The Structure and the Development of the Chondrocranium of *Varanus*.

Part I. The development of the ethmoidal region.

(With 16 figures)

By

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Varanus occupies an important position among the Lacertilia. It is connected on the one hand with the extinct mosasaurs while on the other it is considered as a near relative of the Ophidia. Curiously enough the development of the chondrocranium of this lizard has not been worked out so far. On the ethmoidal region, however, two papers have been published. Pratt (1948) deals with the ethmoidal region of a number of lizards and *Sphenodon* so that his description of *Varanus* is quite brief. Bellairs (1949) describes in good detail the varanid snout. Both these papers are based on juvenile specimens and naturally a number of points remain unexplained. The development of the ethmoidal region shows the presence of a few structures which were either overlooked by the previous workers or were simply lacking in the sub-adult specimens. Apart from its phylogenetic importance *Varanus* is used as a lacertilian type in the degree courses of the various universities of India and thus information on the different aspects of its developmental morphology was long due.

So far, only three detailed descriptions of the development of the chondrocranium of the Lacertilia are available. That of de Beer (1930) deals with the chondrocranium of *Lacerta* and is mainly based on the Van Wijhe preparations. El-Toubi and Kamal (1959, 1961 a & b) describe in good detail the chondrocranium of *Chalcides* and *Ptyodactylus*. They have used projection drawings for the graphical reconstructions of the developmental stages. The

present paper deals with the development of the ethmoidal region of *Varanus*. My observations on the development of the other regions of its chondrocranium will follow soon.

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Material and Method

The eggs of *Varanus bengalensis* were collected locally. The area round about Saugar abounds in these lizards but the eggs are rather difficult to get. *Varanus* is reported not to lay eggs in captivity and hence a search was made for them with the help of a local tribe of hunters known as *Moghia*. Indiscriminate digging of the burrows is dangerous as they may be harbouring poisonous species of snakes. The burrows are found in red *morram* near the boundaries of cultivated fields, sandy hillocks and sometimes even by the side of the road. When the burrow is recognised as such by the foot-prints of the lizard, the soil is carefully removed.

The eggs were collected from the burrows from July to September. They were kept in ordinary soil in wooden trays at the room temperature. The eggs are very sensitive to variations of heat and cold and the mortality is very high.

Healthy embryos were fixed in Bouin's fluid and sectioned at $20\ \mu$ except the first stage which was sectioned at $15\ \mu$. Both transverse and longitudinal sections were cut and stained with Mallory's triple stain. This stain gave quite satisfactory results. A number of embryos were prepared by Van Wijhe's method substituting Victoria blue for the Methylene blue. The Victoria blue was found a quite satisfactory stain for the varanid embryos. The embryos were stained for seven days and then dissected in 90% alcohol. However, only at 73 mm. whole length that the ethmoidal region could be distinguished. As pointed out by de Beer (1930), the difference between the Van Wijhe preparations and the sectioned embryos is remarkable.

The study in main was made from the graphical reconstructions using an oculometre disc. The magnification used for all stages was 50 times but that of 400 times was invariably applied for look-

ing into the details. Camera lucida drawings were used for reconstructions from longitudinal sections.

The age of the earliest embryo could not be determined. However, it appears to be about a month old. The approximate ages and the whole lengths of the various stages are as follows:—

Stage 1	44.75 mm.	T. S.	One month.
Stage 2	52.50 mm.	T. S.	45 days.
Stage 3	57.20 mm.	L. S.	45 days.
Stage 4	75.20 mm.	T. S.	59 days.

Intermediate Stages:

	74.00 mm.	L. S.	59 days.
	78.00 mm.	T. S.	63 days.
	70.60 mm.	L. S.	63 days.
	94.20 mm.	L. S.	73 days.
Stage 5	104.60 mm.	T. S.	67 days.

As the above table shows, there is apparent discrepancy between the age and the length of the embryos. A burrow contains about 35 eggs laid by a single female but probably they are deposited by intervals in batches. The above stages for the study of the ethmoidal region were carefully selected from a number of available embryos. Embryos used for Van Wijhe preparations measured 52 mm., 58 mm., 62 mm. and 73 mm. respectively without any reference to age.

Observations

Stage 1

(44.75 mm. whole length)

There is no indication of any skeletal element at this stage. The nasal organs are seen in the form of more or less a straight tube opening to the out on the anterior side while backwards it pushes the buccal epithelium to form an opening into the oral cavity. Medially the tube shows the olfactory sac. There are two knob like bulgings on the olfactory sac. The posterior one of these two bulgings represents the organ of Jacobson. (Fig. 1).

Fig. 1.

Stage 2

(52.50 mm. whole length)

The nasal septum appears in the middle line dividing the nasal organs of the two sides. Anteriorly the nasal septum shows a slight depression but the rostral wings are not yet in evidence.

Fig. 2.

Posteriorly it continues between the eyes and up to the parachordals. There is no indication of its double origin. The nasal septum and the trabecula communis were never found separated. The nasal septum has a distinct perichondrial covering but the chondrification has not progressed sufficiently. The most interesting feature which the nasal septum shows at this stage is the extension of its perichondrial covering dorsally on both sides. (Figs. 2 and 3). Below this

Fig. 3.

extension runs the medial ramus of the ethmoidal nerve. It passes to the tip of the snout through it. This extension is the beginning of the rostral element that takes part in the formation of the nasal capsule.

