Aspects of the ontogenesis of the avian columella auris

A.L. Smit and G.H. Frank

Observations on embryological material from *Spheniscus demersus, Acridotheres tristis, Geopelia cuneata* and *Gallus domesticus* strongly suggest that the avian stapes represents part of an infrapharyngohyal while the rest of the pharyngohyal material (supra- plus infrapharyngohyal) together with the epihyal and a secondary laterohyal component form the extracolumella. The latter structure bears three so-called processes: the supracolumellar arcade or process (de Beer's lateral prong) whose inner limb is derived from the suprapharyngohyal and the outer limb (comprising at least part of the intercalary) from the laterohyal blasteme; the tympanic process (extracolumellar process) also derived from laterohyal blasteme; and the infracolumellar process (formed by the distal tip of the epihyal and a composite interhyal) which is continuous with the ceratohyal in most birds. Our investigation suggests that the supposed great variation in the development of the columella among birds is a fallacy.

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Waarnemings op embriologiese preparate van *Spheniscus demersus, Acridotheres tristis, Geopelia cuneata* en *Gallus domesticus* dui sterk daarop dat die stapes by voëls deel van 'n infrafaringohiale verteenwoordig terwyl die res van die faringohiale materiaal (supra- plus infrafaringohiale) saam met die epihihiale en 'n sekondêre laterohiale komponent die ekstrakolumella vorm. Laasgenoemde struktuur dra drie sogenaamde uitsteeksels: die suprakolumellaar-uitsteeksel of -arkade ('lateral prong' van de Beer) waarvan die 'binnebeen' van die suprafaringohiale afkomstig is en die 'buitebeen' (wat minstens 'n deel van die interkalare insluit) deur die laterohiale blasteem bygedra word; die timpaniese uitsteeksel of ekstrakolumellaar-uitsteeksel wat ook van die laterohiale blasteem afkomstig is; en die infrakolumellaar-uitsteeksel (gevorm deur die distale punt van die epihiale en 'n saamgestelde interhiale) wat by meeste voëls aaneenlopend met die keratohiale voorkom. Ons ondersoek dui daarop dat die vermeende groot variasie wat ten opsigte van die ontwikkeling van die kolumella by voëls sou bestaan, 'n dwaling is.

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A.L. Smit and G.H. Frank
Department of Zoology, University of Durban-Westville,
Private Bag X54001, Durban 4000

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It has been repeatedly stated that the avian columella auris consists of a proximal bony stapes and a distal cartilaginous extracolumella. On this statement general consensus has been reached, but in regard to terminology and the origin of the different parts, confusion still prevails.

Work on the crocodile (Frank & Smit 1974) and the ostrich (Frank & Smit 1976) produced a model which attempted to explain conditions present at the upper end of the reptilian hyoid arch in terms of those existing in their rhipidistian ancestors. This model also offered some clarification of the homologies and synonymies of the columellar processes in diapsid reptiles and their descendants. Some important observations and deductions such as the contributions of the laterohyal component to the columella and the composition of the so-called infracolumellar process in birds, however, remained to be verified.

In view of certain reservations expressed by us regarding Crompton's (1953) observations on the jackass penguin *Spheniscus demersus,* we undertook a thorough investigation of conditions in this bird coupled with similar studies of the Indian mynah *Acridotheres tristis,* the Australian laughing dove *Geopelia cuneata,* and the domestic fowl *Gallus domesticus.*

Although based on four birds belonging to four widely divergent families this work has revealed a fundamentally similar ontogeny in all of them. Thus to avoid repetition the four studies have been combined into one general account. Only where important differences have been found are these described in greater detail. The illustrations are, however, not generalized but are reconstructions from actual specimens.

Material and Methods

The penguin embryos were collected on St Croix Island near Port Elizabeth and those of the Indian mynah from nests found in the suburbs of Durban. The other two birds were both bred in captivity in the Zoology Department of the University. The methods employed in the preparation of the material are similar to those described in previous papers (Frank 1954, Frank & Smit 1974, Frank & Smit 1976). Almost all specimens were cut in two planes, *viz* sagittally and then transversely, frontally or horizontally, thus providing additional information. In all a series of 35 penguin embryos were studied and 50 detailed reconstructions were prepared. Similarly, there were 13 embryos and 28 reconstructions of the mynah, 11 embryos and 14 reconstructions of the dove, and 7 embryos and 12 reconstructions for the fowl. Only contour reconstructions were made as we consider them to be more accurate and informative than those done by the graphic technique. By the above combination of techniques at least four reconstructions, each from a different viewpoint, can be made of the columella auris of a particular specimen.

Description of the development

First phase: the hyoid arch anlage

In the earliest stages, the avian hyoid arch anlage is represented by a thin, almost shapeless, aggregation of mesenchyme lying below the otic vesicle and between the dorso-ventrally elongated pharyngeal outpushings of the spiracular and first branchial pouches (Fig. 1A). These evaginations meet corresponding shallow ectodermal invaginations of which part of the first will become the external auditory meatus, while the endodermal part of the second pouch is closely associated with the more ventral termination of the hyoid anlage. The mass of mesenchyme mentioned above must represent the primary hyoid arch. not, as yet, separated into its component (pharyngo-, epi-, and ceratohyal) elements. These anlagen of the elements all appear simultaneously. Soon afterwards some additional, usually very faint, mesenchyme appears in the position of the future laterohyal (lateral limb and tympanic process) anlage (Figs. 1A and B, 3A and D: *lathy*).

It is important to note that in these early stages the visceral arch anlagen are intimately applied to the pharyngeal pouch endoderm and are no doubt receiving cellular increments from this region; in many places the two entities cannot be separated (Fig. 4A: *spirpoc* and *suphar*).

