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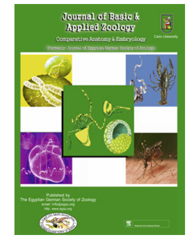

Studies on the ontogeny of *Streptopelia senegalensis aegyptiaca* (latham 1790) 5 – The development of the viscerocranium

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Abstract The present article shows the following points: The quadrate and Meckel's cartilages have separate centres of chondrification. A symphsis Meckelii is absent. Meckel's cartilage has three processes. These are processus mandibularis externus, processus mandibularis internus and retroarticularis. The quadrate cartilage has five processes; orbitalis, medialis, lateralis, oticus and the ventral articular processes. The columella auris has two centres of chondrification, a medial otostapedial centre (the stapes) and a lateral hyostapedial centre.

Introduction

The avian viscerocranium has been described by several investigators (De Beer and Barrington, 1934; Slaby, 1951; De Kock, 1955; Crompton, 1953; Frank, 1954; Fourie, 1955; Engelbrecht, 1958; Müller, 1963; Til-Macke, 1969; Mokhtar, 1975; Abd El-Hady and Zaher, 1999 and El-Shikha, 2011). Although these works furnish a good survey on the avian viscerocranium, certain problems are still present in this subject which the authors have attempted to solve. This attracted the attention of the authors to cast light on the study of the ontogeny of the viscerocranium of *Streptopelia senegalensis aegyptiaca*.

The present work is the fifth one in the series of publications carried out by the authors to study the ontogeny of the chondrocranium of Streptopelia senegalensis aegyptiaca. In previous four publications, Zaher and Riad (2009, 2012a,b, in press) studied the development of the early, and intermediate stages as well as the optimum and post hatching stages of the chondrocranium of *Streptopelia senegalensis aegyptiaca*.

Material and method

The present article needs the study of the viscerocranium of three embryos of *Streptopelia senegalensis aegyptiaca* with the total body lengths of 30, 34 and 62 mm. The heads of embryos were stained in toto with Borax carmine, then serially sectioned. The sections were counterstained with picroindigocarmine. From these sections, graphic reconstruction of views of the visceral arches in only three ontogenic stages (30, 34 and 62 mm lengths) were drawn and explained in detail.

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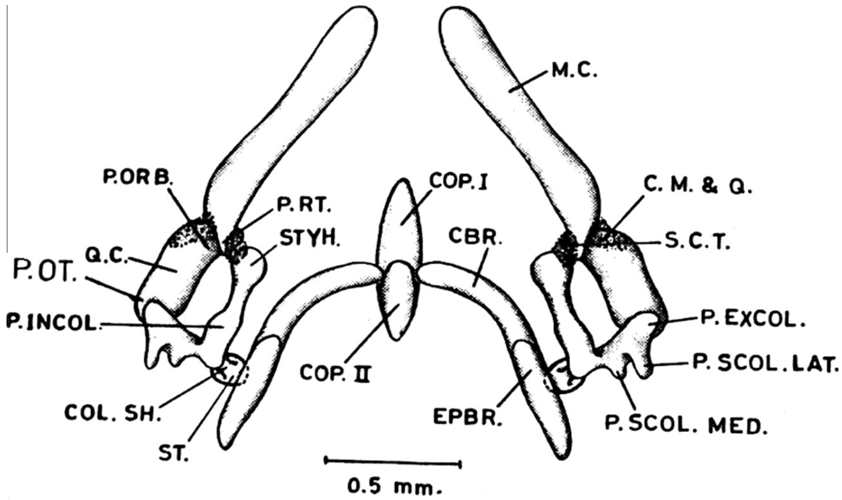

Figure 1 Graphic reconstruction of the viscerocranium of stage I (30 mm embryo) of *Streptopelia*.

Observation

Investigation of the viscerocranial elements of the present stage of *Streptopelia* (stage 1, 30 mm total body length) shows the prior appearance of the two quadrate processes, these are the processus oticus (Fig. 1[1], P.O.T.) and processus orbitalis (Fig. 1, P.ORB.).

The processus oticus develops as a stout cylindrical outgrowth from the postero-lateral extremity of the quadrate.

The processus orbitalis (Fig. 1, P. ORB.) extends in the form of a stout process from the upper portion of the quadrate cartilage.