Apart from the nasal septum and its perichondrial extensions no other condensations are seen at this stage. The nasal organs however have undergone great change. Among them can be recognized the following: Anterior external nostril, Anterior nasal tube, Anterior chamber and the Olfactory chamber. The small

anterior nasal tube opens to the outside by the anterior external nostril. The anterior chamber has a minute opening into the olfactory chamber. The walls of the olfactory chamber are thick. In the earliest stage there was no distinction between the anterior nasal tube and the anterior chamber. A slight bending and the thick walls of the anterior chamber now make the distinguishing characters between the two. The olfactory chamber has grown transversely and shows three bulgings foreshadowing the lateral recess and the conchal zone. The duct of the organ of Jacobson makes its appearance so that the organ has a distinct identity. Further the duct becomes curved and carries the dome of the organ towards the anterior side. The dome itself undergoes a half fold so that the organ becomes crescent shaped and its lumen is reduced. It is partly covered by the olfactory chamber on the dorsal side.

Stage 3

(57.20 mm. whole length)

Cell condensations now appear over the nasal organs. Among them can be recognized, the parieto-tectal, the paranasal, sphenethmoid commissure, aditus conchae, rostral wing, lamina transversalis anterior and the planum antorbitale. (Figs. 4 and 5).

Even at this early stage the boundaries of the parieto-tectal and the paranasal can not be demarcated. Roughly speaking the parieto-tectal condensation covers the anterior chamber dorsally. It does not very much extend to the sides. Posteriorly it is continuous with the paranasal but the arrangement of the cells is such that their meeting place can be recognized at the aditus conchae. The foramen epiphaniale has not been formed but the cells through which the ramus lateralis of the ethmoidal nerve passes are stained deeply. This ramus at the second stage passed by the side of the nasal organs but now it passes over them and the parieto-tectal condensation through the incipient foramen epiphaniale.

The sphenethmoid commissure is in continuation with the paranasal as a process. The olfactory nerve passes in between this process and the condensation of the planum supraseptale.

The aditus conchae at this stage appears as the lateral extension and the meeting place of the parieto-tectal and the paranasal. It is not very deep and it lies in the groove separating the lateral recess and the main olfactory chamber.

The rostral wings appear as the lateral extension of the anterior

Fig. 4.

tip of the nasal septum. They are faintly marked.

The lamina transversalis anterior shows a crescent shaped condensation in front of the organ of Jacobson. The condensation follows the curvature of the dome of that organ.

The planum antorbitale lies against the antorbitale space of the nasal sac between it and the orbit. The condensation of the planum antorbitale is stained deeper than all the others. Medially it touches the nasal septum but laterally it does not reach the capsule wall.

Among the nasal organs further growth has taken place. The lateral recess now appears as a fingershaped outgrowth from the olfactory sac. The new changes among the nasal organs are the formation of the large antorbitale space, elongation of the anterior chamber and the appearance of foldings on the wall of the olfactory

sac. The foldings are those of the conchal zone. Thus except the nasal and the lachrymal glands all others nasal organs have been formed at this stage. (Fig. 5).

Fig. 5.

Stage 4

(75.20 mm. whole length)

Perichondrial wall has appeared round the condensations so that the nasal capsule takes a definitive shape and the chondrification centres can now be recognized. (Figs. 6 and 7).

The nasal septum is in fully cartilaginous condition. Anteriorly it ends in a flattened rostrum with the lateral wings. The ramus medialis of the ethmoidal nerve passes over these lateral wings. There is no foramen apicale. (Fig. 8).

The perichondrial extension of the second stage has formed a sheet of cartilage on either side of the nasal septum. This cartilage forms the medial boundary of the anterior cupola as well as the median dorsal roof of the nasal capsule. This rostral element represents the dorsal plate. There is a groove running in the median dorsal line in between the dorsal plates of the two sides. The bottom of the groove is formed by the dorsal edge of the nasal septum. The dorsal plate is reduced in the middle region of the nasal septum. (Fig. 9).

The covering wall round the parieto-tectal condensation has not been fully formed. Some cells from the perichondrial extension of the nasal septum appear to have migrated to form a wall round the parieto-tectal but many perichondrial cells are being formed in

Fig. 6.

situ. There is also differential staining of the various areas in the parieto-tectal. At about the middle there is a large gap of unchondrified area representing the fenestra superior, though the real fenestra superior is absent in *Varanus*. The anterior part of parieto-tectal curves to form the anterior cupola. It however does not reach sufficiently lower down to enclose a foramen apicale. The anterior cupola is continued on the side forming the superior alar process. This process covers and partly folds round the anterior nasal tube. A new condensation has appeared at the place where the anterior nasal tube bends into the anterior chamber. This condensation is hammer shaped in reconstruction. It hangs from the lateral edge of the anterior cupola and is the beginning of the inferior alar process. (Fig. 8). The side wall of the nasal capsule shows a small cut through which passes the duct of the lateral nasal gland.

