

**THE EARLY ONTOGENY OF THE COLUMELLA AURIS OF
CROCODILUS NILOTICUS AND ITS BEARING ON PROBLEMS
CONCERNING THE UPPER END OF THE REPTILIAN HYOID ARCH**

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ABSTRACT

The columella auris in *Crocodylus niloticus* has been found to comprise the two upper segments of the hyoid arch, viz., a forked pharyngo-hyal and an epi-hyal. To these two primary arch divisions becomes added a latero-hyal component derived from delaminating subepidermal blasteme. The crocodylian stapes represents the infra-pharyngo-hyal; the suprastapedial stem (or basal portion of the lacertilian dorsal process) represents the supra-pharyngo-hyal while the extrastapedial represents essentially the epi-hyal to which latero-hyal material contributes the tympanic process as well as the suprastapedial (or lacertilian intercalary). The lateral limb of the so-called lateral prong of the reptilian and avian columella auris is also a latero-hyal derivative. It is concluded that in reptiles and birds: (a) the lateral limb and intercalary represent the dorsal articular head of the rhipidistian hyomandibula, (b) the proximal end of the epi-hyal represents its ventral articular head and (c) the so-called Huxley's foramen is the original passage between the two. Since the lacertilian internal process arises from the pharyngo-hyal it cannot represent the original rhipidistian quadrate-hyomandibular articulation.

INTRODUCTION

Reviewing the literature on the reptilian and avian columella auris one is struck by the paucity of recent investigations. The field is dominated by the writings of the comparative anatomical giants of the previous century and the first quarter of the present century, Parker, Gaupp and Versluys in particular. As Jollie (1971b) remarked in another but similar context, "we are reduced to weighing opinions rather than reviewing facts". The observations and conclusions of these older workers are used over and over again simply because thorough detailed descriptions by modern workers on the entire development of the columella in key forms are few and far between.

The problem of synonymous terms and the resultant confusion in the literature on the columella auris is immediately obvious even to the casual reader. Some authors have used descriptive topographic terms while others have tended to use terms with a morphological connotation. Often there is a lack of precision on the exact anatomical limits of a particular morphological entity. With these difficulties in mind the present authors thought that it would be useful to undertake a thorough re-investigation of the development of the columella auris and its processes in lower tetrapods (especially reptiles and birds) and to compare these with the upper half of the hyoid arch and its processes in ancestral forms. In this way it was hoped that the contradictory descriptions and confusing terminology could be clarified and a model might suggest itself which would not only reflect observed facts more accurately but also stimulate subsequent research.

Crocodylus niloticus was chosen for this study since the material was readily available and could serve as an excellent starting point for subsequent research on birds. The first worthwhile

contribution to our knowledge of the columella auris in crocodiles was that of Parker in 1883 with descriptions of the development of the columella in *C. palustris* and *Alligator mississippiensis*. Parker's work was followed by Shiino (1914) on *C. porosus* and Goldby (1925) on *C. palustris* or *porosus* and *A. mississippiensis*. However, the latter contributions added very little to that of Parker so that our knowledge of conditions in crocodiles has remained incomplete and unsatisfactory.

Since a full explanation of the terms employed in the descriptive part of this work would have been too long to be dealt with here the reader is referred to the discussion and particularly to Figure 13 (page 80).

MATERIAL AND METHOD

The eggs for this investigation were collected by Ranger A. C. Pooley of the N'dumu Game Reserve in northern Zululand. Since their age was unknown the embryos were roughly classified according to size. However, previous experience has taught that size is seldom indicative of the stage of development and the present work confirmed this.

The material was fixed either in formalin, Allen's fluid or Susa and subsequently preserved and simultaneously decalcified in Allen's fluid. No difference in the effect of these various fixatives on the subsequent staining of the material could be detected. Bulk-staining was done in Carazzi's haematoxylin and counterstaining after serial sectioning at 15 μ in Patay's double stain (Gray 1954). Very young amniote material which has been kept for some time is particularly difficult to stain effectively and differentiation was poor though adequate for the purpose. Some twenty of the sectioned specimens were selected for use in the present work and in most cases transverse, horizontal and sagittally sectioned specimens were available for each stage studied. Many embryos were sectioned sagittally up to the centre line then re-embedded and sectioned either horizontally or transversely making graphic reconstructions unnecessary. It is the opinion of the authors that the margin for error in graphic reconstructions is greater than in direct contour reconstruction and should be avoided whenever possible. Thus only contour drawings were executed in the present work. These were compiled directly under a microscope equipped with a drawing tube.

As Holmgren (1940) and Jollie (1971b) have recommended, these observations start with the first mesenchymatous condensations to appear; long before matrix is deposited between the cells. When the blastematos precursor to a structure is first laid down no perichondrium or limiting membrane is present and even during chondrification no definite boundaries exist between the cells and matrix of the cartilage or its precursors and the surrounding connective tissue. The reconstructions of early stages presented here should be interpreted in this light. The exact limits to any structure are somewhat arbitrary but, it is hoped, consistent in all stages.

DESCRIPTION OF THE DEVELOPMENT

Stage 1

The parachordals are the first part of the chondrocranium to appear. A small quantity of intercellular matrix becomes visible between the cells surrounding the notochord and immediately

anterior to it in the region of the acrochordal. Boundaries are indistinct. The matrix between the cells of the pilae antotympanae and orbital cartilages is just visible but here too distinct boundaries are absent. Mesenchyme is beginning to concentrate in the region of the future trabeculae, as yet unattached to the parachordals and without matrix. The ganglia of the branchial nerves, the eyes and otic vesicles are, however, well-formed.

Rather conspicuous at this stage are dense subepidermal blastemes applied to the postero-dorsal wall of each of the four pharyngeal pouches. This blasteme is particularly noticeable in the region of the future hyoid arch and undoubtedly provides the material for the epibranchial geniculate ganglion of VII and will later contribute to the columella. It consists of well-rounded cells packed close to the basement membrane of the thickened epidermis; the basement membrane is intact and at this stage there are no signs of active delamination, that is, elongation of the cells towards the place where the future arches will later appear. The otic vesicles lie above and between the spiracular and first branchial pharyngeal pouches.

Stage 2

When the mandibular and hyoid arches first appear as discrete blastematous tracts (Figure 1) the hyoid anlage is more advanced (more intercellular matrix present) than that of the mandibular arch. A little blasteme now outlines the ventral aspect of the otic capsule. At this stage the proximal end (the epal element: *epi*) of the elbowed hyoid arch blasteme lies immediately postero-ventral to the dorsal pocket at the top of the spiracular pouch (part of the medial recess of Goodrich 1915) (*spir poc*). Medial to the epihyal a faint blastematous tract of pharyngohyal tissue (not shown in Figure 1) passes dorso-mediad below the hyomandibular trunk of VII in a gentle curve to end without demarcation against the blasteme of the otic capsule. Except for the concentric arrangement of the cells of the pharyngohyal it is not possible to distinguish between the blasteme of the otic capsule and that of the pharyngohyal at the point where they meet. This element of the hyoid anlage is far less well-developed than the rest. The anlage of the interhyal (*inter*) lies postero-ventral to the epihyal and is marked off from the latter by a slight constriction. The arch is elbowed at this point so that the most ventral part, that is, the ceratohyal (*cerato*), lies antero-ventral to the interhyal. The densely mesenchymatous interhyal nodule lies more mediad than either the epihyal above or the ceratohyal below it. From the material at our disposal it would appear that the crocodilian interhyal forms from primary arch material only and does not receive secondary additions from subepidermal blasteme as has been reported for the interhyal of bony fish (Bertmar 1959).

Unfortunately a dense sub-epidermal blasteme devoid of all intercellular matrix lies ventrally around the distal tips of the mandibular and hyoid arches (*blast*) and around the external openings of the mouth and pharyngeal pouches thus effectively masking any incipient structures which may lie between the ceratohyal and the mandibular arch. In later stages these elements are connected.

The first pharyngeal pouch forms a well-developed spiracular crest (*spir crest*) between the anlagen of the mandibular and hyoid arches. The dorsal pocket (*bran poc*) of the second pouch (1st branchial) is connected to this crest by a horizontal ridge below which the interhyal lies in a small depression. The crest of this pouch lies between the hyomandibular trunk of VII (*hyo*) and the glossopharyngeal nerve and separates the hyoid and basilingual blastemes from each

other. As is to be expected, the hyomandibular trunk passes dorso-medially over the pharyngo-hyal and curves down to innervate the depressor mandibulae musculature which is developing posterior to the arch. As it passes over the pharyngo-hyal it gives off a short branch which probably represents the chorda tympani. This passes anteriorad over the epihyal laterally between the tip of the latter and the main trunk of the nerve.