The two rami of Meckl's cartilage extend antero-medially on both sides of the elements of the neurocranium. Each ramus lies in the form of a thick cylindrical rod. The anlage of the processus retroarticularis (P.RT., Fig. 1) projects postero-laterally as a small procartilaginous protrusion from the posterior end of the Meckel's cartilage. In a ventral view (Fig. 1), the anterior tips of the two rami of Meckl's cartilage are situated medially near each other but without contact. On the other hand, the posterior extremities of the rami are far apart from each other.

The stapes (ST., Fig. 1) is in the form of a rough oval procartilaginous mass which does not differentiate into any components.

The faint connective tissue band which connects the two components of the columella auris converts now into a dense connective strand which later chondrifies as the coulmellar shaft (Fig. 1, COL. SH.).

The outer extracolumellar portion reaches the procartilaginous phase. This represents the processus extracolumellaris (Fig. 1, P.EXCOL.). The proximal tip of the hyostapes extends anterolaterally as the procartilaginous processus infracoulmellaris (Fig. 1, P. INCOL.). The upward continuity of the latter process represents the stylohyal (STYH., Fig. 1).

In the present stage two copulae can be easily differentiated from each other. These are a dorsal copula 1 (Fig. 1, COP. I.) and a ventral copula II (Fig. 1, COP. II.). At the point of contact between the two overlapping copulae, the anlage of the ceratobranchial of the first branchial arch (Fig. 1, C.BR.) extends postero-laterally.

When the present stage is reached (stage 2, total body length 34 mm), the quadrate cartilage shows an advanced rate of chondrification and develops another two new processes, the medial process of the quadrate (Fig. 2, P.MED.) and processus lateralis (Fig. 2, P. LAT.). The medial process of the quadrate develops from its medial surface at the base of the processus orbitalis as a short, thick and stout process. The processus lateralis represents a slight undulation extending at the lateral wall of the quadrate cartilage.

The processus oticus is now well developed and shows a considerable increase in length when compared with the slightly smaller processus orbitalis.

One of the novelties of the viscerocranium of *Streptopelia* in the present stage, is the regression of the quadratopolar commissure. Its remains are the processus pterygoideus and basalis (Fig. 3, P. PT. & P. BAS.). By the end of this stage, the basal process is completely atrophied.

One of the important changes in the viscerocranium of the present stage of *Streptopelia* (stage 2 total body length 34 mm) is a progress in the rate of chondrification and an increase in the length of Meckel's cartilage. The anterior ends of the two rami of Meckel's cartilage come nearer to each other. However, there is no actual fusion between them. The medial side of the articular region shows a triangular projection. This represents the rudiment of the processus mandibularis internus (Fig. 2, P.MAN. N.).

It can be easily detected that a considerable chondrification has taken place in the hyoid arch elements. Thus in the columella auris, the stapes becomes now well chondrified with a

[1] *Abbreviations:* C.BR, ceratobranchial; COL. SH, columellar shaft; COP.I, first copula; Cop.II, second copula; EP.BR, epibranchial; FOR. HUX, Huxley's foramen; M.C, Meckel's cartilage; P.BAS, basal process of the quadrate; P.EXCOL, processus extracolumellaris; P.INCOL, processus infracolumellaris; P.LAT, processus lateralis of the quadrate; P.LNG, processus lingualis; P.MAN. EX, processus mandibularis externus; P.MAN IN, processus mandibularis internus; P.MED, medial process of the quadrate; P.ORB, processus orbitalis; P.OT, processus oticus; P.PT, processus pterygoideus; P.RT, processus retroarticularis; P.SCOL. LAT, processus supracolumellaris lateralis; P. SCOL. MED, processus supracolumellaris medialis; P.V.ART.Q, ventral articular process of the quadrate; PARAG.C, paraglossal cartilage; Q.C, quadrate cartilage; S.COL.ARC, supracollumellar arcade; ST, stapes; STYH, stylohyal.