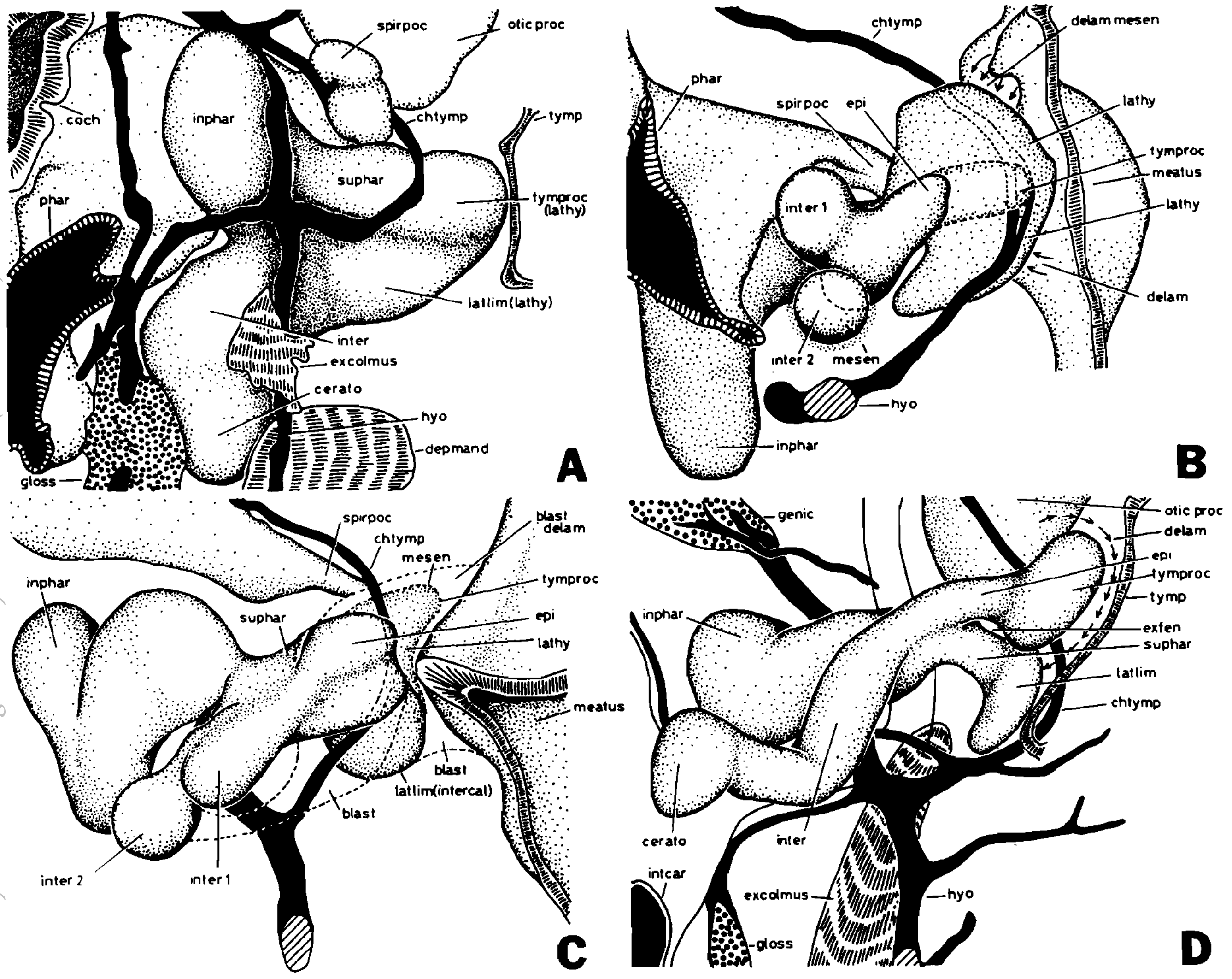

Fig. 1 (As an aid to orientation, part of the external auditory meatus and developing tympanum is shown. Abbreviations as on p. 29.)

A, Mynah: Posterodorsal view of the hyoid arch anlage in the first phase of development. B, Penguin: Ventral view of the hyoid arch anlage in the second phase of development. The ceratohyal anlage has been omitted to reveal the double interhyal anlage. The denser anlage of the tympanic process and chorda tympani may be seen buried within the general laterohyal blasteme. Arrows indicate what appear to be cells migrating towards the laterohyal blasteme from below the epithelium of the meatus. The basement membrane of the latter is discontinuous. Since it is homocontinuous with the otic capsule the boundaries of the infrapharyngohyal are indistinct. C, Penguin: Ventral view of the columella in about the third phase of development. The ceratohyal has again been omitted. The track of blasteme which appears to have delaminated from the tympanic region is shown by broken lines. Note the clear space in the region where the extracolumellar fenestra would normally lie. D, Dove: Ventral view of columella to show the path of cells (arrows) apparently migrating from the dorsal diverticulum of the spiracular pocket to the lateral limb. The internal carotid artery with stapedial (orbital) branch is shown only in outline.

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An important landmark in the region is the hyomandibular trunk (*hyo*) of the facial nerve which passes over the hyoid anlage and may, as for example in the penguin, even at this early stage give off a short twig which passes anteriad. This, although it does not yet reach the mandibular arch anlage, no doubt represents the beginnings of the chorda tympani nerve.

Another observation in the case of the penguin is that in a very early stage the ceratohyal is intimately associated with the first branchial pouch, that is, the pouch behind the spiracular pouch, and appears to be receiving cellular increments from this region. Thus branchial pouches both anterior and posterior to a particular visceral arch may be involved in the formation of that arch. The relationship between the branchial pouches and the arches is probably an inductive one.

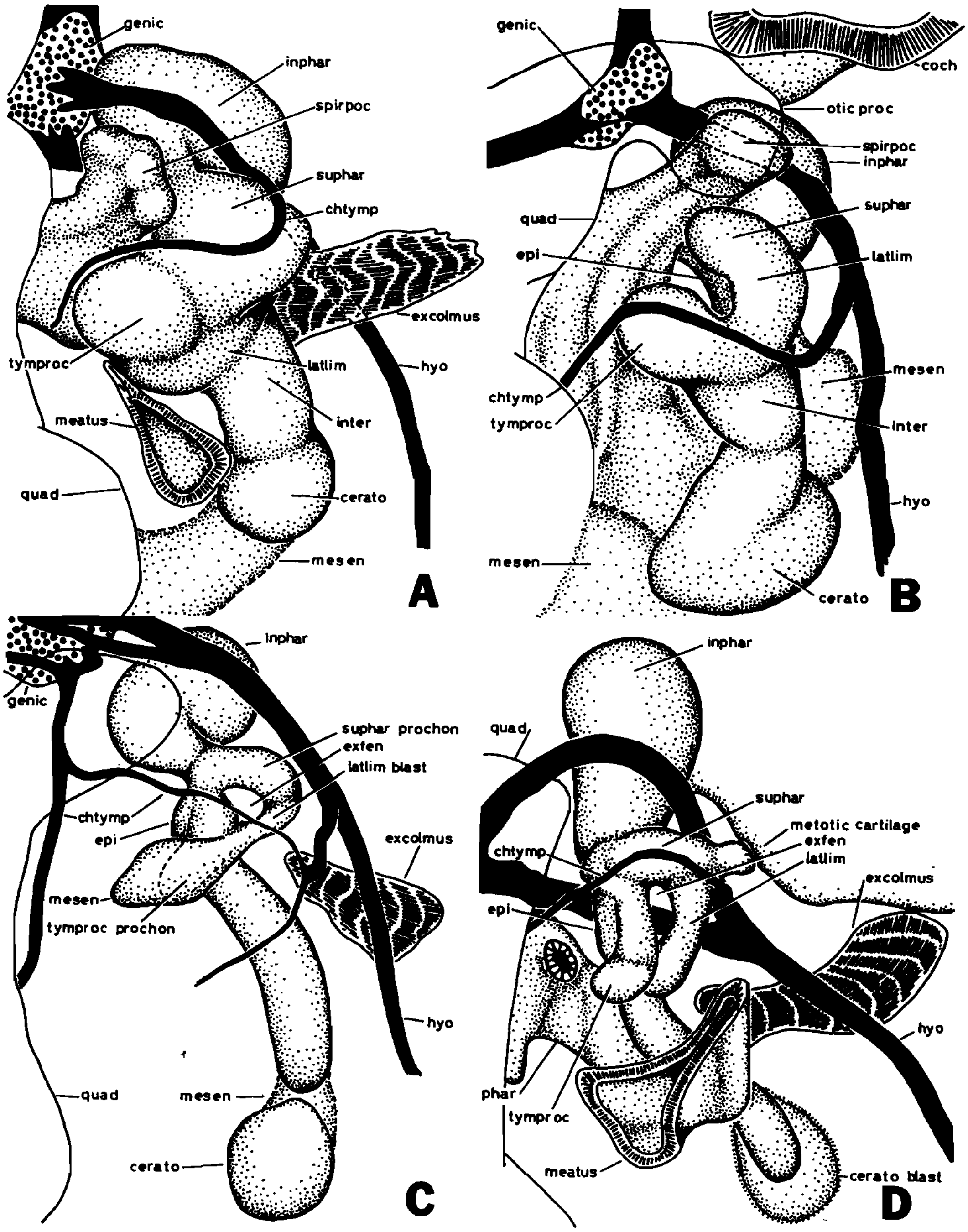

Fig. 2 (As an aid to orientation, the outline of part of the quadrate and its otic process has been included. Abbreviations as on p. 29.)

A, Mynah: Lateral view of the hyoid arch anlage in the first phase of its development. The nebulous laterohyal blasteme lying lateral to the tympanic process and suprapharyngohyal anlagen and chorda tympani nerve has been omitted from the illustration. The hyomandibular trunk passes through the extracolumellar muscle. B, Dove: Lateral view of the hyoid arch anlage in the late first phase of its development. The general laterohyal blasteme is omitted. There appears to be delamination proceeding from the dorsal spiracular pocket towards the infrapharyngohyal. A cellular aggregation lies postero-medial to the epi-interhyal junction and may represent the secondary interhyal blasteme.
C, Fowl: Lateral view of the columella in the third to fourth phase of development. A blastematous laterohyal lies lateral to and homocontinuous with both the tympanic process and the lateral limb. Note how only a small part of the chorda tympani lies in the conventional position while the greater part of the nerve runs direct from the ganglion of VII to the inside of the mandibular arch.
D, Mynah: Lateral view in the fourth phase of development showing the unusual position of the lateral limb. The tip of the ceratohyal is buried in very dense blasteme.

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Second phase: early cell migration

Following closely upon the previous stage in which endodermal participation in the development of the primary arches seems probable, there is a stage which is characterized by what appears to be active delamination and cell migration from below both ecto- as well as endodermal epithelia.

