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STUDIES ON THE ONTOGENY OF *STERPTOPELIA* *SENEGALENSIS AEGYPTIACA*

1. DESCRIPTION OF THREE EARLY DEVELOPMENTAL STAGES

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Abstract. The present article studies the development of some neurocranial elements in three early embryonic stages of *Streptopelia*. The collected data are compared and discussed with those of the previously studied avian neurocrania.

Key words: development, neurocranium, *Streptopelia*, early stages.

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Исследования онтогенеза *Streptopelia senegalensis aegyptiaca*. 1. Описание трех ранних стадий развития. - М.М. Захер, А.М. Риад. - Беркут. 18 (1-2). 2009. - Описаны три ранние эмбриональные стадии малой горлицы. Собранные данные сравниваются с другими результатами развития нейрокраниума птиц.

INTRODUCTION

The development of the avian chondrocranium is now regarded as well known. The earliest classical work was published by W.K. Parker (1866) on the structure and development of the skull in the ostrich tribe. Later he added more publications on the skull of birds (Parker, 1869, 1875, 1877, 1888, 1891a, 1891b).

De Beer and Barrington (1934) gave a detailed account of the development of the chondrocranium of *Anas*. Brock (1937) was the first to cast some light on the problematic phylogeny of the Ratitae by her study on the chondrocranium of the ostrich.

Later, further crania of birds belonging to different orders were examined (Slabý, 1951a, 1951b, 1952, 1958; Crompton, 1953; Fourie, 1955; Engelbrecht, Van, 1958; Müller, 1961; Til, 1969).

Recently F.M. Mokhtar (1975) gave a comprehensive study on the craniogenesis of two birds. These are *Upupa epops major* and *Merops superciliosus persicus* (order Coraciiformes). More recently Mokhtar et al. (1983), Zaher et al. (1991), Zaher and Abdeen (1991), Abd El-Hady (2008a, 2008b, in press) studied the crania of *Pterocles*, *Passer*, *Charidrius*, *Galinula*, *Bubulcus*, *Corvus*, *Hirundo* and *Coturnix* respectively.

Since birds form a closed phylogenetic

group, it seems difficult to judge upon the affinities of some structures of the chondrocranium due to their different modes of formation in different species. Examples to these structures are the maxillo-turbinal cartilage, the metotic cartilage, the infra-carotid commissure, and the tectum synoticum.

The authors cannot claim, hence, that the development of the chondrocranium of other different birds belonging to uninvestigated orders in exactly similar to that of any investigated species.

Beyond all what has been mentioned above, there comes a facile assumption that the universal tabulated taxonomy of each order of birds (Peters, 1945; Thomson, 1964) would be more appropriate if it could be possibly verified from an ontogenetical review since birds of the same order should have nearly the same ontogenetical relations. Thus in dealing with the ontogeny of some species of birds belonging to one order, the ontogenetical affinities between them should be considered as well as the difference if there are any. An example to this is the prediction put forward by some authors that *Pterocles alchata caudacutus* is not a Columbiformes. Prof. Dr. Walter Bock from the Columbia University of the States, by his personal contact with Prof. Dr. Hammouda from the Cairo University denies this idea completely and believes that it is quite incorrect.



Thus Prof. Dr. Hammouda and his colleagues suggested that a detailed developmental history for *Pterocles alchata caudacutus* and another typical species of Columbiformes is deemed worthy to confirm the exact relationships of *Pterocles* to the order Columbiformes. Surprisingly enough is the findings of Dr. F.M. Mokhtar, Dr. M.M. Zaher, and Prof. Dr. H.G. Hammouda in a series of four publications, that the chondrogenesis of *Pterocles* shows great affinity to bee eaters (Meropidae, Carciiformes) and the wavers (Ploceidae, Passeriformes). In spite of the fragmentary data observed by Smith (1905) and Til (1969) in *Columba livia*, a detailed study for the chondrogenesis of a typical Columbiformes becomes now a necessity. The chosen species in the present study is *Streptopelia senegalensis aegyptiaca* from suborder Columbae, family Columbidae. It is thus the aim of the present study to elucidate the typical Columbiformes affinities and to judge upon the observed affinities of *Pterocles* as stated by Dr. F.M. Mokhtar and Dr. M.M. Zaher and to compare between both affinities as far as the chondrogenesis is concerned.

The present article in the series deals with the developmental study of 3 early stages of *Streptopelia*. It is followed by the study of the development of the neurocranium of the intermediate stages, the optimum stage, the ethmoid region of a nestling stage, as well as the ontogeny of the visceral arch skeleton of the bird. Moreover, in a separate article, the major affinities and differences between *Streptopelia* and *Pterocles* will be listed and discussed.

MATERIAL AND METHODS

It was found convenient to choose *Streptopelia senegalensis aegyptiaca* to be the aim of the present study as it furnish's a successful possibility of obtaining a complete set of embryos and nestlings of different developmental stages. Actually, it was possible to collect very early embryos from newly laid eggs up to very late ones, and some nestlings.

Living and healthy embryos of *Streptopelia* were removed from their shells and quickly put in aqueous Bouin's fluid for a time ranging between 24–48 hours according to the size of the embryo. The embryos were then washed for several days with 70% alcohol, after which they were preserved in alcohol of the same concentration. The embryos were classified according to the total body length. The specimens were stained in toto with borax carmine for a period ranging from 24–72 hours. Excess stain was removed by differentiating the embryos and nestlings in 1% acid alcohol for several hours followed by washing with 70% alcohol. Before embedding in paraffin, the dehydration process was carried out till 100% alcohol.

After embedding in paraffin, serial transverse sections were cut 10, 15 and 20 microns in thickness according to age. The serial sections were counterstained with picroindigo-carmine.

In a few of the older embryos in which the dermal bones were present, the counterstaining was with azan. In other embryos, mounting the sections without further staining, surprisingly, proved to be perfectly favourable for the identification of cartilage. Other stains used were Haematoxylin-Eosin and Mallory triple stain. In late embryos decalcification was necessary before cutting and even before staining in toto.

For the present study, nine successive stages with total body lengths: 23.6 mm, 24.8 mm, 25.6 mm, 26.8 mm, 28.0 mm, 33.0 mm, 39.0 mm, 53.0 mm (optimum stage) and 64.0 mm. Nestling stage were chosen and fully described. In addition to the series of transverse sections of these stages sagittal sections of 15 microns thick were also cut for the embryos having nearly the same total body lengths.