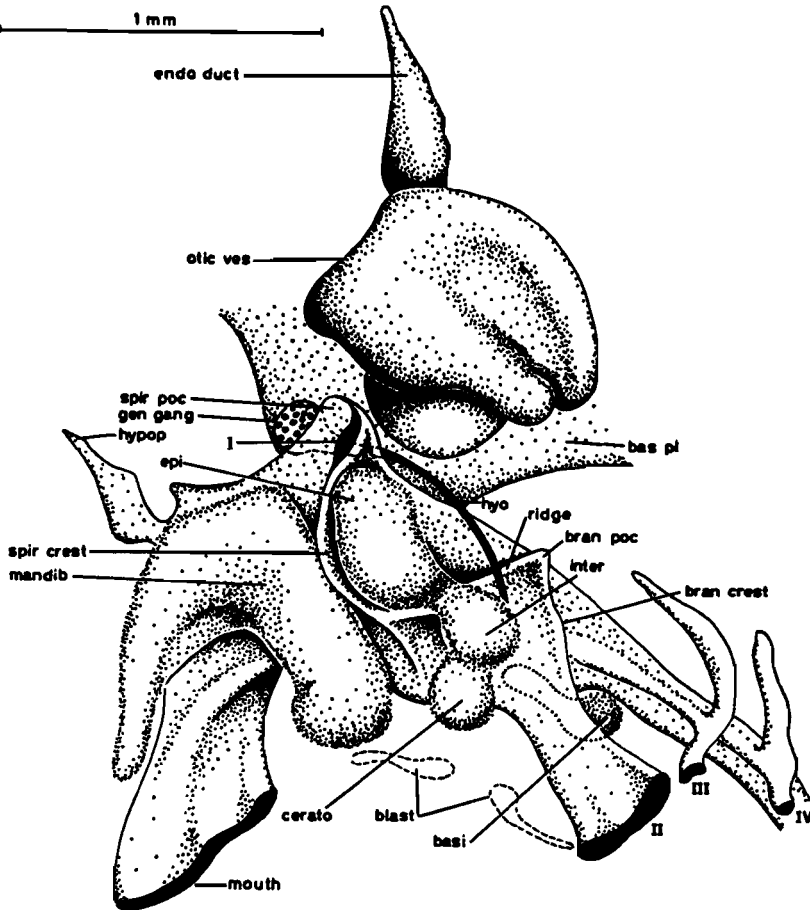


FIGURE 1

Lateral aspect of the visceral arch anlagen and pharyngeal pouches in stage 2 of the development. I is the dorsal division of the first visceral or spiracular cleft. II to IV are the second to fourth clefts; also shown are their more dorsally situated pouches. Note how the crest of the spiracular pouch (*spir crest*) and that of the first branchial pouch (*bran crest*) completely separate the first three visceral arches from each other. The dense subepidermal blastemes (*blast*) are more extensive than the dotted outlines would imply. (For other abbreviations see p. 88.)

Stage 3

As development proceeds the pharyngohyal blasteme begins to differentiate into a supra-pharyngohyal (the suprastapedial stem of Parker 1883) and an infrapharyngohyal (future stapes) (Figure 2: *supra* and *infra*). A limited amount of delamination would appear to be taking place between the dorsal pocket and horizontal ridge (*ridge*) of the spiracular pouch towards the supra-pharyngohyal anlage. The epithelia of both these spiracular evaginations lack basement membranes at this stage and are surrounded by dense mesenchyme. This implies a secondary addition of sub-epidermal (thus laterohyal) blasteme to the supra-pharyngohyal material. In this way a composite structure (the suprastapedial complex) which is the homologue of the lacertilian dorsal process is formed (*cp* Figure 13). There is thus reason to believe that an intercalary (Parker's suprastapedial) is present in *C. niloticus* though not as an independent chondrification as in *C. palustris* (*cf.* Parker 1883). As a whole, the pharyngohyal blasteme is less well-developed than either the epi- or the interhyal below it. The epihyal now has a nebulous connexion via a dorso-lateral blasteme (future tympanic process or insertion plate) with the early beginnings of the tympanum (*tym proc*). Immediately ventro-lateral to this process active delamination and cellular streaming may be observed between the thickened epidermis, which lacks a basement membrane in this area, the tympanic process also suggesting contributions

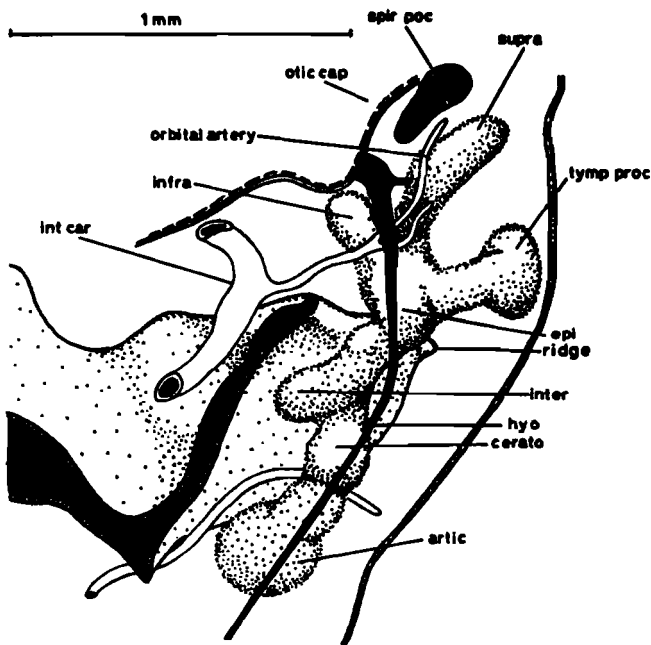


FIGURE 2

Posterior aspect (looking craniad) of the columella auris; stage 3. The shape and size of the anlagen of the supra-pharyngohyal and tympanic process are only approximate as they are still very nebulous at this stage and have sub-epidermal cells streaming towards them. (For abbreviations see p. 88.)

from the laterohyal blasteme. It might be useful at this point to refer to the reptilian hyoid arch as depicted in Figure 13 which shows the full laterohyal involvement in columella structure. In fronto-transverse sections it may be observed that the dark-stained interhyal blasteme lies almost transversely with its most ventral termination ending freely, medial to its connexion with the ceratohyal (Figures 2 & 3: *inter*). The latter has become slightly denser. The dense mesenchyme which lay between the distal tips of the mandibular and hyoid arches in stage 1 recedes sufficiently for a slight discontinuity to be observed in some embryos between these two anterior arches. This gap between the articular region of Meckel's cartilage and the ceratohyal soon becomes bridged by a thin mass of mesenchyme (shown but not labelled in Figure 2) which is separated from both structures by slight constrictions. It may thus represent a separate arch element.

The relative positions of the various elements of the hyoid arch to the first and second pharyngeal pouches is unchanged. Both the head vein and the hyomandibular trunk run outside the mesenchymatous beginnings of the otic capsule dorsal to the infrapharyngohyal and medial to the suprapharyngohyal anlage, that is, they have the typical rhipidistian and tetrapod relationships.

Although the various components and processes of the columellar anlage become gradually

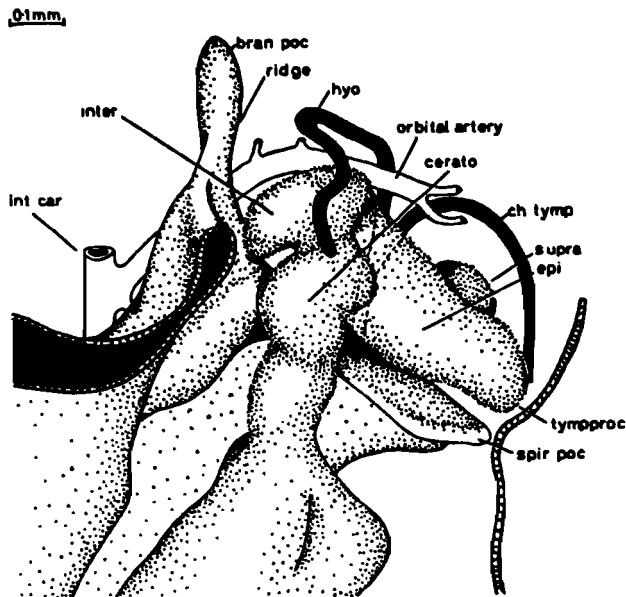


FIGURE 3

Ventral aspects of the columella auris and caudal extremity of Meckel's cartilage to show the connexion between the two structures. The medially directed tip of the interhyal is also clearly seen. The pharyngohyal components of the columella are obscured in this view by the spiracular pouch outpushings. (For abbreviations see p. 88.)

demarcated from each other and the surrounding mesenchyme the entire hyoid complex is still continuous. A similar situation exists between the infrapharyngo-hyal (stapes) and the otic capsule; the prospective foot-plate of the stapes is denser than the capsular blasteme but is devoid of any definite boundaries. The inter- and ceratohyal segments may most easily be distinguished in frontal sections. The interhyal is characterized by its dense appearance with traces of intercellular matrix while the ceratohyal has a very definite concentric cell arrangement which distinguishes it from the mesenchymatous condensation which links it with the caudal extremity of Meckel's cartilage. Externally the points of contact between these structures are marked by slight constrictions (Figure 3).

It should be noted that in each case the interhyal has been identified as that swelling of the hyoid blasteme lying between the crests of the first and second pharyngeal pouches immediately below and in the pocket formed by the horizontal ridge joining the two pouches. It also lies more mediad than either the proximal end of the ceratohyal or the medial termination of the epihyal (Figures 2 & 3).

The chorda tympani is not easy to follow in sagittal sections but in frontal sections it may be seen to come off the hyomandibular trunk of VII above the infrapharyngo-hyal (stapes) and medial to the suprapharyngo-hyal (suprastapedial stem of Parker 1883) to pass round lateral to the latter. It ends in these early stages near the dorsal extremity of the otic process of the quadrate, far lateral and dorsal (Figure 3: *ch tym*).

Stage 4

Initially the epi-, inter- and ceratohyal are far better developed than the pharyngo- and latero-hyal blastemes (*i.e.* than the stapes, the suprastapedial stem, the suprastapedial and the tympanic process). Conditions are thus similar to those existing in actinopterygians where Bertmar (1959) found that the pharyngo element often 'grew out of' the epi element. Likewise he found that the latero elements differentiated on the epi element from the dorso-lateral blasteme. The blastematos link (Figure 4: *mesen*) between the ceratohyal and the articular region of Meckel's cartilage is also less well-defined than the other elements of the arch. The epihyal at this stage appears as a dense curved, blastematos rod with a little matrix between its cells (*epi*). To its ventro-caudal tip is attached the similarly developed interhyal, the joint between them marked by an area of less dense mesenchyme. The interhyal (*inter*) is a distinct, medially directed knob of procartilage which lies postero-medial to the ceratohyal blasteme. From the proximal tip of the epihyal a thinly mesenchymatous infrapharyngo-hyal (*infra*) (stapes) extends mediad towards the developing capsule and a similarly developed suprapharyngo-hyal (suprastapedial stem) (*supra*) reaches up beside the spiracular pouch which is still surrounded by dense subepidermal blasteme.