As the various elements of the columella become distinct, although remaining homocontinuous, cell migration, apparently from the region of the dorsal diverticulum of the spiracular pouch as well as the floor of the shallow depression representing the external auditory meatus, is initiated (Figs. 1B and 3A: *delam*). This dorsal diverticulum lies almost vertical, interposed between the otic

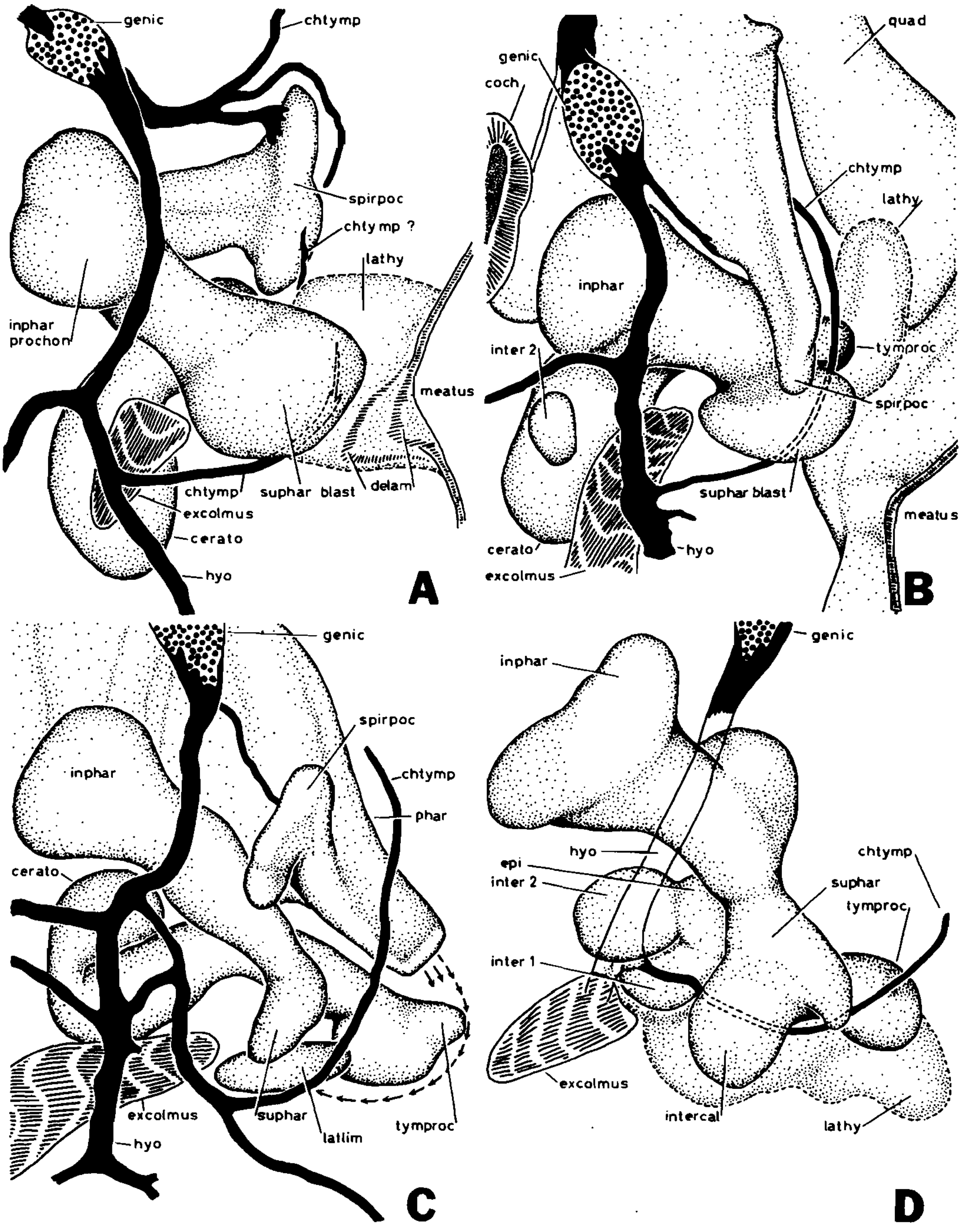

Fig. 3 A, Fowl: Dorsal view of the hyoid arch anlage in late first phase of development - it is still homocontinuous. The laterohyal blasteme lying between the meatal epithelium and the suprapharyngohyal anlage appears to be a delamination product of this epithelium since the latter's basement membrane is discontinuous. Isolated nerve fibres are present in the conventional position occupied by the chorda tympani.
B, Dove: Dorsal view of the columella in the early third phase of development. Note the evanescent secondary interhyal anlage of this specimen. Although extensive delamination seems already to have occurred the meatal epithelium remains discontinuous. The almost procartilaginous infrapharyngohyal overlies and is homocontinuous with the densely blastematous epihyal; the supracolumellar arcade is early blasteme. C. Dove: Dorsal view of the columella in the fourth phase of development. Much of the prospective tympanic epithelium still lacks a basement membrane and appears to be contributing cells to the suprapharyngohyal region. There also appears to be active cell migration (arrows) between the region of a dorsal pouch of the pharynx and the lateral limb region. D, Penguin: Dorsal view of the columella in the third phase of development. Infrapharyngohyal, suprapharyngohyal and epihyal are homocontinuous but, while the infra- and suprapharyngohyal are blastematous, the epihyal is very early procartilage. Laterohyal blasteme extends proximad from the tympanum parallel to the epihyal but contacts the latter only proximally and distally as well as the suprapharyngohyal on its ventral surface. The chorda tympani penetrates this nebulous blasteme.

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process of the quadrate and the anlage of the supracolumellar arcade. From the anterior surface of the diverticulum migration can most easily be seen proceeding towards the otic process of the quadrate. Of the four birds studied possibly the clearest evidence of cell migration from the dorsal diverticulum could be seen in the dove. Early in development the extreme dorso-distal part of this pocket has the appearance of a placode, and between this particular region and the infrapharyngohyal anlage there appears to be a stream of mesenchyme. Also between the latero-ventral ridge-like edge of the pocket and the anterior surface of the epi-interhyal region there is a stream of cells. The latter gives the appearance of proceeding specifically towards the primary interhyal component of a composite interhyal (Fig. 1B: *phar, inter* 2).

Between the posterior surface of the dorsal spiracular diverticulum and the epithelium of the prospective tympanum there is at this point in the development a large, nebulous mass of what has been equated with gill-ray or laterohyal mesenchyme (Figs. 1B: *delam, mesen;* 3A: *lathy, delam;*