The transverse sections of the 9 selected stages were drawn by the projector with magnification 30 $\times$ or 40 $\times$. From the drawings of these sections accurate graphic reconstructions of the chondrocranium till the optimum stage were made. The elements of the viscerocranium were reconstructed in a ventral view. As regards stage IX of the nestling only few transverse sections were chosen and drawn for

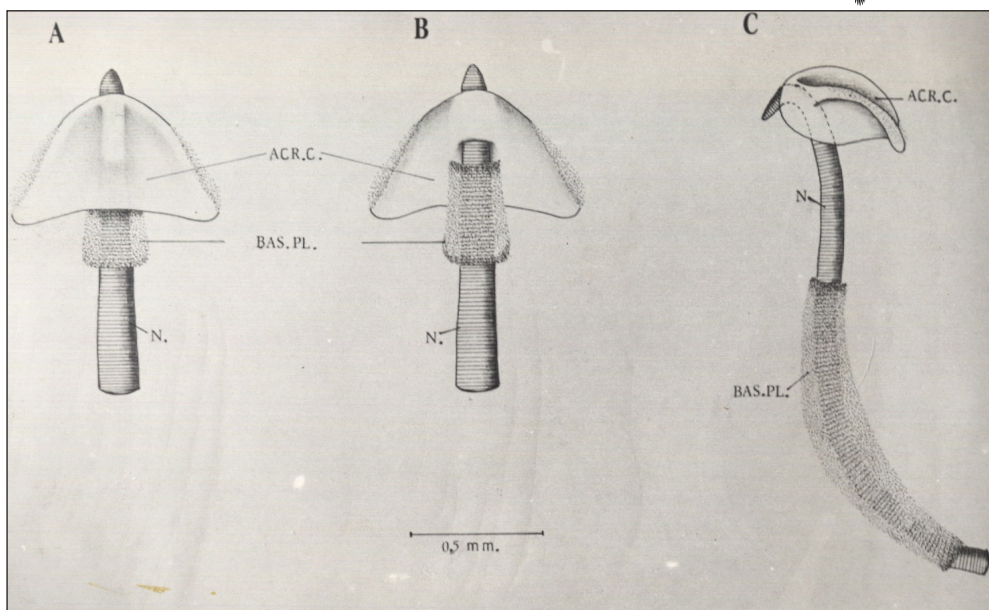


Fig. 1. Graphic reconstructions of the neurocranium of stage I in *Streptopelia senegalensis*.

A – in a dorsal view; **B** – in a ventral view; **C** – in a lateral view.

Рис. 1. Графическая реконструкция нейрокраниума *Streptopelia senegalensis* на стадии I.

the nasal capsule to illustrate the chondrocranial changes which have taken place.

RESULTS

Stage I

Total body length of embryo: 23.60 mm

Figures: 1–2

Only in this stage of *Streptopelia*, and not before, that the early signs of the cartilaginous skull are indicated by the appearance of the primary mesenchymal anlagen of the acrochordal cartilage and the parachordal cartilage or the basal plate.

The mesenchymal condensation of the acrochordal anlage (Fig. 2, ACR. C.) is seen as a thick dorsally concave rectangular plate transversally disposed below the mesencephalon (MESEN.), and directly behind the hypophysis cerebi.

The oculomotor nerve (N. III), on both sides, traverses freely the lateral border of the acrochordal anlage (Fig. 2). In a dorsal

or ventral view of the chondrocranium (Figs. 1A, 1B), the acrochordal plate is triangular in shape with the broad base of the triangle disposed posteriorly.

In a lateral view (Fig. 1C), the acrochordal plate is oval-shaped. The anteriormost portion of the notochord is completely embedded in the anterior one third of the plate. From Figure 1, it is evident that the notochord is slightly tapers interiorly. Directly behind the anterior third of the acrochordal anlage, the notochord is seen projecting from the ventral surface of the plate, then steeply declines downwards.

The anlage of the parachordal plate (BAS. PL.) appears simultaneous with the acrochordal blasteme from an isolated centre of chondrification. Its paired origin could not be observed. The parachordal anlage lies some distance behind and far below the acrochordal blasteme. As it is evident from the reconstruction figures of this stage (Fig. 1A–1C), the parachordal blasteme is in the form of an elongated cylinder surrounding the notochord.

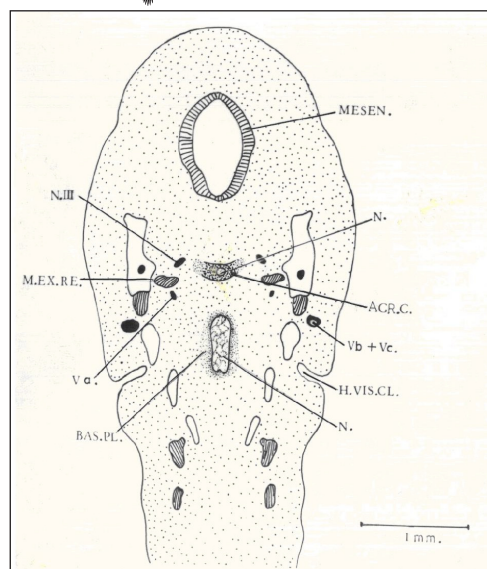


Fig. 2. Transverse section passing through the head region of stage I in *Streptopelia senegalensis* just posterior to the hypophysis cerebri.
Рис. 2. Поперечный разрез стадии I через область гипофиза.

The anterior margin of the parachordal cylinder is blunt. However, this margin does not show any sign of bifurcation.

Seen laterally (Fig. 1C) the chordal region of the chondrocranium shows the beginning of formation of a smooth S-shaped structure. Lang (1952), in her work on the cranial flexure of birds, has named this curvature «lordosis» of the basal region.

Stage II

Total body length of embryo: 24.80 mm

Accurate head length: 2.82 mm

Figures: 3–5

Several steps of development are apparent in the chordal region of the present stage of *Streptopelia*. The parachordal plate which would be more appropriately termed the basal plate, has achieved its co-extension and fusion with the acrochordal plate. The basal plate is now a well defined thick plate. It comprises the basal region of the chondrocranium bounded

anteriorly by the acrochordal plate and posteriorly by the atlas vertebra.

The mesenchymal cells, at the anterior margin of the parachordal plate of the previous stage, extend anteriorly and upwards round the notochord, as well as laterally, eventually they merge completely with the whole ventral and posterior surface of the acrochordal plate, but a clear line of demarcation is evident between them (Fig. 4). The basal plate and the acrochordal element have now the typical smooth S-shaped form of the young avian chondrocrania. The angle between them is a wide one of about $\pm 120^\circ$ and accordingly the lordosis of the chordal region is more pronounced than before.

In its development, the basal plate of *Streptopelia* is thus initially complete and its anterior region does not bifurcate to enclose a posterior basicranial fenestra. Later on, this fenestra will appear by a process of resorption in pre-existing cartilage.

In the present stage of *Streptopelia*, a remarkable change has occurred concerning the relation of the notochord to the basal plate. It is now completely embedded in the plate and cannot be seen either in a dorsal or in a ventral view of the chondrocranium except its anterior tip (Fig. 3–4). The anterior tip of the notochord is flexed downwards and pierces the anteroventral surface of the acrochordal to project for a little distance in the hypophyseal incisure (Fig. 3–4, HYPO. INC.). By such a course, the anterior region of the notochord becomes distinctly S-shaped.