In a slightly more advanced embryo the elements of the pharyngo-hyal (stapes and suprastapedial stem (Figures 5 & 6: *infra* and *supra*) appear to be more closely associated, likewise the tympanic process (*tym proc*) appears to be associated with the epihyal. But distinct boundaries between the columella and its various processes and the proximal tip of the infrapharyngo-hyal and the otic capsule do not exist. However, as development proceeds a line of mesenchyme separating the pharyngo- and epihyal tissue first becomes more distinct (Figure 7: *infra*, *epi*) and thereafter gradually fades so that the two elements eventually become intimately fused to one another.

The stem of the ceratohyal becomes, in comparison with the columella auris, relatively long in keeping with the increasing dorso-ventral extension of the quadrate (Figure 8). There is also a gradual straightening out of its elbowed condition associated with this growth. In contrast to its persistently mesenchymatous dorsal tip, the stem of the ceratohyal and especially the bridging mass of mesenchyme (first seen in stage 3) which joins it to the articular region of Meckel's cartilage, is very well chondrified (Figure 8). The dorsal tip lies distinctly anterior to the ventral tip of the interhyal (Figure 7: *inter, cerato*). The stapes differentiates into an antero-posteriorly elongate oval plate (Figure 8: *st plate*) lying free in the fenestra ovalis and attached near its

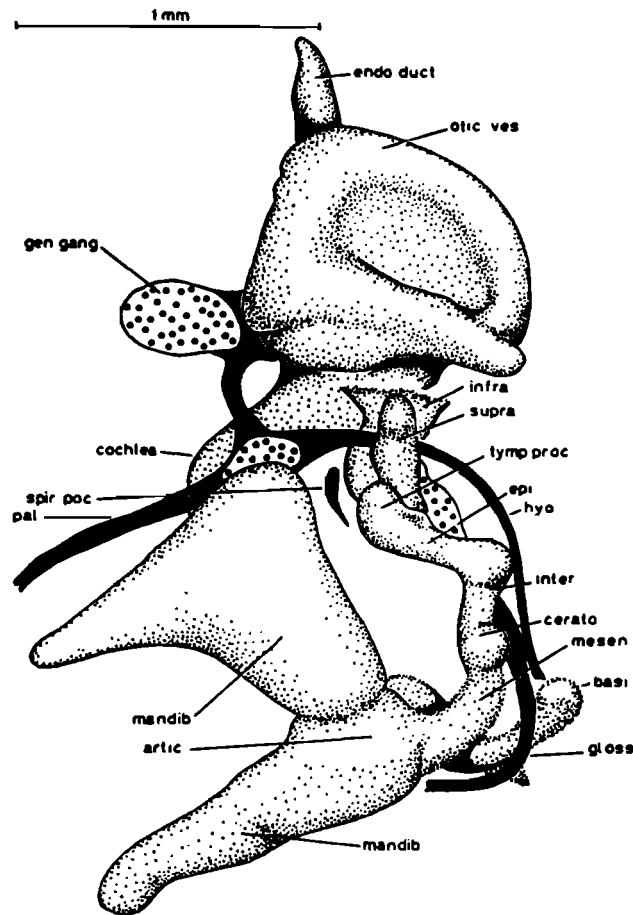


FIGURE 4

Lateral aspect of the first three visceral arches in stage 4. Only the most dorso-lateral tip of the spiracular pouch (*spir poc*) is shown, serving as a land-mark. Note that the basilingual cartilage (*basi*) lies more mediad and is separated by the glossopharyngeal nerve and first branchial pouch structures from the hyoid visceral arch. (For other abbreviations see p. 88.)

anterior edge to the stem of the columella. The extreme edge of the suprapharyngo-hyal element is now firmly attached by connective tissue to the ventro-lateral aspect of the otic process of the quadrate (*supra, otic proc*).

During development a muscle has made its appearance lying between the ventro-lateral edge of the parotic process (Figure 11: *par proc*) and that area of the tympanum to which the tympanic process (*tym proc*) and the distal tip of the epi-interhyal (*inter*) is attached (see also Figure 9). From its position it is probably the extracolumellar muscle (Goodrich 1915) also observed by Goldby (1925) in the alligator. At the point where the early anlage of the squamosal bone overlies the otic process of the quadrate an aggregation of connective tissue extends antero-laterally to the point where the tympanic process is inserted on the tympanum. This is probably the homologue of the lacertilian extra-columellar ligament. A mesenchymatous postero-ventrally directed pars inferior of the tympanic process (Figure 9: *tym proc*) has made its

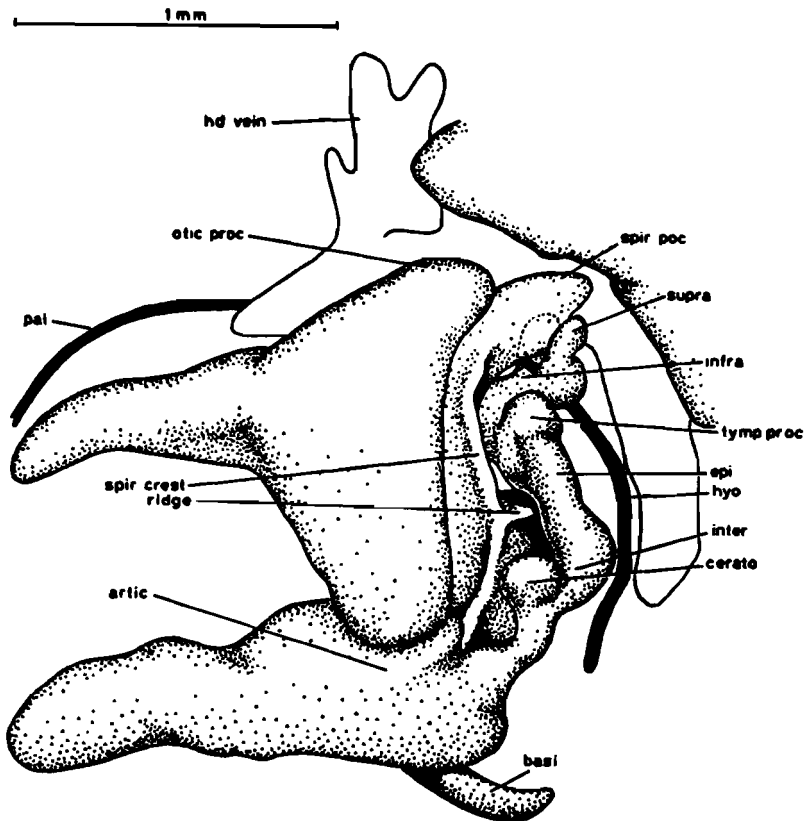


FIGURE 5

Lateral aspect of the columella of a late stage 4. Only the spiracular pouch and its crest and part of the head vein are shown. (For abbreviations see p. 88.)

appearance. Later this structure develops a small, medially directed knob. The chorda tympani branches off from the hyomandibular trunk low down, immediately posterior to the interhyal (Figure 11), then passes dorsad and laterad to the supratharyngohyal (suprastapedial stem) to fade out in the wall of the dorsal diverticulum of the tympanic cavity.

Stage 5

The aggregation of connective tissue reported from the previous stage has now developed into a ligamentous thickening lying within the tympanum and connecting the tympanic process to that part of the suprastapedial complex (*cp.* stage 3, p. 63) attached to the edge of the tympanum (Figure 11: *lig*). The impression is that the otic process of the quadrate, the suprastapedial complex and the tympanic process and epihyal are joined by this ligament where they lie in the plane of the tympanic membrane. (The positions of these structures relative to each other are best seen in Figure 10). The insertion plate of the tympanic process is roughly triangular in shape with its apex ventral; it pushes the tympanic membrane outwards so that the latter has a squat

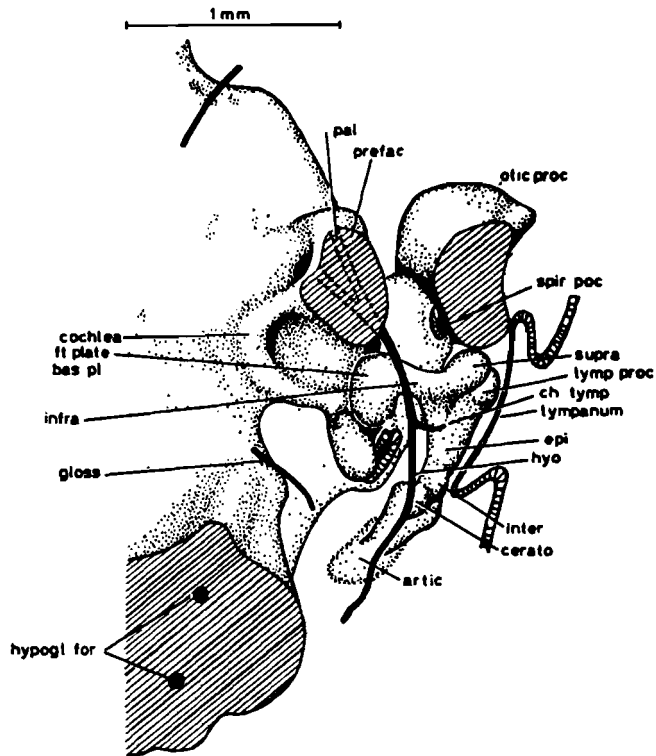


FIGURE 6

Postero-dorsal aspect of the basal plate, partly formed cochlear capsule and columella in a late stage 4. Portions of the spiracular pouch have been omitted so as not to obscure the columellar structures. (For abbreviations see p. 88.)