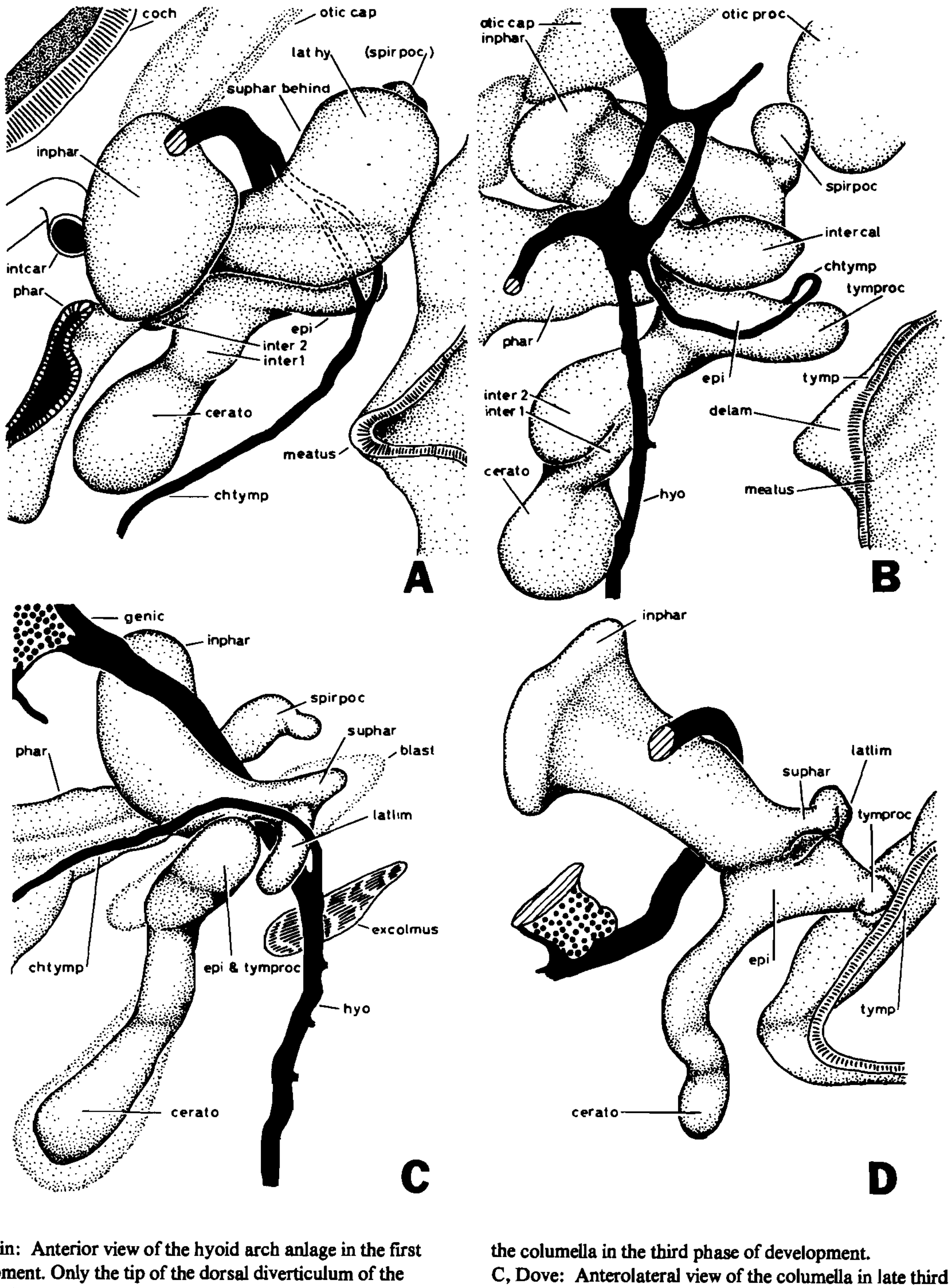

Fig. 4 A, Penguin: Anterior view of the hyoid arch anlage in the first phase of development. Only the tip of the dorsal diverticulum of the spiracular pocket is shown since the latter obscures the anlage in an anterior view. Much of the meatal epithelium lacks a basement membrane but no delaminating cells could be seen. The suprapharyngohyal blasteme is closely associated with and appears to be receiving cellular increments from the region of the spiracular pocket. The infrapharyngohyal anlage and cochlear capsule are homocontinuous, both with slight matrix. B, Penguin: Posterior view of the columella in the third phase of development.
C, Dove: Anterolateral view of the columella in late third phase. The meatal epithelium has a discontinuous basement membrane with blasteme lying between the latter and the tympanic process and lateral limb. D, Mynah: Anterodorsal view of the columella in late fourth phase with much fusion of the elements. Supra- and infrapharyngohyal and lateral limb are homocontinuous, as are the tympanic process, epi-, inter-, and ceratohyal elements.

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4A: *lathy, meatus*). This mesectoderm is destined to contribute to the lateral limb of the supracolumellar arcade and to the tympanic process. At this stage, however, there are no indications of its ultimate destiny but its origin seems quite clearly to be the tympanic region. Since the tympanic epithelium lacks a distinct basement membrane the contiguous mesenchymal mass can be presumed to have been produced by delamination at the basement membrane of the epithelium. In the case of the dove it is interesting to note that although delamination appeared to be proceeding generally from below the tympanic epithelium, no activity could be found in the immediate vicinity of the future tympanic process.

In these early stages, the chorda tympani, before passing anteriad to the mandibular arch anlage, lies buried in the aggregation of densely stained laterohyal mesenchyme mentioned above (Fig. 1B: *chtymp*). This nerve will eventually tend to overlie the supracolumellar arcade (that is, dorsal rather than posterolateral) in the mynah and the dove (Fig. 2D and 4C: *chtymp*) but in the penguin it lies close to the root of the medial limb of the supracolumellar arcade (Fig. 5A). Except for its most dorsal remnant (the so-called 'intercalary') the lateral limb of the penguin's supracolumellar arcade is absent.

Peculiar to the penguin, the chorda tympani often splits as it passes over the columella to recombine soon after (Figs. 1B and 4A). It acts as a useful landmark in these early stages: medioventral to it lies the prospective epihyal, while antero-dorsal lies the blasteme of the intercalary, and laterally, as mentioned above, there are considerable quantities of laterohyal blasteme. Below, the chorda tympani is taken as roughly marking the boundary between the blastematous epihyal and its mesenchymatous laterohyal prolongation, the tympanic process (Fig. 1C: *epi, tymproc*).

Goodrich's (1915) observations on the course of the chorda tympani in the fowl are essentially correct. It is pretrematic and pretympanic. However, in addition to the large main trunk passing down to the inside of Meckel's cartilage anterior to the columella, in all early stages examined, we found traces of a small nerve tract lying in the conventional position for the chorda tympani. In the oldest stages

