THE MORPHOGENESIS OF THE AVIAN COLUMELLA AURIS WITH SPECIAL REFERENCE TO *STRUTHIO CAMELUS*

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ABSTRACT

The columella auris of the ostrich is derived as in the crocodile from three sources; the two upper segments of the hyoid arch (pharyngohyal and epihyal) and a laterohyal component. The latter contributes the homologue of the crocodilian suprastapedial (or lacertilian intercalary) as well as the tympanic process and the material of the lateral limb (which is not lacking as stated in the literature) of the lateral prong (supracolumellar arcade). Conditions in *Struthio camelus* confirm the views expressed by the authors in their paper on *Crocodilus niloticus* regarding the homologies of the columellar processes. The avian infracolumellar process represents the crocodilian infrastapedial plus the interhyal which in addition to primary arch material, includes a secondary subepidermal part. The ceratohyal (usually called stylohyal in the literature) remains attached to the columella through the infracolumellar process.

INTRODUCTION

Despite the mass of evidence that has accumulated in the literature devoted to the development and anatomy of the columella auris of birds, great uncertainty still exists with regard to the exact homology of its constituent parts. As yet no unifying concept of the calibre of the Reichert-Gaupp thesis (Gaupp 1913) on the mammalian auditory ossicles has appeared. Unfortunately, with the increase in literature there has been a corresponding increase in terminological and interpretational confusion. As Toerien (1971) has remarked, the terminology of this region in birds is probably more confusing than any other domain of vertebrate morphology. The present investigation was thus undertaken with some trepidation. Although it deals with the ontogeny of the ostrich columella it is also a tentative attempt to bring some order into the chaos existing in the literature and to collate previous workers' results. Hopefully the unified concept presented here will stimulate others into an investigation of its validity.

MATERIAL AND METHODS

The microtome sections used in this work are those prepared by one of the authors in 1952 and housed in the Zoological Institute of the University of Stellenbosch. Our grateful thanks to Professor C. A. du Toit for the loan of this material. A full description of the material and its preparation may be found in a paper by Frank (1954).

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At the earliest stage in which the various components of the hyoid arch anlage become differentiated (6,8 mm embryo, Figure 1) the hyomandibular trunk of VII (*hyo*) passes freely over the infrapharyngohyal (*infra*) but the orbital artery (*orb art*) appears, at this stage, to pierce the general blastematous infrapharyngohyal condensation; it is thus possible to speak of a stapedial fenestra (not shown in Figure 1). A general laterohyal blasteme lies laterally, extending between the distal tips of the suprapharyngohyal (*supra*), the epihyal (*epi*), and the most proximal parts of the external auditory meatus or depression (*meatus*) (see also insert in Figure 3 and consult Figure 10 for orientation).

Evidence of active cellular delamination from the most dorso-distal portions of the pharyngeal pouches is very distinct in the ostrich. This is especially true in the earliest stages when only a general condensation of mesenchyme is visible below the otic vesicle and anterior to both the spiracular and first branchial pouches. There are, for instance, clear signs of cellular streaming towards the pharyngohyal blasteme (and the otic process of the quadrate). These delaminating cells together with a later subepidermal addition from the region of the future tympanic membrane (see later) form the laterohyal blasteme, which according to Bertmar (1959) probably includes original gill-ray material.

When the suprapharyngohyal (*supra*), and the distal delaminating laterohyal blasteme (*lat lim*) associated with it, first appear (Figures 1 and 2), they are closely applied to the posterodorsal tip of the spiracular diverticulum (*spir poc*). However, the latter's basement membrane is intact at this point and no delamination seems to be taking place from this area. As shown in Figure 1 the homocontinuous anlagen of the intercalary (*supra & intercal*) and tympanic process (*tymp proc*) derived from the laterohyal blasteme are slightly more advanced than that of the lateral limb (*mesen*) itself. Immediately medio-ventral and quite discrete, lies the epihyal element (*epi*) which in turn is attached by less dense mesenchyme to the ceratohyal anlage (*cerato*). The mesenchyme (*mesen*) which links these two elements is more concentrated on the medial surface of the epihyal in a manner strongly reminiscent of the interhyal blasteme of the crocodile. In the latter animal the interhyal develops from a distinct, medially directed knob of dense mesenchyme (Frank & Smit 1974). In the ostrich this portion of the arch blasteme reveals the same characteristics but is not as discrete in appearance.

In a slightly older 9,2 mm embryo (Figure 3) there is still distinct cellular streaming, in wide arcs, from blastematous areas subjacent to the epidermis ventral to the tympanum and to the antero-dorsal and ventral surfaces of the dorsal spiracular diverticulum (these surfaces lack basement membranes; a characteristic of active delamination according to Jollie, 1971) towards the suprapharyngo-, epi- and interhyal blastemes (*supra, epi, inter*). There is thus direct evidence of cellular delamination from below epithelia of both ectodermal as well as endodermal origin. However, as mentioned earlier the posterodorsal surface of the diverticulum appears to contribute no delaminating material. Conditions at this stage are very similar to those existing in early crocodilian embryos; the ceratohyal's proximal tip (*cerato*) lies medial to the distal tip of the interhyal blasteme (*inter*), and the distal tip of the suprapharyngohyal (*supra*) lies immediately postero-ventral to the dorsal diverticulum of the spiracular pouch (*spir poc*). The tympanic membrane will develop at the end of the external auditory meatus (at this stage only a superficial

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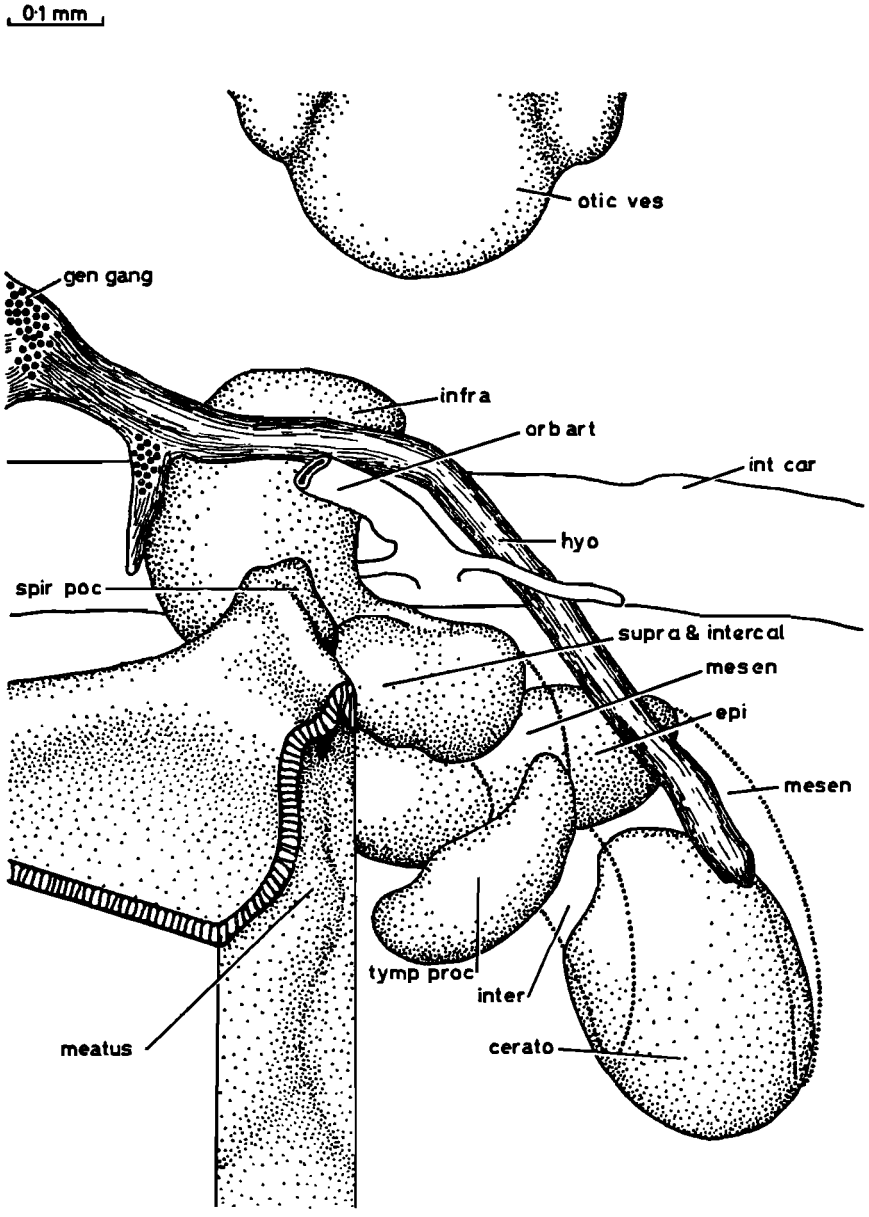

FIGURE 1

Thick sagittal section of the 6,8 mm embryo showing the lateral aspect of the hyoid arch anlage and related structures. Delaminating blasteme (shown with dotted lines) is streaming in the region of the tympanic process and suprapharyngohyal. Portions of the spiracular pouch and external auditory meatus are also shown. For abbreviations see page 182.