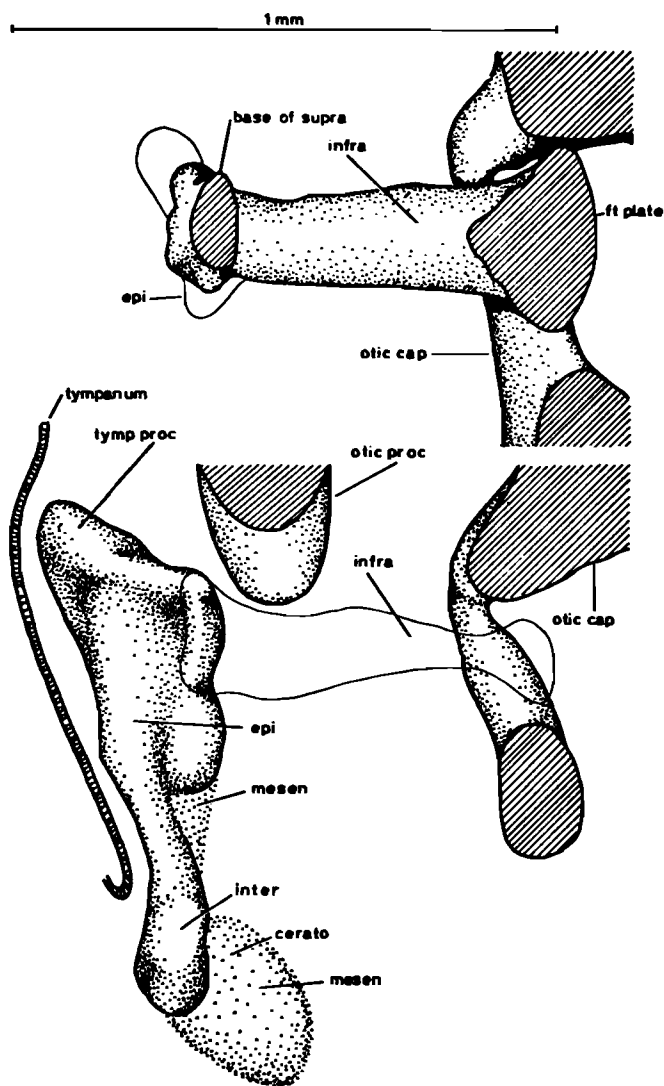


FIGURE 7

Posterior aspect of the infrapharyngo-hyal (above) and the epihyal (below) looking forward. Only the base of the supra-pharyngo-hyal and the proximal part of the cerato-hyal are shown. The two elements of the columella have been separated along the line of mesenchyme dividing them and depicted separately to show their essentially separate nature. In the lower illustration, that part of the infrapharyngo-hyal which connects with the epihyal is given in outline to show the relatively small area of contact between them; in the upper illustration a part of the epihyal is similarly shown in outline. (For abbreviations see p. 88.)

conical form. The epihyal below the tympanic process (that part of the epihyal referred to by Parker as the infrastapedial) has become very much flattened and lies at right angles to the surface of the tympanum (Figure 10: *epi*); its entire edge from top to bottom attached to the membrane. The membrane itself lies obliquely, facing postero-ventrally outwards. The outer opening of the external auditory meatus lies almost directly below it, very near the jaw articulation.

The several elements comprising the columella auris are now becoming more closely united. The interhyal (Figure 12: *inter*) appears as a slightly curved rod of cartilage in homo-continuity with the ventral tip of the epihyal (*epi*) (infrastapedial) and the knob-like dorsal tip of the ceratohyal (*cerato*). The transition from epihyal to interhyal lies on the edge of the tympanum and can only be recognised by the abrupt change of form as one passes from *epi*- to interhyal; there

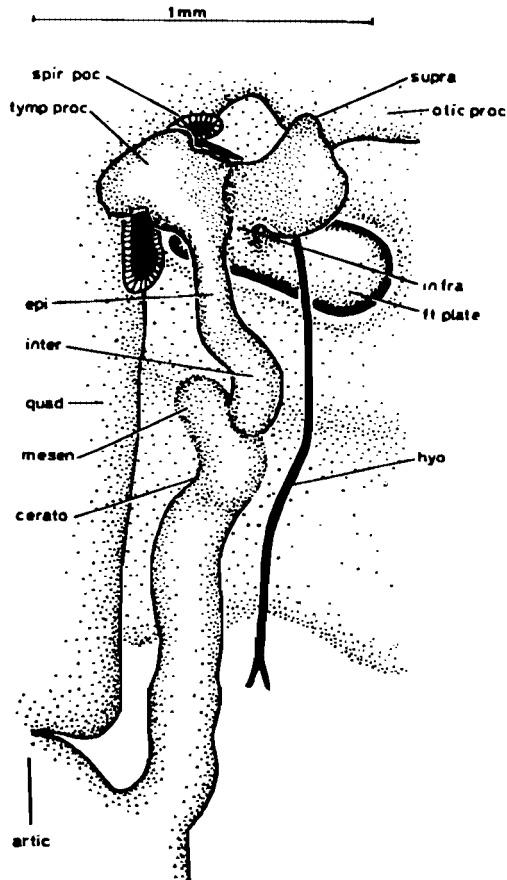


FIGURE 8

Lateral aspect of the columella auris and its processes showing the great extension and straightening of the ceratohyal alongside the quadrate. Only the tip of the dorsal pocket of the spiracular pouch is shown to serve as a land-mark. Part of the otic capsule and basal plate also appear. (For abbreviations see p. 88.)

is no longer any other demarcation. The expanded dorsal flange of the suprastapedial complex (Figure 9: *supra*) is applied to the outer surface of the otic process (*otic proc*) of the quadrate and overlain in turn by the anlage of the squamosal bone. The tympanic cavity has a dorsal diverticulum (presumably part of the anterior, outer recess of Goodrich 1915), which separates the suprastapedial complex from the quadrate's otic process. However, dorsally, the upper extremities of both these structures lie closely applied to one another.

A rather well-developed fan-shaped muscle first evident in stage 4 (p. 67), the extracolumellar muscle, innervated by several branches of the hyomandibular trunk lies outside this nerve.

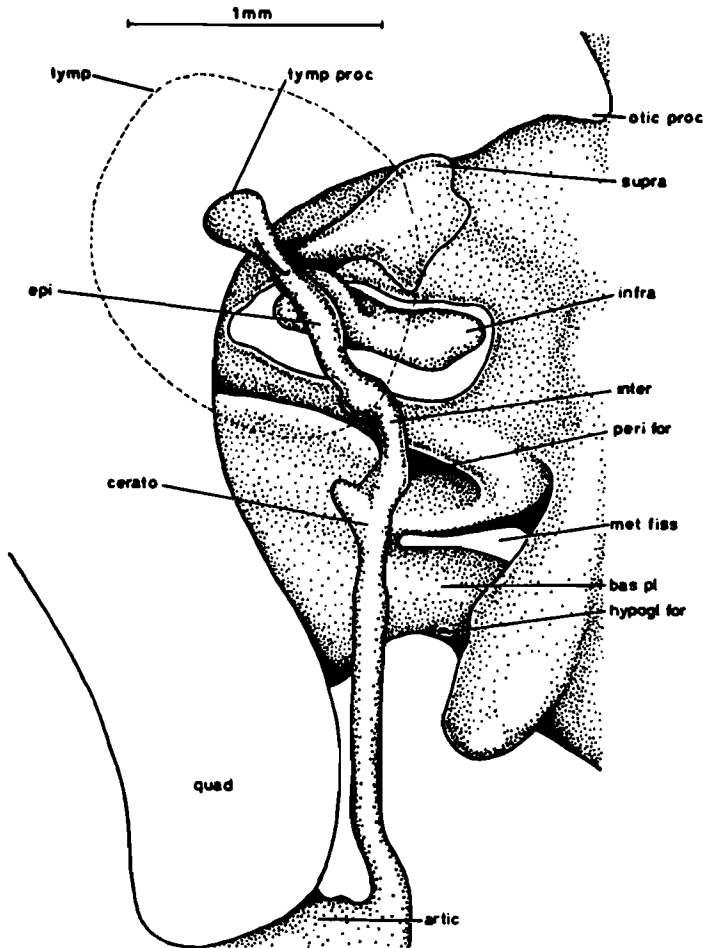


FIGURE 9

Lateral aspect of the columella and surrounding structures in an early stage 5. The quadrate (*quad*) is only shown in outline and the edge of the tympanum (*tym*) with a dotted line. The crest of the parotic process is shown but not labelled. (For other abbreviations see p. 88.)

Its origin is on the parotic process of the otic capsule (it is also overlain by the squamosal bone), its insertion on that edge of the tympanum which lies between the distal tips of the suprastapedial complex and the epihyal. A separate slip of this muscle inserts on the ventral tip of the epihyal itself and has fibres curling round the ventral edge of the tympanum. It is innervated by a separate branch of the hyomandibular nerve.