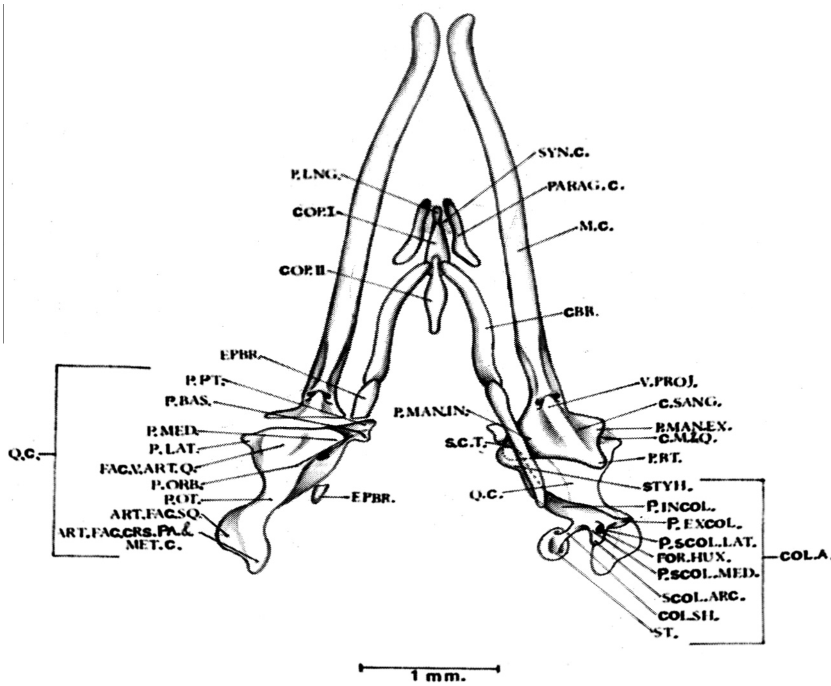

Figure 2 Graphic reconstruction of the viscerocranium of Stage II (34 mm embryo) of *Streptopelia*.

circular outline. Also, the processus extracolumellaris shows a higher degree of chondrification.

Also, the processus infracolumellaris shows an advanced rate of chondrification. It is somewhat elongated antero-ventrally with its stylohyal.

In the present stage, a procartilaginous epibranchial (Fig. 3, EP. BR.), belonging to the first branchial arch, is now differentiated in prolongation with the distal margin of the ceratobranchial. However, both elements are separated by a thin zone of mesenchymatous tissue. The epibranchial is a stout cylindrical rod that projects posteriorly in a latero-ventral direction. Its distal portion is still developed without definite boundary from the surrounding mesenchyme.

The elements of the median copulae (Copula I and Copula II) are now well chondrified.

The second copula of the stage is restricted to the ventral surface of the first copula.

One of the novelties of the visceral arch skeleton of the present stage is the development of the paraglossal cartilages.

In the present stage, the paraglossal cartilages are well chondrified (Fig. 2, PARAG. C.). They are now elongated, rod-shaped and have remarkably increased in length in the antero-medial direction. They are disposed now anteriorly and laterodorsally to the first coupla(). Their anterior halves approach each other in the sagittal plane, but without real fusion. However, the posterior halves of the two paraglossals diverge towards the posterior direction without any connection between them.

In the optimum stage of *Streptopelia* (stage 3 total body length 62 mm), the quadrate cartilage is a massive structure and shows an exceptional increase in size. It develops a new process, the ventral articular process (Fig. 3, P.V. ART. Q.).

All the previously described processes of the quadrate are now extensively enlarged and become more heavily chondrified than before. However, the processus basalis and basipterygoideus are completely disappeared when the optimum stage is reached.

Meckel's cartilage has grown further forward in the form of a very long stout rod. It is almost circular in cross section through its whole length, except its anterior end which is triangular in shape and its posterior articular region which is extensively enlarged. The two rami of Meckel's cartilage approach each other gradually towards the sagittal plane, but they never fuse even in the 82 mm nestling stage. This means that the symphysis meckelii is absent in *Streptopelia*.

The articular region of the Meckel's cartilage becomes now massive and heavily chondrified. It has three distinct processes; the processus mandibularis externus (Fig. 3, P. MAN. EX.) which tapers towards the antero-lateral direction, the processus mandibularis internus (Fig. 3, P. MAN. IN.) which extends postero-medially as an intensively enlarged triangular process and the processus retroarticularis which protrudes postero-laterally and represents the longest process.

The processus extracolumellaris (Fig. 3, P. EXCOL.) has elongated antero-medially, and the processus infracolumellaris (Fig. 3, P. INCOL.) anteriorly. Moreover, the distal tip of the processus infracolumellaris medialis extends ventrally and merges with the distal tip of the processus infracolumellaris lateralis. Thus a supracolumellar arcade (Fig. 3, S. COL. ARC.) is developed enclosing, together with the medial and lateral processes, a narrow foramen that allows the passage of a minute blood vessel. This is Huxley's foramen (Fig. 3, FOR. HUX.).

