A comparative study of the morphology of the chondrocranium of *Dendroaspis angusticeps* and *D. polylepis polylepis*

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The essential features of the chondrocrania of both *D. angusticeps* and *D. polylepis polylepis* are very similar and conform closely to the platytrabic ophidian type. Specialized features such as a marked reduction of the solum nasi, as well as of the orbitotemporal region of the chondrocranium are noticeable. The basal plate and the occipital and auditory regions do not differ in important respects from those described in other snakes. Taxonomic justification for the separation of these elapids into two distinct species is adequately confirmed by structural differences between their chondrocrania.

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Wesenlik toon die chondrokraniums van *D. angusticeps* en *D. polylepis polylepis* groot ooreenkoms en beide sluit nou aan by die platibasiese skedelpatroon by slange. Gespesialiseerde kenmerke soos reduksie van die neuskapselvloer sowel as van die orbitotemporaalgebied is opvallend. Die basaalplaat en die oksipitaal- en oorkapselgebiede verskil ook nie in belangrike opsigte van dié wat in ander slangsoorte beskryf is nie. Taksonomiese regverdiging vir twee aparte spesies word voldoende deur strukturele verskille tussen die chondrokraniums bevestig.

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The chondrocrania of the two species of *Dendroaspis viz. D. angusticeps* and *D. polylepis polylepis* have never been studied. Both snakes were originally regarded by Smith (1849) as colour varieties of a single species (Fitzsimons 1962). From a study of the external features, it is evident that differences do exist between the two, especially with regard to the scale count. The object of this investigation was *inter alia* to see whether the separation of these two snakes into two distinct species on the basis of external features and scale count could be substantiated by additional information revealed by a comparative study of the chondrocrania.

Although the fully formed chondrocranium of snakes is fairly well understood, some doubts and obscurities still remain. In the hope that further light might be shed on some of the problems in ophidian cranial morphology, a careful investigation of some young embryos of *D. polylepis polylepis* was also made.

Material and Technique

A batch of newly laid eggs of *D. polylepis polylepis* was obtained from the Fitzsimon's Snake Park, Durban. These were kept in damp soil at room temperature.

The heads of the following embryos of *D. polylepis polylepis* were sectioned:

10-day-old embryo
15-day-old embryo
20-day-old embryo
25-day-old embryo
30-day-old embryo
50-day-old embryo
Late embryo just prior to hatching.

The heads of the embryos were sectioned at 10 μm. The serial transverse sections of the earlier embryos, ranging from 10 to 30 days, were stained either with haematoxylin and acid fuchsin or haematoxylin and alcoholic eosin, both combinations giving satisfactory results. The late embryos were stained in Mallory's triple stain.

A complete set of slides of the head of an embryo of *D. angusticeps*, sectioned at 10 μm and stained in Bismarck brown and eosin, was loaned to me by Professor A.L. Smit of the Department of Zoology, University of Durban-Westville. The exact age of this embryo could not be ascertained. However, it represented a relatively late stage since the chondrocranium was well formed and