Except that the sculpturing of the columella becomes more elaborate no radical changes were observed in the oldest embryos studied (Figure 12). The suprastapedial complex tends to

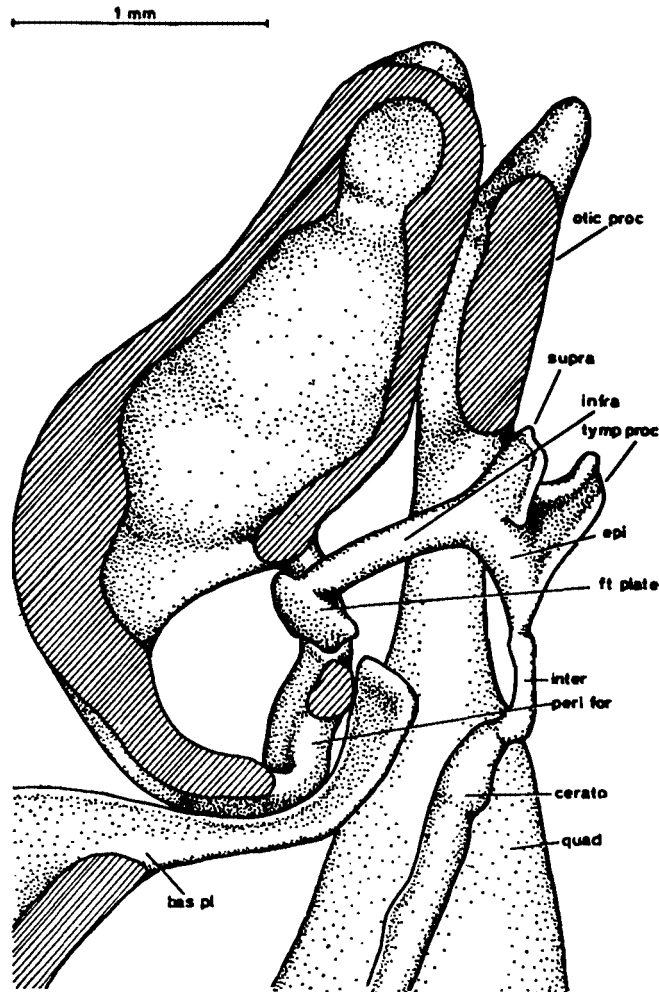


FIGURE 10

Thick section through the otic capsule and basal plate showing the posterior aspect of the columella. The same structures appear in Figure 9 but from a different viewpoint. (For abbreviations see p. 88.)

curve more and more postero-ventrally until its distal tip almost meets the dorsal tip of the interhyal-epihyal junction (best seen in Figure 11). Starting off as a moderate amount of connective tissue running between these two parts, the dense band of tissue (a ligament) first mentioned in stage 5 soon develops between the ventral extremity of the suprastapedial complex and the epi-interhyal junction on the edge of the tympanum (Figure 11: *lig*). The suprastapedial complex

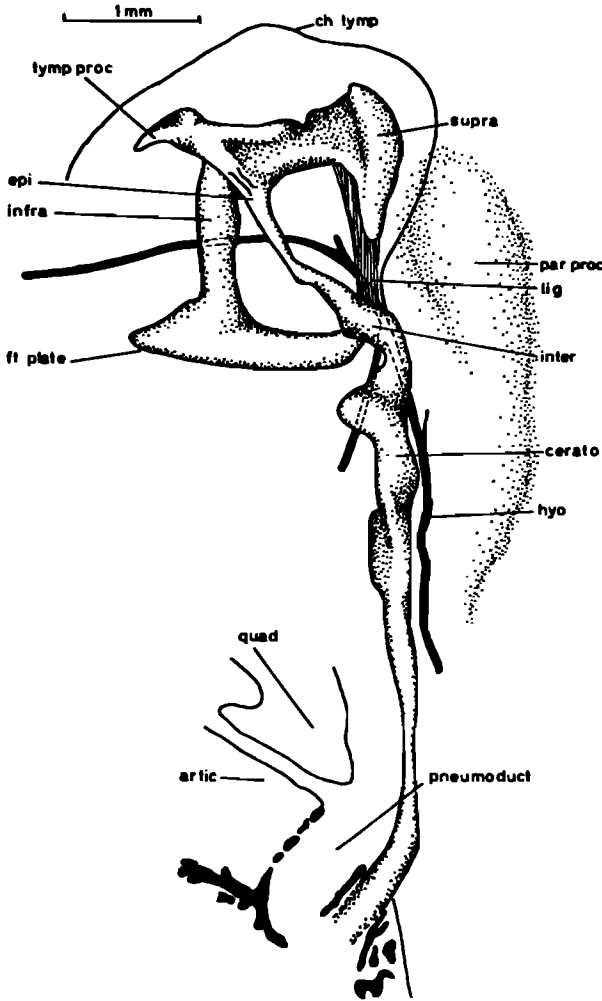


FIGURE 11

Ventro-lateral aspect of the columella auris and associated structures. An outline of the articulation between the quadrate and Meckel's cartilage is included to show the position of connexion between the mandibular and hyoid arches and the entrance of the pneumoduct into the lower jaw. The positions of the parotic process of the otic capsule and the course of the hyomandibular trunk and chorda tympani nerve are also shown in part

(For abbreviations see p. .88)

which has a distinct ridge inserted on the edge of the tympanum is, as mentioned before, firmly attached by dense connective tissue to the otic process of the quadrate. The latter is interposed between the suprastapedial complex and the parotic process.

The hyomandibular trunk of the facial nerve passes above the columella and then curves postero-ventrad towards the depressor mandibulae muscle. As it curves over the columella it gives off numerous branches to the extra-columellar muscle. After leaving the hyomandibular trunk at about the level of the interhyal, the chorda tympani (Figure 11 : *ch tym*) passes anteriad, above the tympanic process and supratharyngo-hyal against the lateral aspect of the otic process of the quadrate. Then, running ventrad anterior to the columella it passes below the tympanic diverticulum on the postero-dorsal surface of the quadrate to enter the lower jaw immediately

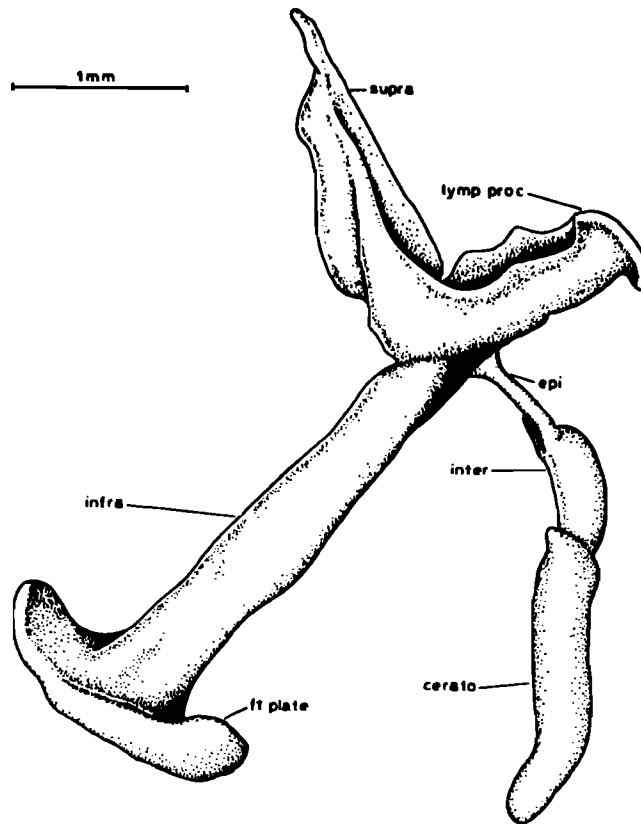


FIGURE 12

Anterior aspect of the columella auris showing the club-shaped distal termination of the ceratohyal (*cerato*) which appears late in stage 5. The very close approximation of the suprastapedial complex and epihyal are hidden in this view. (For other abbreviations see p. 88.)

behind the articulation and anterior to the point of attachment of the ceratohyal (not shown in Figure 11). It is at this point that a pneumoduct, connected with the tympanic cavity enters the lower jaw.

By this time the ceratohyal is enclosed in a narrow bony channel between the quadrate and the otic capsule; it is this part which was observed to degenerate in later stages until only a slight ossified eminence marks where it was attached to the lower jaw. The remaining portion of the ceratohyal is club-shaped and lies within the confined limits of the cranioquadrate passage (Figure 12: *cerato*). The interhyal retains its distinctive curved shape, its upper curve attached to a tenuous epihyal. The tympanic process has developed a small fenestra in its outer flange. The infrapharyngohyal element of the columella becomes ossified externally from its foot-plate up to the point of attachment of the supratharyngohyal (suprastapedial stem).

DISCUSSION

The main division of the columella auris

Parker (1883) observes that the columella arises as two separate pieces in *Crocodylus*: a proximal segment (which gives rise to the stapes as well as to a process to which the suprastapedial becomes attached) and a distal segment or extrastapedial (Figure 13). Goldby (1925) distinguishes between medial and lateral divisions. These coincide with Parker's divisions as well as with Hoffman's otostapes and hyostapes (Hoffman 1889). This is essentially the situation in *Crocodylus niloticus* and in the penguin (*Spheniscus demersus*, Crompton 1953). Crompton uses the terms pharyngohyal and epihyal for the two main divisions and these terms are preferable to those used in the older literature since they describe more accurately the origin of the columella in the light of present knowledge (see later).

The term 'extrastapedial' is used by Parker for the distal segment in *Crocodylus* and refers to what Goldby calls the primary (embryonic) division of the columella. It has, however, been used by several authors in the past as a synonym for 'extracolumella' which refers to a segment which arises during the secondary division of the columella, *i.e.* to the segment which remains cartilaginous when the stapes ossifies. This has caused much confusion and should be avoided. It is suggested here that the terms extracolumella and stapes should be used for the secondary division as they are used by Versluys (1903 & 1936). The extracolumella includes the extrastapedial of Parker plus the distal part of the pharyngohyal. The stapes represents the lower division of the pharyngohyal, probably the infrapharyngohyal (see later). The term columella or columella auris should be used for the whole structure (extracolumella plus stapes).

Parker's infrastapedial in *Crocodylus* is the distal part of the epihyal, it is not, nor was it considered by him to be, a separate entity. In *Crocodylus* the interhyal becomes detached from the epihyal in older embryos (Versluys 1903 & 1936); apparently these embryos were older than the oldest specimen available to us. In lacertilians the ceratohyal detaches from the columella probably through atrophy of the interhyal (*cf.* Versluys 1903). Since the interhyal most probably forms the tip of the infracolumellar process in birds generally (*cf. inter alia* Crompton 1953 & Frank 1954), the latter process is not homologous with the crocodilian infrastapedial (Figure 13). In the crocodilian embryo according to Parker the epihyal (Parker's extrastapedial) gives rise to the infrastapedial which connects with the ceratohyal through a separate cartilaginous piece the

'epihyal'. Versluys also calls the independent chondrification an 'epihyal'. In this he follows Parker who derives the whole columella from a pharyngohyal and it therefore follows that the next segment should be an epihyal. Goldby who considers this structure (Parker's 'epihyal') as the dorsal swollen tip of the ceratohyal in *Crocodylus* sees no harm in the use of the term 'epihyal' provided no homology is attached to it. Crompton calls the homologue of Parker's epihyal, 'ceratohyal' in *Spheniscus*.