The stylohyal (Fig. 3, STYH.) represents the anterior continuation of the processus infracolumellaris (Fig. 3, P.INCOL.). It extends medially and lies apart from the posterior extremity of Meckel's cartilage.

The median copulae mass shows a considerable increase in length and growth. The thin zone of mesenchyme, separating the two copulae in the sagittal plane, has disappeared with

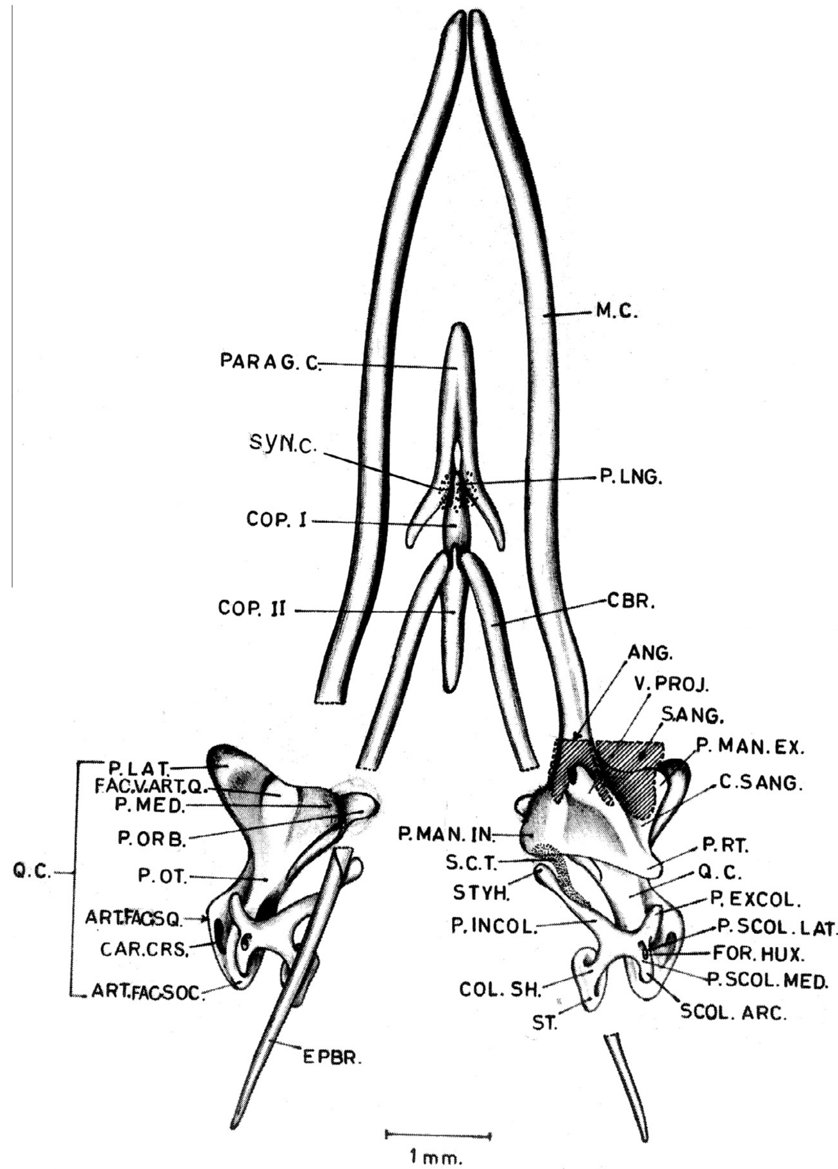

Figure 3 Graphic reconstruction of the viscerocranium of the optimum Stage (62 mm embryo) of *Streptopelia*.

the complete coalescence of the two copulae (Fig. 3, COP. I. and COP. II.).

A short median process extends towards the anterior direction and in continuity with the anterior tip of the first copula. It is homo-continuous with the first copula and prolongs anteriorly as a small stout cartilaginous process with a blunt anterior margin. It represents the processus lingualis (Fig. 3, P. LNG.). In addition, the ceratobranchials and the epibranchials are notably elongated and their articulation becomes more accentuated. The posterior end of the epibranchial lies now far past the hind margin of the processus retroarticularis.

