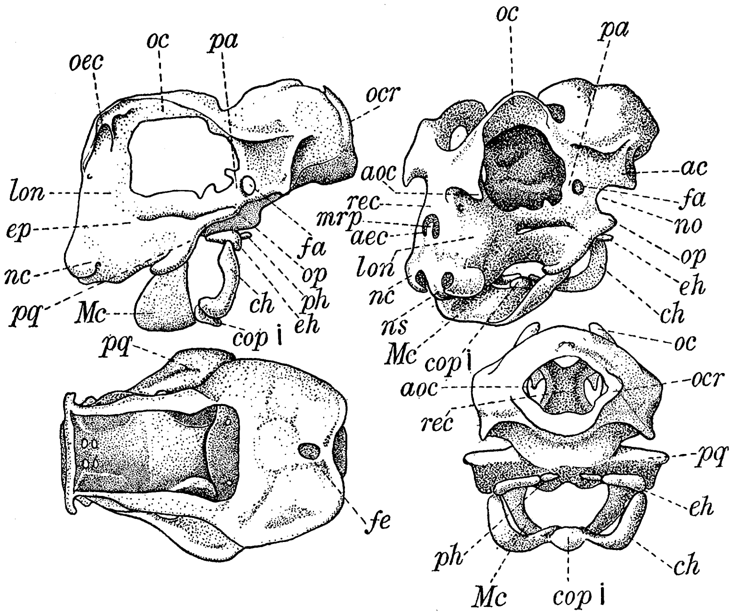


FIG. 2—Views of wax model of skull of 6-months embryo of *Chimæra colliei*, after BASHFORD DEAN, redrawn and labelled.

process is only feebly developed and represented by a part of the subocular shelf, it is probable that the major part of the basal connexion in *Callorhynchus* is formed by the basal process.

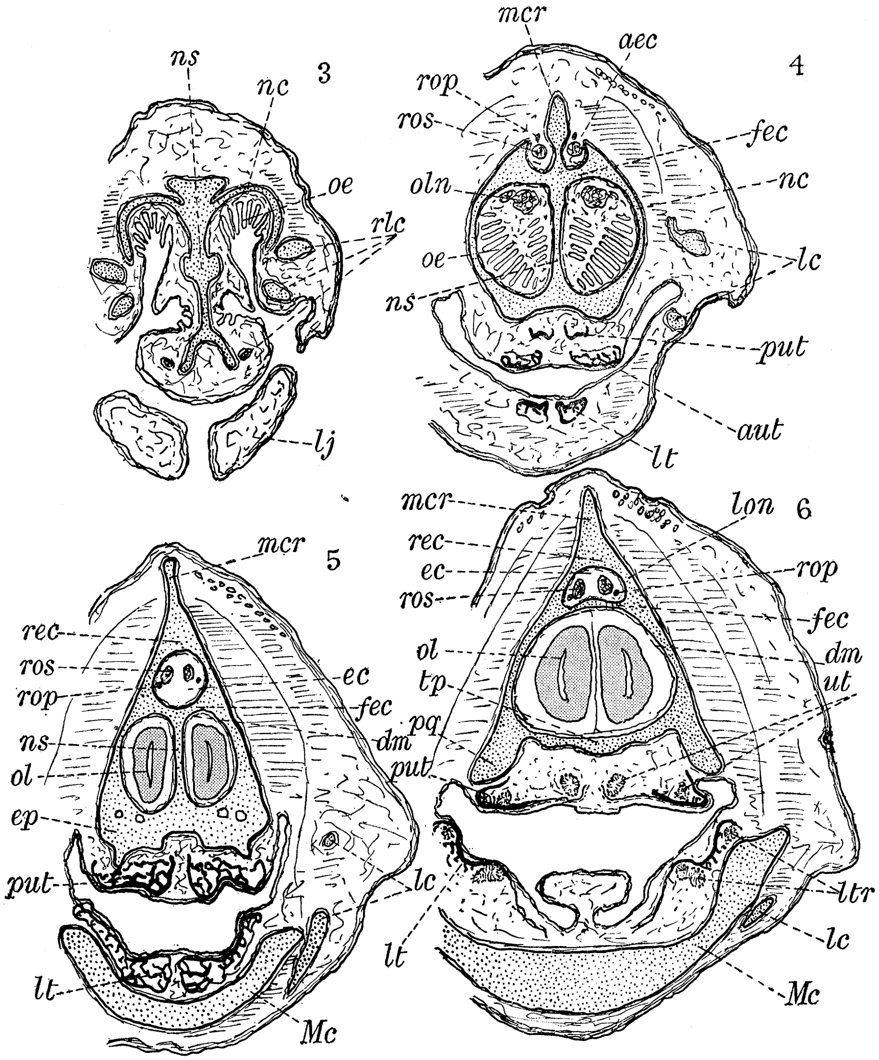
In most forms which possess both otic and basal connexions there is an open passage—the cranio-quadrate passage (Goodrich, 1930)—between the neurocranium and the pterygo-quadrate, and through this passage the palatine and hyomandibular branches of the facial nerve run downwards, the vena capitis lateralis runs backwards, and the orbital artery runs forward.

In *Callorhynchus*, the two foramina which transmit, the one, the palatine nerve and the orbital artery, the other, the hyomandibular nerve and the vena capitis lateralis, are separated by a short region of fusion between the pterygo-quadrate and the neurocranium. As a result, the cranio-quadrate passage is divided into two, and is therefore not easily recognizable at first sight. Its true morphological relations are, however, typical; and the cartilage, which thus divides it in two, bears all the relations of a post-palatine commissure, which is of wide occurrence in other forms.

Attention must now be turned to the relations of the efferent pseudobranchial artery. This artery, which represents the dorsal portion of the original mandibular vessel (de Beer, 1924, *b*), is of interest because of the difference in relations which it shows in Selachii and in Teleostomi. In the latter group the efferent pseudobranchial artery runs dorsally and inwards beneath the pterygo-quadrate, and then runs *underneath* (ventrally to) the trabeculæ to join the internal carotid artery just as it enters the cranial cavity through the hyophysial fenestra. In the Selachii, on the other hand, the efferent pseudobranchial artery again passes ventromedially to the pterygo-quadrate, but it then runs *above* (dorsally to) the trabecula and thus enters the cranial cavity independently and from the side, before joining the internal carotid (Allis, 1923, *a*; de Beer, 1924, *b*).

It is therefore of interest to find that in *Callorhynchus* the relations of the efferent pseudobranchial artery are similar to those shown by Selachians. The only differences are matters of detail, and concerned with the facts that in *Callorhynchus*, (i) there is no pseudobranch (doubtless connected with the early closure of the spiracle), (ii) the internal carotid arteries are completely aborted and do not even enter the skull (presumably consequent on (i), since there is now no interruption to the flow of blood in the efferent " pseudobranchial " artery, which in Holocephali thus furnishes the sole supply of blood to the brain); and (iii) the arteria ophthalmica magna is absent.

In the Holocephali therefore, owing to the extensive fusion of the pterygo-quadrate with the brain-case, the efferent pseudobranchial artery as it runs upwards finds itself caught in between the pterygo-quadrate and the trabecular plate, and passes through a canal. On the median side of this canal there is a small opening through which a branch of the efferent pseudobranchial artery runs inwards, ventrally to the trabecula, towards the subcranial hypophysial sac. This median opening of the canal is formed by a short discontinuity between the pterygo-quadrate and the trabecula, on the ventral side of the efferent pseudobranchial artery. The upper opening of the canal leads into the orbit, fig. 9, but the artery immediately penetrates the dura mater and enters the cranial cavity; its passage through the orbit, which is lengthy in Selachians, is thus extremely short in Holocephali.