It is suggested here that the term 'epihyal' for the separate blastematous interhyal anlage should be abolished and the structure be called interhyal (or stylohyal). We must look upon this structure as a separate hyoid element which has been inherited from the fish ancestors of vertebrates where it has precisely the same relations to the hyomandibula and the ceratohyal (cf. Jarvik 1954).

Problems concerning the upper end of the hyoid arch

At this stage brief reference must be made to the double-headed rhipidistian hyomandibula. The 'double-headed' view was originally propounded by Schmalhausen (1923). He maintains that in Selachii the hyomandibula (an epihyal) articulates with the neurocranium through a head of pharyngohyal origin, medially to (below) the head vein; in Teleostomi the hyomandibula is attached to the neurocranium directly or possibly through a fused 'extrapharyngohyal' laterally to (above) the head vein. Both these articulations were originally present in bony fishes and are retained by tetrapods, one on each side of the head vein. He unfortunately makes no mention of the lateral commissure in bony fish or its composition. Since then a double-headed hyomandibula has been recorded, *inter alia*, by Romer (1937 & 1941) in his work on *Megalichthys*, by Jarvik (1954) in *Eusthenopteron* and by Thomson (1966 & 1967) in *Ectosteorhachis*. But Jarvik contends that the rhipidistian hyomandibula is of epihyal origin exclusively, since the supra- and infrapharyngohyal are incorporated into the braincase. Thus the rhipidistian hyomandibula with its two articular heads is an epihyal which articulates with the suprapharyngohyal (lateral commissure) and infrapharyngohyal (otic shelf or auditory ledge) which are fused to the neurocranial wall.

Bertmar's (1959) work on *Neoceratodus* strengthens Jarvik's theory in regard to the fusion of the supra- and infrapharyngohyal material onto the neurocranium. Additional support for Jarvik comes from Jollie (1962 & 1971a & b) and Nelson (1969) who are both of the opinion that in fish separate supra- and infrapharyngo elements probably never existed in the pro-otic arches but tended to be incorporated into the braincase early in gnathostome history to form, for example, the lateral commissure in bony fish. This incorporation of pharyngohyal elements into the neurocranium must have occurred at a time when the mandibular arch became attached to the hyoid arch and must be seen as an adaptation to the newly acquired suspensorial function of the hyomandibula (see later).

Schmalhausen (1923) refers to the forked upper end of the hyoid arch in tetrapods. He identifies a medial element (pharyngohyal) represented by the stapes and a lateral element (hyomandibula or epihyal) represented by the extracolumella with its tip, the dorsal process. In this Schmalhausen is followed by Versluys (1924 & 1936) and Sushkin (1927). Similarly de Beer (1937) speaks of a 'medial prong' or pharyngohyal and a 'lateral prong' or epihyal. Visser (in press) is also in broad agreement that the reptilian stapes represents an infrapharyngohyal but

suggests that the dorsal process is not an epihyal but a suprpharyngohyal.

In the interim both Eaton (1939) and Romer (1941) had compared the amphibian and reptilian stapes with the ventral head of the rhipidistian hyomandibula and the reptilian dorsal process with the rhipidistian dorsal head thus confusing the issue and leaving the pharyngohyal elements unaccounted for. Westoll (1943) unfortunately strengthened this view by drawing attention to the hyomandibular trunk of VII which passes backwards in tetrapods between the stapes and dorsal process as it does between the two heads of the rhipidistian hyomandibula.

In his work on the morphological significance of the auditory ossicle in reptiles Hoffman (1889) referred to the confusion that existed regarding the origin of the stapes. Today, almost a hundred years later, there still remains considerable confusion on the phylogenetic as well as the ontogenetic origin of what de Beer calls the 'medial prong' and the 'lateral prong' of the tetrapod columella auris (Figure 13).

The medial prong (stapes or processus ventralis: Westoll 1943)

Without reviewing the literature on the capsular and/or hyoid origin of the tetrapod stapes, it will be suggested here that the stapes is derived from the hyoid arch. In this regard experimental work such as that of Toerien (1963 & 1965) is more convincing than the descriptions of developmental stages of Reinbach (1950 a & b) and Barry (1956). The last two authors claim a capsular and a palatoquadrate origin for the two primary divisions of the amphibian columella with no contribution from the hyoid. Reinbach also claims a capsular origin for the proximal division (Reinbach's pars optica) of the reptilian columella auris.

If the stapes, then, is a hyoid derivative, which part of the hyoid arch does it represent? To answer this, reference to the fish ancestors of tetrapods is necessary. As mentioned earlier, Jollie (1971 a & b) supports Jarvik (1954) who states that the entire pharyngohyal element probably became incorporated into the neurocranium very early in gnathostome evolution. One could follow this up with the suggestion that the incorporation could have taken place at a time when the palatoquadrate reached the hyoid arch and the latter assumed a suspensorial function. Incorporation of the pharyngo-element would *inter alia* result in a firmer support for the hyomandibula and better protection for the head vein. Although highly speculative it may be assumed that in the rhipidistian embryo the pharyngohyal arose independently of the neurocranium. The suggestion put forward by Jollie (1968), namely, that originally the pharyngohyal tissue was an integral part of the endocranium becoming free only later in evolution, is not supported here. If Jollie is right then one could reason that the tissue is a secondary addition to the hyoid arch and thus primarily not part of it. Conditions in Rhipidistia would then have been similar to those in *Neoceratodus* (Bertmar 1959) where the hyoid arch is in early development complete and independent. Later the pharyngohyal element (infra plus supra) fuses with the neurocranium in the position of the lateral commissure of bony fishes. Fox (1963 & 1965) calls this structure in *Neoceratodus* the otoquadrate cartilage and considers it homologous with the lateral commissure of teleostomes.

A lateral commissure or bony covering of the jugular canal is absent in tetrapods (Romer 1941; Hotton 1960) so that the head vein runs 'exposed' between the medial and the lateral prongs. Jollie (1971b) explains the condition in tetrapods by assuming that in tetrapods part of the lateral commissure (pharyngohyal element) does not become incorporated into the skull but

remains separate, its ventral part (infrapharyngo-hyal) forming the stapes. This view seems probable if one bears in mind that in the autostylic tetrapods the hyoid has lost its suspensorial function and thus its need for a dorsally extending brace. Its pharyngo element, which in Rhipidistia, as in *Neoceratodus*, fuses with the neurocranium during ontogeny now remains separate and available to participate in sound conduction. It now follows that Bertmar (1962) and Visser (in press) are justified in regarding the boundary between the two primary divisions (Hoffmann's otostapes and hyostapes) of the columella as the original discontinuity between the pharyngo-hyal and the epihyal. The absence of a lateral commissure and otic shelf (*i.e.* pharyngo-hyal material) in the neurocranial wall of tetrapods and the homocontinuous embryonic origin of the stapedia and capsular blastemes in most forms is also explained.

With the probable exception of Urodela where the pharyngo-hyal element is incorporated into the floor of the auditory capsule forming the otoquadrate (post palatine) cartilage (Fox 1963 & 1965), the proximal segment of the tetrapod columella auris would thus represent the pharyngo-hyal. On the balance of the evidence therefore we have to conclude that the so-called medial prong of the tetrapod columella is derived from pharyngo-hyal material probably representing an infrapharyngo-hyal.

The lateral prong

The lateral prong is not a unit-structure, but represents material from several sources (Figure 13). De Beer (1937) refers to this complexity of structure when he states that the lateral prong may include: (1) the intercalary, (2) the dorsal process connecting the intercalary with the infrapharyngo-hyal and forming the medial boundary of the extra-columellar (Huxley's) fenestra, and (3) a structure which he (de Beer) calls the laterohyal. The latter connects the intercalary with the epihyal (hyostapes) and forms the lateral boundary of the extracolumellar fenestra. It is essential that an attempt should be made to determine the morphological significance of the 'three' structures involved, namely: intercalary and/or dorsal process and the so-called 'laterohyal' of de Beer. This, of course, also involves the so-called Huxley's foramen. For descriptive purposes we distinguish here between the medial limb (including the intercalary) and the lateral limb of the lateral prong.

The medial limb

Parker (1883), in his work on *Crocodylus*, distinguishes between what he calls the suprastapedial (intercalary or laterohyal of Versluys 1903 & 1936) and a suprastapedial stem or stalk or ascending process (our suprapharyngo-hyal) (Figure 13.) He claims that the suprastapedial is clearly distinct from the suprastapedial stem; it is a special hyoid element not found in normal branchial arches. The suprapharyngo-hyal projects dorsally from the lateral end of the proximal segment or infrapharyngo-hyal. The suprastapedial plus suprapharyngo-hyal of *Crocodylus* are homologous with the dorsal process plus intercalary of lacertilians (Versluys 1903). The suprastapedial (intercalary) in *Crocodylus* takes, however, no part in the attachment of the quadrate to the skull as it does in lizards since it lies lateral to the quadrate. A separate origin for the suprastapedial (intercalary) could not be ascertained in *Crocodylus niloticus* but there is undoubted evidence of cells delaminating from the dorsal pocket of the spiracular pouch towards the tip of the suprapharyngo-hyal (see description stage 3).