The aditus conchae, curiously enough has not chondrified so far. But it has extended lower down forming a fold on the ventral side. This fold is the beginning of the concha. Laterally the fold is in

Fig. 7.

Fig. 8.

Fig. 9.

continuation with the medial wall of the lateral recess capsule. The concha like its predecessor, the aditus conchae, is only a condensation at this stage. The characteristic cavity of the concha, as seen in the sections of the later stages is not yet in evidence. The aditus conchae and the nasal concha are full of blood capillaries.

The paranasal has taken upon itself the task of forming a covering for the lateral recess of the olfactory sac. The conchal fold extends in to this newly formed capsule, dividing its cavity longitudinally into right and left parts and vertically into the dorsal and ventral parts. The foldings of the lateral recess fit snugly over this conchal ridge. The capsule of the lateral recess is only partly chondrified and is open at the dorsal side. The conchal ridge is not visible from this dorsal opening at this stage.

The ramus lateralis of the ethmoid nerve passes through a small foramen epiphaniale. The foramen is not visible from either the dorsal or the ventral side as it lies in the lateral inpushing of the parieto-tectal. It only roughly represents the meeting place of the parieto-tectal and the paranasal cartilages.

The sphenethmoid commissure is under the same perichondrial wall as the paranasal but a careful scrutiny showed that it has a separate centre of chondrification. With the growth of the nasal

capsule the planum supraseptale has been left backwards so that the sphenethmoid commissure now joins its anterior prolongation (the pre-optic root) enclosing the foramen olfactorium evenhens for the entry of the olfactory nerve.

The planum antorbitale has extended considerably. Laterally it has joined the paranasal wall while medially it abuts against the nasal septum. It is in advanced stage of chondrification.

On the ventral side the condensation of the lamina transversalis anterior has spread and chondrified into a plate which is in continuation with the nasal septum medially while laterally it bends slightly to end in a process. The lamina transversalis anterior not only covers the organ of Jacobson but it also sends a cartilaginous piece to support it. (Fig. 6).

The paraseptal cartilage makes its appearance as a thin rod of cartilage starting from the lamina transversalis anterior and running by the side of the nasal septum. It ends freely in the posterior region.

There are two maxillary processes. The anterior maxillary process is in continuation with the planum antorbitale but with a separate centre of chondrification. The posterior maxillary process is not joined to the nasal capsule.

The nasal organs are now grown sufficiently. They approach the adult condition. The bending of the anterior nasal tube into the anterior chamber is sharply marked. The other novelty is the appearance of the lateral nasal gland. It arises from near the posterior end of the anterior chamber as an outgrowth. This outgrowth (duct) passes through a cut in the lateral part of the parieto-ectal to reach the anterior end of the aditus conchae. At the tip of the duct some glandular cells are differentiating. Its lumen is full of dividing cells.

The duct of the organ of Jacobson now opens separately. From its opening runs a groove up to the choana. The two lachrymal glands make their appearance. Both arise from a higher and a lower punctum from the lower eye-lid. They are in continuation with the epithelium of the conjunctiva. The duct of the upper lachrymal gland opens near the internal opening of the choanal tube. The duct of the lower lachrymal gland forms a connection with the duct of the upper gland near its opening. The duct of the lower lachrymal gland then runs closely above the choanal groove to reach the duct of the Jacobson's organ. After opening into the duct of the Jacobson's organ, it ends blindly.

Intermediate Stages

The embryos of 70.60 mm., 74.00 mm. and 78.00 mm. whole length resemble the 75.20 mm. embryo. There is general growth of the ethmoidal region but nothing new appears.

At 94.20 mm. whole length, the ventral nasal gland makes its appearance as well as a process of the parieto-ectal cartilage to support it. This embryo approaches the next one in many respects.

Stage 5

(104.60 mm. whole length)

All the elements of the nasal capsule are now fully chondrified. In many respects this stage comfortably passes into the sub-adult condition described by Bellairs (1949).

Fig. 10.

The nasal capsule has an elongated form. (Figs. 10 and 11). Anteriorly it is narrower but becomes broader posteriorly due to the presence of the recess capsule. The roof of the capsule is formed on each side by the dorsal plate and the parieto-tectal. There is a groove running in the median line. Anteriorly the parieto-tectal is free from the nasal septum. This unattached portion forms a slightly dome shaped covering over the anterior chamber and is known as the anterior cupola. The margin of the anterior cupola is not smooth. The rough margin is partly due to the presence of three cartilaginous nodules. One of them, the middle one is in close contact amounting to fusion with the anterior wall of the cupola (Fig. 12). There are indications of at least two more condensations which however do not chondrify. The foramen apicale is not en-

Fig. 11.

Fig. 12.

closed and the median ramus of the ethmoid nerve passes over the rostral wings towards the tip of the snout. Laterally the anterior cupola is continued into a processus alaris superior. The inferior alar process, which was observed as a hammer-shaped condensation hanging from the lateral wall of the anterior cupola at the 75.20 mm. whole length stage, has now chondrified. The top of the hammer forms two round pieces which join the handle of the hammer to the superior alar process and the lateral wall of the cupola. (Fig. 13).