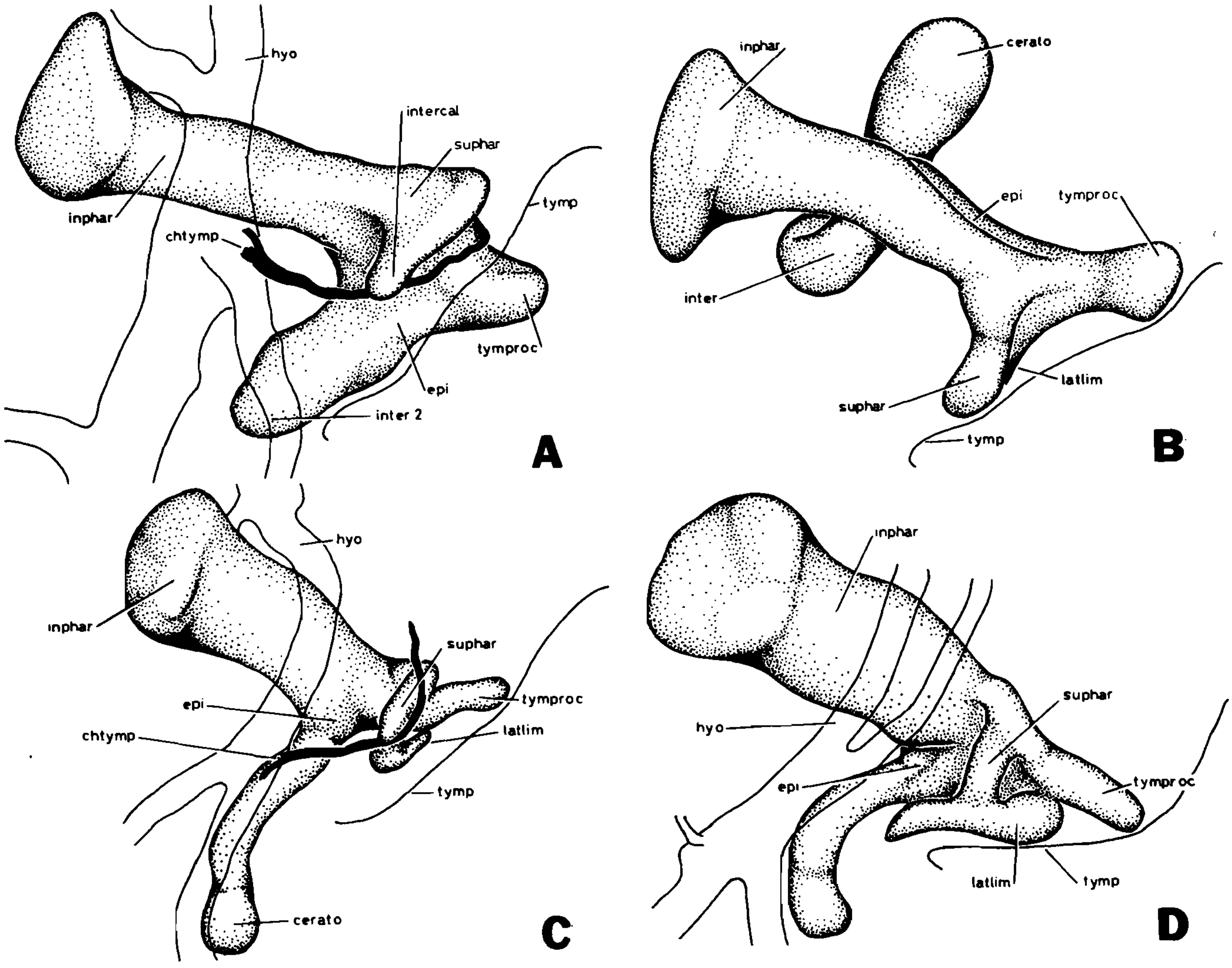

Fig. 5 (In these reconstructions the hyomandibular trunk is shown only in outline, the chorda tympani in solid black and the relative position of the tympanum is indicated by a single line. Abbreviations as on page 29.)
A, Penguin: Posterior view of the columella in a late stage of development; the primary arch interhyal has been obliterated. The ceratohyal has been left out of the illustration. B, Dove: Posterodorsal view of the columella at a late stage of development.
C, Mynah: Posterior view of the columella at a late stage of development. D, Fowl: Posterodorsal view of the columella at a late stage of development. The ceratohyal has been left out of the illustration.

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available it could not be traced (Fig. 2C and 3A: *chtymp*).

It is approximately at this stage of development of the penguin that Crompton (1953) (his stage II, p. 89) describes 'a nodule of blastematous tissue' lying between the processus oticus and the metotic cartilage which he homologizes with the reptilian intercalary. A careful study was made of all the penguin embryos of the same approximate age which were available to us but nothing resembling or lying in the position of this blastematous nodule could be found. Laterally overlying the distal tip of the columella, the more posterior part of the otic process and the earliest beginnings of the metotic cartilage, there is the relatively massive but nebulous laterohyal blasteme already described, but it occupies neither the position of the reptilian intercalary nor that of the nodule mentioned by Crompton.

Third phase: delimitation of arch elements

The spatial relationships of the avian arch elements are unusual, especially in the case of the penguin. Those of the mynah and fowl are probably the closest to the reptilian, with the dove falling somewhere in between (Fig. 6). As the various arch elements in the penguin become clear the infrapharyngohyal appears more or less vertically disposed, meeting the suprapharyngohyal at an angle. The latter element is almost horizontal and anteromedial to the latero-

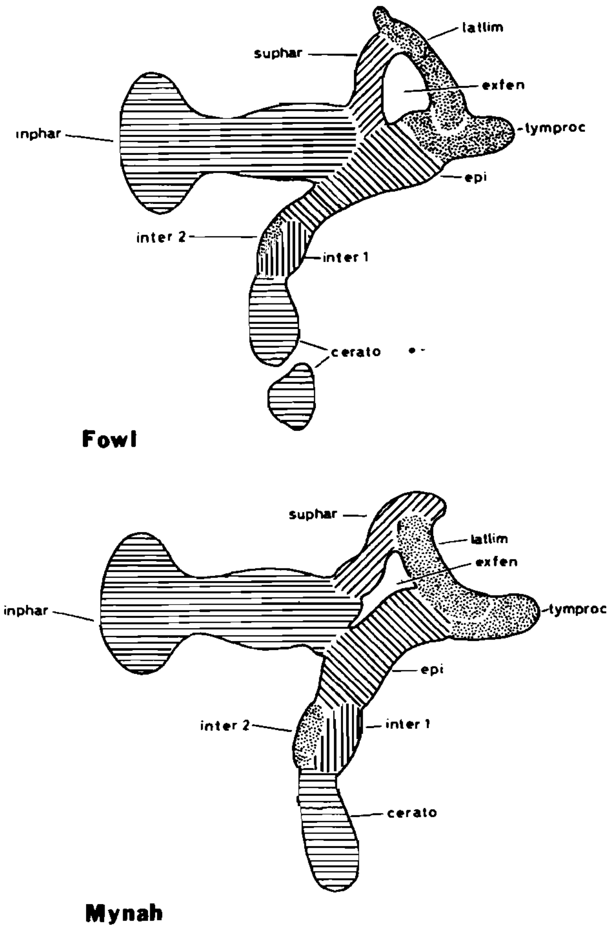

Fig. 6 Diagrammatic representation of the columella and its constituent elements in the four birds covered by this study.

Abbreviations

blast	blasteme	*inter 2*	secondary arch component of the interhyal
cerato	ceratohyal	*intercal*	intercalary
coch	cochlear part of otic capsule	*latlim*	lateral limb of the lateral prong
chtymp	chorda tympani	*lathy*	laterohyal blasteme
depmand	musculus depressor mandibulae	*mesen*	mesenchyme
delam	path of migrating cells which appear to have delaminated from under the epithelium	*meatus*	most proximal part of developing external auditory meatus
epi	epihyal	*otic cap*	otic capsule
excolmus	extracolumellar muscle	*otic proc*	otic process of quadrate
exfen	extracolumellar fenestra	*phar*	pharynx
genic	geniculate ganglion of VII	*prochon*	procartilage
gloss	glossopharyngeal nerve and ganglion	*quad*	outline of quadrate
hyo	hyomandibular trunk of VII	*spirpoc*	dorsal pocket of the spiracular pouch
inphar	infrapharyngohyal	*suphar*	suprapharyngohyal (medial limb of lateral prong)
intcar	internal carotid	*tymp*	position of developing tympanum
inter 1	primary arch component of the interhyal	*tymproc*	tympanic process (insertion plate)

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hyal blasteme (Figs. 1C and 3D: *suphar, inphar, lathy, intercal*). At this stage it protrudes slightly laterad to this blasteme as a small process. The epihyal lies more medial than usual, almost parallel and for much of its length contiguous with the suprapharyngohyal. Laterally it is continuous with the tympanic process, while medioventrally it curves down and with the interhyal element it forms the infracolumellar process.

The dove columella is very similar. As the infrapharyngohyal is more horizontally disposed it makes contact over a limited area with the epihyal at the point where they meet tangentially. Here the proximal end of the suprapharyngohyal meets both the infrapharyngohyal and the epihyal (Figs. 3B and C, 4C: *inphar, epi, suphar*). In the mynah and fowl the suprapharyngohyal is almost vertically disposed to the epihyal, and it is the lateral limb which is more or less posterior and parallel to the epihyal-tympanic process axis in the earlier stages (Figs. 2C and D: *latlim, tymproc*).

Initially the avian infrapharyngohyal anlage tends to be very diffuse with only slight traces of matrix between its widely dispersed cells. In other words it is in an early prochondral condition. It never exhibits the densely blastematous condition so characteristic, for instance, of the epihyal. There is in the penguin (in complete homocontinuity with, and quite indistinguishable from, the infrapharyngohyal) a part of what can only be the ventrolateral wall of the cochlear capsule (Figs. 1B and 4A: *inphar, otic cap*). Except for this latter structure the capsule is open in this region. The cochlear capsule of the fowl and mynah is even more retarded in its development. It becomes quite clear only after the infrapharyngohyal is well established. In the dove, in direct contrast, the fenestra ovalis is lacking and a dense mesenchymatous capsular wall underlies the foot-plate of the infrapharyngohyal anlage. However, here the two structures may be separated since the infrapharyngohyal is procartilaginous.

Adjacent to the infrapharyngohyal lies the nebulous mass of laterohyal mesenchyme within which is hidden the suprapharyngohyal anlage as well as the laterohyal derivatives (the lateral limb and/or intercalary and the tympanic process) (Figs. 4A and 1B: *inphar, suphar, lathy*). While the infrapharyngohyal tends to be procartilaginous this laterohyal is purely mesenchymatous to blastematous. Unlike the crocodile the avian infrapharyngohyal and suprapharyngohyal are not always clearly independent anlagen; their stage of development is often very similar and their anlagen homocontinuous. They tend to meet each other at an obtuse angle to form a distinct elbow. Particularly in the mynah and the fowl the suprapharyngohyal protrudes as a small process beyond the point where the anlage of the lateral limb is attached (Figs. 2D and 5D: *suphar, latlim*).