FIGS. 3-6—Selected transverse sections through 95 mm *Callorhynchus*. (3, section 61, 2, 9; 4, section 59, 4, 4 ; 5, section 57, 3, 4 ; 6, section 54, 1, 3.)

With regard to the blood-vessels of *Callorhynchus* in general, a comparison of our fig. 1 with ALLIS' (1912) fig. 1 showing the branchial vessels in *Chimæra*, reveals a general similarity between the two fish. In one respect, however, they show an interesting difference. PARKER (T. J., 1886), in describing the vessels of *Callorhynchus*, showed that there is only one efferent artery in each branchial arch in this form, which we can confirm. This condition is, however, not constant in Holocephali, for in *Chimæra*, ALLIS (1912) has shown that there are two efferent arteries in each branchial arch, much as in Selachians. We have, however, found that in the ventral part of the branchial arch in *Callorhynchus* there is a tendency for the efferent artery to fork, and it is possible that the condition in *Callorhynchus* should be regarded as a secondary simplification from that which is found in *Chimæra* and throughout the Selachians.

From what has already been said it should be clear that the morphological relations of the pterygo-quadrate in Holocephali are quite typical and similar to those found in Selachians; the apparent differences are due to the topographical distortion brought about by the anterior position of the mouth and small gape of the jaw, and by the extensive fusion of the pterygo-quadrate with the brain-case. These are specializations not without parallel in other forms.

The morphology of the pterygo-quadrate in Holocephali is therefore clear; unfortunately the same cannot be said of its embryology. Neither our specimen nor the older (85 mm) one described by SCHAUINSLAND (1903, fig. 124) gives any clue to the method of origin of the pterygo-quadrate. SCHAUINSLAND'S younger (60 mm) specimen, reproduced in fig. 16, shows the ethmoid and otic fusions already present, but the intermediate region of the pterygo-quadrate is still for a considerable distance free from the neurocranium, leaving a large gap through which the palatine and hyomandibular nerves, the orbital artery, and the vena capitis lateralis must pass, though he does not indicate them.

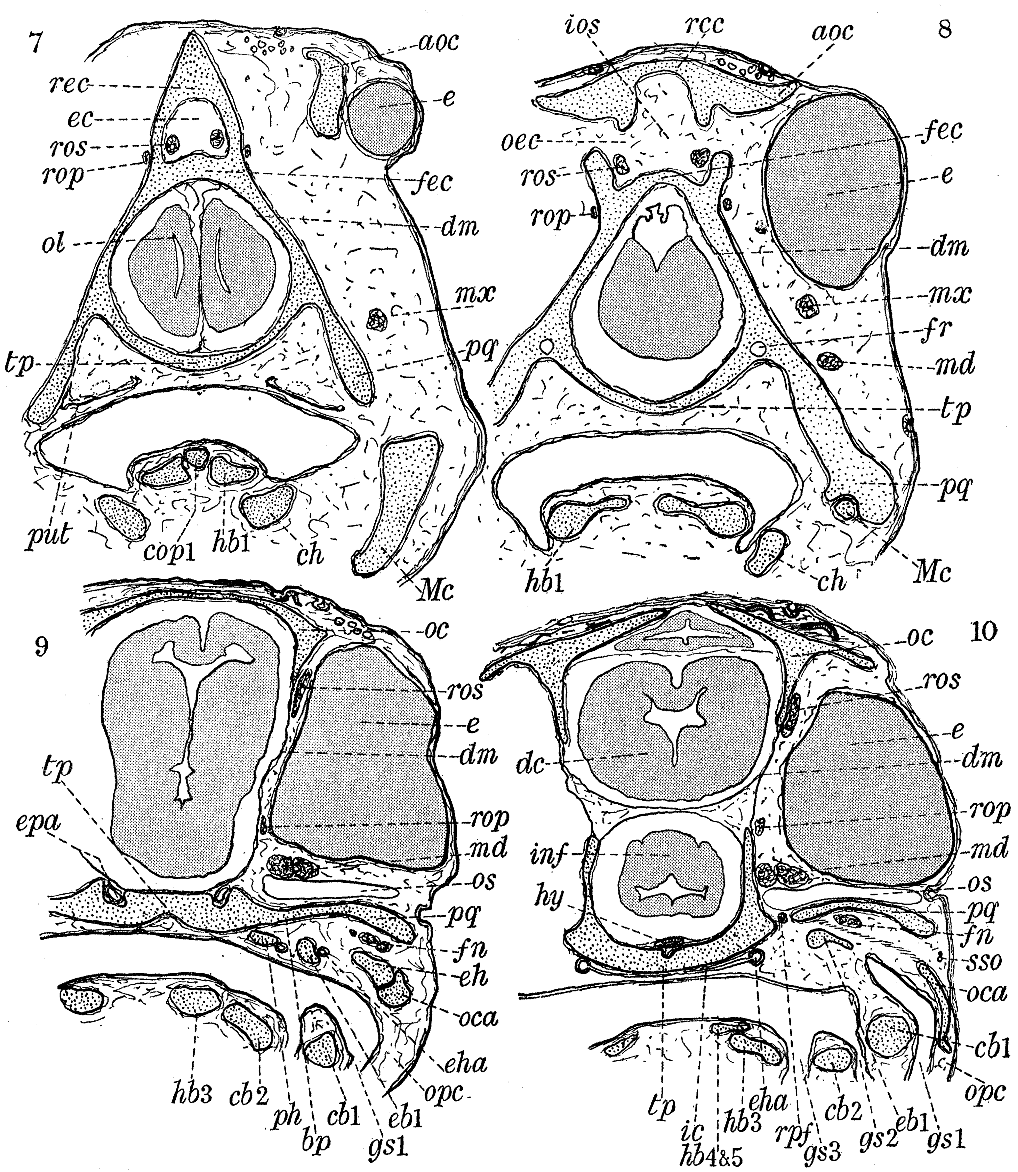
DEAN (1906) reconstructed the chondrocranium of a 6 months' embryo of *Chimæra* and figures it (fig. 84). Unfortunately, it is very sparsely labelled, and no indication is given of the relations of the neighbouring blood-vessels and nerves. From what we now know of these relations in *Callorhynchus*, and from a comparison of DEAN'S figure with adult specimens, it is, however, possible to identify a number of structures, and we have accordingly redrawn DEAN'S figures, fig. 2, and labelled them as fully as we are able.

While agreeing in general lines with *Callorhynchus*, DEAN'S specimen of *Chimæra* shows a deep notch immediately ventral to the foramen antoticum, in the position where the otic process of *Callorhynchus* stretches back to join with the auditory capsule. It looks, therefore, as if in *Chimæra* at this stage, the otic process were still incompletely chondrified.

ii—*The Skeleton of the Hyoid Arch*

In the skeleton of the hyoid arch, HUBRECHT (1877) found three cartilages on each side, which SCHAUINSLAND (1903) identified as pharyngohyal, epihyal, and ceratohyal elements; these elements corresponding serially to the pharyngobranchials, epibranchials, and ceratobranchials behind them. The interest of this state of affairs is clear, for if SCHAUINSLAND is right, then the Holocephali present a case of a hyoid arch skeleton which is scarcely if at all modified from the condition of the branchial arches, and in respect of the hyoid arch they would be the most primitive living Gnathostomes known.

Careful contemplation of Schauinsland's figures, however, raised the possibility of a doubt, for he shows this pharyngohyal in contact with the first epibranchial. Might it be, therefore, that his pharyngohyal is really the first pharyngobranchial, his first pharyngobranchial really the second, and so on? Without indication of the relations of the neighbouring blood-vessels and nerves it is impossible completely to dispel this doubt from Schauinsland's work, and we accordingly investigated the matter in our specimen of *Callorhynchus*.