Behind the point of contact of the notochord with the cerebral surface of the basal plate and backwards, as well as in the occipital region, the notochord occupies a central position and shows no irregular horizontal curvature (Fig. 5). Later, it will tend to have a cerebral position inside the basal plate.

In the present stage of *Streptopelia*, behind the posterior edge of the basal plate, four segmental sclerotomic incomplete rings are discrete around the notochord. The rings are incomplete both dorsally and ventrally. Comparison with later stages reveals that the two

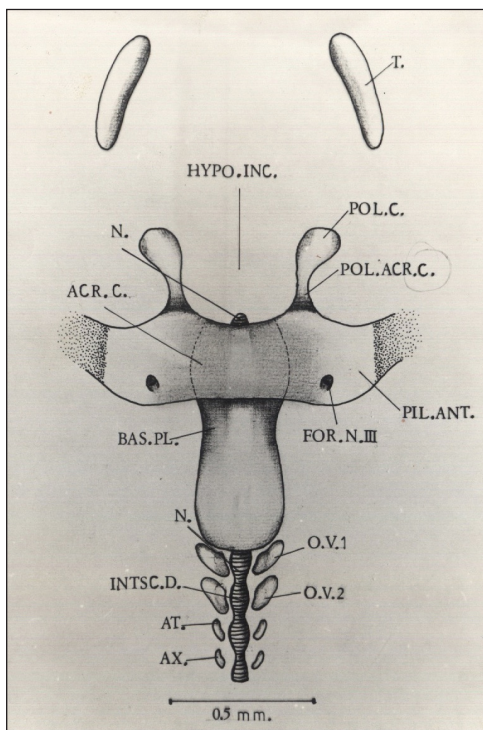


Fig. 3. Graphic reconstruction of the neurocranium of stage II of *Streptopelia senegalensis* in a dorsal view.

Рис. 2. Графическая реконструкция нейрокраниума на стадии II, дорсальный вид.

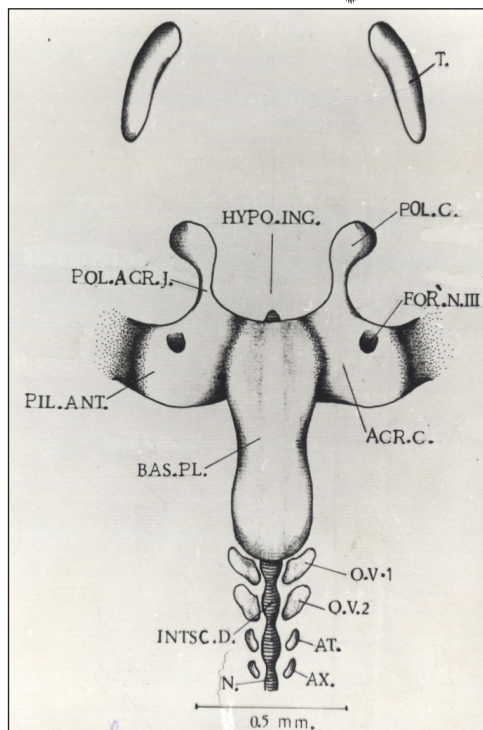


Fig. 4. Graphic reconstruction of the neurocranium of stage II of *Streptopelia senegalensis* in a ventral view.

Рис. 4. Графическая реконструкция нейрокраниума на стадии II, вентральный вид.

anterior rings lying close to the basal plate represent the first occipital vertebra (O.V.1) and the second occipital vertebra or the proatlas vertebra (O.V. 2). These two anlagen will later synchondrose with each other and with the nasal plate. The third and fourth rings will be identified respectively as the first and second cervical vertebrae i.e., the atlas (AT.) and the axis (AX.).

In the occipital region, the notochord shows a moniliform appearance having three dilatations which represent the intersclerotic dilatations presumably belonging to the last three occipital vertebrae (Fig. 3–5, 6A; INTSC. D.).

The acrochordal plate of the present stage of *Streptopelia* is fairly well developed. It is now rectangular in shape, and more thick than before.

Laterally on each side the lateral sides of the acrochordal plate expand in the dorsal direction into a large rectangular structure which represents the pila antotica. It passes over into a diffuse structure without any definite boundaries. This structure is the future anlage of the posterior orbital cartilage.

The first sign of chondrification of the prechordal region starts in the present stage. Almost at the same time, two structures have made their appearance. These are; the paired independent trabeculae (T.) and the paired polar cartilages (POL. C.) already fused to the acrochordal plate by the polar acrochordal junctions (POL. ACR. J.).

The trabeculae basis cranii (T.) appear in this stage as two independent densely blastematos bars in the mid orbital region beneath the floor of the fore-brain. These

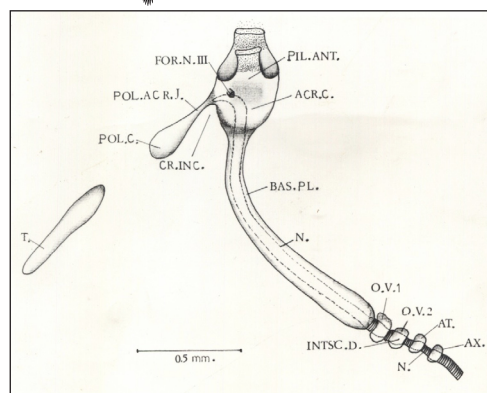


Fig. 5. Graphic reconstruction of the neurocranium of stage II of *Streptopelia senegalensis* in a lateral view.

Рис. 5. Графическая реконструкция нейрокраниума на стадии II, латеральный вид.

bars are long, stout and uniformly thick. They are widely separated from each other. This gives the impression as if the skull is destined to be platytrabic instead of tropytrbic. In a lateral view (Fig. 5), each trabecula shows an acute declining position with its posterior tip remarkably elevated than its anterior one. Because of the mesocephalic flexure, the long axis of the trabecula makes less than a right angle with that of the acrochordal and basal plate. The trabeculae are far apart from the anterior surface of the polar anlagen behind.

In the present stage, the paired polar anlagen (POL.C.) have also made their appearance situated posterodorsal and medial to the trabeculae crani between the latter and the acrochordal plate. From the postero-medial surface of each polar element a densely mesenchymatous strip is prolonged posteriorly upwards. It is fused to the antero-lateral surface of the acrochordal plate by a considerable broad base and the line of fusion is quite discernible.

In *Sterptopelia* the junction durates relatively longer since it is traced just before the fifth stage is reached.