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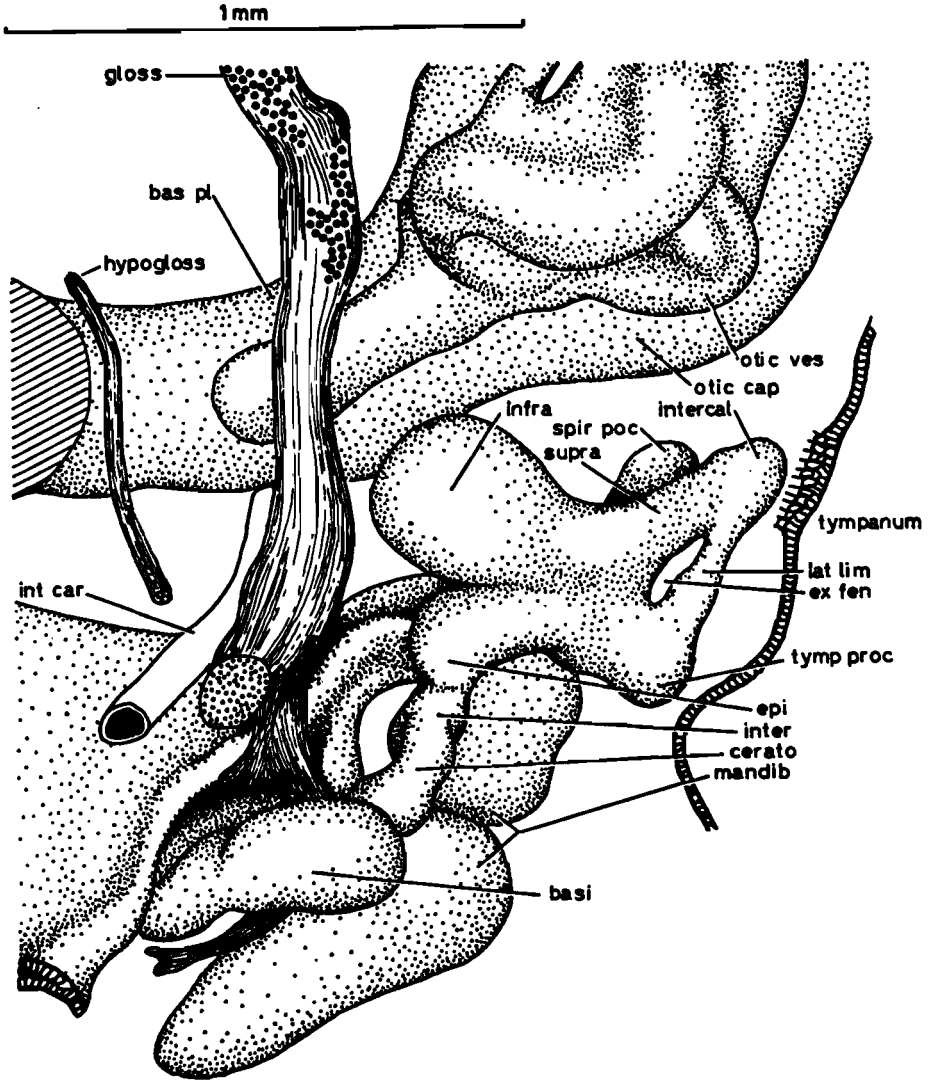

FIGURE 2

Posterior aspect (looking craniad) of the columella auris of an 8,2 mm embryo. Part of the pharynx, spiracular pouch and developing external auditory meatus have been included. There is subepidermal delamination proceeding in the region of the developing tympanum. That part of the interhyal lying in front of the ceratohyal consists of dense mesechyme. For abbreviations see page 182.

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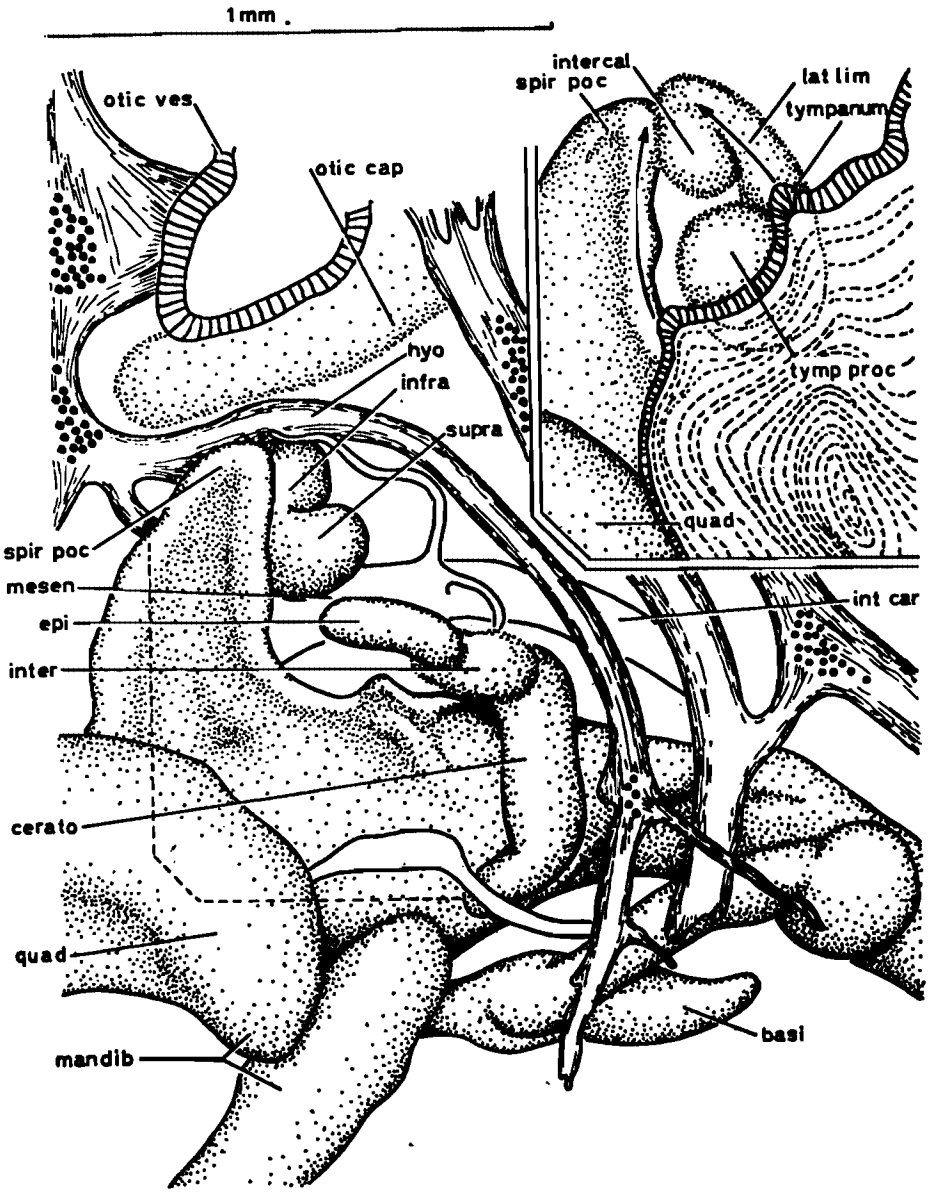

FIGURE 3

Lateral view of the procartilaginous hyoid arch anlage of a 9,2 mm embryo with the densely mesenchymatous laterohyal blasteme shown separately in the insert. In the latter diagram arrows mark the direction of streaming blasteme from the area of the future tympanum towards the laterohyal. For abbreviations see page 182.

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depression) somewhat ventro-lateral to the spiracular diverticulum and adjacent to the incipient tympanic process (Figure 3 insert: *tymp proc*).

In reconstructions made from transverse sections (8,2 mm embryo, Figure 2) the various elements of the developing columella auris are easier to identify. A well-developed supra- plus infra-pharyngohyal (*supra & infra*) are joined by less dense mesenchyme to the epihyal (*epi*). The laterohyal blasteme to which delaminating cells are still being contributed forms a lateral limb (*lat lim*), an intercalary (*intercal*) and an incipient tympanic process (*tymp proc*). Between the anlagen of the medial (*supra*) and the lateral limbs (*lat lim*) lies an area of less dense mesenchyme which represents the extra-columellar fenestra or Huxley's foramen (*ex fen.*). The inter- and ceratohyal (*inter & cerato*) are characteristic in appearance and position and can be easily identified at this stage. Both have a small core of procartilage surrounded by a mass of deeply stained mesenchyme. Sagittal sections from a slightly larger embryo (8,4 mm, not reconstructed) shows that this mesenchyme actually links the ceratohyal with the retroarticular process of Meckel's cartilage as it does in the crocodile.

The three main elements of the hyoid arch of the ostrich are most clearly observed in a 9,2 mm embryo. These are the pharyngo-, epi- and ceratohyal (Figure 3: *supra, epi, cerato*). They are joined by less dense mesenchyme of which that part lying between the epi- and ceratohyal is particularly noticeable and has been identified as representing the interhyal (*inter*). The latter, unlike in the crocodile, gradually loses all traces of separate identity as development proceeds and when chondrification sets in becomes intimately connected with the epihyal above and the ceratohyal below. The nebulous laterohyal blasteme lies between the main arch anlage and the epidermis on the outside, especially in the area where the tympanum will form in later stages. As previously mentioned (page 160) there is, particularly in this stage (9,2 mm, Figure 3 insert), active delamination taking place between the area of the external auditory meatus and the laterohyal blasteme.