Below the pharyngo-elements lies the anlage of the epihyal. As seems to be characteristic of birds, the epi-, inter- and ceratohyal flow into one another without definite boundaries when they first appear. However, the epihyal soon becomes densely blastematous while that portion of the infracolumellar process identified as the interhyal becomes late blasteme, that is, it acquires traces of matrix while the knob-like ceratohyal, like the infrapharyngohyal, becomes prochondral (Fig. 4B: *epi, inter, cerato*).

In the mynah, as mentioned above, the lateral limb of the supracolumellar arcade has an unusual position; it lies posterior and parallel, not vertical, to the epihyal-tympanic process anlage. The latter lies between it and the dorsal diverticulum of the spiracular outpushing (Fig. 2D: *tymproc, latlim, phar*). Distally, the tips of the lateral limb and the tympanic process are buried for a long time in the general laterohyal blasteme and are consequently virtually indistinguishable from one another in their more lateral parts. Thus although a complete extracolumellar fenestra may already exist in both the mynah and dove, its boundaries consist almost entirely of dense blasteme. The only part of the lateral limb represented in the penguin is its extreme dorsodistal tip, the so-called intercalary. This almost independent aggregation of cartilage lies posteriorly near the distal tip of the suprapharyngohyal (Fig. 3D: *intercal, suphar*).

At this stage in the development the epihyal of the penguin tends to lag behind the primary arch interhyal in its development. The latter element tends to be very densely blastematous, similar to that reported for the crocodile. Thus the two elements may be distinguished without much difficulty. An additional landmark in the region of this primary interhyal component is the blastematous proliferation on the posteromedial aspect of the infracolumellar curve. This is considered to represent the secondary sub-epidermal contribution to the interhyal. This secondary interhyal blasteme is at first somewhat poorly developed, its mesenchyme concentrically organized without matrix. In the penguin this element comes to lie in a direct line with the infracolumellar part of the epihyal and eventually appears simply as an extension of this element; it is better developed than in any of the other three birds studied. It is this secondary interhyal component which in the penguin persists as the distal tip of the infracolumellar process, while the primary interhyal component eventually regresses to less dense mesenchyme and obliterates (Figs. 4B and 5A: *epi, inter 1* and *2*). In this way the ceratohyal of the penguin becomes detached from the rest of the columella. Except for a single dove embryo which demonstrated a discrete aggregation of mesenchyme on the postero-medial aspect of the infracolumellar process (Fig. 3B: *inter 2*), evidence of the secondary interhyal is almost entirely lacking in the other birds studied. On the other hand, the primary interhyal in the dove, mynah and fowl remains connecting the epihyal with the ceratohyal in one continuous sinuous rod (Fig. 1D, 4D and 5). Some tendency to regression of the primary interhyal was detected in the oldest embryos of both the mynah and dove but it never completely obliterates as it does in the penguin. Only the extreme knob-like tip of the ceratohyal becomes separated from the rest of the infracolumellar process in the fowl. Thus in this latter bird the process must contain some cerato-material; its length confirms this (Fig. 2C: *cerato, mesen*).

In all four birds there is a thin but distinct tract of mesenchyme connecting the ventro-distal tip of the ceratohyal with the posterior tip of the retro-articular process of Meckel's cartilage during a considerable part of the early embryology. In all cases its disappears later on (Figs. 2A and B: *mesen*).

Fourth phase: late cell migration

For an appreciable period in the very early embryology the ventral ends of the visceral arches (mostly cerato-elements) are intimately associated with the endodermal pharyngeal wall and would appear to be receiving sub-epithelial

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increments from there. This latter arch element cannot easily receive sub-epidermal delaminated material since the depressor musculature of VII lies between it and the ectoderm.

The region of the prospective tympanum, like the dorsal diverticulum of the spiracular pocket, remains throughout an important source of delaminating material. For example, in the penguin the laterohyal blasteme is broadly applied to that area of the external auditory meatus which will eventually become the tympanum. For protracted periods patches of this epithelium lack a basement membrane. This laterohyal blasteme of the penguin passes in a broad arc from the tympanic process from which it is initially indistinguishable round posteriad, mediad and under to mingle with the blasteme of the 'intercalary' and the secondary interhyal. Posterior to the pharyngo-epihyal shaft of the columella there remains a conspicuous clear space which doubtless represents an incipient extracolumellar fenestra, except that in the case of the penguin this never develops further since its lateral limb fails to meet the columellar shaft (Figs. 1C and 3D: *delam, blast, lathy*). The mesenchymatous arc thus only represents the path of migrating cells from the region of the epithelium to the 'intercalary' and secondary interhyal regions.

The mynah also contributes indirect evidence of a dual origin to the interhyal. When the primary arch structures (including the region of the infracolumellar process) are procartilaginous there is in this region an additional, chiefly mesenchymatous, part, which lies closely applied and posterior to the primary interhyal and no doubt represents the secondary interhyal anlage. Clear arcs of mesenchyme, such as reported above for the penguin, were not, however, in evidence here. The converse would also seem to occur; late in the embryology of the dove the laterohyal blasteme receives cells from the region of the endodermal spiracular diverticulum in addition to an 'ectodermal' contribution (Fig. 3C: *phar, latlim*).

The 'extracolumellar muscle'

At the point where the epihyal leaves the infrapharyngohyal, the former curving down as part of the infracolumellar process and the latter curving up to the developing cochlea, lies a small slip of muscle (Fig. 1A: *excolmus, depmand*). This small detached part of the depressor musculature of VII is always more or less clearly associated with the distal part of the infracolumellar process, and early in the embryology of, for example, the mynah and penguin appears to 'insert' on the interhyal and connective tissue of the prospective tympanum. It has its origin on the metotic cartilage-basal plate region posterior to the columella and runs directly anterodorsad to insert in the older embryos mainly on the fibrous tissue making up the tympanic membrane, but also on the connective tissue sheathing the infracolumellar process (Figs. 2D and 3D: *excolmus*)

The muscle thus occupies a similar position and probably acts in a similar fashion to the extracolumellar muscle found in the crocodile and alligator. However, in these birds, it lies medial to the hyomandibular trunk of VII which also innervates it and therefore, according to Goodrich's (1915) criterion, it cannot be regarded as homologous with the reptilian extracolumellar muscle but rather with the mammalian stapedial muscle. In early stages in the mynah the nerve trunk passes *through* the muscle so the distinction is probably not valid (Fig. 2A: *excolmus*).

Discussion

In an earlier work (Frank & Smit 1976) we contended that the avian columella auris was formed from primary gill-arch material representing the upper two segments of the hyoid arch (the pharyngohyal and the epihyal) with a secondary addition of delaminated laterohyal material. Ventrally, in most species investigated, a ceratohyal becomes attached to the columella through a distinct interhyal.

In regard to the most proximal segment of the adult columella, *viz* the stapes or medial prong of de Beer (1937), the available evidence suggests its derivation from an infrapharyngohyal. This matter has been dealt with in some detail in papers on the crocodile (Frank & Smit 1974) and ostrich (Frank & Smit 1976) and will not be pursued further. However, the origin, composition and homologies of the distal extracolumellar part with its processes, the so-called supracolumellar arcade (lateral prong of de Beer 1937) and the infracolumellar process need further clarification. The third process of the extracolumella, the tympanic process, has also been dealt with in the earlier papers.

The supracolumellar arcade

The medial limb of the supracolumellar arcade

The supracolumellar arcade usually consists of two processes (the medial and lateral limbs), often enclosing the foramen of Huxley or extracolumellar fenestra (Frank & Smit 1976). The medial limb arises as a derivative of the pharyngohyal or proximal primary segment (otostapes of Hoffmann 1889) in all five species of bird investigated by us (see also Müller 1963, Frank & Smit 1976) and most probably represents a suprapharyngohyal. It is interesting to note that Crompton (1953) maintains that the ostrich and the penguin represent "opposite extremes in the avian columella auris. In the latter only the p. supracolumellaris lateralis develops, while in the ostrich only the p. supracolumellaris medialis chondrifies" (p. 126). Crompton's remark in regard to the ostrich has already been refuted (Frank & Smit 1976) and his contention that the ostrich columella "appears to be primitive" put into perspective.