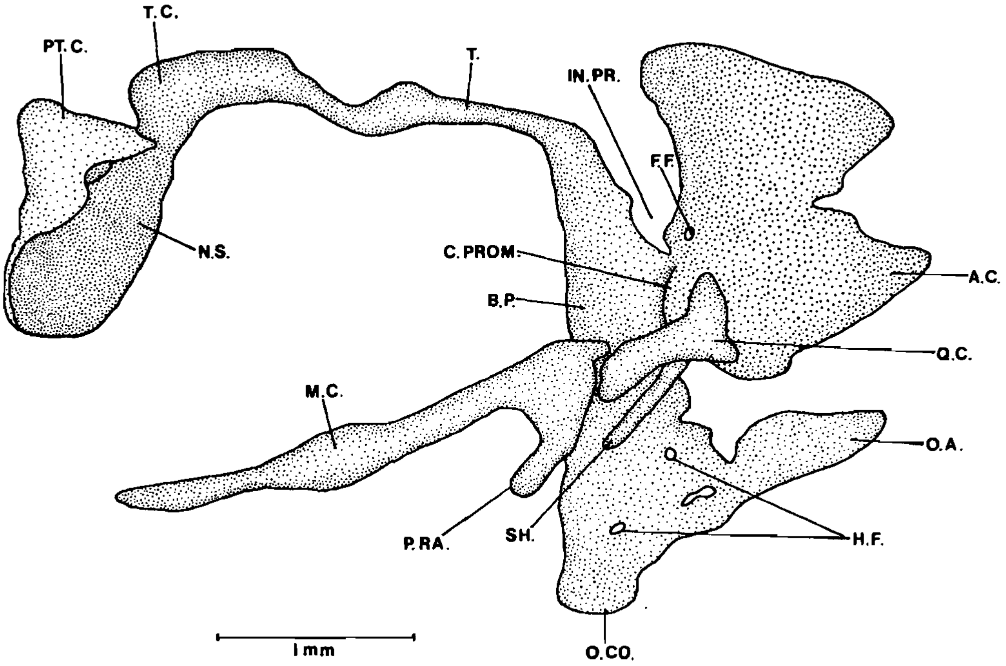

Fig. 1 Graphic reconstruction of the blastematous chondrocranium of a 25-day-old embryo of *D. polylepis polylepis* as seen in lateral view. (See Table 1 Key to anatomical drawings.)

ossification had already begun in the basioccipital and basisphenoid regions.

Graphic reconstructions of the dorsal, ventral and lateral views of the chondrocrania of both species as well as of the viscerocranium of *D. angusticeps* were made according to the method described by Pusey (1939). The blastematous chondrocranium of a 25-day-old embryo of *D. polylepis polylepis* was also reconstructed.

The Neurocranium

Ethmoid region

The chondrification of the ethmoid region of snakes is retarded. Although the parachordals in a 15-day-old embryo of *D. polylepis polylepis* are discernible, the parietotectal cartilage and the nasal septum are not yet represented in mesenchyme. In the 25-day-old embryo of the same species, however, the nasal septum and part of the medial wall and roof of the capsule have appeared in a blastematous condition.

Chondrification of the nasal septum precedes that of the other structures in the nasal region. In the 25-day-old embryo, the nasal septum lies almost at right angles to the trabeculae cranii (Fig. 1). This appears to be a common feature in the embryos of snakes. During ontogeny, the nasal capsules are gradually displaced dorsad. In the 50-day embryo of *D. polylepis polylepis*, where the chondrocranium is fully formed, the nasal septum lies in almost the same horizontal plane as the trabeculae cranii

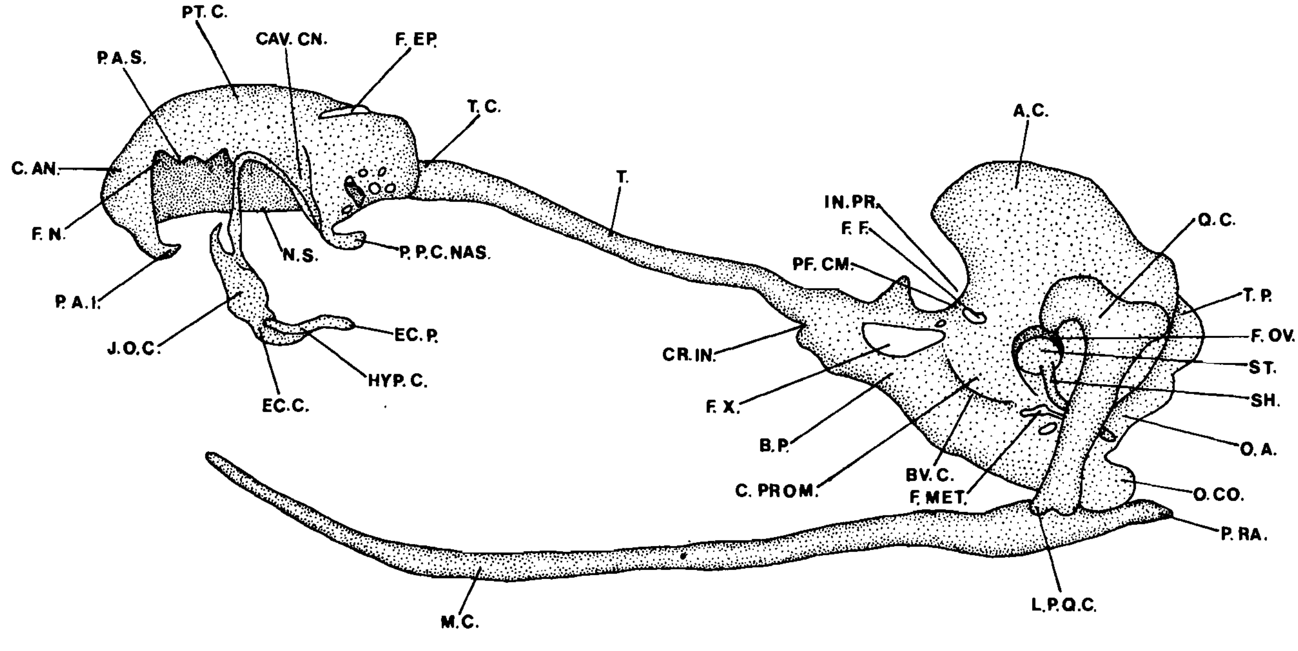

Fig. 2 Graphic reconstruction of the chondrocranium of a 50-day-old embryo of *D. polylepis polylepis* as seen in lateral view. (See Table 1 Key to anatomical drawings.)