Histologically, the polar anlagen and the polar acrochordal junctions in the present stage of *Streptopelia* can be easily distinguished

from the acrochordal plate which shows a more advanced degree of chondrification. However, careful investigation of the series of transverse sections of this region shows also that the polar anlagen can easily be demarcated from the polar-acrochordal junctions.

Now, with the appearance of the elements comprising the prechordal region of the chondrocranium, a large and extensive anterior basicranial incisure or hypophyseal incisure (HYPO. INC.) could roughly be delimited. It is confined to the arbitrary area bordered posteriorly by the anterior surface of the acrochordal plate, postero-laterally by the polar anlagen and polar acrochordal junctions. Anteriorly it is wide opened and the two trabeculae are so far to be considered as its antero-lateral borders. Below the point where the polar acrochordal junction and the acrochordal plate are flexed at an acute angle to one another (Fig. 5), a passage called the lateral carotid incisure is formed (CR.INC.). It is bordered anteriorly by the posterior edge of the polar acrochordal junction, dorsally by the connection of the latter with the acrochordal plate and posteriorly by the antero-ventral surface of the acrochordal cartilage by the antero-ventral surface of the acrochordal cartilage and the basal plate.

Stage III

Total body length of embryo: 25.60 mm

Figures: 6–12

At this stage, the lordosis of the basal plate is more pronounced than before as the gradual posterior shift of the dorsal surface of the acrochordal plate is still proceeding. Accordingly, the angle between the basal plate and the acrochordal cartilage is still a wide one but less than before ($\pm 120^\circ$).

In the present stage of *Streptopelia*, the basal plate is a well defined thick plate. It shows a remarkably increase in breadth on both sides of the notochord. With the coalescence of the two occipital vertebrae and their absorption in the basal plate, this latter will lengthen in the posterior direction. It now



comprises the basal region of the chondrocranium bounded anteriorly by the acrochordal plate and posteriorly by the atlas vertebra. Midway its length, the basal plate shows a shallow compression from side to side. Here it is induced by the expected encroachment of the cochlear portions of the auditory capsules on the lateral sides of the basal plate. Along its anterior half the median dorsal distinct elevation formed by the complete embedding of the notochord is evident, but posteriorly it is no more pronounced.

The line of demarcation between the basal plate and the acrochordal cartilage is still evident but less than before (Fig. 8–9). With the completion of chondrification in this particular region of the basal plate no initial posterior basicranial fenestra is formed.

The relation of the notochord to the basal plate is rendered constant as mentioned in the previous stage. The moniliform appearance of the notochord in the occipital and cervical regions is still apparent and the three interclebotomic dilatations previously observed are becoming more accentuated.

In the occipital region, the first occipital vertebra (O.V.1) is synchondrosed with the basal plate (Fig. 6A–B). Its hypocentrum (O.V.1.H.Y.) is easily distinguished as a slight concentration of cells in the procartilage of the basal plate.

The second occipital vertebra (proatlas) in the present stage of *Streptopelia* still appears as an independent thick mass in its way to be absorbed in the basal plate. Its hypocentrum (Fig. 6B, PROAT. HY.) projects ventrally below the level of the hypocentrum of the first absorbed vertebra and is situated some distance in front of the hindmost edge of the basal plate in a position corresponding to that of the origin of the definitive occipital arch (the hindmost arch; Fig. 9, O.A.). The pleurocentrum of the proatlas vertebra (PROAT. PL.), which represents the future occipital condyle (O.C.) is slightly raised than the level of the basal plate (Fig. 6A). The atlas and axis vertebrae are well recognized. The latter is still incomplete dorsally. The atlas and axis

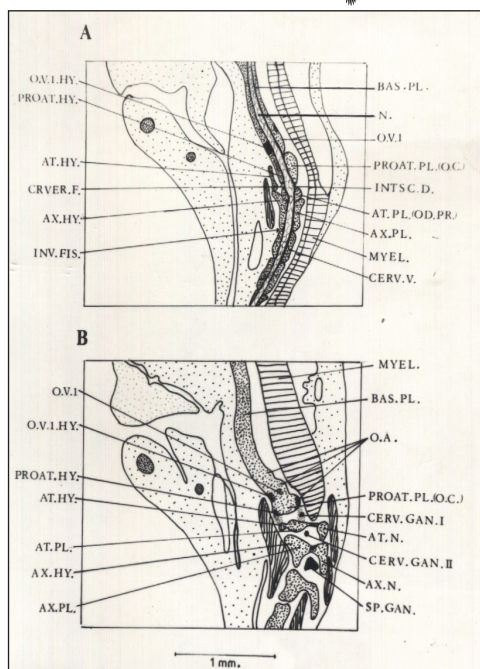


Fig. 6. **A.** Sagittal section through the 25.5 mm T.B.L. embryo of *Streptopelia senegalensis*. **B.** Parasagittal section through the same embryo illustrating the nature of the occipito-atlantic joint.

Рис. 6. Сагиттальный (А) и парасагиттальный (В) разрезы эмбриона длиной 25,5 мм.

vertebrae have well marked hypocentra (AT. HY., AX. HY.). The pleurocentrum of the atlas is destined to give rise to the odontoid process (OD. PR.). The rudiment of this process holds a mesenchymatous connection with the posterior margin of the basal plate, i.e. with the pleurocentrum of the proatlas vertebra, while a similar connection is traced between the atlas and the proatlas hypocentra (Figs. 6A–B). However, these connections are of a short duration and disappear directly after the complete absorption of the proatlas vertebra in the basal plate.

The neural arches of the atlas and axis vertebrae (AT. N., AX. N.) arise from paired centres of chondrification which are independent of the pleurocentral anlagen.

In *Streptopelia*, two fused occipital verte-

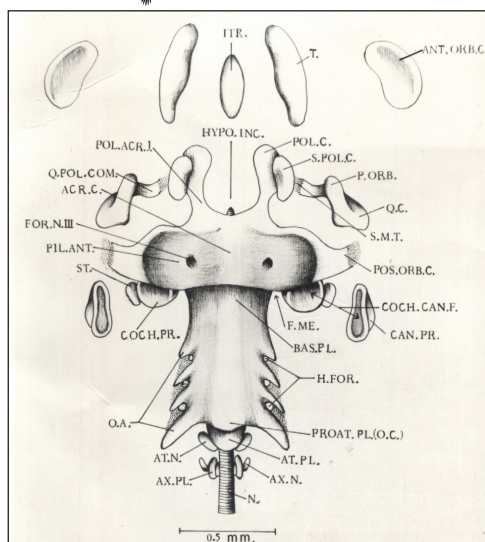


Fig. 7. Graphic reconstruction of the chondrocranium of stage III of *Streptopelia senegalensis* in a dorsal view.

Рис. 7. Графическая реконструкция хондрокраниума на стадии III, дорсальный вид.