Figs. 7-10—Selected transverse sections through 95 mm *Callorhynchus*. (7, section 50, 3, 3; 8, section 48, 1, 1; 9, section 35, 2, 3; 10, section 29, 2, 2.)

The reconstruction shown in fig. 1 proves without doubt that Schauinsland was right, and that his pharyngohyal is rightly so called. In the first place, the pharyngohyal here does not quite touch the first epibranchial, and so there is no reason to suspect the pharyngohyal of being an element belonging to the first branchial arch. Secondly, a comparison of the relations in *Callorhynchus* with those in a Selachian such as *Heterodontus* (DE BEER, 1924, *a*, fig. 7) shows that there is a close correspondence, the only difference (apart from topographical distortions) being that in *Heterodontus*, the pharyngohyal is absent and the epihyal-hyomandibula is so large that it touches the auditory capsule. It is to be noticed that the skeleton of the hyoid arch is very similar to that of the branchial arches behind it; so similar indeed as to make it almost impossible to imagine that the hyoid arch in Holocephali is other than primitive.

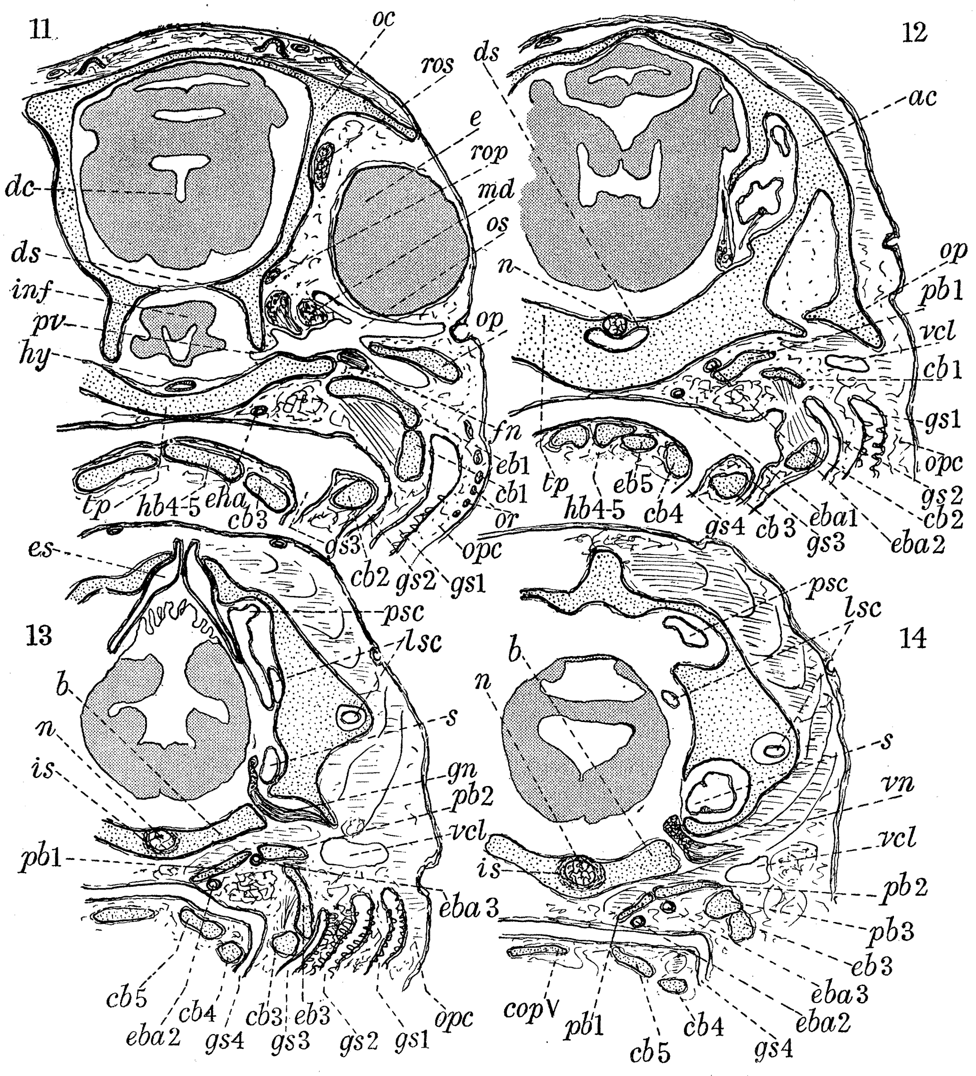
It may seem surprising that it should be the epihyal and not the most dorsal element of the hyoid arch which in Selachians and all other Gnathostomes becomes the hyomandibula or columella auris, and reaches the auditory capsule. The explanation is doubtless that given by ALLIS (1915), viz., that the dorsal ends of the pharyngeal elements converge towards the middle line beneath the vertebral column and skull, and that their ventral ends articulate not with the dorsal ends but with the posterior edges of their respective epal elements; the dorsal ends of the latter are therefore free to extend upwards. An example of this in the first branchial arch is seen in the sturgeon (DE BEER, 1925, fig. 14).

The primitive nature of the hyoid arch in Holocephali must be taken as evidence that in their lineage the hyoid arch skeleton never assumed a suspensorial function as in amphistylic or hyostylic forms, for this would have entailed the loss of the pharyngohyal and the specialization of the epihyal as in Selachians. A return from the hyostylic or amphistylic condition to that of the Holocephalian is most unlikely. At the same time, the presence of an otic process in Holocephali proves that this structure was already in existence before the epihyal-hyomandibula became suspensorial. The existence of the pharyngohyal in Holocephali is therefore supported by the results of this paper. It entails certain important consequences, however, which are referred to below (p. 308).

iii—*The Ethmoidal Canal*

A glance at transverse sections through the anterior region of the Holocephalian skull reveals the presence, figs. 4–8, of a canal, the ethmoidal canal, the relations of which are by no means clear. The ethmoidal canal is continuous posteriorly with a space which opens into the orbit on each side. This space which we propose to call the interorbital space is dorsal to the dura mater, and therefore strictly extracranial, although it is covered over by a cartilaginous roof. It may here be noted that the skull in the adult Holocephalian has a large and high interorbital septum, dorsal to the brain-case. At the stage here studied, however, and in those studied by SCHAUINSLAND and DEAN, the interorbital septum has not yet been formed, and the eyes are still widely separated, with the brain between them, figs. 8, 9, 10. As the roof of the skull gets lifted higher and higher the interorbital space will become compressed from side to side.

The interorbital space, then, leads into the hinder part of the ethmoidal canal (which, like it, is strictly extra-cranial), and gives passage to the superficial ophthalmic nerve, which runs forwards in the ethmoidal canal. A little further forward, the ophthalmicus profundus nerve leaves the orbit and enters the ethmoidal canal by piercing the cartilage of its side wall. Both superficial and profundus nerves then run forwards within the ethmoidal canal to its anterior opening, through which they emerge on to the snout.



FIGS. 11-14—Selected transverse sections through 95 mm *Callorhynchus*. (11, section 26, 2, 3; 12, section 21, 1, 3; 13, section 10, 1, 3; 14, section 6, 1, 3.)

Throughout its length, the ethmoidal canal is dorsal to the anterior part of the cranial cavity containing the forebrain, and to the cavity of the nasal capsules, and separated from them by a cartilaginous floor which at this stage is complete, figs. 5, 6, 7, and 8.