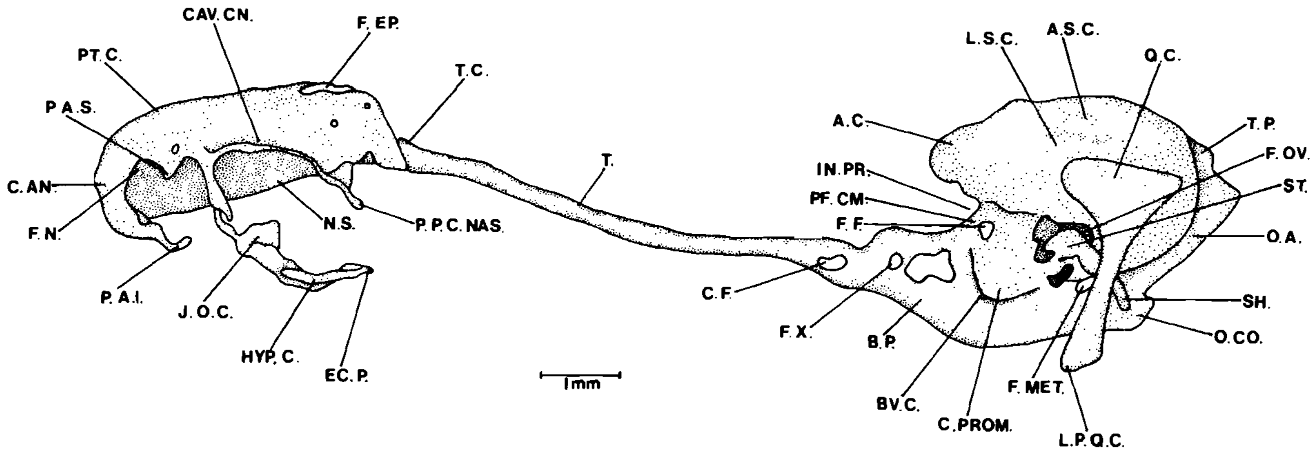

Fig. 3 Graphic reconstruction of the fully formed chondrocranium of *D. angusticeps* as seen in lateral view. (See Table 1 Key to anatomical drawings.)

(Fig. 2) and appears as an anterior continuation of the fused trabecular rods. In both species of *Dendroaspis*, this septum is a vertical unfenestrated plate that lies between the nasal capsules. It is relatively high in the middle but its height gradually decreases both anteriorly and posteriorly.

Except for some minor variations, the fully formed nasal capsules of both species of *Dendroaspis* are similar. They are of a delicate nature and conform in all essential respects to the ophidian pattern.

A pair of dome-shaped structures, the cupolae anteriores, extend beyond the tip of the nasal septum. On either side of each anterior cupola is a large fenestra narina (Figs. 2 and 3). This fenestra is incomplete posteriorly because the processus alaris superior and the processus alaris inferior remain widely separated from each other. The processus alaris inferior is a long tapering process that extends in a posterolateral direction from the floor of each anterior cupola (Figs. 2 and 3). In contrast to this structure, the processus alaris superior is rather inconspicuous.

The lamina orbitonasalis forms the posterior border of the foramen olfactorium advehens and also of the nasal capsule. In both species of *Dendroaspis* this foramen is closed off posteriorly by the fusion of the lamina orbitonasalis (planum antorbitale) with the nasal septum (Figs. 4 and 5). This fusion occurs in the region of the trabecula communis.

In the 25-day-old embryo of *D. polylepis polylepis* the foramen olfactorium advehens is still incomplete posteriorly. Although the blastematous rudiments of the nasal septum, the trabeculae cranii and the medial wall and roof of the nasal capsule are indistinct, the lamina orbitonasalis is not represented even in the mesenchymatous condition. The lamina orbitonasalis appears late in the ontogeny of *D. polylepis polylepis* and is fused to the nasal septum in the 50-day-old embryo where the chondrocranium is fully formed. This connection must therefore be regarded as a secondary condition.