The roof extends sufficiently backwards to cover the planum antorbitale. The sphenethmoid commissure starts from the posterior part of the roof to join the anterior prolongation of the planum suprasetale as in the previous stages but a cut has appeared near its medial union for the passage of the blood vessels.

Side wall of the nasal capsule is formed by the lateral extension of the parieto-tectal and the paranasal. The parieto-tectal is sufficiently curved to support the elongated nasal chamber. It gives out two processes laterally. The first of the two lies a little behind the end of the lamina transversalis anterior. It is a bifid process. (Figs. 11, 14 and 15 A). The tip of the ventral nasal gland rests in the depression on this process. The second process lies quite near to the first one. The duct of the lateral nasal gland passes over it towards the aditus conchae. This process also supports the place of origin of the ventral nasal gland and its duct.

The paranasal forms the recess capsule and the part of the nasal concha. The lateral nasal gland lies at the mouth of the concha while the concha itself is full of blood capillaries. In a ventral reconstruction of this stage the concha is only partly visible. The figure 16 shows the relationship of the concha with the surrounding structures.

The nasal septum is unfenestrated and is connected to the roof

Fig. 13.

for the most part. Posteriorly the roof and the nasal septum are separated and in the space so created lie the olfactory nerves. Posteriorly the nasal septum is in continuation with the interorbital septum.

The fenestrae superiores and lateralis are absent. The foramen epiphaniale has the same relationship but it has shifted from near the aditus conchae to the posterior side of the roof. It lies in the same segment from which arises the sphenethmoid commissure.

The maxillary processes are now well developed. They are now displaced towards the anterior side.

In the floor, the lamina transversalis anterior covers the organ of Jacobson from all sides except the dorsal. It further gives rise to an ectochoanal cartilage, which lies by the side of the duct of the organ of Jacobson.

The paraseptal cartilage does not reach the planum antorbitale. But the planum shows an anteriorly directed process towards the paraseptal. It is the posterior remnant of the once continuous

Fig. 14.

paraseptal cartilage.

Among the nasal organs the novelty of this stage is the appearance of a ventral nasal gland. It arises by a broad base from the anterior chamber but becomes narrower as it proceeds away from it. Near its origin the lumen is filled with round glandular cells which have migrated from the interior of the anterior chamber. (Fig. 15 B).

The lachrymal glands and their ducts have become thicker. The important development is the appearance of a flap on which the upper duct opens. The lower duct also reaches the same place and is in intimate relationship with the opening of the upper duct by a short connection. The upper duct opens on a raised epithelial cone on the flap. The flap lies in the ventral conchal zone near the inner opening of the choanal tube. (Fig. 16).

Fig. 15A, B.

Discussion

The ethmoidal region of *Varanus*, while showing the typical lacertilian organization is distinguished by a number of characteristic features of its own. The factors which have influenced its peculiar development are the following:—

- 1—Early development of the dermal bones.
- 2—Archaic features.
- 3—Functional adaptations.

How these factors bring about the changes in the basic elements of the ethmoidal region is seen by the consideration of the characteristic individual parts as follows.

Fig. 16.

1—The Rostral Process—In *Varanus* the nasal septum is continued in front into a rostral process. The lateral wings of the same develop a little later. Such a rostral process has not been described in any other lacertilian so far and is a characteristic feature of the ethmoid region of *Varanus*. This feature is associated with the absence of a foramen apicale. The lateral wings are meant to support the medial ramus of the ethmoid nerve. The lateral wings are joined to the medial edge of the anterior cupola in *V. salvator* and *V. niloticus* (Bellairs, 1949), so that a gutter is formed in front carrying the medial ramus and blood vessels. These are species differences but they clearly point to the generic feature of the rostral process. (Fig. 10, 11)

2—Nodules of Cartilage—Three nodules of cartilage are found on the ventral side of the anterior cupola. They were noted by Bel-

lairs (1949) in the sub-adult specimens but at my fifth stage of development they are in slightly different positions and relationship. These nodules of cartilage in my opinion represent the remnants of the connection between the rostral wings and the anterior cupola. Further they may be the front wall of the anterior cupola which is incomplete and leaves a gap for the medial ramus of the ethmoid nerve. The early development of the bones renders it unnecessary to form a cartilaginous gutter. The medial ramus is very efficiently supported by the premaxilla and the septomaxillary. (Fig. 11)

Among other lizards the foramen apicale is generally enclosed. It is present in *Lacerta* (de Beer, 1930) and *Eumeces* (Rice, 1920). In *Calotes*, Ramaswami (1946) describes a feature of some interest. There is a common large foramen apicale through which the medial branches of both sides pass out. It is clear that the foramina apicales in *Calotes* have become secondarily fused together. In any case the large common foramen apicale represents a stage towards the complete disappearance of the medial wall of the anterior cupola as in *Varanus*. El-Toubi and Kamal (1961a, b) point out a shifting of the foramen apicale from the ventral wall of the cupola towards the medial wall of the same during the development of the gecko, *Ptyodactylus*.