The head vein (*hd vein*), orbital (stapedial) artery (*orb art*) and hyomandibular trunk (*hyo*) curve down over the columella auris in this region (Figures 6–9) but they are not closely associated with it. The next significant development is a lengthening, similar to that in the crocodile, of the ceratohyal. When this occurs neither the otic capsule (*otic cap*) nor the various elements of the hyoid arch are more than very dense mesenchyme but the epi-, inter- and ceratohyal are rapidly losing their separate identity (10,7 mm embryo, Figures 4 & 5: *epi, cerato*). The laterohyal is, however, still distinguishable by its mesenchymatous nature (Figure 6: *lat lim*). A small discontinuous part of this blasteme, still receiving delaminating increments, lies above the pharyngohyal and immediately medial to the orbital artery (Figure 4: *intercal*). It appears to belong to the laterohyal blasteme and probably represents the autonomous anlage of the intercalary but its exact significance is uncertain. It is absent in later stages.

Transverse sections of a slightly older embryo (11,6 mm, Figure 7) reveal that the extra-columellar fenestra has disappeared, the area having become filled with denser mesenchyme (*mesen*). Both the intercalary (*intercal*) and tympanic portions (*tymp proc*) of this laterohyal blasteme are extending laterad. The intercalary lies immediately posterior to the otic process of the quadrate (*otic proc*) while the latter is applied to the developing tympanic membrane (see also Figure 8: *tymp proc*). Horizontal sections of a 12,3 mm embryo reveal that the pharyngo- and epihyal anlagen (Figure 8: *infra, supra & epi*) have not yet completely fused with each other.

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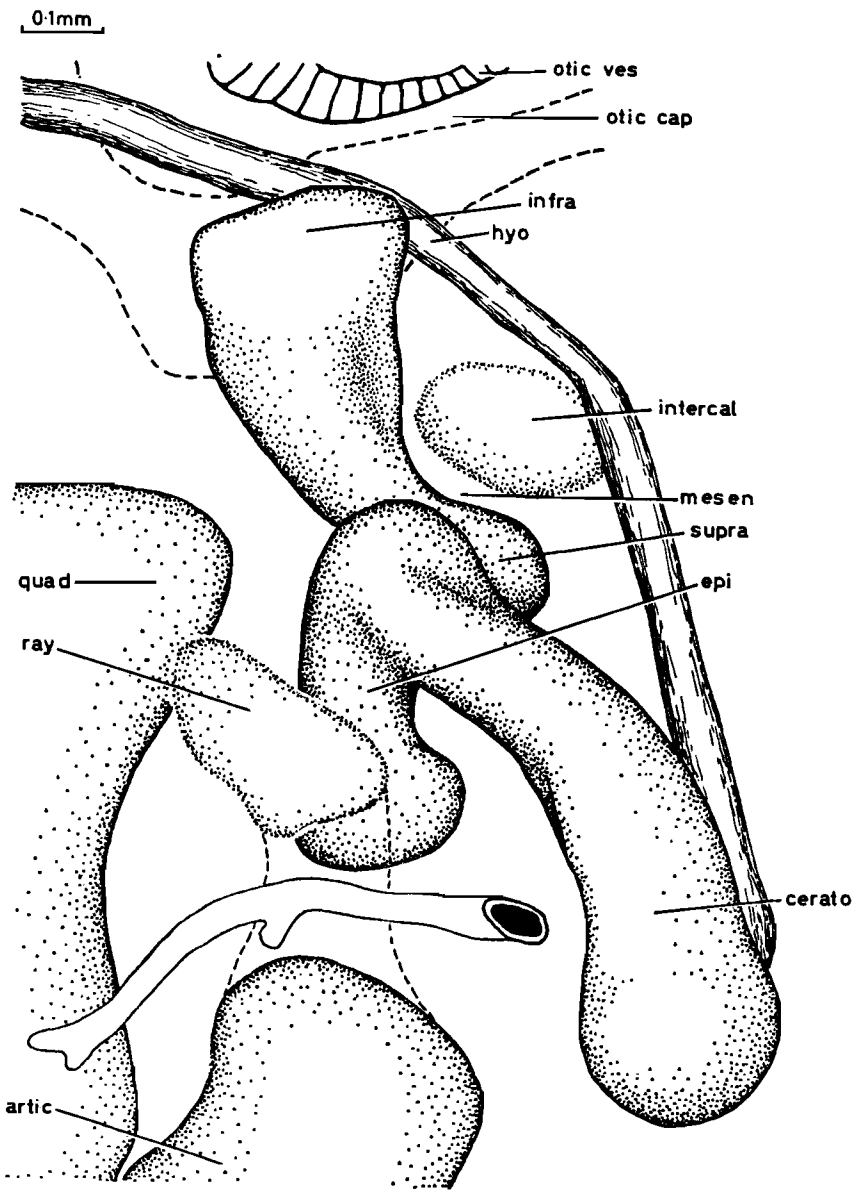

FIGURE 4

Thick sagittal section from a 10,7 mm embryo to show the medial aspect of the hyoid and mandibular arch anlagen. The dense blasteme identified as the intercalary is without matrix; the suprapharyngohyal appears to condense in its more ventral parts. A similar blasteme is associated with the retro-articular part of Meckel's cartilage. It has been provisionally identified as a mandibular ray. For abbreviations see page 182.

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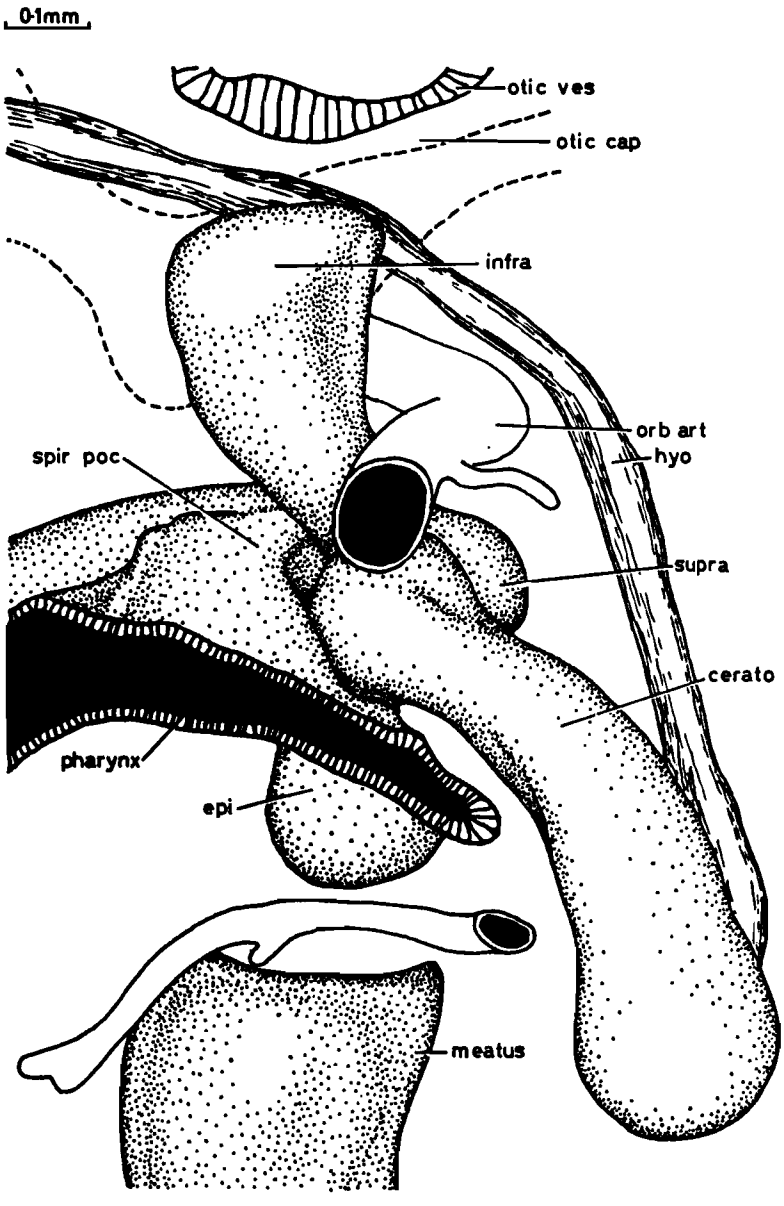

FIGURE 5

Thick sagittal section similar to Figure 4 but with the spiracular evagination and external auditory meatus inserted. Much delamination seems to be taking place from the posterior edge of the spiracular pocket towards the pharyngohyal, epihyal and interhyal. The mandibular ray (Figure 4) lies immediately anterior to the pocket and is receiving no subepidermal contributions. For abbreviations see page 182.