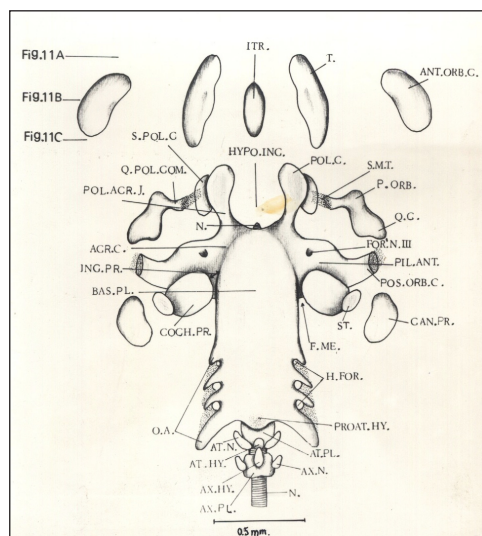


Fig. 8. Graphic reconstruction of the chondrocranium of stage III of *Streptopelia senegalensis* in a ventral view.

Рис. 8. Графическая реконструкция хондрокраниума на стадии III, вентральный вид.

brae form the hind end of the basal plate. Just posterior to these incorporated vertebrae, the hypocentrum of the atlas vertebra as well as its pleurocentrum (future odontoid process) and its basidorsals are discrete. In this region, the notochord occupies a central position and is completely embedded in the pleurocentrum of the second occipital vertebra i.e. the proatlas vertebra, while its hypocentrum lies by a little distance in front of the hind edge of the basal plate (Fig. 6A). This indicates that the pleurocentrum of the proatlas vertebra will form the hindmost region of the basal plate, and within the latter the hypocentrum of this vertebra will be also incorporated. This the occipito-atlantic joint in the present study falls in between two vertebrae (the proatlas and the atlas) i.e. intrasegmental.

In the present stage, the posterior region of the basal plate is pierced, on each side, by three oval-shaped hypoglossal foramina implying the development of four distinct arches.

Between these arches narrow fissures are created which serve to accommodate the

hypoglossal nerve roots. The dotted lines in the reconstruction figures of this stage (Figs. 7–9) indicate the erstwhile contours of the occipital arches. The enclosure of the hypoglossal foramina has been progressed when the dorsal free ends of the occipital arches come to merge together.

In the present stage of *Streptopelia*, the posterior occipital arch continues to grow and forms the main or definitive occipital arch. It represents the posterolateral extension of the basal plate without any line of demarcation between them. Each arch is in the form of a thick stout cylindrical cone. Posteriorly, it diverges and extends in a gentle uprising manner.

The median acrochordal cartilage is reasonably well developed. It is now fairly chondrified and shows a remarkable expansion in the lateral and posterior directions.

The lateral expansion of the acrochordal cartilage is the pila antotica. It is in a considerably more advanced state of chondrification than in the previous stage. As stated before, the boundary between the acrochordal cartilage

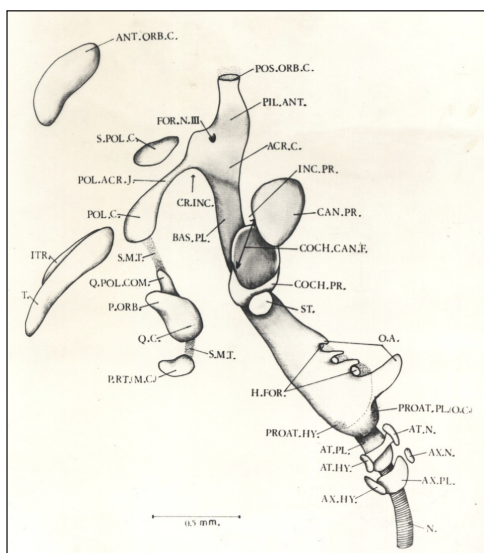


Fig. 9. Graphic reconstruction of the chondrocranium of stage III of *Streptopelia senegalensis* in a lateral view.

Рис. 9. Графическая реконструкция хондрокраниума на стадии III, латеральный вид.

and the pila antotica is the oculomotor canal. Progressive deposition of intercellular substance in the undifferentiated diffused tissue lateral to the pila antotica has increased the size of this tissue. This is the first formation of the posterior orbital cartilage (POS. ORB. C.) which later forms the postero-median and posterior boundary of the eye region. It is impossible to ascertain the boundary between the pila antotica and the posterior orbital cartilage. It is thus evident that the pila antotica and the posterior orbital cartilage are the direct continuity of the lateral border of the acrochordal cartilage. The three elements have thus one centre of chondrification.

Particularly interesting in the present stage is the beginning of chondrification of the auditory capsule. On each side of the basal plate and nearly midway along its whole length, a cochlear and a canalicular anlagen for each auditory capsule are recognized (COCH. PR., CAN. PR.). Each anlage has a separate centre of chondrification quite isolated from each other and clearly distinct from the basal plate.

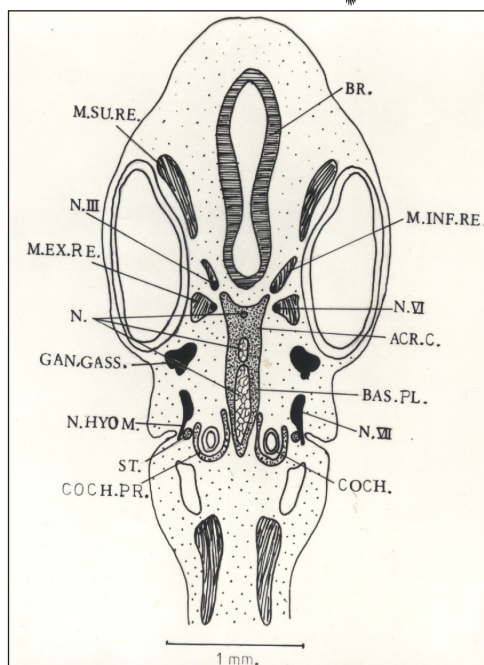


Fig. 10. Transverse section in the chordal region of stage III of *Streptopelia senegalensis*.

Рис. 10. Поперечный разрез хордальной области на стадии III.

The canalicular portion is histologically less differentiated than the cochlear portion.

The cochlear anlage is a wide opened roughly oval cup-shaped structure. It represents the medial and ventro-medial walls of the future cochlear portion. In the present stage, the cochlear portion does not encroach on the lateral side of the basal plate (Fig. 10).