The intercalary (suprastapedial) of lacertilians represents the tip (pars dorsalis) of the dorsal process (Versluys 1903). It is situated between the quadrate and the crista parotica (Gaupp 1900) or processus paroticus (Versluys 1903) or paroccipital process (Goodrich 1930). As it arises from a separate cartilaginous centre it may be considered a separate entity in lacertilians. Versluys, however, came to a contrary conclusion in spite of certain observations including the following: (a) In very young *Lacerta* embryos (blastematos stage), there is a condensation of cells which extends from the skin towards the columellar blasteme lateral to the head vein. In this cell-aggregation (according to Versluys) the dorsal process arises on the distal end of the pharyngo-hyal (otostapes) and forms part of it. Its dorsal tip ultimately lies between the upper end of the quadrate (which lies lateral and anterior) and the parotic process (which lies caudal, medial and dorsal). The tip chondrifies independently of the columella and Versluys (1903 & 1936) prefers to call it the intercalary or laterohyal. (b) In *Calotes* (Versluys 1903) a cartilaginous process grows from the intercalary towards the columella in the connective tissue strand which connects the intercalary with the columella. In *Lacerta* this connective tissue strand between the intercalary and the columella disappears in the adult. (c) In *Platydactylus* (Versluys 1903) the intercalary arises as a completely independent nodule unattached to the otostapes (pharyngo-hyal). The intercalary is connected only to the lateral end of the columella by an extracolumellar ligament.

Now, despite the fact that in all three cases mentioned the intercalary chondrifies independently of the columella, Versluys is very definite that the intercalary is basically an integral part of the columella and that its independent origin is a secondary condition. It would, however, be interesting to investigate the opposite view, viz., that an independent intercalary reflects a primary condition.

It is quite clear from Wyeth's (1924) description that his 'suprastapedial process' in *Sphenodon* represents the lateral limb of de Beer's lateral prong and not the medial limb as does Parker's suprastapedial stem in *Crocodylus*. It originates from the antero-dorsal surface of the distal extremity of the epihyal or extrastapedial cartilage (Hoffmann's hyostapes). The medial limb of the lateral prong (Parker's suprastapedial stem) Wyeth calls the recurrent process and it is interesting to note that it grows from the intercalary towards the columella. The intercalary, therefore, arises independently of the pharyngo-hyal (otostapes). According to Reinbach (1950 a & b) the intercalary in reptiles arises independently of the columella in close association with the dorso-caudal tip of the quadrate. Crompton (1953) speaks of two supracolumellar limbs in most birds; a medial one (processus supracolumellaris medialis) and a lateral one (processus supracolumellaris lateralis). Both arise from the columella auris, the lateral one from the lateral surface of the epihyal (hyostapes) and the medial one from the infrapharyngo-hyal (otostapes). In the penguin, however, he finds very interesting conditions since the medial limb or processus supracolumellaris medialis (Parker's suprastapedial stem) is lacking and a nodule of blastematos tissue arises, continuous with the lateral limb, between the otic process of the quadrate and the metotic cartilage. Crompton considers this structure (which later disappears) as a probable homologue of the intercalary of reptiles. In spite of Parker's view that there does not appear a distinct intercalary (Parker's suprastapedial) in birds one is inclined to support Crompton in considering the transient structure an intercalary. The important fact here is that in the penguin the intercalary appears to arise independently of the pharyngo-hyal (otostapes).

RHIPIDISTIAN HYOID ARCH

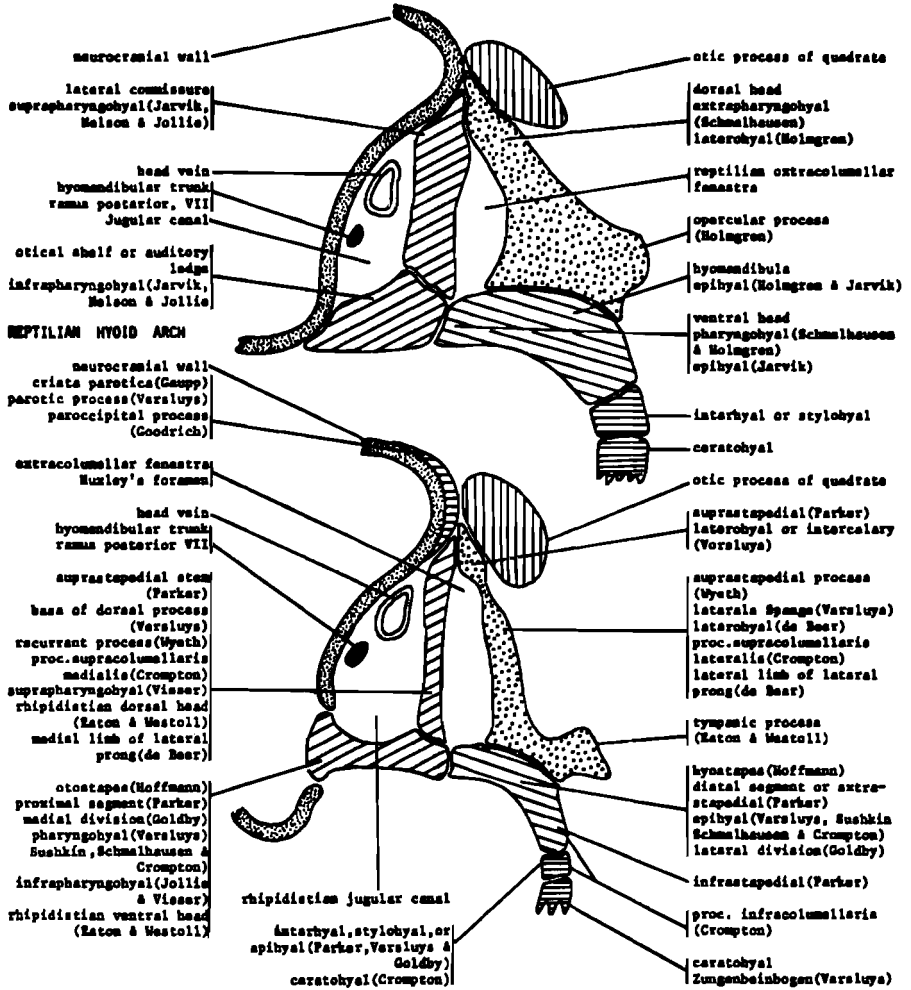


FIGURE 13

Diagram illustrating rhipidistian and reptilian hyoid arch derivatives and their synonymy.

The question now arises; if the intercalary is not derivable from the pharyngohyal (otostapes), and its separate origin is primary, what does it represent in a morphological sense? To answer the question we have to refer to fishes again. Holmgren (1943) found that to the posterior border of the crossopterygian hyomandibula is plastered a ray bar of which the upper part forms the upper (posterior) articular head and the lower part the opercular process. The upper articulation of the crossopterygian hyomandibula, he says, is thus between a hyomandibular ray and the neurocranium. The former is attached to the skull dorsal to the head vein.

According to Bertmar (1959) who made a detailed study of the development of *Neoceratodus*, the hyomandibula in adult Dipnoi and Teleostomi consists of an epihyal and a 'laterohyal'. The latter obtains a connection with the neurocranium dorsal to the head vein; caudally it forms a small opercular process. The laterohyal arises separately from the epihyal and comes from a subepidermal blastema and thus represents fused hyal rays. In Bertmar's opinion the laterohyal probably also forms the lateral (dorsal) articulation in crossopterygians. In this he follows Holmgren (1943).

Now if Eaton (1939) and Westoll (1943) are correct in homologizing the dorsal articulation of the crossopterygian hyomandibula with the upper end (intercalary) of the processus dorsalis of the reptilian columella, then we might consider the intercalary as being derived from a hyal ray. It is interesting to note that Reinbach (1950b) derives the anuran pars externa (according to him the homologue of the reptilian dorsal process) from a mandibular gill ray.

If one now recalls Versluys' (1903) description of a cell condensation in a very young *Lacerta* embryo (in which the dorsal process forms) extending from the skin towards the columellar blasteme (lateral to the head vein), one is compelled to reason that the so-called dorsal process is composed not only of hyoid arch material but that its tip includes a secondary addition of material from subepidermal mesenchyme which suggests the incorporation of hyal ray material.

The idea expressed here is that the intercalary (suprastapedial) represents a remnant of the hyal ray which assisted in the attachment of the rhipidistian hyomandibula lateral to the head vein. The suprastapedial stem (Parker 1883) which is ontogenetically clearly a derivative of the medial division of the columella (pharyngohyal) is considered the homologue of the supra-pharyngohyal. In Rhipidistia the hyal ray component of the hyomandibula is also attached proximally to the homologue of the suprapharyngohyal (the lateral commissure) (Figure 13.)

The lateral limb

Versluys (1898, 1903 & 1936) states that in Gekkonidae the ceratohyal (Versluys' Zungenbeinbogen), after it has become detached from the columella, does not remain free dorsally but grows upwards behind the tympanum towards the parotic process and becomes attached to a cartilaginous structure on the process. This cartilaginous structure is continuous with the intercalary but does not arise from it.

In *Sphenodon*, with a rudimentary tympanum, the ceratohyal remains continuous with the columella (Versluys 1898, 1903, 1936; Wyeth 1924). This continuity, according to Wyeth, persists throughout development and into the adult stage. The continuity must thus be considered as primary. The 'lateral prong' of *Sphenodon* has both a medial as well as a lateral limb (de Beer's laterohyal; Versluys' 'laterale Spange') with an extracolumellar fenestra (also called Huxley's foramen) between the two. Versluys compares the lateral limb in *Sphenodon* with the

upper part of the ceratohyal ('Zungenbeinbogen') in Gekkonidae. He considers the condition in *Sphenodon* to be the result of a similar upgrowing of the ceratohyal (which does not become detached from the columella as in Gekkonidae which Versluys considers as more primitive than *Sphenodon* in this regard) towards the parotic process and the intercalary while remaining in cartilaginous continuity with the extracolumella laterally.