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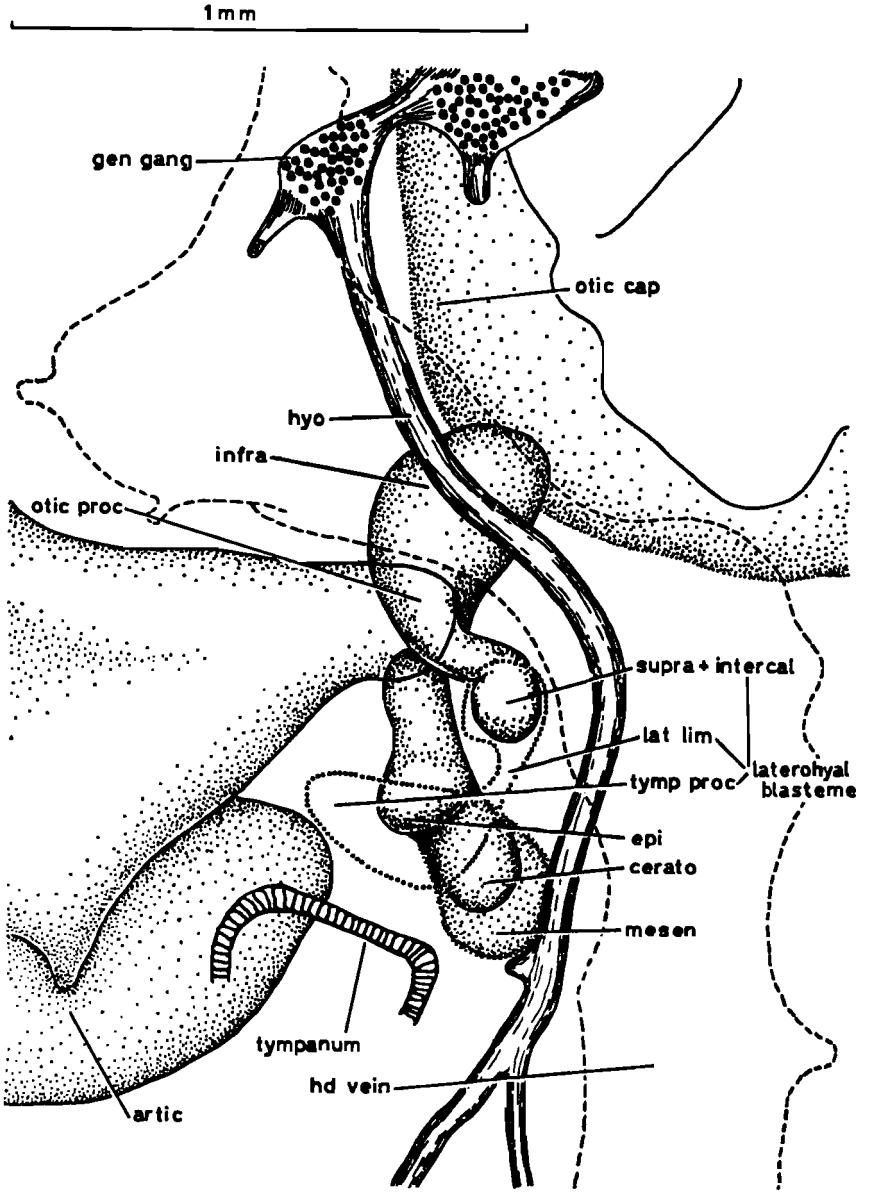

FIGURE 6

Dorso-lateral view of the developing columella auris of an 11,0 mm embryo with the laterohyal blasteme, tympanic area and head vein shown in outline. The otic process of the quadrate has also been left in outline. In these sections the interhyal appears as a dense mediad-directed mesenchymatous anlage. For abbreviations see page 182.

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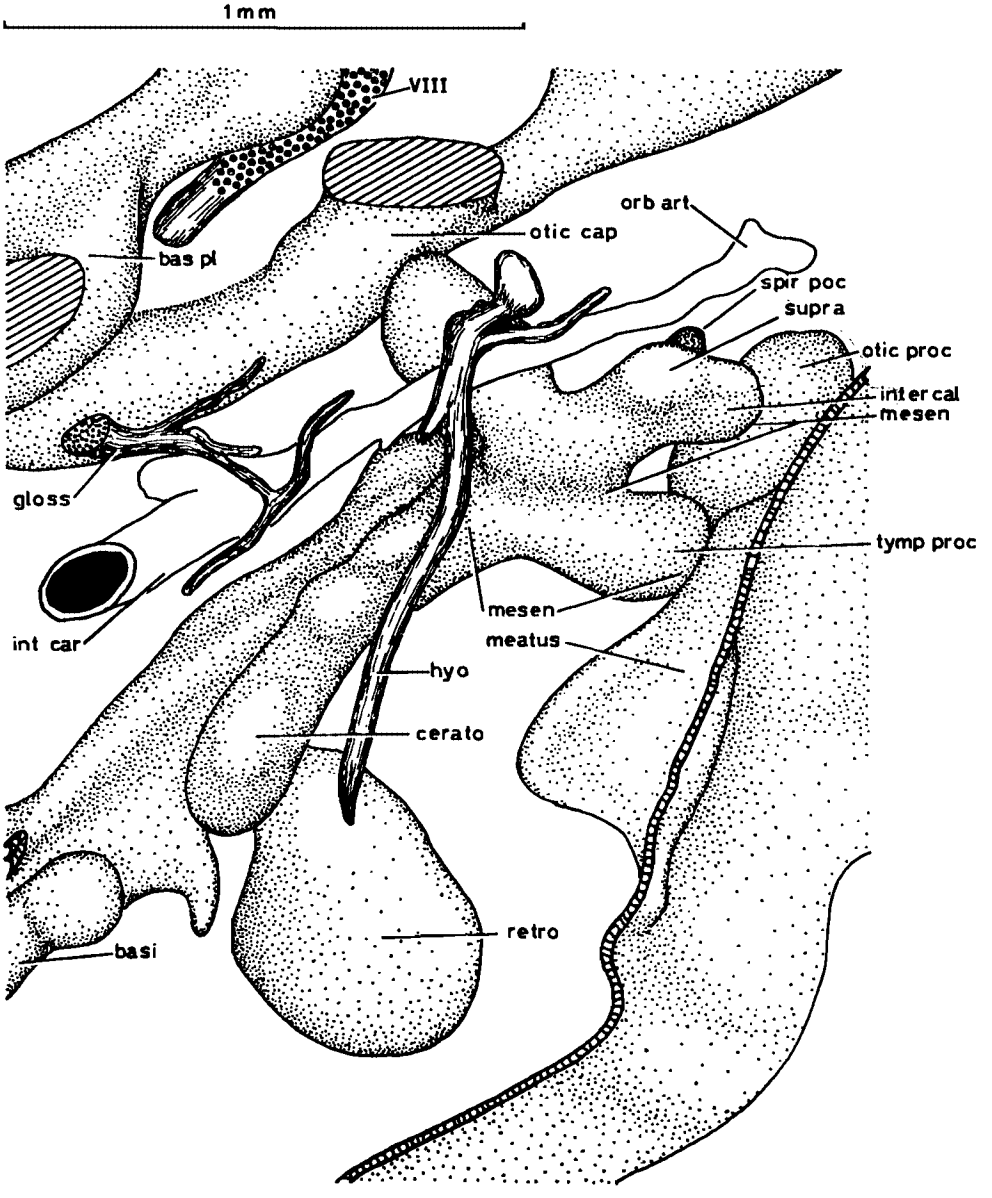

FIGURE 7

Thick fronto-transverse section from an 11,6 mm embryo showing the developing columella auris and associated structures from behind looking craniad. The line of contact between the pharyngohyal and epihyal is still mesenchymatous, as is the homocontinuous interhyal link between epihyal and ceratohyal. For abbreviations see page 182.

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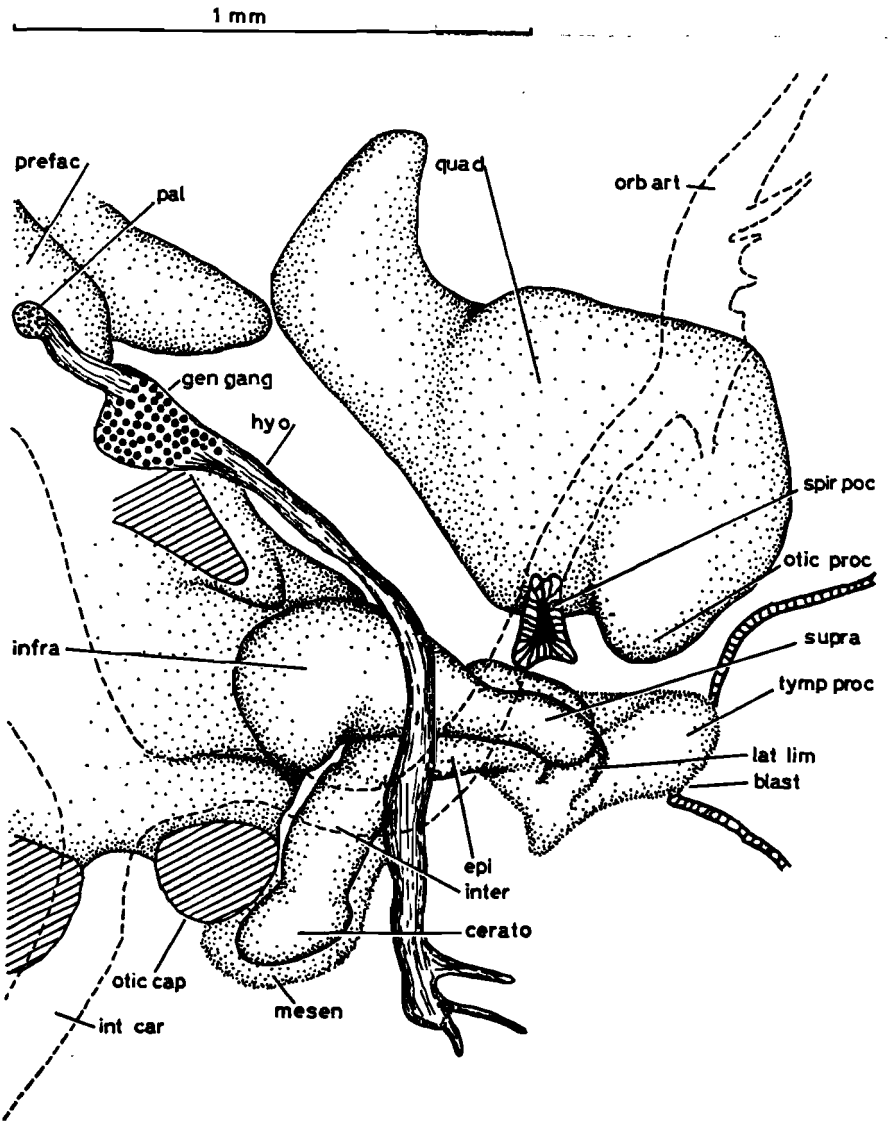

FIGURE 8

Dorsal view of the columella auris and associated structures of a 12,3 mm embryo with the course of the internal carotid and orbital arteries superimposed in outline. Mesenchymatous laterohyal blasteme still receiving delaminated material from the tympanic area is shown by stippling. For abbreviations see page 182.