Lateral to and separated from the cochlear portion by a wide fissure is the anlage of the canalicular portion. It is roughly triangular and cup-shaped with its large aperture directed medially. It covers the lateral and posterior surfaces of the faintly indicated semicircular canals. The cochlear and canalicular anlagen face each other by their large apertures but the latter anlage lies slightly posterior and dorsal to the former (Fig. 9). By such a disposition of the two anlagen, a large vacuity is created between them which corresponds to the cochleo-canalicular fissure. Through the dorsal

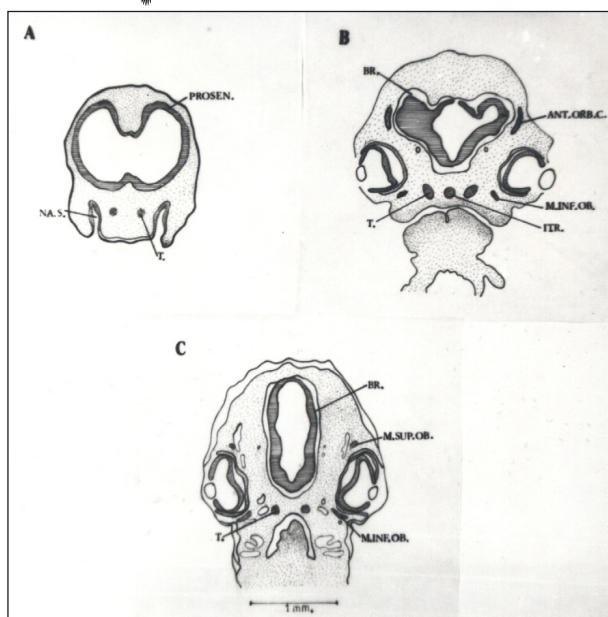


Fig. 11. **A.** Transverse section passing through the anterior region of the head of the 25.6 mm embryo of stage III of *Streptopelia senegalensis*. **B.** Transverse section passing through the anterior orbital region of the same embryo. **C.** Transverse section passing through the mid orbital region of the same embryo.

Рис. 11. Поперечные разрезы через три области эмбриона на стадии III.

orifice of the referred vacuity (COCH. CAN. F.) all the branches of the auditory nerve enter the auditory capsule.

In the present stage, between the pila antotica, the rudiment of the posterior orbital cartilage and the anlagen of the auditory capsule, an extremely wide incisura prootica can roughly be delimited. It is bordered anteriorly by the pila antotica and the primary anlage of the posterior orbital cartilage, ventro-medially by the lateral edge of the basal plate and posteriorly by the cochlear portion of the auditory capsule where it is confluent with the cochleo-canalicular fissure.

Also in the present stage of *Streptopelia* it is hardly possible to delimit a fissura metotica (F.ME.), bordered anteriorly by the cochlear portion of the auditory capsule, ventrally and

medially by the lateral edge of the basal plate and posteriorly by the occipital arch. Through the wide opened fissura metotica the glossopharyngeal, the vagus and spinal accessory nerves leave the cranial cavity.

The incisurae metotica and prootica are still confluent together and with the cochleo-canalicular fissure. This is due to the absence of the basal articulation between the cochlear portion and the basal plate and to the fact that the auditory capsule still lacks the anterior, posterior and ventral walls (Figs. 8–9).

In the present stage of *Streptopelia*, new prechordal elements have made their appearance. These are: The median isolated intertrabecula (ITR.), the paired independent anterior orbital cartilages (ANT. ORB. C.) and the paired independent suprapolar cartilages (S. POL. C.).

In the present stage of *Streptopelia*, just below the brain (BR.) three distinctly isolated entities are evident. The two lateral entities are

the trabeculae cranii. In the midline between them an independent condensation of dense blasteme becomes more clearly demarcated from its surroundings. There can be no doubt that this isolated blastematous nodule is nothing but the inter-trabecular element of Suschkin (1899) and Bellairs (1958).

It is evident from the reconstruction figures of this stage (Figs. 7–9) that the antero-posterior extension of the intertrabecular nodule occupies a middle position in between the two trabeculae cranii without any sign of contact between them.

In the anterior orbital region of this stage of *Streptopelia* and laterally on both sides, a procartilaginous anterior orbital plate extends dorso-medially over the eye, lateral to the brain and just in front of the rudiment of the



muscle superior oblique (Fig. 11) B, C, ANT. ORB. C., M.SUP.OB.). Its faint proximal mesenchymatous end lies quite apart from both the trabecula of its side and the intertrabecula condensation without any sign of mesenchymal connection between these entities. This finding is of real importance since it assures that the anterior orbital cartilage has a separate centre of chondrification.

The trabeculae cranii (T.) become well chondrified than in the previous stage. They increase remarkably in thickness throughout their whole length and become more stout than before. They elongate and approach the anterior borders of the polar cartilages behind, but still a wide distance is evident between them.

The polar cartilages (POL.C.) of the present stage have distinctly increased in size. They are now oval shaped with their matrix becoming considerably denser, together with that of the polar acrochordal junctions which are now more stout. In a lateral view (Fig. 9), the polar cartilage curves downwards. The ventro-lateral surface of the polar cartilage is in mesenchymatous connection with the processus orbitalis of the quadrate though the procartilaginous quadratopolar commissure.

The hypophysial incisure (HYPO. INC.) of the present stage is confined to the extensive triangular space bordered posteriorly by the anterior surface of the achrochordal cartilage, laterally, by the polars and the posterior tip of the intertrabecula that forms the apex of the triangle. Thus the incisure has been now roughly delimited but it is still a wide open space anteriorly.

Dorso-lateral to each polar cartilage and its polar-acrochordal junction another pair of prechordal elements has appeared from isolated centres of chondrifications. These are the suprapolar cartilages (S. POL.C.), its blasteme is already faintly discernible in the 25.3 mm embryo as a large oval nodule surmounting the dorsolateral region of the polar cartilage with a considerable distance separates them. This separating distance could be homologized with the ophthalmic incisure of other birds.

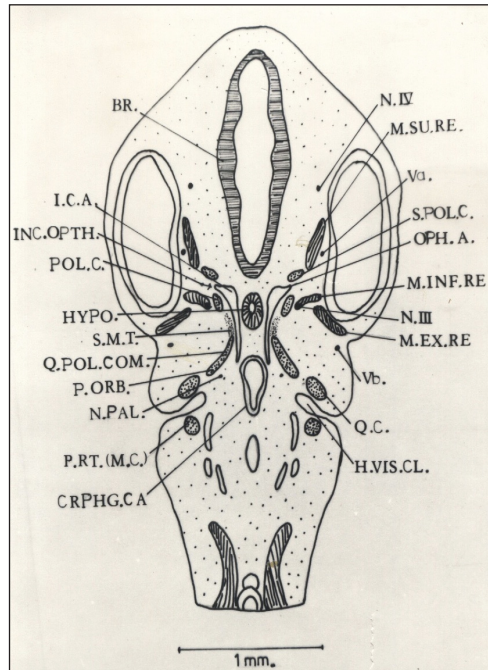


Fig. 12. Transverse section passing through the posterior orbital region at the level of the polar anlagen of stage III of *Streptopelia senegalensis*.

Рис. 12. Поперечный разрез через заднюю орбитальную область.