3—Superior and Inferior Alar Processes—are usually present in lizards to support the fenestra narina. (*Lacerta*, de Beer 1930; *Mabuya*, Rao and Ramaswami 1952; *Calotes*, Ramaswami 1946).

In *Ptyodactylus* the superior alar process is completely lacking (El-Toubi and Kamal, 1961b). In *Varanus*, Bellairs (1949) reports a small projection on the superior alar process and interprets it as the inferior alar process. The development of *Varanus* however shows the presence of a well formed inferior alar process. It hangs from the anterior cupola (parieto-tectal) ventrolaterally. The elongation of the anterior naris into a well formed anterior nasal tube has brought about this change. Inferior alar process of Bellairs (1949) does not appear to perform any special function. The most that can be said regarding it is that it supplements the function of the real processus alaris inferior. (Fig. 11, 13)

4—Ventral Nasal Process—Two processes hang down from the lateral wall of the nasal capsule from the parieto-tectal cartilage behind the termination of the lamina transversalis anterior. The first of these two has not been reported so far in any lizard except *Varanus*. It is meant to support the ventral nasal gland. It may be called

as the "Ventral Nasal Process" to distinguish it from the next "Lateral Nasal Process" over which passes the duct of the lateral nasal gland. (Fig. 11, 13 and 15A)

5—The presence of a ventral nasal gland is rather unexpected in *Varanus*. Pratt (1948) however finds one in *Sphenodon*. This gland appears to be a vestigial organ and perhaps is not present in the adult as Bellairs (1949) has not mentioned it in his description of the sub-adult. The presence of a ventral nasal gland is an archaic character. (Fig. 15A, 15B)

6—No zona annularis is formed in *Varanus*. This feature is related to the early formation of the septomaxillary bone in this region. But for this bone the parieto-tectal and the lamina transversalis anterior would meet and a zona annularis would be formed. The organ of Jacobson is also not covered dorsally by the cartilage due to the formation of the septomaxillary bone over it. In *Eumeces* (Rice, 1920), *Calotes* (Ramawami, 1946) and *Mabuaya* (Rao and Ramawami, 1952) no zona annularis is formed. It is however present in *Lacerta* (de Beer, 1930). El-Toubi and Kamal (1961a, b) report an interesting condition in *Ptyodactylus*. At 26.5 mm. whole length the parieto-tectal is connected with the lamina transversalis anterior but at 37.8 mm. stage, when the chondrocranium is fully formed the connection disappears. In *Varanus* the connection is not present at any stage but the septomaxilla is wedged between the two from the beginning.

7—Concha—is formed by the parieto-tectal and the paranasal cartilages. The conditions leading to the formation of the concha may be summarized as follows:

The parieto-tectal as we have seen gives out processes to support the emergent structures from the nasal sac. In my opinion the lateral recess primitively originated as a glandular process from the olfactory sac like the ventral and the lateral nasal glands. To support this the parieto-tectal came out with a process. The appearance of a separate cartilage (Paranasal) forming the capsule of the now overgrown lateral recess and extending to meet the process given out by the parieto-tectal would result in the formation of the aditus conchae. If no nasal concha develops, there would be a vertical pillar of cartilage hanging there as is seen in *Calotes* (see further). The concha during the development is nothing but the extension of the aditus conchae. A cavity is formed later giving it the characteristic shape. The concha may extend into the capsule of the lateral recess as in *Varanus*. (Fig. 16)

The aditus conchae, more than the foramen epiphaniale, denotes the line of fusion of the parieto-ectal and the paranasal. The foramen epiphaniale changes its position during the development. It however keeps its position in that segment of the paranasal from which arises the sphenethmoid commissure (*Lacerta*, de Beer 1930). In the fully formed chondrocranium the foramen epiphaniale can not give reliable information as to the boundaries of the parieto-ectal and the paranasal cartilages. If, however, a median line is drawn through the course of the aditus conchae and the concha, it will show the extents of the parieto-ectal and the paranasal even in the adult specimens.

In *Calotes*, Ramaswami (1946) is evidently under misconception when he says, "The pillar separating the olfactory from the extraconchal recess does not represent the fused posterior walls of the conchae nasales since the aditus concha in all the Lacertilia is posterior to the epiphaneal foramen". From his diagrams and sections, it is clear that the vertical pillar does represent the aditus conchae and its extension. The foramen epiphaniale in *Calotes* is pointed out by him as the demarcating orifice between the paranasal and the lamina orbitonasalis. The foramen epiphaniale, as I said before, does change its position during the course of development. But in *Calotes* also it lies in the segment connecting the paranasal and the sphenethmoid commissure as is evident from the dorsal view of the nasal capsule of the 8 mm. head length embryo given by Ramaswami (1946).

In *Mabuya* (Rao and Ramaswami, 1952) the concha is not typically formed as in *Lacerta*. In *Ptyodactylus*, El-Toubi and Kamal (1961 b) point out the presence of a third element, the posterior extension of the lamina transversalis anterior, taking part in the formation of the concha. As the geckos are primitive and degenerate in many features, it is difficult to say whether it is a secondary feature.