Discussion

The simultaneous chondrification of the two elements of the mandibular arch in *Streptopelia* seems to be a common feature for the viscerocranium of the described birds. However, de Beer and Barrington (1934) found that the quadrate cartilage has a prior appearance than Meckel's cartilage. The present study proves the presence of two separate centres of chondrification for the two mandibular arch components. This condition is identical to that detected in *Spheniscus* (Crompton, 1953), *Struthio* (Frank, 1954), *Fulica* (Til-Macke, 1969), *Upupa* (Mokhtar, 1975), *Corvus* (Zaher et al., 1991), Hirundo (Abd-El-Hady, 2000) and *Columba*(El-Shikha, 2011). Moreover, this is identical to what was observed in *Lacerta* (De Beer, 1937). Accordingly, such a character may be regarded as a primitive one. On the contrary, the anlagen of the quadrate cartilage and Meckel's cartilage are in continuity in *Anas platyrhynchos* and *Passer domesticus* (Kallius, 1905) as well as in *Pyromelana* (Engelbrecht, 1958).

The present investigation reveals that in *Streptopelia* the quadrate cartilage shows the common avian features. Thus, the basal process is ephemeral. The processus orbitalis has a prior appearance as compared with the processus oticus. The ventral articular process is more delayed in appearance. An identical condition is observed by Engelbrecht (1958), Müller (1963), Til-Macke (1969), Mokhtar (1975), Zaher (1984) and Zaher et al. (1991) in *Pyromelana*, *Rhea*, *Fulica*, *Upupa*, *Charadrius* and *Corvus,* respectively. In few cases, the processus orbitalis and processus oticus appear simultaneously prior to the ventral articular process (De Beer and Barrington, 1934; Slaby, 1951 and Crompton, 1953).

In *Streptopelia*, a gradual regression takes place in the ventral surface of the quadratopolar commissure. Accordingly, it becomes discontinuous and all what remains out of the commissure are the ephemeral basal process of the quadrate and the basipterygoid process. This is identical to the condition present in *Pyromelana* (Engelbrecht, 1958), *Fulica* (Til-Macke, 1969), *Upupa* and *Merops* (Mokhtar, 1975), *Corvus* (Zaher et al., 1991) and *Coturnix* (Abd El-Had, 2008). However, de Beer and Barrington (1934) found that, in Anas, the quadratopolar commissure is completely regressed and thus the basal as well as the basipterygoid processes are wanting.

In *Streptopelia*, the quadratopolar commissure is entirely visceral in origin and its connection to the neurocranium is secondary. This confirms Engelbrecht (1958) in *Pyromelana*. This condition is also observed in *Upupa* and *Merops* (Mokhtar, 1975), *Corvus* (Zaher et al., 1991) and *Coturnix* (Abd El-Hady, 2008).

In *Streptopelia*, the basipterygoid process chondrifies in the dorsal portion of the quadratopolar commissure. This means that it has a visceral origin and its connection to the neurocranium is secondary. This confirms the findings of Engelbrecht (1958), Mokhtar (1975), and Zaher et al. (1991) in *Pyromelana*, *Merops*, *Charadrius* and *Corvus,* respectively. However, in *Spheniscus* (Crompton, 1953) and the Ostrich (Frank, 1954) the process is homologized with the pharyngeomandibular of selachians because it has a separate centre which later chondrifies in continuity with the neurocranium.

In *Streptopelia*, the processus retroarticularis shows a delayed appearance as compared with Meckel's cartilage. This represents a common feature in the avian literature (Crompton, 1953; Til-Macke, 1969; Mokhtar, 1975; Zaher et al., 1991 and Abd El-Hady, 2008). However, Frank (1954) stated that in *Struthio*, the processus retroarticularis appears at the same time with Meckel's cartilage, while Engelbrecht (1958) considered that in *Pyromelana* the process in question has a prior appearance as compared with Meckel's cartilage.

In *Streptopelia*, the processus mandibularis externus and internus are well developed. The latter has a prior appearance. Such a condition is the same in *Rhea* (Müller, 1963), *Fulica* (Til-Macke, 1969) and *Corvus* (Zaher et al., 1991). However, in *Upupa* (Mokhtar, 1975), the processus mandibularis externus has a prior appearance. It is of interest to mention that De Kock (1955), Fourie (1955) and Engelbrecht (1958) denied the presence of the processus mandibularis externus in *Sturnus*.