It is Crompton's (1953) remark that in the penguin only the lateral limb of the supracolumellar arcade chondrifies that attracts attention. In the penguin a single limb chondrifies (no complete supracolumellar arcade is formed) and since this process arises, according to Crompton, from the lateral aspect of the epihyal (hyostapes of Hoffmann 1889), he homologizes it with the lateral limb of other birds. We do not, however, share this opinion since in our penguin material a suprapharyngohyal clearly distinct from an infrapharyngohyal (which gives rise to the stapes) is formed. It is the extreme dorsolateral tip of the suprapharyngohyal which gives rise to the single limb in the penguin. When the suprapharyngohyal and the infrapharyngohyal merge into one another they contribute, together with the epihyal, to the shaft of the columella. Thus in the penguin the suprapharyngohyal lies parallel to the epihyal so that the boundary line between the supra- and the epihyal runs along the length of the shaft, and the morphologically proximal (or upper) end of the epihyal in this bird comes to lie laterally. This condition has also been suggested by

Toerien (1971) for the grebe *Podiceps* and the duck, and it would seem that this tendency exists to a greater or lesser degree in most birds (*cf.* the ostrich: Frank & Smit 1976). Toerien's (1971) remark that because of this the line originally separating the pharyngohyal from the epihyal does not correspond to the line separating the stapes from the extracolumella is irrelevant in this context. The two lines separate the primary and secondary segments of the columella respectively and do not, in any case, correspond. As shown in some detail in a previous article (Frank & Smit 1976) the primary division lies between the pharyngo- and epihyal while the secondary division lies entirely within the pharyngohyal as in *Lacerta* (Versluys 1903).

Toerien (1971) also concludes that the situation in birds, where the boundary line between the suprapharyngohyal and the epihyal runs along the shaft of the columella, implies that the so-called "lateral supracolumellar process described in at least some adult specimens, probably corresponds to the processus supracolumellaris medialis of the embryo" (p. 25). In the case of the penguin we are in complete agreement. The single limb which in the penguin arises from the distal aspect of the suprapharyngohyal appears to be situated on the epihyal laterally; hence Crompton's observational error. Brock (1937) is correct in considering the process in the penguin as the medial limb (medial supracolumellar process, her dorsal process). In this regard she treats the penguin and the ostrich alike. However, it has been pointed out (Frank & Smit 1976) that although the process in the adult ostrich appears single it includes lateral limb material. An extracolumellar fenestra is absent since it is filled with mesenchyme and cartilage in later stages. Crompton's (1953) conclusion that in the ostrich and the penguin the columella represents opposite extremes is invalid.

The lateral limb of the supracolumellar arcade

Attention was first drawn to the not inconsiderable contribution of the so-called laterohyal blasteme to the extracolumella of birds by Frank & Smit (1976). The failure to recognize this contribution has, we believe, led to the incorrect interpretation of the homologies of certain parts. Crompton's (1953) observation that in the penguin his processus supracolumellaris lateralis (actually the medial limb, as shown above) develops from the lateral aspect of the epihyal has led to Müller's (1963) remark that this is not true for all birds since in many cases the lateral limb arises separately from the epihyal or hyostapes. Müller cites Suschkin (1899), Stellbogen (1930), Freye (1952/53) and Werner (1960) in support of his contention.

To this can be added our own observations on the ostrich (Frank & Smit 1976) and Schestakowa's (1934) on the goose. Even though Toerien (1971) could not observe a separate origin for the lateral limb in the grebe (he also derives it from the epihyal) one is inclined to think that an origin separate from the epihyal must be postulated for birds generally.

The discrete nature of the lateral limb is indicative of an important morphogenetic process first described in fishes by Holmgren (1940) and Jarvik (1959), but recently found to occur with equal frequency in higher vertebrates, namely the addition of secondary arch material, in this case, to the distal segment of the adult columella. Conditions in the four birds investigated confirm that, in the ostrich (Frank & Smit 1976), primary arch material receives considerable secondary accretions in the form of delaminated material from below the ectodermal epithelium, especially from the region of the future tympanic membrane. This appears to be particularly extensive in the case of the penguin. According to Hay (1964) and Moss (1968 a and b) the epidermis (ectoderm) plays an active role in the process of delamination as pictured by Holmgren (1940) and Jarvik (1959). The biochemical details do not concern us here; it is however, necessary to take cognizance of the fact that the epithelium itself is not the source of the cellular components of the delaminated tissue. These delaminating cells derive ultimately from the neural crest or ectomesenchyme (Hay 1964, Moss 1968 a and b). Jollie's (1971) observation that in *Squalus* "there is evidence of continued epidermal origin of the subepidermal layer of cells and movement from here to the deeper skeletal regions" (p. 31) needs additional verification. According to Moss (1968 b) the epidermal cells have the capacity to interact with the neural crest derivatives in a "well regulated sequence of inductive interactions" (p. 366) and the site of the interaction is the basement membrane. This probably explains the indistinct basement membrane at delamination sites (Jollie 1971). Our observations in the crocodile and all birds investigated point clearly towards delamination also occurring on the inside of the dorsal spiracular diverticular endoderm and pharyngeal endoderm. It would also appear that there is some mixing of this latter material with the general laterohyal blasteme.

That gill pouch endoderm is essential for gill arch formation in amphibians was established experimentally by Balinsky (1948) who found a close causal relationship between the presence of gill pouch endoderm and the gill arches. When the former is absent the arches do not chondrify. He ascribes this phenomenon to a kind of inductive action of the pouch endoderm, under whose influences the neural crest (mesectoderm or ectomesenchyme) situated against its inner surface chondrifies and becomes incorporated piecemeal ('Stück für Stück') into the arches. This finding is significant and (with our own observations in the crocodile and birds) is an indication that gill pouch and pharynx endoderm is probably essential for gill arch formation in vertebrates generally and that primary arch material may still be added to the already formed primary arches in later stages.

Delamination of material from below the pharyngeal endoderm of the ostrich has been reported (Frank & Smit 1976) but no distinction was drawn between this material and the laterohyal blasteme derived from sub-epidermal delamination. Our present, more extensive, bird material shows that additional sub-endodermal blasteme becomes added to all the upper segments of the hyoid arch, namely infra-, supra-, epi-, inter- and ceratohyal. One is inclined to suggest that all additional material that becomes incorporated into the arches from inside the endoderm is prospective primary arch material and that it should be distinguished from secondary sub-epidermal laterohyal blasteme, which in bony fish is the source of gill ray material (Bertmar 1959) and not primary arch material as such. However, as indicated above, there is some mixing of the two blastemes in birds and a strict distinction between the two is not possible. Thus our avian material suggests that after initial primary arch formation there is no specificity, that is, endodermal delaminating products

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contributing exclusively to the primary arch, and ectodermal products contributing exclusively to the secondary (gill ray or laterohyal) arch elements. In other words, subepithelial products of both ecto- and endodermal origin contribute to primary as well as secondary arch elements so that the individual elements would appear to be of mixed origin.

As has been mentioned earlier a single supracolumellar process exists in the penguin but in the other three species investigated (mynah, dove and fowl) a complete supracolumellar arcade with extracolumellar fenestra (Huxley's foramen) is formed. The lateral limb (lateral supracolumellar process) is clearly derived from the laterohyal blasteme. This is also true for the so-called 'intercalary' which appears to be the extreme dorsal tip of the lateral limb. It must be clearly understood that the structure called 'intercalary' in birds is presumably homologus with the similarly named structure in *Lacerta* (Versluys 1903) but it does not occupy the same position between the otic process of the quadrate and the auditory capsule. The lateral prong in birds is relatively much smaller than in lizards and ends freely dorsally (de Beer 1937). The 'intercalary' cartilage of the penguin is situated at the tip of the medial limb and must be looked upon as nothing more than the dorsal part of an incipient lateral limb. This reminds one of the observations of Stellbogen (1930) and Freye (1952/53), namely, that the lateral limb of adult birds frequently appears as a process of the medial limb.

Crompton's (1953) reference to the presence of a "nodule of dense blasteme" continuous with the dorsal end of the medial limb (Crompton's lateral process) in early stages and situated between the otic process of the quadrate and the metotic cartilage, and which later atrophies when chondrification sets in, could not be verified with the material at our disposal. Crompton regards this structure as probably homologous with the reptilian intercalary. This view was accepted by the present authors in a previous paper (Frank & Smit 1974). However, in view of our own observations in the penguin, we must now conclude that this is not the structure designated 'intercalary' by us in the penguin.