8—It was observed that as the orbit grows the maxillary processes move with it. Thus it appears that the maxillary processes are primarily meant to support the ever enlarging eyes during the development. (Fig. 6, 7 and 10, 11) and perhaps also the lachrymal ducts. In *Lacerta*, de Beer (1930, 1937) considers the posterior maxillary process as representing the ethmoidal attachment of the pterygoquadrate to the planum antorbitale. Such a connection could only be speculated at the second stage of development in *Varanus*. In *Ptyodactylus* the anterior maxillary process is completely absent.

(El-Toubi and Kamal, 1961) in *Calotes* and *Mabuya*, the processes are attached to the lamina orbitonasalis.

It is important to note that the maxillary processes arise at the same time as the lachrymal ducts. (Pratt, 1948)

9—The planum antorbitale shows a process both anteriorly and posteriorly (Fig. 11). The anterior one represents the posterior section of the paraseptal cartilage. Ramaswami (1946) wrongly calls this projection as representing the "reminiscence of the paranasal connexion" in *Calotes*. The posterior process appears to be a bulging and without any special significance. Ramaswami (1946) has however named it as the posterior laminal process in *Calotes*.

In *Lacerta* (de Beer, 1930) and in *Ptyodactylus* (El-Toubi and Kamal, 1961) the planum antorbitale arises independently while Pratt ('48) considers it to be an extension of the paranasal. In *Varanus*, it arises as a separate condensation and with a separate centre of chondrification.

10—Pratt (1948) considers the sphenethmoid commissure as the rostral element which appears in the embryo as anterior free prolongation from the fused planum suprasetale. Actually the sphenethmoid commissures arise from the paranasal. They may reach the anterior prolongation of the planum suprasetale (*Lacerta*, *Calotes*, etc.) or may remain incomplete as in *Ptyodactylus* (El-Toubi and Kamal, 1961).

11—Except Pratt (1948), the nasal organs in lizards have not been in general described along with the development of the ethmoidal region. The important conclusion which emerges from the simultaneous study is the fact that the cartilages arise in response to the appearance of the nasal organs.

12—The lachrymal glands and their ducts present some features of interest. (Fig. 15B, 16). There are two lachrymal glands, which may be called as the upper and the lower according to their position of origin. The upper duct opens on an epithelial cone on a flap near the inner opening of the choanal tube. The lower forms a connection with the upper at this place and then continues its course to open into the duct of the organ of Jacobson, where it further ends blindly. It appears that this complicated connection and the opening of the upper lachrymal duct on the raised epithelial cone together form a controlling mechanism for the flow of the lachrymal secretion. In semi-deserticolous forms like *Varanus bengalensis*, the watery secretion is of utmost importance. Functional aspects of the flap and the connection may be explained as follows:—

a—When dry air enters the nasal organs, the flap hanging into the ventral conchal zone is stimulated and the secretion of the upper lachrymal duct is poured to moisten the surrounding area.

b—The epithelial cone on the flap will allow the secretion to flow slowly and evenly. This is an adaptation par excellence.

c—The connection between the upper and the lower ducts at this place controls the quantity of the flow in the two directions according to the emergent necessity of the fluid in the organ of Jacobson or the ventral conchal zone and the choana. The pressing of the palate by the prey or the tongue may be a further source of stimulation.

d—The blind ending of the lower lachrymal duct on the medial side of the duct of the Jacobson's organ is to keep a drop or two handy of the excess secretion to be poured into the duct of the Jacobson's organ when required.

The dorsal plate

The roof and the side wall of the nasal capsule in Lacertilia are considered primarily to be made up of two cartilages—the parietotectal and the paranasal. Pratt (1948) pointed out the existence of a third element, which he called as the Dorsal plate. According to him the dorsal plate is demarcated from the capsular element by the foramina apicale and the epiphaniale, and the fenestrae lateralis and superior. Thus his conception of the rostral element, the dorsal plate, is rather quite extensive.

In *Varanus*, at the 52.50 mm. total length there is an extension of the perichondrial wall dorsally on both sides of the nasal septum. At 57.20 mm. stage the cells are seen on the upper side of this extension. At 75.20 mm. the cartilage appears. It has extended slightly but it is still uncovered on the dorsal side by a perichondrium. Lateral to this, perichondrium is being formed both on the upper as well as on the lower sides of the condensation. Further lateral, the cells are in strong concentration. Under high power the cells are seen in strings and take intense blue stain. (Fig. 9).

The area with the perichondrial extension from the nasal septum partially answers to the Pratt's idea of a rostral element. It is however seen that the rostral element does not form a continuous sheet over the nasal septum as Pratt would have it. It is present separately on both sides of the nasal septum. It is a bilateral structure and but for the presence of a perichondrial extension of

the nasal septum from the earliest stage, it can as well be said to be a parieto-tectal cartilage. It appears that the cells bud off from the perichondrial extension from the beginning. These cells move further laterally. The trabecula communis, extension of which forms the nasal septum, would thus appear to be more than a mere median cartilaginous bar separating the nasal organs of the two sides. However the perichondrial cells are also formed in situ at the extreme end of the side wall. Thus in any case the presence of a bilateral rostral element taking part in the formation of the nasal capsule can not be denied. Towards the posterior side the extent of the rostral element is the same as in the anterior region and there is no ground to accept its boundary upto the foramen epiphaniale. At the least the presence of the rostral element may be considered as a passing phase in the development of the ethmoidal region.