The absence of a true symphysis Meckelii is observed in *Streptopelia* as in almost all described birds e.g. *Spheniscus* (Crompton, 1953), *Nyctisyrigmus* (Fourie, 1955), *Pyromelana* (Engelbrecht, 1958), *Merops* (Mokhtar, 1975), *Corvus* (Zaher et al., 1991 and Abd El-Hady, 2008). However, the presence of a true symphysis Meckelii is observed by De Kock (1955), Webb (1957) and Mokhtar (1975) in *Sturnus*, *Struthio* and *Upupa,* respectively.

In *Streptopelia*, the columella auris has the typical avian pattern. The processus supracolumellaris medialis has an otostapedial origin, i.e. it originates from the distal tip of the columellar shaft. However, the avian literature shows a wide controversy regarding the origin of the processus supracolumellaris lateralis. Suschkin (1899), De Beer (1937) and Müller (1963) state that this process originates as an isolated anlage.

Engelbrecht (1958) states that in *Pyromelana*, the lateral and medial processes are formed when the supracolumellar process chondrifies and leaves a small area at its base devoid of any deposit (Huxley's foramen). Stellbogen (1930), Freye (1952–1953) and Warner (1960) report that the processus supracolumellaris lateralis in birds represents a continuation of the processus supracolumellaris medialis that does not reach the processus extracolumellaris, but ends in the region of the ligamentum ascendens. The present investigation confirms the findings of Crompton (1953), Til-Macke (1969), Mokhtar (1975) and Zaher et al. (1991). Thus, the processus supracolumellaris connects the processus medialis with the root of the processus extracolumellaris.

In *Streptopelia*, the stylohyal has no separate centre of chondrification, since from the beginning of its development, it represents the anterior continuity of the processus infracolumellaris. Such a condition is similarly described by Engelbrecht (1958), Mokhtar (1975), and Zaher et al. (1991) in Pyromelana, Upupa and *Corvus* respectively. However, an isolated stylohyal, having an independent centre of chondrification from the processus infracolumellaris, is described in Gallus (Sonies, 1907), *Spheniscus* (Crompton, 1953), Rhea (Müller, 1963) and Sturnus (De kock, 1955).

In *Streptopelia* as commonly found in the described birds, the median unpaired copulae mass is formed by the fusion of two centres of chondrification. This is identical to those found in *Fulica* (Til-Macke, 1969), Upupa, (Mokhtar, 1975), *Corvus* (Zaher et al., 1991) and Hirundo (Abd-El-Hady, 2000).

In *Streptopelia*, as commonly found in birds, the two copulae appear simultaneously. However, in Anas (De Beer and Barrington, 1934), copula I appears first.

The present study shows that from the very beginning the ceratobranchial anlage runs in imperceptible fusion with the blastema of the second copula. This is similar to the condition found by Crompton (1953), Til-Macke (1969), Mokhtar (1975), Zaher et al. (1991) and Abd El-Hady and Zaher (1999) in their described birds. Their separation takes place in a later developmental stage. However, in *Anas* (De Beer and Barrington, 1934), *Phalacrocorax* (Slaby, 1951), *Struthio* (Frank, 1954) and *Pyromelana* (Engelbrecht, 1958), the ceratobranchial has an isolated centre of chondrification. Whatever the exact origin of the ceratobranchial may be there is nothing that could weigh against regarding the second copula as a basibranchial element in birds.

In *Streptopelia*, the ceratobranchial element, undoubtedly, belongs to the first branchial arch (the third of the whole series). In the present study, as found in the majority of the described birds, no anlage of the second branchial arch could be traced. In reptiles, such a structure has a common existence and it develops further in later ontogeny.

The paraglossal cartilages, which are found in *Streptopelia* have a general occurrence in all the described birds.

The present study describes a paired origin for the paraglossal cartilages. This feature is commonly found in the described birds. However, their later fusion is not manifested. Crompton (1953) and Fourie (1955) describe in *Spheniscus* and *Nyctisyrigmus,* respectively a thin cartilaginous bridge connecting the posterior diverging parts of the paraglossals, thus a median foramen is created between them.

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