In both species of *Dendroaspis*, the foramen epiphaniale is an elongate fissure that lies dorso-lateral and slightly anterior to the foramen olfactorium advehens (Figs. 4 and 5). The lateral branch of the profundus nerve (ramus lateralis nasi) emerges through this foramen (Fig. 6) and innervates the lateral nasal gland. The medial ethmoidal branch (ramus medialis nasi) runs alongside the nasal septum and emerges ventral to each anterior cupola.

A simplified type of concha nasalis is present in the nasal capsule of *D. angusticeps* where the cavum conchale resembles a U-shaped trough (Fig. 6). This trough is

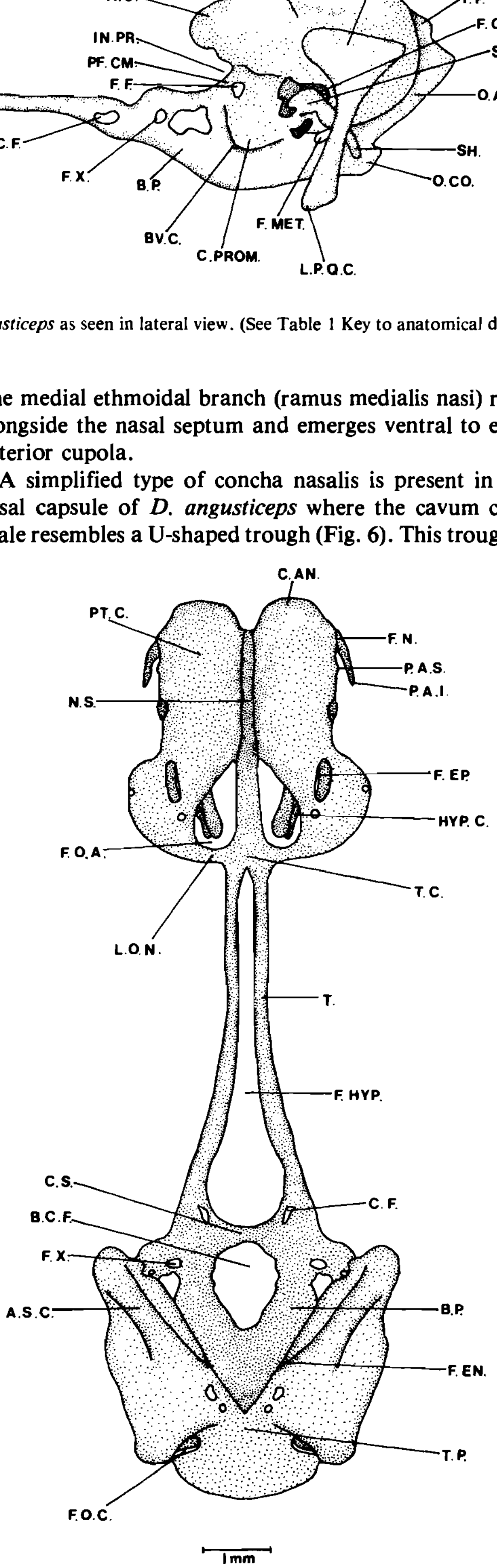

Fig. 4 Dorsal view reconstruction of the fully formed chondrocranium of *D. angusticeps*. (See Table 1 Key to anatomical drawings.)