Wyeth, however, describes the origin of the lateral limb (his suprastapedial process) as arising from the epihyal (extrastapedial) distally. According to Reinbach (1950 a & b) the lateral limb in *Sphenodon* (Reinbach's processus anterior) forms as a result of an upgrowing of the hyoid where, during development, the epihyal (Reinbach's pars externa or pars hyalis) meets the pharyngo-hyal (Reinbach's pars interna or pars otica), thus from the proximal end of the epihyal. Reinbach's description would seem to confirm Versluys' deduction.

In *Crocodylus* (Parker 1883; Versluys 1903; Goldby 1925; de Beer 1937) the interhyal (Parker's 'epihyal') or connecting piece between the epihyal (infrastapedial) and the ceratohyal loses its cartilaginous continuity with the epihyal and becomes connected to the supratharyngo-hyal by means of a ligament. In this way the lateral limb (laterohyal of de Beer) to 'Huxley's foramen' is formed. According to Reinbach (1950b) the 'hyoid' (interhyal?) in *Crocodylus* grows upwards behind the tympanum and connects with the 'dorsal process'.

Both Versluys (1903 & 1936) and de Beer (1937) compare conditions in *Crocodylus* with conditions in Gekkonidae and *Sphenodon*. According to them the so-called 'laterohyal' in all these forms represents the tip of the ceratohyal. Even at this stage one has difficulty in agreeing with Versluys and de Beer. Conditions in *Crocodylus niloticus* are slightly different from those described by Parker, Versluys and Reinbach in other species of *Crocodylus*. The interhyal (Parker's epihyal) is still (in the oldest embryo examined) (Figure 12: *inter*) in cartilaginous continuity with the distal tip of the epihyal (infrastapedial), but very conspicuous is a ligament (Figure 11: *lig*) connecting the epihyal-interhyal with the distal tip of the suprastapedial complex. The latter curves more and more postero-ventrally until its distal tip almost meets the epihyal-interhyal, thus creating the impression of a lateral limb.

In most birds a cartilaginous continuity exists throughout life between the columella auris and the upper end of the ceratohyal (Versluys 1903; Marinelli 1936). The continuity in birds (cf. *inter alia* Parker 1883; Goodrich 1915; Gaupp 1906; Toerien 1971) is, however, between the distal tip of the epihyal (infrastapedial) and the interhyal or stylohyal (so-called 'epihyal tip of the ceratohyal of some authors) as in *Crocodylus*. Conditions in *Spheniscus demersus* are (in spite of what Crompton states) probably the same as in birds generally. A cartilaginous continuity between the columella and the interhyal (Crompton's ceratohyal) persists as the processus infracolumellaris.

Conditions in birds are interesting; they resemble *Sphenodon* in the possession of a lateral limb (the avian processus supracolumellaris lateralis) but on the other hand they resemble *Crocodylus* in the partial atrophy of the ceratohyal. Such a situation is difficult to assess. Again Versluys (1903) and de Beer (1937) are inclined to homologize the lateral limb (laterohyal of de Beer, laterale Spange of Versluys) of birds with the interhyal (so-called 'epihyal') in *Crocodylus* and the lateral limb of the extracolumellar fenestra in *Sphenodon*. It must now be clear from the above that the homology between the crocodylian interhyal and the avian processus supracolumellaris lateralis cannot be accepted - birds have both. The same can be said of *Sphenodon*

where the homologue of the reptilian interhyal must be present in the continuous hyoid arch. Ontogenetically the processus supracolumellaris lateralis in birds arises ostensibly from the epihyal (distal segment of the columella). What does this structure (as well as the 'lateral limb' in *Sphenodon*) represent in a morphological sense?

In order to throw more light on the problem we have to return to the condition in fish. In hyostylic rhipistidian fish the ceratohyal (posterior ceratohyal – Jarvik 1954) as well as the quadrate are attached to the distal end of the hyomandibula (Westoll 1943; Eaton 1939). Between the hyomandibula (epihyal) and the ceratohyal a separate interhyal or stylohyal occurs (Jarvik 1954). This situation could have been retained in the first tetrapods where hearing was most probably effected through bone conduction only (Tumarkin 1968).

If we accept Tumarkin's view that the first tetrapods depended on bone conduction, functional continuity demands the coexistence in time of a bone-conducting mechanism as well as an air-conducting mechanism during the transition from bone-conduction to air-conduction among tetrapods. This transitional stage could have appeared already among the labyrinthodonts where indications of the presence of a tympanum exist (Sushkin 1927; Barry 1963). Tumarkin's suggestion that all tetrapods – amphibians and reptiles – made use of bone-conduction only up to almost the end of the Permian seems highly improbable. It is, however, clear from Sushkin (1927) that bone-conduction remained a very important mechanism in synapsid (quadrate-columellar conduction) and early 'diapsid' (hyoid-columellar conduction) reptiles. The ancestral 'diapsid' line (lines) seems to have retained the original ceratohyal-hyomandibular junction (through the interhyal) and to have combined air-conduction with hyoid-columellar conduction.

In the light of the above it is contended here that *Sphenodon* (with hyoid columellar continuity) represents the primitive lepidosaurian condition. This view is in agreement with Gaupp (1913), Goodrich (1930) and Tumarkin (1968). It rejects Versluys' theory (1903) which considers the *Sphenodon* condition as secondary since it evolved from a 'primitive lacertilian' condition with a detached ceratohyal. The gekkonid condition where the ceratohyal attaches to the parotic process (not to the columella) as well as the condition where the ceratohyal ends free dorsally (as in most lacertilians – Versluys 1903; Gaupp 1913) must be considered secondary.

We must visualize a primitive lepidosaurian (or rather 'diapsid') condition where the ceratohyal is attached to the columella and where the 'lateral prong' is composed of both a medial and a lateral limb. From such a basic pattern can be derived not only the *Sphenodon* condition but all lacertilian types (cf. Barry 1963; Olson 1966; Gans & Wever 1972) as well as conditions in crocodiles and birds.

The complete absence from the earliest embryonic stages of the ventral ends of the hyoid arches (basi- and hypohyals) in *Crocodylus niloticus* (unpublished data) and the embryonic cartilaginous continuity between the ceratohyal and Meckel's cartilage suggests a secondary strengthening of bone-conduction in archosaurian ancestors with the substitution of the ventral ends of the mandibular arch as a conduction route in the absence of the basi-hypohyal complex. This linking of the more posterior cerato-elements by means of so-called terminal commissures is common in urodeles (Fox 1959). Crocodiles and birds (and probably dinosaurs) must have later returned to exclusive air-conduction as a result of the atrophy of the ceratohyal but with retention of the interhyal.

Holmgren (1943) expresses the view that the processus opercularis in Rhipidistia is derivable

from hyal ray (laterohyal) material. This is, according to Bertmar (1959), also the case in Dipnoi and Teleostomi. Eaton (1939) and Westoll (1943) derive the insertion plate (Westoll's *processus tympanicus*) of the reptilian columella auris from the rhipidistian opercular process. If this is so then the reptilian tympanic process should also represent (or at least include) laterohyal material.

According to Romer (1941) Eaton's view cannot be validated by available fossil evidence and to our knowledge the situation has not changed. One is thus compelled to test Eaton's theory with ontogenetic evidence. Again the evidence is scanty, but significant. In both *Struthio* (unpublished data) and in *Crocodylus niloticus* the blasteme giving rise to the tympanic process (*processus extracolumellaris* in birds) arises from a sub-epidermal delamination situated ventrolaterally on the dorso-lateral aspect of the curved epihyal and lags slightly behind in development if compared with the epihyal and the interhyal. The traditional opinion that it represents hyoid arch (epihyal) material does not seem likely from the specimens at our disposal. Since the tympanic process appears to include laterohyal material there is much merit in Eaton's theory.

It is the opinion of the authors that the lateral limb part of the lateral prong does not represent the tip of the ceratohyal, nor is it homologous with the interhyal (Parker's epihyal) of *Crocodylus*. The structure arises ontogenetically in *Sphenodon* and birds on the lateral aspect of the columella (*cf.* Wyeth 1924; Crompton 1953) and must consist of laterohyal material. The structure is absent or reduced in *Crocodylus* and is probably represented by the pars superior of the insertion plate of *Lacerta* (*cf.* also Parker 1879; Crompton 1953).

From what has been said above it follows that the lateral limb (together with the intercalary) constitutes a morphological entity which represents the dorsal or lateral articular head of the rhipidistian hyomandibula. The presence of a lateral limb is therefore, a primitive characteristic. It is incorrect to state categorically that the reptilian dorsal process is the homologue of the rhipidistian dorsal (lateral) articular head.

The presence of the so-called extracolumellar fenestra or Huxley's foramen can now also be explained morphologically (the chorda tympani does not pass through it as claimed by Baird, 1970). It must represent the original passage between the two articular heads of the rhipidistian hyomandibula; it has exactly the same boundaries; laterally, the so-called lateral limb originating from the laterohyal blasteme (the *processus supracolumellaris lateralis* of birds, laterohyal of *Sphenodon* and the dorsal articular head of the rhipidistian hyomandibula); medially, the so-called medial limb originating from the suprapharyngohyal blasteme (the *processus supracolumellaris medialis* of birds, base of the lacertilian dorsal process and the lateral commissure of Rhipidistia); ventrally the proximal end of the extrastapedial from epihyal blasteme (the hyostapes of reptiles and birds and the ventral articular head of the rhipidistian hyomandibula).

A word on the lacertilian internal process (quadrate process) is necessary. From the foregoing it must be clear that the *processus internus* cannot represent the original hyomandibula-quadrate connection. It is a secondary structure that evolved later in lacertilian ancestors since, according to our theory, the original hyomandibula-quadrate junction was discarded in the lepidosaurian line. However, the most convincing evidence against the 'original junction' view is the fact that the internal process arises from the pharyngohyal (otostapes) (Versluys 1903 & 1936) whereas the original junction lay between the epihyal (hyomandibula) and the quadrate. *Sphenodon*, where the internal process is lacking (Versluys 1903), most probably represents the primary condition.

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