In attempting to provide a solution of the problem presented by the ethmoidal canal, ALLIS (1917, 1926) put forward the view that this cartilaginous floor to the ethmoidal canal, which forms at the same time a roof above the forebrain, is the product of the trabeculæ, and he stated that the outlines of the ethmoidal canal (or chamber) " as seen in median vertical longitudinal section, strongly suggest that the (ethmoidal) chamber and the posterior portion of the entire cranial cavity were once continuous, and have been separated from each other by the coming together of the orbits above the forebrain. If this be so, the trabeculæ would form the roof of the forebrain chamber, and not its floor." This strange view then entails further hypotheses concerning the cartilaginous floor upon which the forebrain rests, and this ALLIS thinks may represent the pterygo-quadrates fused in the middle line, possibly together with " intertrabecular tissues."

We know, however, of no acceptable evidence in favour of such an interpretation, nor of any valid reason why the Holocephali should depart so extraordinarily from the general morphological plan, which holds in all other vertebrates. It would be necessary to assume that the forebrain comes to lie in a space which extends down between the trabeculæ, and somehow gets into communication with the nasal capsules *ventrally* to the trabecular plate ; on the other hand, ALLIS' original forebrain chamber, the ethmoidal canal, is not lined by the dura mater at all, and the superficial and profundus ophthalmic nerves pass through it ; these nerves are not to our knowledge found running through any part of the cranial cavity in any vertebrate. ALLIS is moved to propose this most extravagant hypothesis because of the relations of the nasal septum and nasal capsules. In order to avoid having to regard these structures in Holocephali as dorsal to the trabecular plate, he makes the trabeculæ bend upward and form the floor of the ethmoidal canal, with the nasal septum and nasal capsule beneath them.

In addition to the intrinsic objections to ALLIS' hypothesis, we have two further grounds for rejecting it. One is that we do not hold the premises from which he starts in regard to the morphology of the trabeculæ to be sound ; the other is that the conditions in Holocephali can be explained, as we believe, more simply and more satisfactorily, on another view, to which we now turn.

The Selachians are the nearest relatives of the Holocephali, and the interpretation of the conditions in the latter can be found in a consideration of the relations of the ophthalmic nerves in the former.

The profundus nerve transverses the orbit (even in *Scyllium* where, as YOUNG (1933) has shown, it is often present although reduced) and pierces the cartilaginous anterior wall of the orbit. Morphologically (DE BEER, 1931), the point of entry represents the original gap (orbitonasal fissure) between the lamina orbitonasalis (hind wall of the nasal capsule) and the true side wall of the skull (preoptic root of the orbital cartilage). As in other forms, however, the profundus nerve never really enters the cranial cavity since it always lies outside the dura mater (*cf.* mammals, and the passage of the nerve through the supracribrous recess, DE BEER, 1929). For a distance which varies in different forms, the profundus runs forward in this position and emerges again through the cartilage by an epiphanial foramen on to the dorsal surface of the nasal capsule.

The superficial ophthalmic nerve leaves the orbit by a foramen distinct from that of the profundus, and which represents the gap between the supraorbital cartilage and the true side wall of the skull. The superficial ophthalmic then finds itself directly on the dorsal surface of the nasal capsule.

The position of the lamina orbito-nasalis is also indicated by the so-called orbito-nasal canal (GEGENBAUR) through which a branch of the facial vein leaves the orbit and runs through a space (termed by ALLIS (1913) the ectethmoidal chamber) to reach a point ventral and median to the nasal capsules. The exact relations of the ectethmoidal chamber vary in different Selachians, but the position of the orbitonasal canal can be relied on as a fixed point, marking the line of attachment between the lamina orbitonasalis and the side wall of the skull. In *Callorhynchus* the orbitonasal canal is present, and transmits a branch of the facial vein in the typical manner.

Another point to notice in Selachians is the universal existence of an unchondrified portion of the roof of the skull in the anterior region, forming a prefrontal or epiphysial fontanelle, or fenestra præcerebralis (ALLIS, 1923, *b*), beneath which the epiphysis is to be found. [In some forms, *e.g.*, *Squalus*, a small epiphysial or pineal foramen is separated off by cartilage from the large prefrontal fontanelle.]

An attempt to depict these relations is given in fig. 15, A.

Now, in Holocephali, the ophthalmic nerves leave the orbit by two foramina (on each side) which have every appearance of being homologous with those in Selachians. Only, instead of emerging freely on to the dorsal surface of the nasal capsules, these nerves here find themselves enclosed in the ethmoidal canal. The latter, then, must represent an originally external space, which has been secondarily roofed over. Why this should have occurred, we are not in a position to give a complete answer, but we can point to a certain typical Holocephalian modification with which the conditions now under discussion must have been concerned—we refer to the development of the interorbital septum. The formation of this structure in Holocephali above the brain results in a lifting up of the roof of the skull to an extent that is quite remarkable. One result of this has been to produce an upward distortion of the lamina orbitonasalis ; this structure in Selachii forms the hind wall of the nasal capsule ; in Holocephali the nasal capsules have no cartilaginous hind wall at all for they are directly continuous by wide apertures with the anterior part of the cranial cavity. The lamina orbitonasalis, here, therefore is displaced dorsally and forms the side wall of the ethmoidal canal as well as the side wall of the nasal capsule. A careful consideration of SCHAUINSLAND's younger stage, reproduced here in fig. 16, will show how the lamina orbitonasalis comes to flank the ethmoidal canal. At this stage the foramina for the superficial and profundus nerves are not yet enclosed, they leave the orbit through a triangular gap between the lamina orbitonasalis, the supraorbital cartilage, and the orbital cartilage.

Another effect of the formation of the interorbital septum is seen by considering what would happen if the skull still possessed the large open and unchondrified epiphysial fontanelle of Selachii. The fontanelle would then point forwards, and by an increasingly wide gap would give vulnerable access to the brain-cavity behind. It is presumably as a measure of increased mechanical security for the skull with its lifted roof that the ethmoidal canal becomes roofed over. But the distinction between this secondary roofing and the true roof of the skull is shown by the persistence up to a certain stage in *Callorhynchus* (fig. 15, C, after SCHAUINSLAND's fig. 125) of what is really a pineal foramen, overlying the epiphysis, and which represents a part of the original epiphysial fontanelle. It may also be noticed that

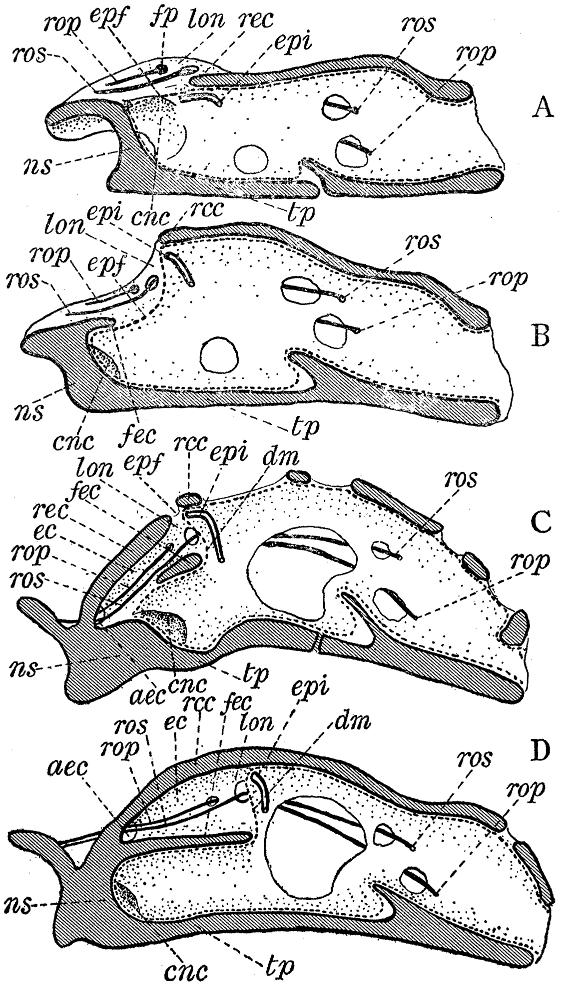


FIG. 15—Diagrams illustrating the morphology of the ethmoidal canal in Holocephali. The observer is looking at the median sagittal cut surface of the right half of the skull, anterior end to the left. A, typical Selachian; B, hypothetical intermediate stage, in which the roof is beginning to rise; C, *Callorhynchus* (early stage, after SCHAUINSLAND) in which the epiphysial fontanelle is still open; D, typical adult Holocephalian with fully formed ethmoidal canal.

while the true roof of the skull is closely associated with the dura mater, the roof of the ethmoidal canal is not.