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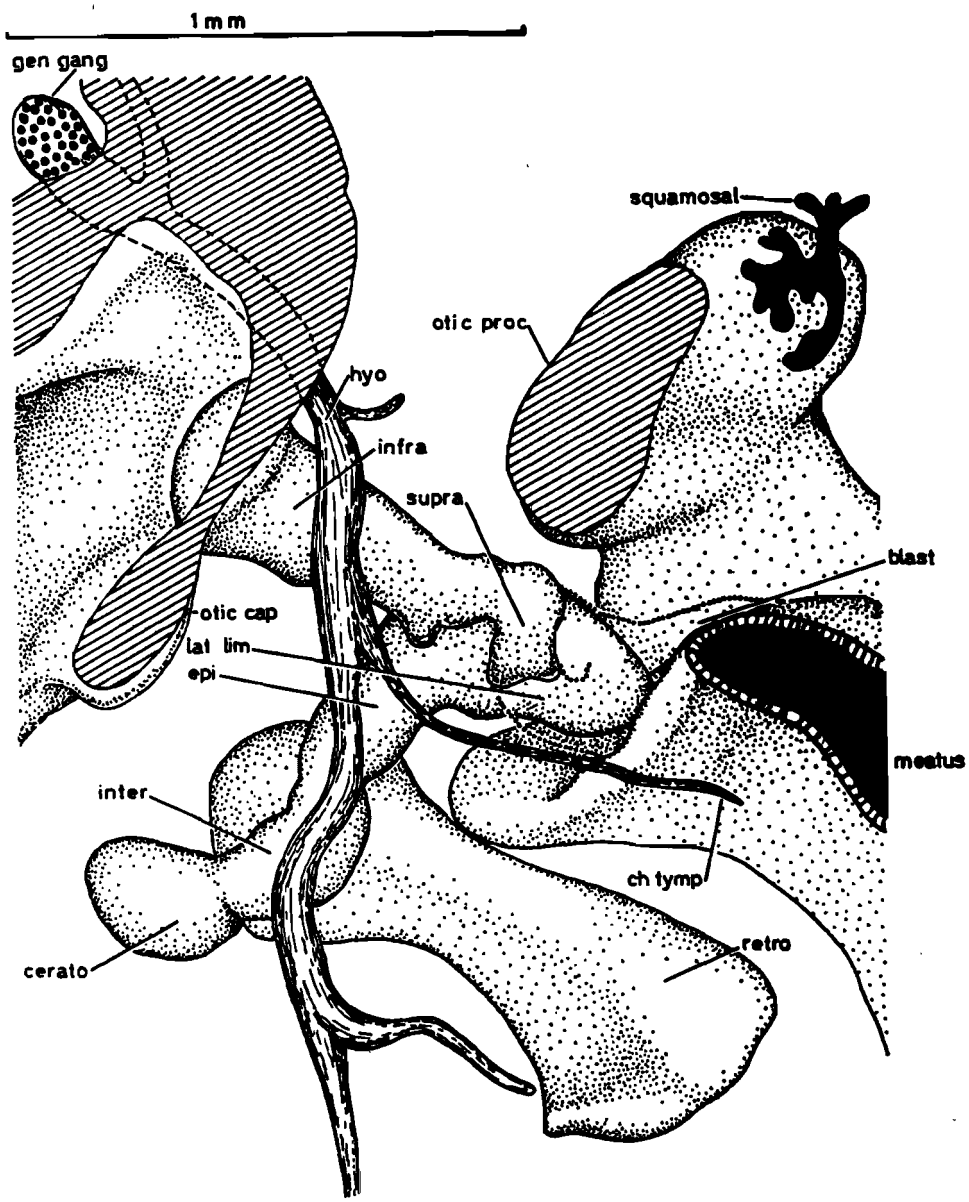

FIGURE 9

Postero-dorsal aspect of the almost fully formed columella auris of a 15,5 mm embryo, looking anteriad. The various arch elements are not yet fully homocontinuous. The tip of the suprapharyngohyal curves ventrad, as it does in the crocodile, and is distally continuous with the laterohyal blasteme. Between the latter and the area of the future tympanum there is much subepidermal activity. For abbreviations see page 182.

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Likewise the interhyal is still identifiable as a more mesenchymatous area within the epi-ceratohyal anlage (*cerato*).

At a later stage (Figure 9) the epi-, inter- and ceratohyal elements (*epi*, *inter*, *cerato*) have become more or less homocontinuous with only slight constrictions marking the points of transition. Separate anlagen for the pharyngohyal and epihyal (*infra*, *supra* & *epi*) are, however, still discernible, joined by less dense mesenchyme. As in the crocodile the interhyal, at this stage, has a characteristic C-shape and the boundary between the epi- and interhyal lies on the ventral edge of the tympanum. The extreme tip of the suprapharyngohyal (*supra*) curves ventrad and passes over into the dense mesenchyme of the lateral limb (and intercalary blasteme?) which is still receiving delaminating cells from the sub-epidermal blasteme of the area of the external auditory meatus (*meatus*). The tip of the tympanic process which appears as a direct extension of the epihyal is also in homocontinuity with this delaminating mesenchyme.

No extra-columellar fenestra can be positively identified in these sections (15,5 mm embryo) but it is possible that with sections cut at exactly the correct angle a thinning of the mesenchyme may still be visible. It would in any case appear that the so-called 'dorsal process' of the ostrich is definitely of dual origin, receiving contributions from both suprapharyngohyal and laterohyal blastemes. A chorda tympani nerve has been provisionally identified (Figure 9: *ch tymp*) as the nerve branching from the hyomandibular trunk; it has the characteristic origin and course over the columella, but unfortunately has not yet reached the lower jaw.

Sagittal sections from a 21 mm embryo (Figure 10) show great similarity with the crocodile at a similar stage of development. The 'dorsal process' (*supra*) has developed a broad flange, the ventral tip of which lies in the edge of the tympanum. This whole process, which shows no sign of a supracolumellar fenestra, lies posterior, not dorsal, to the columella near the metotic cartilage. The tympanic process too, like that of the crocodile, has an extended ridge in contact with the tympanum. The distal tip of the ceratohyal ends freely and far medial to the retroarticular process of Meckel's cartilage.

DISCUSSION

Of all parts of the avian columella auris, the greatest confusion and uncertainty revolves around the distal, cartilaginous part, the extracolumella. In the light of the present work it has become clear that the extra-columella in the ostrich is derived, as it is in the crocodile (Frank & Smit 1974), from three sources:

(1) A contribution from the pharyngohyal blasteme (Hoffman's otostapes) which includes the medial limb of De Beer's (1937) lateral prong; called by Crompton (1953) and Müller (1963) the processus supracolumellaris medialis. This process represents the suprastapedial stem (but not the suprastapedial as such) of the crocodile (Parker 1883; Sonies 1907; Frank & Smit 1974) as well as the ligamentum intercalare-columellare of lizards (Dombrowsky 1925; Freye 1952/53) (Figures 2 and 11).

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(2) An epihyal representing the fish hyomandibula and contributing to the stem of the columella. Distally this goes over into the proximal part of the so-called infracolumellar process of birds. This proximal part of the process represents the infrastapedial (or infrastapedial process) of the crocodile (Parker 1883; Frank & Smit 1974) (Figures 2 and 11).

(3) The laterohyal component which forms the lateral limb: the processus supracolumellaris lateralis of Crompton (1953), or the laterohyal process of the lateral prong of De Beer (1937). In addition it contributes to the homologue of the lacertilian intercalary (the crocodilian suprastapedial) and the tympanic process. The latter term has been recommended by Frank & Smit (1974) after Westoll (1943) in preference to the term 'extracolumellar process' commonly used in avian terminology, as the latter is liable to be confused with Versluys's (1903) 'extracolumella' which represents the entire cartilaginous distal part of the adult columella auris.

