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A review on the avian viscerocranium

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Abstract The avian viscerocranium has been described by several investigators. It was perceived that a review on the ontogeny of the avian viscerocranium would be very useful to enrich the knowledge on this subject. The present article casts light on the avian viscerocranium starting from the early stages up to fairly late ones.

Contents

The avian viscerocranium has been described by several investigators such as De Beer and Barrington (1934), Slaby (1951), Crompton (1953), Frank (1954), De Kock (1955), Fourie (1955), Engelbrecht (1958), Müller (1963), Macke (1969), Mokhtar (1975), Zaher et al. (1989, 1991), Abd El-Hady and Zaher (1999), El-Shikha (2011) and Zaher and Riad (2013).

The present authors perceived that a review on the ontogeny of the avian viscerocranium would be very useful to enrich the knowledge of this subject. The present article casts light on the avian viscerocranium starting from the early stages up to fairly late ones.

A review on the avian neurocranium was previously prepared and published by the present authors (Zaher and Abu-Taira, 2013).

The fact that the elements of the mandibular arch chondrify at the same time seems to be universal in all the birds so far described such as *Upupa* (Mokhtar, 1975), *Passer* (Zaher et al., 1989), *Corvus* (Zaher et al., 1991), *Gallinula* (Abd El-Hady and Zaher, 1999), *Hirundo* (Abd El-Hady, 2000), *Coturnix* (Abd El-Hady, 2008), *Columba* (El-Shikha, 2011) and *Streptopelia* (Zaher and Riad, 2013). The only exception is the condition found in *Anas* (De Beer and Barrington, 1934), where the quadrate cartilage has a prior appearance.

Of special interest in the avian viscerocranium is the presence of separate centres of chondrification for the two components of the mandibular arch which are syndesmotically connected together from the very beginning. This condition is found in *Spheniscus* (Crompton, 1953), *Struthio* (Frank, 1954), *Upupa* (Mokhtar, 1975), *Passer* (Zaher et al., 1989), *Hirundo* (Abd El-Hady, 2000), *Columba* (El-Shikha, 2011) and *Streptopelia* (Zaher and Riad, 2013). In *Anas* (De Beer and Barrington, 1934), *Phalacrocorax* (Slaby, 1951) and *Fulica* (Macke, 1969), separate centres for these components do occur

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but no author has pointed out whether a syndesmotic connection is present or not. Whatever the case may be, this condition is reminiscent with what has been referred to by Shanker (1926) in *Chrysemys* and by De Beer (1937) in *Lacerta*. Thus in the above mentioned birds, the presence of separate centres of chondrification for the quadrate and Meckel's cartilages could be regarded as a primitive character. On the other hand Kallius (1905) states that both anlagen of the mandibular components are continuous with each other. In *Pyromelana* (Engelbrecht, 1958) the quadrate and Meckel's cartilage develop from one anlage.

In *Passer* (Zaher et al., 1989), the elements of the mandibular arch have a precocial appearance relative to the other chondrocranial entities, similar to that mentioned in *Lacerta* (De Beer, 1937) and in Ophidia (Kamal and Hammouda, 1965a, b). In *Anas* (De Beer and Barrington, 1934), the quadrate cartilage appears in a late stage and Meckel's cartilage has a more delayed appearance. In all other described birds, *Upupa* (Mokhtar, 1975), *Corvus* (Zaher et al., 1991), *Hirundo* (Abd El-Hady, 2000), *Coturnix* (Abd El-Hady, 2008) and *Columba* (El-Shikha, 2011), the mandibular anlagen develops in a comparatively older stage than described in *Passer* (Zaher et al., 1989). However, in *Phalacrocorax* (Slaby, 1951), Meckel's cartilage and the elements of the hyoid arch have a prior appearance than any other chondrocranial elements. In this respect, it seems possible to consider the condition in *Passer* (Zaher et al., 1989) and *Phalacrocorax* (Slaby, 1951) as a primitive feature.

The common avian pattern of the quadrate cartilage shows an ephemeral basal process. The processus oticus develops exceptionally late, when compared with the processus orbitalis. The ventral articular process has a more delayed appearance. This seems to be the condition in *Struthio* (Brock, 1937; Frank, 1954 & Lang, 1956), *Pyromelana* (Engelbrecht, 1958), *Rhea* (Müller, 1963), *Fulica* (Macke, 1969). Although these three processes are conspicuous in the quadrate of the majority of described birds such as *Hirundo* (Abd El-Hady, 2000), *Coturnix* (Abd El-Hady, 2008), *Columba* (El-Shikha, 2011) and *Streptopelia* (Zaher and Riad, 2013), yet the processus orbitalis is absent in *Nyctisyrigmus* (Fourie, 1955).