Through it the ophthalmic artery (Fig. 12, OPH. A.) leaves the cranial cavity.

DISCUSSION

The study of the early stages of *Streptopelia* corroborates that the basal plate is the product of fusion of three distinct elements. These are the parachordal plate, the acrochordal cartilage and two discrete occipital vertebrae.

The verdict that the acrochordal anlage and the parachordal plate in *Streptopelia* have a simultaneous appearance prior to any other chondrocranial element and that the former has an accelerated chondrification than the latter does not confirm the finding of Parker (1891a) in *Apteryx*, Sonies (1907) and Van Wijhe (1907) in *Anas* and *Gallus*, De Beer and Barrington (1934) in *Anas*, Mokhtar (1975)



in *Upupa* and *Merops* and Mokhtar et al. (1983) in *Pterocles*, Zaher and Abdeen (1991) in *Charadrius*, Zaher et al. (1991, 1993) in *Corvus* and *Passer*, Abd El-Hady (2008a) in *Coturnix* that the acrochordal anlage is the first chondrocranial element to appear. In *Phalacrocorax*, as maintained by Slabý (1951b), the parachordal plate appears first, and soon grows rostrally as two anterior parachordals which enclose the posterior basicranial fenestra. This latter is closed anteriorly when the anterior parachordals share in developing a transverse bar which represents the acrochordal anlage.

The fact that parachordal plate in the present study has one centre of chondrification contradicts the view of Goodrich (1930) and De Beer (1937) about the exact nature of the parachordal plate in vertebrates in general. In *Streptopelia* the paired origin of the parachordal plate is not observed in any developmental stage. In support to this view, all investigators who dealt with the early ontogeny of the chondrocranium of birds (Suschkin, 1899; Sonies, 1907; Jäger, 1926; Lutz, 1942; Slabý, 1951b; Frank, 1954; Til, 1969; Mokhtar, 1975; Mokhtar et al., 1983; Zaher, Abdeen, 1991; Zaher et al., 1991, 1993; Abd El-Hady, 2008a) describe a mode of formation for the parachordal plate as in *Streptopelia* and assert its unpaired nature. Even De Beer and Barrington (1934) confirm the single origin of the parachordal plate in *Anas*, but indicate it as a secondary modification. However, among birds so far described, the only exception is the condition mentioned by Parker (1891a) in *Apteryx*, where the parachordals remain distinctly paired until a late ontogenetic stage and anteriorly the basal plate is pierced by the posterior basicranial fenestra. Thus Sonies is of the opinion that the basal plate is a composite structure. Crompton (1953) has also the same view in *Spheniscus* beyond the fact that this latter bird lack a basicranial fenestra. Undoubtedly, this is not applicable in the present study since it has been proved, ontogenetically, that the basal plate has no initial composite nature.

In *Tinnunculus* (Suschkin, 1899), *Pyromelana* (Engelbrecht, Van, 1958), *Upupa*

and *Merops* (Mokhtar, 1975) and *Pterocles* (Mokhtar et al., 1983), *Charadrius* (Zaher, Abdeen, 1991), *Corvus* (Zaher et al., 1993), *Coturnix* (Abd El-Hady, 2008a) the basal plate, similar to the condition described in *Streptopelia* lacks a basicranial fenestra in the early developmental stages, but later by resorption of cartilage, the fenestra is formed. Among the other described birds, the Emu (Lutz, 1942), the Nightjar and the Ostrich (Frank, 1954) and *Fulica atra* (Til, 1969), a posterior basicranial fenestra is completely absent in all ontogenetic stages.

It is worthy to mention that the initial absence of the posterior basicranial fenestra, in the early stages of *Streptopelia* as well as in the majority of described birds, is reminiscent with what is recorded in Diponi, the early developmental stages of Urodela, Anura, Lacertilia, Crocodilia (De Beer, 1937) and Ophidia (Kamal, Hammouda, 1965), it is thus possible to consider the absence of such a fenestra in some birds (either in early developmental stages or during all ontogenetical stages) as a primitive phylogenetic character. If the fenestra later appears by a process of absorption of cartilage in some of these forms, it should be considered as a secondary modification. If such a supposition comes true, it will be difficult to explain the condition of *Anas*, *Gallus* and *Phalacrocorax*. Also it seems bewildering to comment on the condition of Crocodilia as why no secondary modification has been realized, when compared with other lower forms as Urodela, Lacertilia and Ophidia.

The fact that in the early stages of development in *Streptopelia* the rostral end of the notochord traverses freely for a little distance through the future hypophyseal fenestra to end just behind the hypophysis cerebri, is reminiscent with the behaviour of the notochord in the early ontogenetical stages of the typical lacertilian and ophidian embryos (Peyer, 1912; De Beer, 1930, 1937; Kamal, Hammouda, 1965). Among the majority of described birds the rostral tip of the notochord is traced in the hypophyseal fenestra during the early developmental stages in a manner slightly less than that described in *Streptopelia*.



What seems peculiar in all birds in general is the strong ventral curvature of the rostral end of the notochord shortly before it leaves the acrochordal cartilage. On the contrary, in Squamata, during the early developmental stages, such a ventral bent of the notochord is unnoticeable (Kamal, Hammouda, 1965). Gaupp (1906) found that, in common with all vertebrates with extreme cranial flexure, the anterior most tip of the notochord curves ventrally, projecting from the ventral surface of the parachordal plate. Gaupp's view confirms the condition in birds, but lizards and snakes seems to deviate probably due to the fact that they are related to those forms with the least cranial flexure.

The S-shaped curvature of the basal plate first described by Suschkin (1899) in *Tinnunculus* also occurs early during ontogeny in all the birds so far described. Lang (1952), in her work on the cranial flexure of birds, has termed this curvature «lordosis» of the basal region. Also the notochord runs in an S-shaped fashion corresponding to the flexure of the basal plate.

The differentiation of the first and second occipital vertebrae in the early stages of development is a clear indication that the posterior end of the base of the skull in *Streptopelia* will be formed by two included vertebrae which are differentiated from their corresponding somites. This fact is of theoretical importance since it further validates the findings and observations of several authors about the segmental nature of the head region in birds (Froriep, 1883; Suschkin, 1899; Jäger, 1926; De Beer, Barrington, 1934; Slabý, 1951b).

Additional evidence of segmentation in the parachordal plate in the bird's skull is noted by the presence of segmental perichordal rings of the last two absorbed cranial vertebrae in an early stage of *Spheniscus* (Crompton, 1953), *Struthio* (Frank, 1954) and *Fulica atra* (Til, 1969).

Müller (1961) and Til (1969) stated that the number of the hypoglossal foramina in birds may be taken as an approximate clue for the number of the included vertebrae.