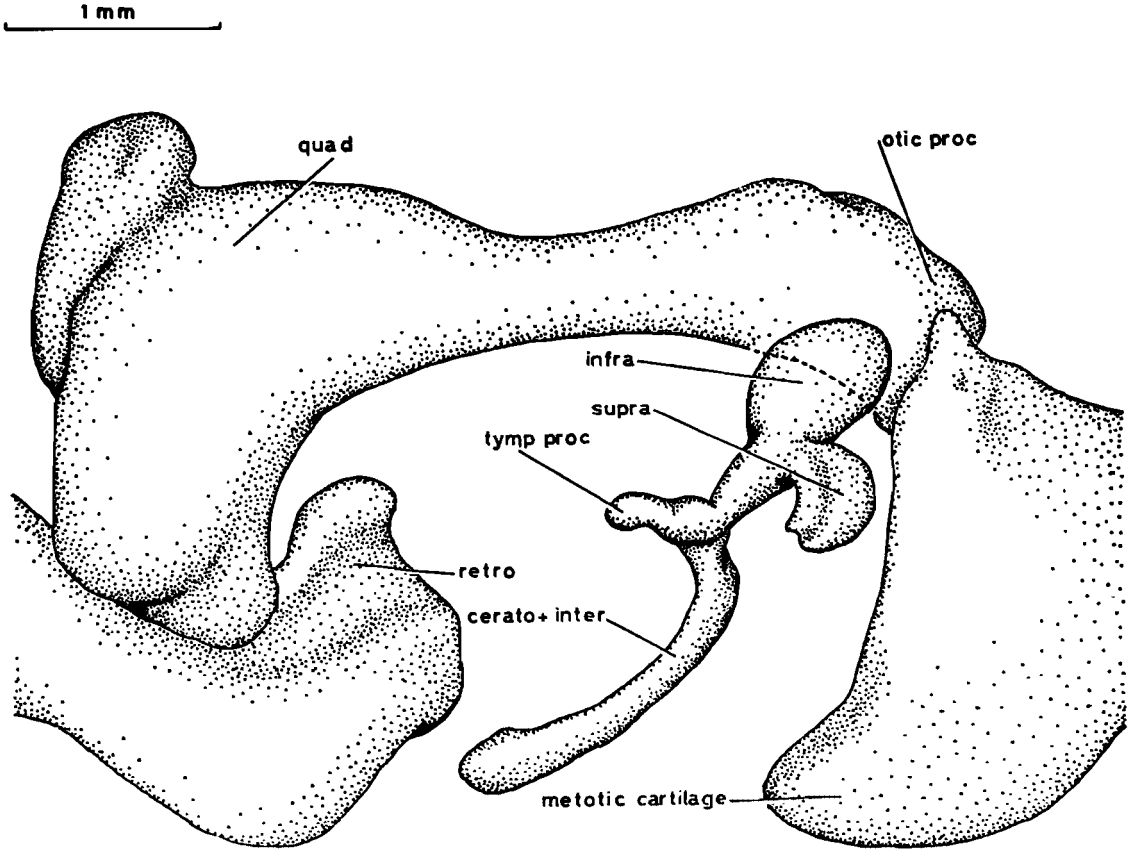

FIGURE 10

Lateral view of the quadrate, metotic cartilage and columella auris in a 21 mm embryo. The distal tip of the ceratohyal lies far medial to the retro-articular process of the lower jar. For abbreviations see page 182.

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The columellar stem

As in the crocodile (and reptiles generally) the avian columella is essentially a hyoid (and hyoid-associated material) derivative. The fact that 'a few cells' of the stapedial footplate may be of capsular origin (cf. Toerien 1971) does not detract from the validity of the statement and should not be elevated to such a level of importance that it confuses the issue.

The adult avian columella auris is roughly divisible into a proximal bony stapes, De Beer's (1937) medial prong, and a distal cartilaginous extra-columella bearing the so-called supracolumellar process which comprises both limbs of De Beer's lateral prong. In their paper on the crocodile, Frank & Smith (1974) point out how much confusion has resulted from the indiscriminate and erroneous use of the term extrastapedial as an alternative to extracolumella. Similarly in the literature on birds we find at the one extreme, Huxley (1869) whose extrastapedial includes, in addition to Parker's extrastapedial part of the proximal primary segment of the columella (Hoffmann's otostapes) and, at the other extreme, Schestakowa (1934) who uses the term 'extrastapedial' for little more than the derivatives of the laterohyal blasteme, that is, the tympanic process and lateral limb but excluding the epihyal.

In the early ostrich embryo (Figures 1, 2 & 3) the discrete blastematous anlagen of the two uppermost elements of the hyoid arch, *viz.*, the proximal pharyngohyal (infrapharyngohyal plus suprapharyngohyal) and the more ventrolateral epihyal correspond in every way to the similarity named parts in the crocodile (Frank & Smit 1974). They also coincide with Parker's (1883) proximal and distal segments (or extrastapedial) as well as Hoffman's (1889) oto- and hyostapes. The possibility that the stapes represents an infrapharyngohyal and not the rhipidistian hyomandibula (*i.e.*, an epihyal) as implied in the older literature (cf. *inter alia* Gaupp 1898; Smith 1905; De Burlet 1934) has been fully dealt with in a previous paper (Frank & Smit 1974). On this theory the epihyal contributes to the extracolumella of the adult, forms the proximal part of the infracolumellar process and receives laterohyal accretions.

In spite of the fact that already in 1903 Versluys had clearly pointed out that in lizards the boundary between the cartilaginous extracolumella and the bony stapes is secondary and does not represent the original boundary between Hoffmann's otostapes (pharyngohyal) and hyostapes (epihyal), considerable confusion in the use of these terms still exists today. Versluys demonstrated that the lacertilian dorsal process, a derivative of the distal part of the otostapes (thus in agreement with Hoffmann), later becomes incorporated in the extracolumella. The new boundary lies within the otostapes and not lateral to it (Gaupp 1906; De Beer 1937). The same situation exists in the crocodile and birds generally (Parker 1883; Crompton 1953; Frank & Smit 1974) where the homologue of the basal part of the lacertilian dorsal process clearly derives from the proximal segment (otostapes or pharyngohyal) of the two primary uppermost segments of the hyoid arch. The parts called stapes and extracolumella in crocodiles and birds are thus exactly homologous with the similarly named parts in lizards.

Engelbrecht (1958) refers to a medial part which gives rise to the bony stapes in *Pyromelana*, and a lateral part which develops into the cartilaginous extracolumella. These terms can only refer to the secondary division of the columella since, according to him, the whole supracolumellar arcade which includes the homologue of the lacertilian dorsal process is associated with the extracolumella; a clear indication that Engelbrecht is not referring to the primary division of the columella. Nevertheless Toerien (1971) seems to think that he is, and this erroneous

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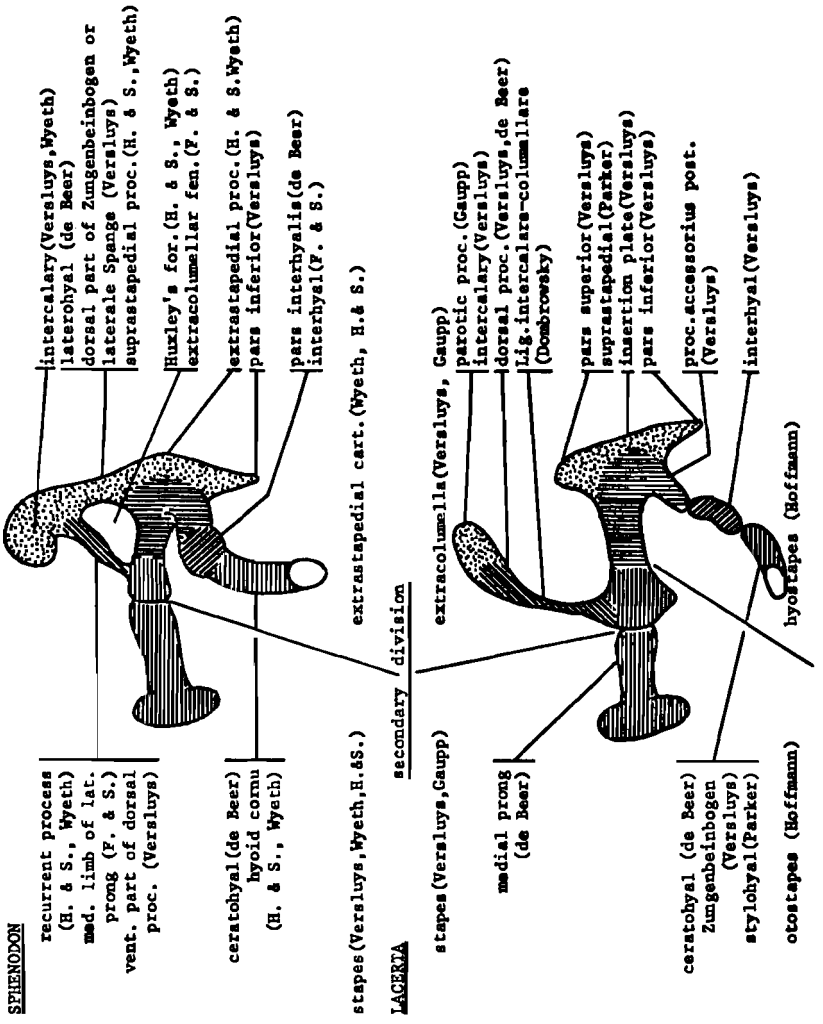