The most recent work on the development of the lacertilian chondrocranium, that of El-Toubi and Kamal (1961a, b) on *Ptyodactylus* however denies totally the presence of a rostral element. Their objections and observations are as follows:—

1. The parieto-tectal cartilage and the dorsal plate, if they are to be considered as separate elements must have two separate centres of chondrification.
2. The two elements have not been observed by the previous workers.
3. Pratt finds only a histological differentiation between the dorsal plate and the parieto-tectal.
4. Pratt regards the cartilage between the fenestrae superiores to be the dorsal plate. In the fully formed chondrocranium of *Ptyodactylus*, the fenestrae are separated from each other only by the dorsal edge of the nasal septum.

The above objections are however not quite tenable. Thus,

1. As I said before, even at the earliest stage the nasal septum shows the lateral extensions of the perichondrium. Naturally we are led to consider it as a separate centre of chondrification or at least as a rostral element that partakes in the formation of the roof of the nasal capsule. The parieto-tectal chondrifies later than the rostral element.
2. The previous authors perhaps did not recognise the importance of the histological differentiation. Indeed thorough morphological and experimental studies are called for to estimate the role of the nasal septum in the formation of the roof of the nasal capsule.

3. Perichondrial wall or its extension is a sufficiently well-established structure to be left aside only as a histological differentiation. Cartilage develops in apposition to the perichondrium. In *Ptyodactylus* the histological differentiation does not occur according to El-Toubi and Kamal (1961).

4. I fully agree with El-Toubi and Kamal as regards the topography of the fenestra superior. In *Varanus*, at the 75.20 mm. whole length, there is an area without the perichondrial wall corresponding to the position of a fenestra superior. (Fig. 7, 9). Further Pratt's contentions as regards the extent of the rostral element are not fully justified by the developmental studies.

Summary

1. In the present work, the development of the ethmoidal region of *Varanus bengalensis* has been studied in five main development stages and four intermediate stages.

2. In Stage I, 44.75 mm. whole length, the skeletal elements do not appear. (Fig. 1). The organ of Jacobson appears as a bulging on the olfactory sac.

3. In stage II, 52.50 mm. w.l., the nasal septum appears in continuation with the trabecula communis. The perichondrium of the nasal septum extends dorsally on both sides. The duct of the organ of Jacobson elongates and connective tissue enters into the fold of the dome. Anterior chamber becomes differentiated. (Fig. 2, 3)

4. In stage III, 57.20 mm. w.l., extensive condensations of the parieto-ectal, paranasal, aditus conchae, rostral wings, lamina transversalis anterior and the planum antorbitale appear. Lateral recess and the conchal zone can be clearly distinguished. (Fig. 4, 5)

5. In stage IV, 75.20 mm. w.l., the perichondrial walls are being formed round the cartilages. The bilateral rostral element taking part in the formation of the nasal capsule is distinguished. The concha appears as a continuation of the aditus conchae. Recess capsule is in the course of chondrification. Foramen epiphaniale is enclosed. Cartilage of Jacobson's organ, lachrymal ducts and maxillary processes appear. Lateral nasal gland is represented by its duct arising from the anterior chamber. There is no foramen apicale. Paraseptal cartilages, sphenethmoid commissures and planum antorbitale are getting chondrified. Condensations of alar processes appear. (Fig. 6, 7, 8, 9)

6. Intermediate stages. General growth occurs. Ventral nasal gland, with a supporting process from the parieto-ectal appears. This process is named as the "Ventral Nasal Process" to distinguish it from the "Lateral Nasal Process" supporting the duct of the lateral nasal gland.

7. Stage V, 104.60 mm. w.l. The nasal capsule is fully chondrified. Three cartilaginous nodules are seen on the ventral side of the anterior cupola. Ectochoanal cartilage appears. (Fig. 10, 11, 12, 13, 14, 15, 16)

8. In the discussion the characteristics of the varanid ethmoidal region are pointed out and their significance is explained along with a few others. Lastly a discussion on the rostral element, taking part in the formation of the nasal capsule, follows.

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Abbreviation to Figures

- A. CH. ; anterior chamber of the nasal sac.
- A. CH.' ; opening of the anterior chamber into the olfactory chamber.
- Ad. Co. ; aditus conchae.
- A. E. N. ; anterior external nostril.
- Ant. Cup. ; anterior cupola.