At later stages in *Callorhynchus* (our specimen) and in *Chimæra* (fig. 15, D, after Allis), the pineal foramen is occluded and the roof of the ethmoidal canal complete as far forward as its anterior opening (paired), where the ophthalmic nerves run out on to the dorsal surface of the nasal capsule, passing laterally to the rostral processes. The position of the original epiphysial fontanelle now follows a curved line, along the anterior part of which the floor of the ethmoidal canal is formed. This floor represents an extension backwards of the cartilage which forms the roof of the nasal capsules, as we have attempted to show in a diagram (fig. 15, B) of a hypothetical intermediate stage.

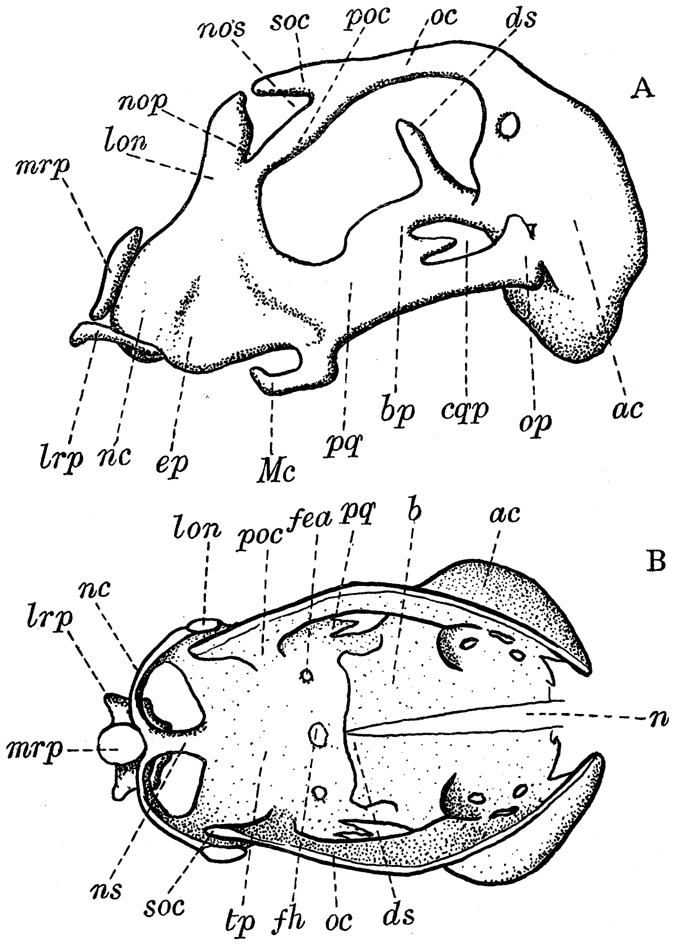


Fig. 16—Views from the left side (A) and from the dorsal side (B) of an embryo of *Callorhynchus* 60 mm long, after Schauinsland, redrawn and labelled.

There is then no reason to postulate far-reaching and fundamental changes in the morphology of the trabeculæ, *etc.*, in order to account for the Holocephalian ethmoidal canal; it is an originally external space; its side walls are formed from the laminæ orbitonasales ; its floor from an extension backwards of the roof of the nasal capsules ; its own roof is a new formation ; it occupies the position of the epiphysial fontanelle in Selachii. Indeed, in spite of the apparent differences, one cannot but be struck by the strong fundamental similarity between Selachii and Holocephali. It is even possible, as ALLIS (1917) suggests, that the medial and the paired lateral rostral processes of Holocephali may correspond exactly to the three limbs of the rostral basket found in Scylliidæ and other Selachians.

If we now turn to the reasons which led ALLIS to regard the trabeculæ in Holocephali as forming the roof instead of the floor of the forebrain cavity, it seems that his view is a consequence of his regarding the nasal septum in Selachii as lying ventrally to the united trabeculæ, whereas the nasal septum in other forms lies dorsally to them. Further (ALLIS, 1913, 1917) he interprets certain descriptions of the development of the ethmoid region of the skull in different forms to mean that the so-called trabecular horns (cornua trabecularum) in Selachii grow dorsally between the nasal sacs instead of laterally beneath the nasal sacs as in other forms. Here we cannot agree with him. After having had the opportunity of studying the development of this region of the skull in all groups of vertebrates we are of opinion that the Selachii form no exception. However, the question of the trabecular horns is in a confused state owing to the fact that PARKER (1878) applied this term to more than one structure. We have accordingly thought it advisable to make a short digression from the Holocephalian skull in order to record our observations on this subject.

iv—*The Trabecular Horns*

In fig. 16, A is shown a ventral view of the ethmoid region of a skull of *Scyllium* (45 mm), omitting the nasal cartilage but including the nasal sac, with its inhalant and exhalant apertures almost separated from one another by a flap (frontonasal process) which projects backwards and outwards.

The median rostral cartilage represents the fused anterior prolongation of the trabeculæ, and gives rise to the nasal septum from which a trabecular horn projects outwards on each side, and on a level with the ventral surface of the rostrum. The trabecular horns are not very long, and they end freely, pointing towards the flaps of the frontonasal processes. To each trabecular horn, near its outer extremity, the anterior wall of the nasal capsule is attached.

The hind wall and part of the side wall of the nasal capsule is formed by the lamina orbitonasalis or planum antorbitale, and the capsule has no cartilaginous floor at all. The junction between the lamina orbitonalis and the side wall of the skull is marked by the foramina for the profundus nerve and for the orbitonasal vein.

Turning now to the conditions (fig. 16, B) which may be taken as typical for all Tetrapods as regards general morphology, the trabecular horns are seen to occupy a position precisely comparable with that in which they are found in Selachii. The relations of the planum antorbitale are also exactly the same, and, indeed, all that is needed to convert the Selachian type into the Urodele is an extension of the trabecular horn to meet and fuse with the ventral edge of the side wall of the nasal capsule. In this way the trabecular horn gives rise to a solum nasi or lamina transversalis anterior, such as is found not only in Amphibia, but also in Reptilia and Mammalia, separating the fenestra narina from the fenestra basalis (or choanalis). A similar conclusion has been arrived at by Allis (1923, *b*), but the conditions in *Chlamydoselachus*, which he studied, are slightly different, and the nasal fontanelle which he shows in this fish, behind the fusion between the trabecular horns and the lamina orbitonasalis (solum nasi) does not serve for the passage of the excurrent aperture of the nasal sac. The point to notice here is that the relations in Selachians of the trabecular horns, and presumably of the trabeculæ, show no departure from the type which is found throughout the remaining vertebrates: viz., they are situated morphologically ventrally and not dorsally to the nasal septum and capsules. There is no reason, therefore, to suspect the existence in Holocephali of so fundamentally exceptional a state of affairs, although the nasal capsule in these forms is much modified, and it looks as if the trabecular horns had here been suppressed.