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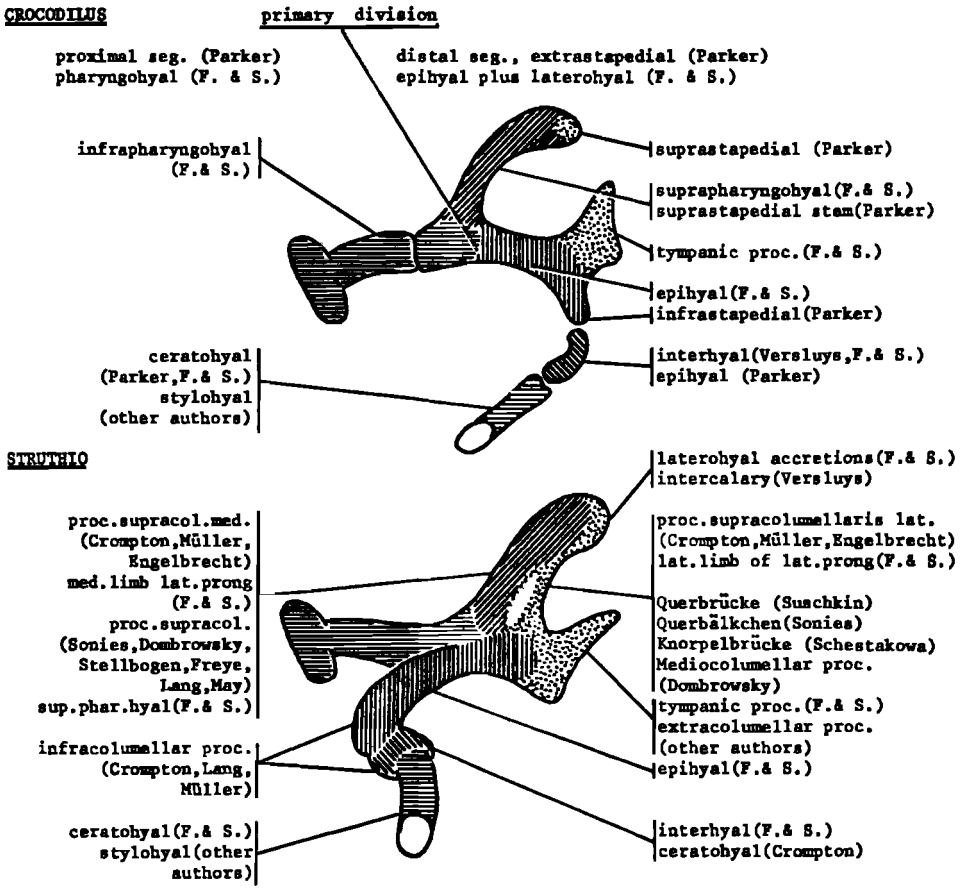

FIGURE 11

Homology and synonymy of the columellar processes of lower tetrapods as interpreted in the present paper. The initials H. & S. and F. & S. refer to the authors Howes & Swinnerton and Frank & Smit respectively. Primary hyoid arch derivatives are hatched, secondary delaminated laterohyal derivatives are stippled.

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deduction of Toerien leads him to conclude that the stapedial and extracolumellar parts in *Podiceps* do not strictly correspond to the similarly named parts in *Pyromelana*. We would, however, suggest that the parts do correspond, for, also in *Podiceps* the homologue of the lacertilian dorsal process is eventually associated with the extracolumellar part.

Since it is continuous with the medial columellar limb the unchondrified portion of the columella of *Podiceps* lying between the distal part of the pharyngohyal and the epihyal must represent the former's contribution to the extracolumella. Thus although Toerien could not establish with certainty the medial limb's derivation from the pharyngohyal, it is highly probable (also in the light of published data) that this structure in *Podiceps* is pharyngohyal in origin.

The lateral prong or supra-columellar arcade

Before discussing the literature which deals with this structure it may be as well to recapitulate briefly some of the more relevant facts on the ontogeny of the lateral limb of the supracolumellar arcade in the ostrich and crocodile (Frank & Smit 1974). As already described, in addition to the usual primary arch elements (*viz.*, pharyngohyal and epihyal), the columella auris of these animals receives important secondary accretions. These arise from subepithelial cellular delaminations which contribute to the formation of the adult extracolumella. A secondary addition of undifferentiated subepidermal mesenchyme to the primary arch material has been described by Holmgren (1940), Jarvik (1959) and Bertmar (1959) in bony fish. It is part of a morphogenetic process which has been called delamination by Holmgren and described by Jarvik as 'the capacity of the outermost parts of the undifferentiated ectomesenchyme, or – in later ontogenetic stages and the adult – of the outermost parts of the corium, to a repeated production of laminae with potentialities to form skeletal structures' (Jarvik 1959: 45). The fact that the same morphogenetic process occurs in the ostrich and crocodile is evidence in favour of Jarvik's statement that 'delamination occurs in all vertebrates from the Ordovician ostracoderms to the modern mammals'. However, there is strong evidence from the ostrich that cells (probably of neural crest derivation) from beneath epithelia of both ectodermal (tympanic area) as well as endodermal (dorsal spiracular diverticulum) origin may participate in the phenomenon of delamination and thus secondarily contribute to hyoid arch structures.

A confusing array of terms has been used to describe the composite lateral prong of the avian columella. De Beer (1937) gives a clear picture of its composition; it includes medial and lateral supracolumellar limbs as well as material representing the lacertilian and crocodilian intercalary or suprastapedial.

Sonies (1907) states that in *Anas* and *Gallus* the processus supracolumellaris and the processus extracolumellaris (tympanic process) are connected by a small 'Querbälkchen' enclosing a foramen intracolumellare (Huxley's foramen). Thus he uses the term 'supracolumellar' for the medial limb only, as does Dombrowsky (1925), Stellbogen (1930), Freye (1952/3), Freye-Zumpfe (1952/3), Lang (1955, 1956) and May (1961) (the term mediocolumellar process being used by some authors for the lateral limb). On the other hand Suschkin (1899), De Burlet (1934), Schestakowa (1934) and De Beer (1937) refer to the medial or inner limb as the dorsal process or suprastapedial, but Crompton (1953), Engelbrecht (1958) and Müller (1963) include both limbs (proc. supracolumellaris medialis et lateralis) in their supracolumellar process.

It is thus clear that whereas some authors use the term 'supracolumellar' (or 'suprastapedial')

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to describe the inner limb only, others include both limbs when referring to the supracolumellar process. We would suggest that in this regard Crompton, Engelbrecht and Müller be followed, or that the two limbs be simply referred to as the medial (inner) and lateral (outer) limbs of the lateral prong or the supracolumellar arcade.

As mentioned earlier, the inner limb of the avian columella is clearly derivable from the proximal hyoid segment (Crompton 1953; Frank 1954; Müller 1963) and most probably represents the suprapharyngohyal. It is thus homologous with the crocodilian suprastapedial stem and the lacertilian ligamentum intercalare-columellare of Dombrowsky (1925). In most birds a structure, probably homologous with the lacertilian intercalary, arises independently, as it does in lizards, of the pharyngohyal. More in harmony with our theories than our findings Brock (1937) reported a short dorsal process (inner limb) in the ostrich terminating in an intercalary which also connected with the extracolumella by means of a lateral limb (laterohyal) so that a foramen is formed. A similar situation exists in *Anser* (Schestakowa 1934) where a separate blastematous anlage appears on the dorsal process (inner limb) of the early embryo. Crompton (1953) describes a separate centre of chondrification in the supracolumellar arcade of *Anas*. He considers this homologous with the independent chondrification (the intercalary) in the reptilian dorsal process. Further, in *Spheniscus* Crompton mentions a transient nodule of blasteme associated with the lateral limb also probably homologous with the reptilian intercalary. Toerien (1971), however, doubts whether the nodule in *Spheniscus* can be homologous with the separate nodules found in *Struthio*, *Anas* and *Anser* or with the mesenchymatous nodule found at the tip of the lateral limb in *Podiceps* as well as the cartilaginous 'Querbrücke' in *Tinnunculus* (Suschkin 1899) connecting the dorsal process with the tympanic process. To the above list may also be added Sonies' (1907 'Querbälkchen' in *Anas* and *Gallus* as well as Schestakowa's (1934) 'Knorpelbrücke' in *Anser*.

By now it must be obvious that the above-mentioned structures do not all represent the same structural unit but that both the homologue of the intercalary as well as the lateral limb of De Beer's lateral prong are involved. Toerien (1971) points out that Suschkin's 'Querbrücke' (which must represent the lateral limb) corresponds to Parker's suprastapedial. Unfortunately he is apparently unaware that Parker (1879, 1883) uses the term 'suprastapedial' differently in lizards and crocodiles. In lizards Parker refers to the pars superior of the insertion plate (the tympanic process) as the suprastapedial (*cf.* also Gaupp 1906; De Burlet 1934), whereas in *Crocodilus* he uses the term suprastapedial for the homologue of the lacertilian intercalary. Dombrowsky (1925) compares the lacertilian pars superior (of the insertion part) with the lateral limb (his proc. mediocolumellaris), which in birds almost always fuses with the intercalary and in lizards with the pars distalis (tympanic process) of the columella auris. Howes & Swinnerton (1903) and Wyeth (1924) consider the homologue of the intercalary in *Sphenodon* as a continuation of the lateral limb which they call the suprastapedial process (the inner limb in *Sphenodon* they call the recurrent process).