In *Streptopelia*, the number of the hypoglossal nerve roots and consequently the num-

ber of the hypoglossal foramina is rendered constant throughout ontogeny being only three on both sides of the basal plate. This implies the development of four occipital arches. Another potent evidence to the segmental nature to the basal plate in birds is the development of the occipital arches and the enclosure of the hypoglossal foramina. These foramina usually lie at the transitional area between the basal plate and the occipital region. This condition is reminiscent with what is mentioned for *Passer* and *Sturnus* (Sonies, 1907).

However, it should be admitted that in the *Streptopelia*, evidence of only two absorbed occipital vertebrae is observed. The occipital vertebra are not distinguished even as sclerotomic ring, nor their hypocentra could be traced. Albeit the distinct development of their neural arches speaks strongly in favour of their earlier assimilation with the basal plate and shows evidence of the metameric segmentation of the latter.

It is evident that commonly in birds the number of the hypoglossal foramina manifests a considerable range of variation. The number may also differ in different developmental stages of the same species and also on both sides of the basal plate of the same embryo. However, Müller (1961) and Til (1969) have referred that the majority of birds possess two hypoglossal foramina in the adult stage. Again the above mentioned data speaks strongly in favour of Rice's (1920) view. Rice gave a list of the number of the hypoglossal foramina in various reptiles and mentioned that the contradictions found in the list are due to specific differences or to individual variation either dependent upon or seemingly accidental. Thus Rice supports the probability that the number of the occurring foramina may differ regardless the age of the embryo.

The development of the auditory capsule from two independent centres of chondrification observed in the majority of described birds. Thus the condition in birds contradicts the view of Noordenbos (1905) who states that generally in vertebrates the cochlear part of the auditory capsule chondrifies in continuity with the canalicular part.



The fact that the cochlear portions, in their earlier development, are initially discrete and quite independent of the basal plate is of theoretical importance since it presents potent evidence against the verdict drawn by Gaupp (1906) that generally in the development of Amniota, because of the intimate fusion between the cochlear portion of the auditory capsule and the basal plate, the former is regarded as an integral part of the latter. The condition found in *Streptopelia* validates the view of Noordenbos (1905), Goodrich (1930), De Beer and Woodger (1930) and De Beer (1937) who point out that the auditory capsule, during the development of the living vertebrates, almost, arises from a centre or centres of chondrification.

The trabeculae basis cranii is a term first used by Rathke (1839) in the study of the chondrocranium of *Coluber*. The independent origin of the trabeculae in birds was referred to by Van Wijhe (1907). It was also observed in *Anas* (Sonies, 1907; De Beer, Barrington, 1934), *Phalacrocorax* (Slabý, 1951b), *Spheniscus* (Crompton, 1953), *Fulica atra* (Til, 1969), *Upupa* (Mokhtar, 1975), *Pterocles* (Mokhtar et al., 1983), *Charadrius* (Zaher, Abdeen, 1991), *Corvus* (Zaher et al., 1993) and in *Coturnix* (Abd El-Hady, 2008c). On the other hand, in *Tinnunculus* (Suskin, 1899), *Struthio* (Brock, 1937; Frank, 1954), *Gallus* (Sonies, 1907; De Beer, 1937) and *Pyromelana* (Engelbrecht, Van, 1958), the trabeculae and polar cartilages are already fused from the early beginning, forming trabeculo-polar bars which, moreover, originate in continuity with the acrochordal plate.

In the present study, the intertrabecula is formed as a clear well defined median isolated entity between the trabeculae cranii. The present result is confirmed by the previous observations in case of *Upupa* (Mokhtar, 1975), *Pterocles* (Mokhtar et al., 1983), *Passer* (Zaher et al., 1991), *Charadrius* (Zaher, Abdeen, 1991), *Corvus* (Zaher et al., 1993), and *Coturnix* (Abd El-Hady, 2008c). On the other hand, the absence of the intertrabecula is recorded in *Anas* (De Beer, Barrington, 1934), *Phalacrocorax* (Slabý, 1951b), *Spheniscus*

(Crompton, 1953), *Struthio* (Frank, 1954), *Pyromelana* (Engelbrecht, Van, 1958) and *Rhea* (Müller, 1961).

In *Streptopelia*, the anterior orbital cartilage has an isolated centre of chondrification, which lies from the very beginning quite apart from the trabeculae and the intertrabecula. The trabecula does not seem to contribute in its development. They lie quite apart from each other. Also the trabecula retains a distinct outline meantime the anterior orbital anlage is fairly developed.

In *Streptopelia*, the anterior orbital cartilage has a prior appearance than the interorbital septum. This latter develops nearly after the anterior orbital cartilage reaches its optimum condition. This result is compatible with the previous observations in case of *Upupa* (Mokhtar, 1975), *Pterocles* (Mokhtar et al., 1983), *Passer* (Zaher et al., 1991), *Charadrius* (Zaher, Abdeen, 1991), *Corvus* (Zaher et al., 1993) and *Coturnix* (Abd El-Hady, 2008b, 2008c).

Parker (1880) was the first to recognize an intertrabecular element in his study on the development of the green turtle, *Chelone viridis*. In other turtles, its existence is asserted by some authors as a well marked wedge between the trabeculae e.g. *Lepidochelys* and *Chrysemys* (Pehrson, 1945) and *Chelydra serpentina* (Bellairs, 1949). Its presence in Crocodilia was observed by Parker (1883). Among other Sauropsida, it may be of rare and transient occurrence, e.g. *Anguis fragilis* (Bellairs, 1958), or absent as in snakes (Kamal, Hammouda, 1965).

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Замітки	Беркут	18	Вип. 1-2	2009	208
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ВТОРАЯ НАХОДКА МАСКИРОВАННОГО СОРОКОПУТА В АРМЕНИИ

Second record of the Masked Shrike in Armenia. - R. Nessing. - Berkut. 18 (1-2). 2009. - Two birds were observed south of Goravan, Province of Ararat (39.88 N, 44.73 E), on 27.06.2009. [Russian].

Маскированный сорокопуд (*Lanius nubicus*) обитает в Западной и Южной Турции, Ливане, Сирии, в приграничной зоне между Ираном и Ираком, в последние десятилетия обнаружен в Болгарии (Lefranc, Worfolk, 1997). Распространение вида изучено недостаточно, возможны находки на гнездовании в других местах Малой Азии и Ближнего Востока (Панов, 2008).

В Армении маскированные сорокопуды впервые были отмечены 30.05.2007 г. на юго-восточных склонах г. Арарат. Пара, за которой велось наблюдение, находилась недалеко от метеорологической станции Амберг (Adamian, Moffatt, 2009).

27.06.2009 г. я наблюдал двух взрослых особей на территории заказника «Горованские пески» южнее с. Горован Араратского р-на (39.88 N, 44.73 E). Были ли эти особи парой, с полной уверенностью утверждать не могу, так как птицы не садились достаточно близко друг к другу. Дистанция между ними сохранялась примерно 35–40 м.

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