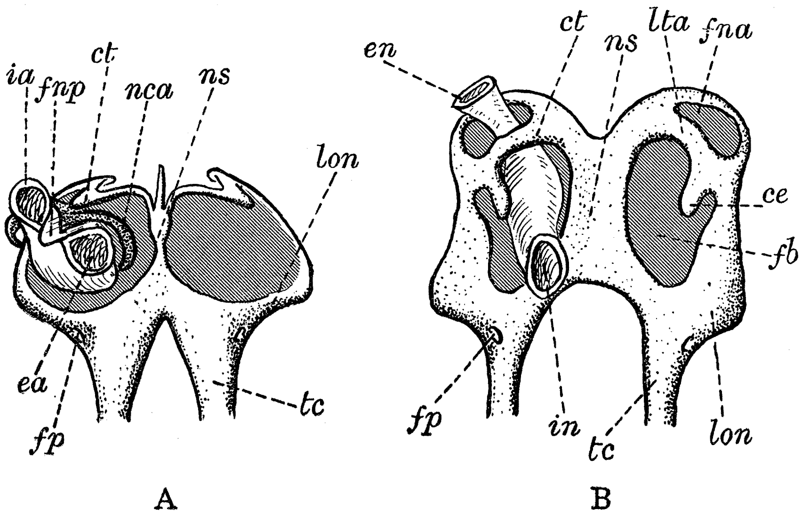


Fig. 17—Ventral views of the anterior region of the chondrocranium in A, *Scyllium* (45 mm), and B, generalized Tetrapod (valid for Urodela, Lacertilia, and Mammalia), to show the morphological relations of the trabecular horns and the formation of the lamina transversalis anterior, separating external from internal nostril.

III—Palæontological Investigations

If it be true that the Holocephali are the most primitive living Gnathostomes, having holostylic jaw suspension, in which the hyomandibula plays no part, it is particularly important to examine the fossil evidence. The Holocephali have hitherto only been known for certain as fossils since the Lias, although it has been

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suggested that they have affinities with the Cochliodonts (SMITH-WOODWARD, 1932). The comparative lateness of the earliest fossils of such an archaic group is very surprising, but recently the discovery of new specimens of *Chondrenchelys problematica* (TRAQUAIR, 1888) from the lower Carboniferous of Eskdale, Dumfriesshire, has revealed characters in this fish which almost certainly relate it very closely to the Holocephali (MOY-THOMAS in a forthcoming work). The importance of *Chondrenchelys* in relation to the present work lies only in the suspension of its jaws, which is of the typical holostylic pattern. The palatoquadrate is fused to the neurocranium, and bears large tooth-plates, and the posterior lateral border of the orbit is bounded by the otic process, the eye being relatively very far posterior. *Chondrenchelys* therefore is the earliest fossil known with holostylic jaw suspension, and shows that this type was fully developed in the Lower Carboniferous.

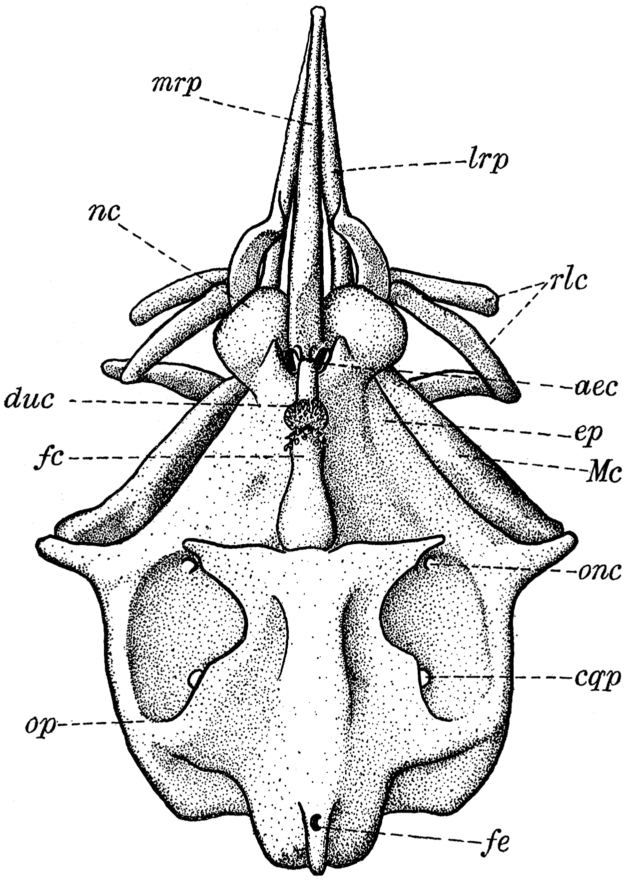

FIG. 18—Dorsal view of the skull of a male specimen of *Callorhynchus*. × ½.

The Jurassic Holocephali are essentially similar to modern forms, which is what would be anticipated in such a primitive group. The best known forms are the Liassic *Squaloraja* (AGASSIZ, 1833, RILEY, 1833, DAVIS, 1872, WOODWARD, 1886, REIS, 1895), *Myriacanthus* (EGERTON, 1872, WOODWARD, 1889), *Acanthorhina* (FRAAS, 1910), and *Ischyodus* (for references see DEAN, 1909), from the Lithographic Limestone. Of these fossils, *Squaloraja* is the best known. *Myriacanthus*, *Acanthorhina*, and *Ischyodus* differ hardly at all from modern forms, and the " hyomandibular " (otic process) has been described as being fused to the neurocranium. But in *Squaloraja*, SMITH-WOODWARD (1886) implies that this region is only fused posteriorly and is free anteriorly, a statement which has not subsequently been contradicted although it is figured fused by REIS (1895). *Squaloraja* is clearly the most important form in connexion with this work and we have therefore to give a brief redescription of its skull, based on the British Museum (Natural History) and Royal Scottish Museum specimens. Our new restoration, fig. 19, can be compared with a dorsal view of the skull of a male *Callorhynchus*, fig. 18, which proves very helpful in interpreting the conditions in *Squaloraja*.