It is suggested here that the fact that in birds the homologue of the intercalary and the lateral limb are often grouped together (and confused with one another), and the fact that Parker uses the term suprastapedial for the intercalary in crocodiles and for the homologue of the lateral limb in lizards (compare also Howes & Swinnerton and Wyeth in *Sphenodon*) conceals a deeper truth. Both structures belong to the same morphological entity and are represented during early

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ontogeny by the laterohyal blasteme. It is thus natural that the structure recognized as the intercalary in birds should appear in close association with the lateral limb, as has been reported by Brock (1937) and by us in *Struthio*, by Compton (1953) in *Spheniscus* and Toerien (1971) in *Podiceps*.

In spite of Crompton's claim of an eiphyal origin for the lateral limb in *Spheniscus*, one must, in the light of ontogenetic evidence in the ostrich and crocodile expect a separate origin (*i.e.*, not derived from epihyal or primary arch material) in birds generally. This view is further substantiated by work done by Suschkin (1899), Schestakowa (1934), Freye (1952/3), Freye-Zumpfe (1952/3) and Müller (1963). Schestakowa's extrastapedial, which according to her gives rise to the lateral limb, arises separately alongside the spiracular pouch in *Anser*, and although she makes no direct reference to cellular delamination both her diagrams and presentation of the facts make one inclined to suspect that such a contribution does in fact take place.

Bertmar (1959) has shown that the laterohyal material (transformed hyal gill rays) of bony fish is derived from delaminating subepidermal mesenchyme. This, together with the observation in the ostrich that ontogenetically the intercalary as well as the lateral limb has a predominantly subepidermal origin, indicates a morphological relationship with hyal ray material similar to that of the crocodile (Frank & Smit 1974). It also follows that the avian lateral limb or processus supracolumellaris lateralis cannot represent the crocodilian interhyal (Parker's epihyal) as Versluys (1903) suggested. Rather the lateral limb represents the dorsal or lateral articular head of the rhipidistian hyomandibula and the extracolumellar foramen the original passage between its dorsal and ventral heads.

This theory, first propounded by Frank & Smith (1974), makes it necessary to reconsider the suggestion by Crompton that the absence of a lateral limb (as was then thought to be the case in *Struthio*) denotes either a primitive or a neotenic condition. However, as this investigation has revealed, laterohyal material is not lacking in the ostrich, but even if it were found to be totally absent in a particular species of bird, this cannot be taken as a primitive characteristic since it is present in the rhipidistian ancestors of tetrapods. Also the fact that a lateral limb often occurs in both the lepidosaurian as well as the archosaurian lines suggests its presence in their common diapsid ancestors and thus that it is, phylogenetically speaking, a very old structure. Thus in comparison with crocodiles, the ostrich, and birds in general, are primitive in this regard, but for the opposite reason that Crompton thought they were. If the lateral limb represents the dorsal head of the rhipidistian hyomandibula and thus phylogenetically a very old structure, then it seems unlikely that its absence would reflect the embryonic condition of ancestral birds, that is, a neotenic condition.

The avian infracolumellar process

Müller (1963) and Toerien (1971) have summarized the literature on the infracolumellar process and the contribution of the so-called 'stylohyal' to it. Two patterns emerge from the literature: an infracolumellar process in the strict sense and an infracolumellar process with a long distal 'stylohyal'. Before discussing the morphological significance of this process in birds a comparison of conditions in the crocodile and the ostrich will be made. Frank & Smit (1974) point out that the avian infracolumellar process is not wholly homologous with the crocodilian infrastapedial process (distal tip of the epihyal) of Parker (1883), since in birds the

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interhyal (Crompton's ceratohyal in *Spheniscus* and Toerien's upper segment of the ceratohyal in *Podiceps*) becomes fused to the distal tip of the epihyal to form the avian infracolumellar process. In older crocodilian embryos the interhyal detaches from the infrastapedial (Parker 1883; Versluys 1903).

In the crocodilian embryo (Parker 1883; Versluys 1903; Gaupp 1906; Frank & Smit 1974) the infrastapedial part of the epihyal is connected to the ceratohyal (stylohyal of some authors) through a distinct interhyal (Parker's epihyal). Ventrally the ceratohyal is at first in cartilaginous continuity with Meckel's cartilage. It is unfortunate that Parker's ceratohyal of crocodiles is mostly called a stylohyal in birds (Suschkin 1899; Sonies 1907; De Beer 1937; Marinelli 1936), since the term stylohyal is also used as an alternative for interhyal (not ceratohyal) in fish (Suschkin 1899; De Beer 1937; Holmgren 1943; Bertmar 1959). The confusion is aggravated by Crompton's observation (1953: 123) that in *Spheniscus* 'within the hypohyal blasteme the large stylohyal cartilage develops'. Crompton thus uses stylohyal as an alternative for hypohyal.

In the ostrich conditions in the blastematous stage are much like those in the crocodile and thus typically archosaurian even to the extent that there is a blastematous connexion between the distal tip of the ceratohyal and Meckel's cartilage. The epihyal is attached by a less densely mesenchymatous interhyal to the ceratohyal below (Figure 1). However, the interhyal blasteme of the ostrich, unlike that of the crocodile, receives additional subepidermal mesenchyme. It is thus of dual origin consisting of primary arch material and subepidermal blasteme like that of bony fish; that is, hyoid arch proper plus hyoid ray (Holmgren 1943; Bertmar 1959). As development proceeds the ostrich interhyal, unlike that of the crocodile, gradually loses its separate identity, and when chondrification sets in it becomes indistinguishably fused to the epihyal above and the ceratohyal below.

In the oldest ostrich embryo examined the epihyal, interhyal and ceratohyal together form a long continuous 'infracolumellar process' (Figure 10). It would thus seem that the long 'interhyal process' of the ostrich (Frank 1954) represents an infracolumellar process plus a ceratohyal and that conditions in the ostrich correspond to those in birds in general where reported observations suggest the addition of ceratohyal material to the infracolumellar process (Müller 1963; Toerien 1971). The small piece of isolated cartilage lying at the tip of the 'processus infracolumellaris' in *Gallus* (reported by Sonies in 1907 and incorrectly homologized with Parker's 'epihyal' of the crocodile by Goodrich in 1915), in *Sturnus* (De Kock 1955) and possibly *Anas* (De Bee r & Barrington 1934) most probably does not represent the whole ceratohyal (stylohyal), if it represents ceratohyal material at all.

One is left with the impression that in the majority of birds ceratohyal material becomes added to the infracolumellar process and that Versluys (1903) is essentially correct when he states that in birds the 'Zungenbeinbogen' retains its connexion with the columella auris as in *Sphenodon* (see also Suschkin 1899; Dombrowsky 1925; De Burlet 1934; Marinelli 1936). Ventrally, however, there is no connexion with the basilingual cartilage as in *Sphenodon*. Two possible exceptions to this rule are *Spheniscus* (Crompton 1953) and *Rhea* (Müller 1963). Additional work is, however, necessary to substantiate and explain conditions in these two birds. Crompton's 'ceratohyal' in *Spheniscus* lies in the same position as the interhyal of the ostrich and undoubtedly represents the same structure. In *Crocodilus*, where no subepidermal addition could be demonstrated, the interhyal (Parker's epihyal) must represent the arch component of this segment.

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Thus the 'uniqueness' of *Spheniscus* (Crompton 1953) lies in its deviation from Versluys's rule rather than in the additional blastematous connexion between the ceratohyal and the columella auris. This 'double connexion' between ceratohyal and epihyal in *Spheniscus* may be secondary and primary arch components of a composite interhyal blasteme similar to that reported by Bertmar (1959) for the bony fish.

Frank & Smit (1974) express the view that the cartilaginous continuity between the ceratohyal and Meckel's cartilage in the crocodile embryo suggest a secondary bone-conducting mechanism in archosaurian ancestors. The fact that such continuity only occurs as a transitory blastematous connexion in the ostrich [also observed in *Struthio* by Peters (1867) and *Rhea* by Gadow & Selenka (1891) but later denied by Stellbogen (1930)] and has never been reported for other birds may mean an early dichotomy in the archosaurs with the ancestors of birds discarding bone-conduction more rapidly than the crocodilian ancestors. On the other hand atrophy of the ceratohyal has gone much further in crocodiles than in birds. In the latter the ceratohyal is still relatively big and usually becomes added to the infracolumellar process. To give a proper explanation to this apparent discrepancy additional work is required.

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ABBREVIATIONS

artic	articular region of Meckel's cartilage
basi	basilingual cartilage
bas pl	basal plate
blast	dense subepidermal blasteme
cerato	ceratohyal
ch tymp	chorda tympani
epi	epihyal
ex fen	extracolumellar fenestra
gen gang	geniculate ganglion
gloss	glossopharyngeal nerve and ganglion
hd vein	head vein
hyo	hyomandibular trunk of VII
hypogloss	hypoglossal nerve root
infra	infrapharyngohyal
int car	internal carotid
inter	interhyal
intercal	intercalary
lat lim	lateral limb of lateral prong
mandib	mandibular arch anlage
mesen	mesenchymatous area
meatus	developing external auditory meatus
metotic	metotic cartilage
orb art	orbital (stapedial) artery
otic cap	otic capsule
otic proc	otic process of quadrate
otic ves	otic vesicle
pal	palatine trunk of VII
prefac	prefacial commissure
quad	quadrate
ray	mandibular ray anlage
retro	retroarticular process
spir poc	dorsal pocket of spiracular pouch
supra	suprapharyngohyal (medial limb of lateral prong)
tympanum	position of developing tympanum
tymp proc	tympanic process (insertion plate)

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