Toerien (1971) makes mention of the great variation that exists in the development of the supracolumellar arcade. As has been shown above the supposed variation results from the confusion of different entities with one another. The only real variation that does exist lies in the degree of reduction of the lateral limb (lateral supracolumellar process). The development in all birds is essentially the same; this is what one would expect.

No significance must be attached to the fact that the chorda tympani nerve in the penguin runs roughly in the position of the extracolumellar fenestra, for in all birds with a complete arcade it tends to overlie the arcade and never runs through the fenestra. In the penguin it probably shifts inwards because of the absence of a complete lateral limb. In all birds the chorda tympani initially runs through the migrating laterohyal blasteme.

Frank and Smit (1974) suggested that the lateral limb of the columella in *Sphenodon* and birds constitutes a morphological entity which represents the dorsal articular head of the rhipidistian hyomandibula. In view of this the Jarvik-Bjerring model (Jarvik 1972, Bjerring 1977), according to which the 'dorsal process' of the reptilian columella is derived from the dorsal articular head of the osteolepiform hyomandibula and composed of hyoid gill ray (laterohyal) material only, cannot be accepted without qualification. The reptilian dorsal process is a composite structure formed proximally from suprapharyngohyal material. This part becomes the ligamentum intercalare-columellare of lizards (Dombrowsky 1925) and the inner limb of the avian supracolumellar process. The tip of the reptilian 'dorsal process' (the intercalary of *Lacerta*) is derived from laterohyal material which also forms the outer limb of the avian supracolumellar process. The base of the reptilian 'dorsal process' thus represents the upper part of the rhipidistian lateral commissure, and its tip part of the dorsal articular head of the rhipidistian hyomandibula.

The infracolumellar process

Both Müller (1963) and Toerien (1971) refer to the great variation that characterizes the development of the infracolumellar process and stylohyal in birds. But here too, as in the case of the lateral limb, our detailed study of more extensive material reveals this to be more apparent than real.

Crompton (1953) states that the infracolumellar process in the penguin differs in its development from that of most other birds investigated. As his description is confusing we were prompted to reinvestigate conditions in this bird and compare them with some other species. This reinvestigation was also necessary in view of our findings in the ostrich (Frank & Smit 1976) and our suspicion that the term stylohyal has been used for different structures by different authors.

Frank & Smit (1976) reported the secondary addition of delaminated sub-epidermal mesenchyme (which forms part of the general laterohyal blasteme) to the primary arch interhyal (connecting the epihyal with the ceratohyal) making this a 'double structure' in the ostrich. This corresponds to the situation in bony fish where Holmgren (1943) and Bertmar (1959) reported a dual origin for the interhyal (also called stylohyal in fish), *viz* a medial primary arch component and a lateral part derived from sub-epidermal blasteme and representing ray material associated with the epihyal. In bony fish this lateral part fuses, upon chondrification, with the medial part into a single structure. In the oldest ostrich embryo examined the composite interhyal forms, with the distal tip of the epihyal (infrastapedial of the crocodile: Parker 1883), an infracolumellar process in the strict sense. In this bird the ceratohyal (Crompton's stylohyal or hypohyal in the penguin) remains attached to this process. A composite interhyal was also found to develop in the other birds we investigated but the contribution of the secondary component in the mynah, dove and fowl is less than in the ostrich.

In the penguin the secondary interhyal blasteme accumulates on the posteromedial aspect of the infracolumellar curve and becomes the more prominent part of a clearly double interhyal with the primary arch interhyal in blastematous continuity with the ceratohyal (stylohyal of other authors). When the secondary component (which seems to represent Crompton's ceratohyal) starts to chondrify, the primary component gradually regresses and ultimately the ceratohyal becomes detached from the epihyal above. When the secondary interhyal component fuses with the epihyal distally it forms a slightly C-shaped infracolumellar process. In the oldest embryos of the

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mynah, fowl and dove investigated the primary interhyal has not become obliterated and attaches the ceratohyal to the epihyal forming a long 'infracolumellar process'. Only in the fowl does the extreme distal knob of the ceratohyal later become separate; the discontinuity lies within the ceratohyal itself. Sonies (1907) is thus justified in considering this isolated piece as the ventral tip of the ceratohyal (Sonies' stylohyal).

It will not be surprising if subsequent work on the crocodile shows that the interhyal (Parker's (1883) epihyal) represents both components of a composite interhyal and not a primary arch component only as suggested by Frank & Smit (1976). According to Parker (1883) and Versluys (1903) this structure in the crocodile separates from the epihyal and becomes attached to the suprapharyngohyal by means of a ligament, thus forming a kind of lateral limb. Versluys (1903) therefore considers Parker's epihyal the homologue of the lateral limb of the supracolumellar arcade in birds. Even if subsequent evidence proves that this structure includes a secondary interhyal it cannot be considered the homologue of the lateral limb of the supracolumellar arcade. Although both structures derive from the same general laterohyal blasteme, conditions in the ostrich, where the secondary interhyal component retains its primary position while separate lateral limb material is clearly incorporated into the "single" supracolumellar process, refute such a deduction.

Thus, variations in the infracolumellar process of birds can be explained partly in terms of the varying degrees in which the two components of the composite interhyal contribute to the adult interhyal. On the one hand there is the penguin where the primary component obliterates, ostensibly completely, leaving the whole ceratohyal separate from the columella and contributing nothing, or at most very little, to the infracolumellar process. On the other hand there are forms (the majority of birds) where the primary interhyal does not obliterate, and forms with the secondary interhyal (the contribution of which can vary) a composite interhyal which connects the ceratohyal with the distal tip of the epihyal forming a long infracolumellar process in the broad sense. It seems that the ostrich occupies an intermediate position, with the secondary component contributing to a relatively large extent to the composite interhyal but without obliteration of the primary interhyal as in the penguin.

The conclusion that is drawn here is that in all birds the development of the so-called infracolumellar process is essentially the same. The primary and secondary interhyal components contribute to a varying degree to the adult interhyal which, with the distal tip of the epihyal, forms the infracolumellar process in the strict sense. When the primary arch component regresses during later development to such an extent that the ceratohyal becomes detached from the columella, the condition that obtains in the penguin results. The earlier remark (Frank & Smit 1974) that conditions in the penguin are probably the same as in birds generally, is thus only partly correct. Subsequent work has indicated that Crompton's (1953) ceratohyal in the penguin represents only the secondary component of the interhyal and not both components of the ostrich interhyal as was suggested by Frank & Smit (1976).

It is also our opinion that some of the great variation that is supposed to exist in the infracolumellar process of birds results from the indiscriminate use of the term stylohyal. Sonies (1907) distinguishes a separate stylohyal (ceratohyal of the present authors) in the fowl and duck which later becomes confluent with the infracolumellar process. An independent cartilaginous piece appears near the ventral tip of his stylohyal in the fowl. This structure Sonies compares with the swollen tip of the ceratohyal (his stylohyal) in the duck and considers it as a piece (of the ceratohyal) that remains independent in the fowl. This has been confirmed by our own observations in the fowl (Fig. 2C: *cerato*).

It would seem that these two ceratohyal components of Sonies are the cause of most of the confusion. Müller (1963) and Toerien (1971) group the fowl with the penguin and consider them as examples where the ceratohyal remains separate from the infracolumellar process. It is, however, quite clear from Crompton's work and our own observations that the two structures involved here are not the same. Crompton's (1953) 'stylohyal' in the penguin corresponds to the entire stylohyal of Sonies (1907), of which the upper part becomes confluent with the infracolumellar process in the fowl, and not to the small ventral isolated piece only.

Müller's (1963) reference to de Beer & Barrington's (1934) observation that in the duck the ceratohyal separates from the infracolumellar process in older stages strengthens the opinion that the small isolated piece of the ceratohyal in the fowl (Sonies 1907) has been incorrectly identified as the entire ceratohyal in some other species of bird by several authors. When this fact is understood much of the confusion in regard to the composition of the 'infracolumellar process' disappears and one is still inclined to agree with Versluys (1903) that in the majority of birds the 'Zungenbeinbogen' (ceratohyal or stylohyal of other authors) retains its continuity with the columella auris as in *Sphenodon* (de Beer 1937).

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