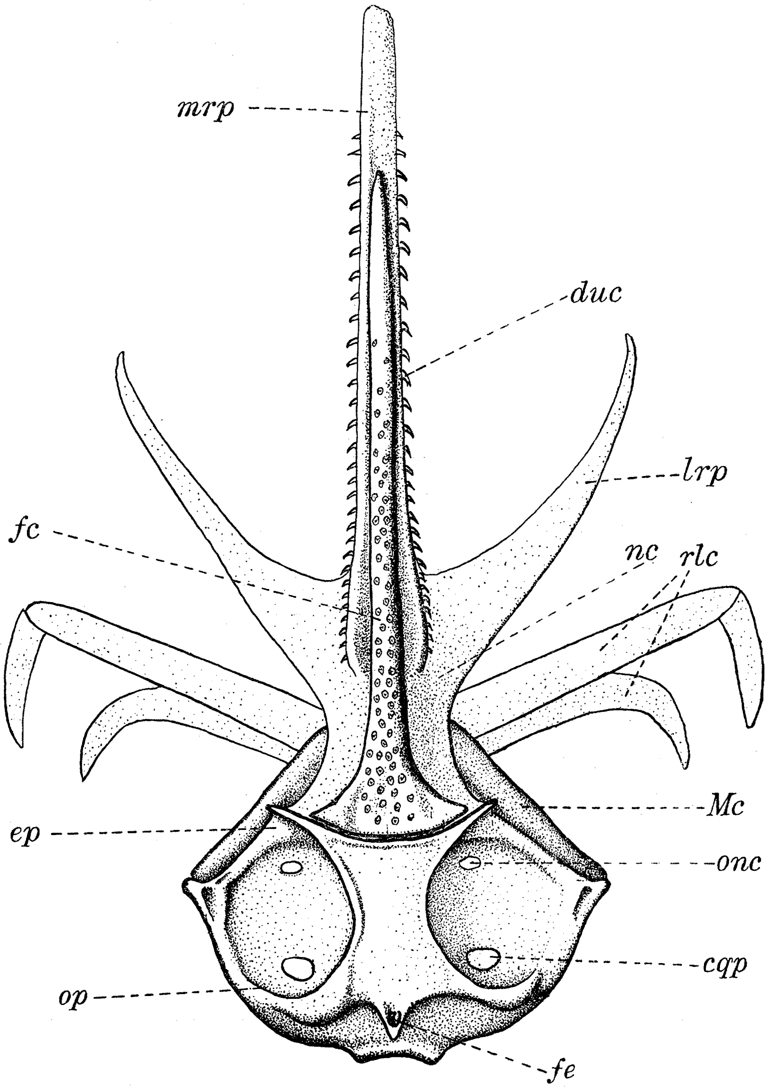

FIG. 19—Dorsal view of the skull of *Squaloraja*. × $\frac{3}{4}$.

The anterior part of the skull bears three elongated rostral processes, the median of which is overlain dorsally by the frontal " spine " or " clasper," and itself overlies the nostrils and nasal capsules. The frontal clasper bears small sharp denticles on the proximal part of its ventral surface, and the median rostral process has a row of similar denticles on each side, which are continued forward to a point just in front of the anterior end of the clasper. Thus there can be no doubt of the prehensile nature of the clasper, which must have worked in conjunction with the median rostral process. The denticles on the latter do not, therefore, fulfil the same function as those carried on the rostrum of the saw-fish, *Pristis* and *Pristiophorus*. The lateral rostral processes do not meet at a point as in *Callorhynchus*, but project out sideways, giving the skull greater broadness, a condition correlated with its dorso-ventral flattening and superficial Ray-like structure. The labial cartilages are placed in almost exactly the same position as those of *Callorhynchus*. The roof of the neurocranium is expanded laterally as in *Callorhynchus*. It is narrowest in the mid-orbital region, being broadened anteriorly to form a base for the frontal clasper. The roof ends posteriorly in a V-shaped prominence situated in the mid-line, pierced by the foramen endolymphaticum. This prominence is continued laterally into ridges behind each orbit. The posterior region of the skull is rounded off and ends in a well-marked concave occipital condyle.

The posterior margin of the orbit is bounded by the otic process (" hyomandibular " of Smith-Woodward) which is continuous with the back of the neurocranium, and with the anterior margin of the orbit. The appearance of a free anterior end to the " hyomandibular " is due to its having a small lateral prominence bearing an articular surface for the lower jaw. The inner side of this otic process passes, however, without a break into the anterior or ethmoid portion of the pterygo-quadrate and into the side of the neurocranium with which it is fused.

The orbit thus has a complete floor which can be seen to be pierced by two foramina : an anterior orbitonasal foramen, and a posterior cranio-quadrate passage. These foramina are fortunately recognizable in the fossils by the upraised rims that surround them.

It is clear that the holostylic type of attachment of the pterygo-quadrate was already in existence in the Carboniferous (*Chondrenchelys*), was well represented in the Jurassic (*Squaloraja* and others), and differed not at all from the conditions in living Holocephali.

Unfortunately we have not been able to study the skeleton of the hyoid arch directly in the fossils, but the condition of the pterygo-quadrate in these early Holocephali enables us to say that as far back as the Carboniferous there is no reason to believe that it differed from the condition at the present day, and there is the strongest presumption that the hyomandibula had no suspensorial function. If it had had such a function and had lost it in the living forms, it is reasonable to suppose that some trace of this would be found in the fossil history. But as we find nothing of the kind, the presumption is that in the Holocephali the skeleton of the hyoid arch never had a suspensorial function.

Note on tooth-plates—Owen (1845) suggested that the Holocephalian tooth-plates were formed by the fusion of simple teeth set horizontally on the jaws, and growing forwards. While we have nothing to add in respect of this interpretation at present, we hope to have the opportunity of studying this problem when suitable material becomes available.

IV—Discussion

The conclusion to which we have been driven, viz., that in the Holocephali the skeleton of the hyoid arch is primitive, non-suspensorial, and necessitates far-reaching revision of our conceptions of the phylogeny of fishes.

In the first place, it is necessary to establish the close nature of the affinity between the Holocephali and the Selachii. A striking similarity between these two groups is provided by the histological picture presented by sections. The staining reactions of the tissues, the size of the cells, the nature of the cartilage, the passage of the efferent pseudobranchial artery dorsal to the trabeculæ, the structure of the membraneous labyrinth, the open ductus endolymphaticus, and numerous other features, impress the observer with the closeness of the affinity between these two groups. In fact, one is quite surprised by the magnitude of the differences of detail which separate them, by means of variations on a common fundamental plan. Not the least interesting feature of these differences is the extraordinary medley of primitive and specialized characters which they involve.

Chief among the primitive features of the Holocephali is the presence of a pharyngohyal element in the hyoid arch, which seems to point to the conclusion that their ancestors never were amphistylic or hyostylic (see above, p. 294).

A primitive feature shown by the Holocephali is the complete cartilaginous floor to the auditory capsule; the glossopharyngeal nerve does not traverse the cavity of the capsule, and there is no lamina hypotica such as exists in Selachians (de Beer, 1931). The otic and basal connexions of the pterygo-quadrate must have been inherited from the non-fused autostylic* or *autodiastylic* common ancestor which Holocephali shared with Selachians. The Holocephali have departed from what

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* The term "autostylic," as one of us has remarked (de Beer, 1931), admits of a certain ambiguity, for while it is commonly applied to forms in which the jaw is fused to the brain-case, it may also be held to mean merely that the hyoid arch plays no part in the suspension, regardless of whether the attachment of the palatoquadrate to the brain-case by its own processes takes the form of apposition only, or of cartilaginous fusion. The latter, wider connotation, appears to be the more proper use of the term, and we may therefore regard as autostylic all Gnathostomes which are neither amphistylic nor hyostylic. (See Goodrich, 1930.)

However, since the non-fused type of attachment is certainly more primitive than the fused, it will obviously be convenient to have a terminology which distinguishes between them. Within the autostylic type, therefore, we may (on the analogy of diarthrosis and synarthrosis) propose *autodiastylic* for the non-fused type possessed by ancestral Elasmobranchs and the Amniote line; *autosystylic* for Dipnoi and Amphibia; while Gregory's term holostylic describes the special autostylic condition found in Holocephali.

must have been the primitive condition by converting these connexions into permanent cartilaginous fusions, thus becoming what Gregory (1904) has called holostylic. Further specializations are the formation of the interorbital septum and ethmoidal canal and the breakdown of the median wall of the auditory capsule. None of these specializations is to be found in Selachians. Nevertheless, in spite of the shiftings and distortions which the Holocephalian's structure must have undergone, they conform closely to the general plan of morphological relations as found in Selachii.

It is at this point of the discussion that a matter of prime importance arises. The conditions found in Holocephali and the close affinity between the latter and the Selachii, suggest that the Selachii are descended from ancestors in which the hyomandibula was not suspensorial, and that the amphistylic and hyostylic conditions evolved within that group. The hyostylic conditions in Selachians must therefore have been evolved independently of the so-called hyostylic condition in Teleostomes; a view which Allis (1918) put forward and which has been favourably considered by Schmalhausen (1923). In this connexion it is important to note that the hyomandibula has different relations to neighbouring blood-vessels and nerves in Selachii and in Teleostomes, and while one of us (de Beer, 1924, *b*, 1925, 1926, *b*) has endeavoured to show that a transition from the one type to the other was not impossible, the evidence could not show that such a transition *did* occur, and is equally consonant with the view, now forced on us by other considerations, that the hyomandibula assumed suspensorial functions independently in Selachii and in Teleostomi.