The fifth process found in the quadrate is the processus lateralis. Actually, this processus is missing in some birds, e.g., *Anas* (De Beer and Barrington, 1934), *Spheniscus* (Crompton, 1953), *Struthio* (Frank, 1954) and *Pyromelana* (Engelbrecht, 1958). In other described birds such as *Upupa* (Mokhtar, 1975), *Corvus* (Zaher et al., 1991), *Coturnix* (Abd El-Hady, 2008) and *Streptopelia* (Zaher and Riad, 2013), the processus lateralis is a well developed structure.

The conspicuous condition of the medial process of the quadrate, which holds fusion with the posterior tip of the pterygoid bone, is a point of difference among the majority of described birds. In some birds, the pterygoid is contiguous with the medial surface of the quadrate, but a medial process as that found in *Passer* (Zaher et al., 1989) is not present except in *Pyromelana* (Engelbrecht, 1958). However, its mode of development in *Pyromelana* is quite different from the condition observed in *Passer* (Zaher et al., 1989). In *Pyromelana* (Engelbrecht, 1958), the medial process of the quadrate develops as a chondrification in the posterior end of the same mesenchymatous tract in which the pterygoid ossifies, thereafter, it acquires fusion with the medial surface of the quadrate. It is thus evident that the medial processes in *Passer* (Zaher et al., 1989) and *Pyromelana* (Engelbrecht, 1958) are not homologous although analogous structures.

The formation of a quadrato-otical joint seems to be a common character in all described birds such as *Spheniscus* (Crompton, 1953), *Nyctisyrigmus* (Fourie, 1955), *Pyromelana* (Engelbrecht, 1958), *Merops* and *Upupa* (Mokhtar, 1975), *Coturnix* (Abd El-Hady, 2008) and *Streptopelia* (Zaher and Riad, 2013), but from one species to another it is not necessarily formed in the same pattern. In the authors opinion the shape of the joint is merely dependent upon the crista parotica formation. In the simplest form the crista parotica is poorly developed. The articular facet of the processus oticus that holds fusion with the crista parotica hardly comes in contact with the referred crista and merges with the antero-dorsal border of the mitotic cartilage. This condition is described in *Struthio* (Frank, 1954), *Pterocles* (Mokhtar et al., 1983) and *Passer* (Zaher et al., 1989). In a more complicated form as in *Anas* (De Beer and Barrington, 1934), *Spheniscus* (Crompton, 1953), *Nyctisyrigmus* (Fourie, 1955), *Pyromelana* (Engelbrecht, 1958), *Rhea* (Müller, 1963), *Fulica* (Macke, 1969) and *Merops* and *Upupa* (Mokhtar, 1975), the crista parotica has a large size, and accordingly there is a tendency in these latter birds that the crista forms a cartilaginous socket without the share of the mitotic cartilage for lodging the posterior extremity of the processus oticus. The condition mentioned in *Passer* (Zaher et al., 1989) is rather similar to that of the above mentioned birds but in *Passer* the crista parotica has no socket but a mere concavity. This has been referred to in the optimum stage. Whatever the case may be, the processus oticus in birds is always provided with articulating surfaces for the attachment with the auditory capsule. This fact led Müller (1963) to conclude that the quadrato-otical joint of birds has no taxonomic importance.

In *Apteryx* (Parker, 1891), *Anas* and *Gallus* (Sonies, 1907), *Sturnus* (De Kock, 1955), *Pyromelana* (Engelbrecht, 1958), *Rhea* (Müller, 1963), *Upupa* and *Merops* (Mokhtar, 1975) and *Passer* (Zaher et al., 1989), other than the dorso-medial facet of the processus oticus of the quadrate which articulates with the concavity of the crista parotica, the dorsolateral facet of the processus oticus has also an articulation with the squamosal. In *Pyromelana* (Engelbrecht, 1958) and *Upupa* and *Merops* (Mokhtar, 1975) this facet is further reinforced by the development of a cartilaginous crest that articulates with the squamosal through a cartilaginous ledge developed by the processus orbitocapsularis. A more or less similar condition is described in *Apteryx* (Parker, 1891), *Anas* and *Gallus* (Sonies, 1907), *Sturnus* (De Kock, 1955) and *Rhea* (Müller, 1963). However, in *Pyromelana* (Engelbrecht, 1958) and *Upupa* and *Merops* (Mokhtar, 1975) this facet is further reinforced by the development of a cartilaginous crest that articulates with the referred ledge.

The term quadratopolar commissure is first used by Engelbrecht (1958) and is preferably kept in the described birds. During ontogeny, it has been shown that the quadratopolar commissure in *Passer* (Zaher et al., 1989) holds the connection between the quadrate and polar cartilage. It passes dorsal to the palatine nerve and its dorsal part helps to bind the lateral carotid foramen. In the fourth stage of *Passer*, the entire commissure is almost cartilaginous. This cartilaginous condition for the commissure is also present in *Upupa* (Mokhtar, 1975) and *Pterocles* (Mokhtar et al., 1983).