- A. N. T. ; anterior nasal tube.
 A. O. S. P. ; antorbital space of the nasal sac.
 A. S. ; anterior space of the olfactory chamber.
 CART. ; nodules of cartilage.
 Ch. ; choanal tube.
 C. L. Rec. ; capsule of the lateral recess.
 C. J. O. ; concha of the Jacobson's organ.
 CO. ; nasal concha.
 CO. Z. F. ; fold in the conchal zone.
 Dent. L. ; dental lamina.
 Dent. R. ; dental ridge.
 d. J. O. ; duct of the organ of Jacobson.
 D. P. ; dorsal plate.
 d. L. N. G. ; duct of the lateral nasal gland.
 d. V. N. G. ; duct of the ventral nasal gland.
 EC. C. ; ectochoanal cartilage.
 F. ep. ; foramen epiphaniale.
 F. S. ; the area without perichondrial wall and low stain representing the fenestra superior.
 Flap lach. ; the flap on which opens the upper lachrymal duct.
 H. G. ; Harderian gland.
 J. O. ; organ of Jacobson.
 J. O. C. ; cartilage of the organ of Jacobson.
 L. L. d. ; lower lachrymal duct.
 L. J. ; lower jaw.
 L. N. G. ; lateral nasal gland.
 L. N. P. ; lateral nasal process.
 L. Rec. ; lateral recess of the nasal capsule.
 L. T. A. ; lamina transversalis anterior.
 L. T. A.' ; posterior end of the lamina transversalis anterior.
 N. S. ; nasal septum.
 O. Ch. ; outer choana.
 Ol. Ch. ; olfactory chamber.
 Ol. S. ; olfactory sac.
 P. Al. Su. ; processus alaris superior.
 P. Al. In. ; processus alaris inferior.
 P. Al. In.' ; early condensation of processus alaris inferior.
 P. Al. In.'' ; processus alaris inferior according to Bellairs (1949).
 P. ANT. ; planum antorbitale.
 Pch. Ext. ; perichondrial extension of the nasal septum.
 P. Mx. A. ; processus maxillaris anterior.
 P. Mx. P. ; processus maxillaris posterior.
 P. N. C. ; paranasal cartilage.
 P. S. S. ; planum suprasedptale.
 P. S. S.' ; anterior prolongation of the planum suprasedptale.
 PS. C. ; paraseptal cartilage.
 PS. C.' ; the process on the planum antorbitale representing the posterior section of the paraseptal cartilage.
 P. T. C. ; parieto-tectal cartilage.
 Ros. P. ; rostral plate. (rostral process).
 Ros. W. ; rostral wing.

Smx.	; septomaxilla.
Sph. C.	; sphenethmoid commissure.
T. C.	; trabecula communis.
U. L. d.	; upper lachrymal duct.
V. N. G.	; ventral nasal gland.
V. N. P.	; ventral nasal process.
I.	; olfactory nerve.
I.'	; nerve to the organ of Jacobson.
Va.	; ethmoid nerve.
Va. m.	; medial ramus of the ethmoid nerve.
Va. l.	; lateral ramus of the ethmoid nerve.

Legends to Figures

- Fig. 1. ; 44.75 mm. embryo. Part of a frontal section showing the nasal organs.
- Fig. 2. ; 52.50 mm. embryo. Frontal section of the ethmoidal region.
- Fig. 3. ; 52.50 mm. embryo. Frontal section of the ethmoidal region a few sections ahead of that shown in Fig. 2.
- Fig. 4. ; 57.20 mm. embryo. Longitudinal section of the ethmoidal region to show cell condensations of cartilages.
- Fig. 5. ; 57.20 mm. embryo. Reconstruction of the nasal capsule from the longitudinal sections in lateral view. All shaded areas show cell condensations. The condensation of the planum supraseptale (the pre-optic root) is only partly shown.
- Fig. 6. ; 75.20 mm. embryo. Reconstruction of the nasal capsule in ventral view.
- Fig. 7. ; 75.20 mm. embryo. Reconstruction of the nasal capsule in dorsal view to show the chondrification centres. $\times 8$, plane of T. S. shown in Fig. 8; $\times 9$, plane of T. S. shown in Fig. 9.
- Fig. 8. ; 75.20 mm. embryo. T. S. through the plane indicated in Fig. 7 and marked $\times 8$.
- Fig. 9. ; 75.20 mm. embryo. T. S. passing through the plane indicated in Fig. 7 and marked $\times 9$.
- Fig. 10. ; 104.60 mm. embryo. Reconstruction of the nasal capsule in dorsal view.
- Fig. 11. ; 104.60 mm. embryo. Reconstruction of the nasal capsule in ventral view. $\times 12$, $\times 13$, $\times 14$ indicate the planes of transverse sections shown in Figs. 12, 13 and 14.
- Fig. 12. ; 104.60 mm. embryo. T. S. through the plane $\times 12$ indicated in fig. 11.
- Fig. 13. ; 104.60 mm. embryo. T. S. through the plane $\times 13$ indicated in fig. 11.
- Fig. 14. ; 104.60 mm. embryo. T. S. through the plane $\times 14$ indicated in fig. 11.
- Fig. 15A.; 104.60 mm. embryo. Reconstruction to show the relationship of the ventral nasal gland and the lateral nasal gland with the processes of the parietotectal in ventral view.
- Fig. 15B.; 104.60 mm. embryo. Reconstruction of the nasal organs in dorsal view.
- Fig. 16. ; 104.60 mm. embryo. Diagram to show the relationship of the concha and the lachrymal ducts with the surrounding structures. The planum antorbitale is only partly drawn. The opening marked X shows the place of entrance of the lateral recess into the capsule of the lateral recess.

(All figures represent $\times 37.5$ of the actual size.)