We are therefore confronted with the picture of a group of fish ancestral to Holocephali and Selachii living in Devonian times, with the autodiastylic type of jaw suspension, and a primitive non-suspensorial hyoid arch skeleton. It now becomes necessary to consider the question of the relationships of this primitive Elasmobranch group to the other types of fish then in existence.

In the Acanthodians, Jaekel (1927) has described an autodiastylic jaw suspension, and the presence of pharyngohyal and epihyal elements in the hyoid arch. In this respect, therefore, the Acanthodians agree with the primitive Elasmobranch group.

Stensiö (1925) expressed the opinion that the Arthrodira were related to the Holocephali, for the reasons that: (i) there is a cranio-vertebral joint; (ii) an operculum of some kind is present; (iii) dentition is similar; (iv) there is a dorsal extension of the pelvic girdle; (v) the general shape of the body is similar, as are (vi) certain characters of the arterial system. To these resemblances, Stensiö (in Säve-Söderbergh, 1934; and 1934) has recently added the following: (vii) the presence of the basal angle; (viii) the direction and shape of the nasal capsule and apertures and the shape of the face; (ix) the form of the anterior part of the cranial cavity; (x) the relations of the biting elements to the endoskeleton; (xi) the rigid fusion in *Pholidosteus* of the palatoquadrate with the neurocranium, in a manner suggestive of the holostvlic suspension of Holocephali.

Further evidence of the Elasmobranch-like shape of the Arthrodira, particularly in respect of the pectoral fin, is presented by Gemündina and Stensiöella (Broili, 1930, 1933).

Stensiö and others have contended that the Elasmobranchs were originally probably heavily armoured, as indeed were the Arthrodira and Cratoselache (Smith-Woodward, 1924), this condition having been gradually lost in later forms. In Holocephali, the dermal plates found in Myriacanthus may therefore be traces of this armour. A progressive loss of bone in the neurocranium of Arthrodires between the Lower and Upper Devonian has been demonstrated by Stensiö (1934).

If it could only be shown that the jaw suspension of Arthrodira was autodiastylic, a good case would have been made out for the existence of an extensive pre-Elasmobranch group from which Acanthodians, Arthrodira, Selachii, and Holocephali could be derived. It may be noted therefore that the Holocephali living to-day, with their non-suspensorial hyoid arch, are the only survivors of this group to have kept this character, and in spite of their specializations in other directions, they must be regarded as representatives of the most primitive living Gnathostomes.

V—Summary

1. In Holocephali—
    - i. a true otic process is present.
    - ii. the hyoid arch possesses pharyngohyal and epihyal elements and is the most primitive known in living forms.
    - iii. The ethmoidal canal is an extra-cranial space, secondarily roofed over in connexion with the formation of the interorbital septum.
    - iv. The auditory capsule has a complete cartilaginous floor, but an incomplete median wall.
2. In Selachii, the trabeculæ and trabecular horns conform to the general type.
3. A description based on new observations is given of the skull in *Squaloraja*.
4. The holostylic type of suspension is found as far back as the Carboniferous period.
5. The affinity between Holocephali and Selachii is close.
6. The suspensorial function of the hyomandibula has been evolved independently in Selachii and in Teleostomi.
7. The possible affinities between Holocephali, Acanthodians, and Arthrodira are discussed.

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VII—Explanation of Lettering

ac, auditory capsule.
aec, anterior opening of ethmoidal canal.
aoc, preorbital cartilage.
apa, afferent pseudobranchial artery.
aut, anterior upper tooth-plate.
b, basal plate.
bp, basal process.
cb 1–5, ceratobranchial of 1st–5th branchial arch.
ce, ectochoanal cartilage.
ch, ceratohyal.
cnc, cavity of nasal capsule.
cop I–V, copula, I to V.
cqp, cranioquadrate passage.
ct, cornu trabeculæ.
da, dorsal aorta.
dc, diencephalon.
dm, dura mater.
ds, dorsum sellæ.
duc, denticles underneath frontal clasper, on median rostral spine.
e, eye.
ea, excurrent aperture of nasal sac.
eb 1–3, epibranchial of 1st–3rd branchial arch.
*eba*1–4, efferent branchial artery of 1st–4th branchial arch.
ec, ethmoidal canal.
eh, epihyal.
eha, efferent hyoidean artery.
en, external nostril.
ep, ethmoid process.
epa, efferent pseudobranchial artery.
epf, epiphysial fontanelle.
epi, epiphysis.
es, endolymphatic sac.
fa, foramen antoticum.
fb, fenestra basalis.
fc, frontal clasper.
fe, foramen endolymphaticum.
fea, foramen for efferent pseudobranchial artery.
fec, floor of ethmoidal canal.
fh, hypophysial fenestra.
fn, facial nerve.
fna, fenestra narina.
fnp, frontonasal process.
fp, foramen for profundus nerve.
fv, foramen for vein.
gn, glossopharyngeal nerve.
*gs*1–4, gill-slit 1–4.
*hb*1–4, hypobranchial of 1st–4th branchial arch.
hf, hypoglossal foramina.
hy, hypophysis.
ia, incurrent aperture of nasal sac.
ic, internal carotid artery.
in, internal nostril.
inf, infundibulum.
ios, interorbital space.
is, invaded sheath of notochord.
lc, labial cartilages.
lj, lower jaw.
lon, lamina orbitonasalis.
lrp, lateral rostral process.
lsc, lateral semicircular canal.
lt, lower tooth-plate.
lta, lamina transversalis anterior.

ltr, lower tooth rudiments.
Mc, Meckel's cartilage.
mcr, median crest.
md, ramus mandibularis trigemini.
mrp, median rostral process.
mv, mandibular vessel.
mx, ramus maxillaris trigemini.
n, notochord.
nc, nasal capsule.
nca, nasal cartilage.
no, notch in position of cranioquadrate passage.
nop, notch for profundus nerve.
nos, notch for superficial ophthalmic nerve.
ns, nasal septum.
oa, orbital artery.
oc, orbital cartilage.
oca, opercular cartilage.
ocr, occipital arch.
oe, olfactory epithelium.
oec, posterior opening of ethmoidal canal.
ol, olfactory lobe.
oln, olfactory nerve.
on, oculomotor nerve.
onc, orbitonasal canal.
op, otic process.
opc, operculum.
or, opercular rays.
os, orbital sinus.
pa, pila antotica.
*pb*1–5, pharyngobranchial of 1st–5th branchial arch.
ph, pharyngohyal.
poc, preoptic root of orbital cartilage.
pq, pterygoquadrate.
psc, posterior semicircular canal.
put, posterior upper tooth-plate.
pv, pituitary vein.
rcc, roof of cranial cavity.
rec, roof of ethmoidal canal.
rhf, ramus hyoideus facialis.
rif, ramus mandibularis internus facialis.
rlc, rostro-labial cartilages.
rop, ramus ophthalmicus profundus.
ros, ramus ophthalmicus superficialis.
rpf, ramus palatinus facialis.
s, saccule.
soc, supra-orbital cartilage.
sso, spiracular sense-organ.
tc, trabecula cranii.
tn, trochlear nerve.
tp, trabecular plate.
ut, upper tooth rudiment.
vcl, vena capitis lateralis.
vn, vagus nerve.