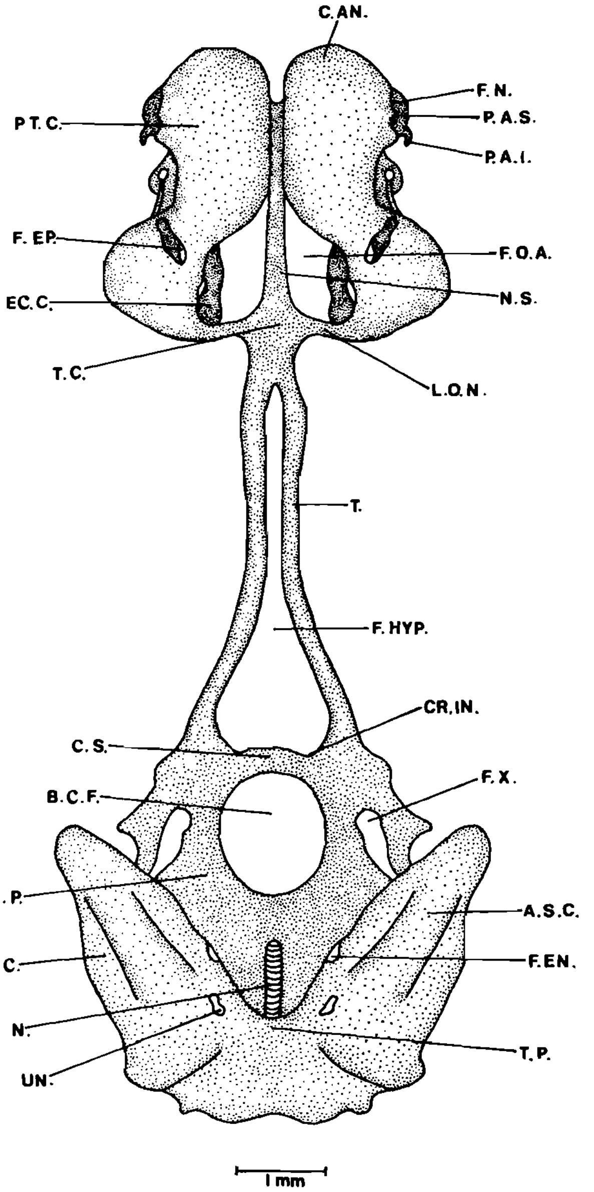

Fig. 5 Dorsal view reconstruction of the chondrocranium of a 50-day-old embryo of *D. polylepis polylepis.* (See Table 1 Key to anatomical drawings.)

shallow anteriorly but gradually deepens posteriorly. The anterior opening of the concha, the aditus conchae is not clearly defined. Posteriorly, the cavum conchale opens ventrolaterally but at its extreme posterior end it is closed by the fusion of the two edges of the U-shaped trough. The lateral nasal glands are not only confined to the cavum conchale but overlie the conchal portion of the nasal capsule. Since in the embryos of *D. polylepis polylepis* the lateral nasal glands develop long after the appearance of the conchal infolding, it seems more likely that it is the nasal epithelium rather than the glands themselves which play a role in its formation. This suggests that the glands are secondary to the conchal infolding.

The paranasal cartilage is present in *D. polylepis polylepis* and contributes to the formation of the concha nasalis. Since this cartilage is present in lizards, its occurrence in snakes indicates a primitive feature. The paranasal cartilage in *D. polylepis polylepis* is attached to the lateral wall of the parietotectal cartilage in the region of the lateral nasal glands. It appears late in the ontogeny and only a small median portion, attached to the lateral wall of the parietotectal cartilage, is retained (Fig. 7). This rudimentary paranasal cartilage contributes to the formation of the anterior part only of the concha nasalis and lies over the lateral nasal gland. It does not play a very prominent role in the formation of the concha nasalis as such.

Solum nasi. Similar to the condition in the Colubridae and Viperidae, the nasal capsules in both species of *Dendroaspis* are almost entirely open ventrally. The anterior cupola has a reduced floor. In both species of *Dendroaspis* there is a small cartilaginous process from the floor of each anterior cupola close to the nasal septum (Figs. 8 and 9).

Jacobson's organ cartilage medially has a cartilaginous ridge projecting into the ventral indentation of the organ (Fig. 6). Jacobson's organ cartilage continues posteriorly as the ectochoanal cartilage. Lying parallel to the ectochoanal cartilage is the rod-like hypochoanal cartilage (Figs. 8 and 9). In both species of *Dendroaspis*, the hypochoanal cartilage is free anteriorly but it is attached to the ectochoanal cartilage posteriorly.

In *D. polylepis polylepis*, a narrow strip of cartilage extends downwards from the paries lateralis nasi to unite with the cartilage of Jacobson's organ (Fig. 2). This cartilaginous connection is, however, absent in *D. angusticeps*

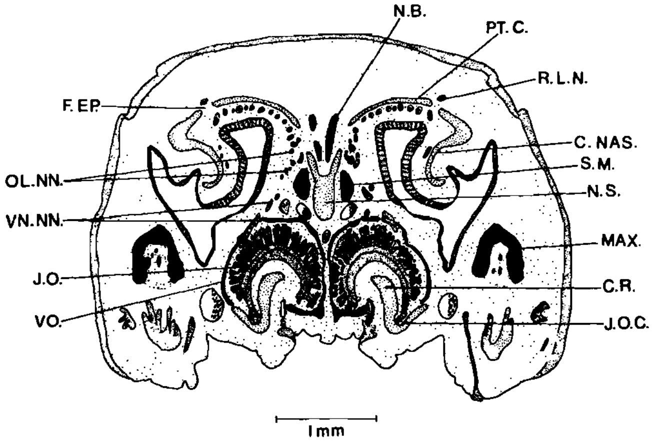

Fig. 6 Transverse section through the nasal capsule of a late embryo of *D. angusticeps* to show the concha nasalis, Jacobson's organ and the vomero-nasal nerves. (See Table 1 Key to anatomical drawings.)

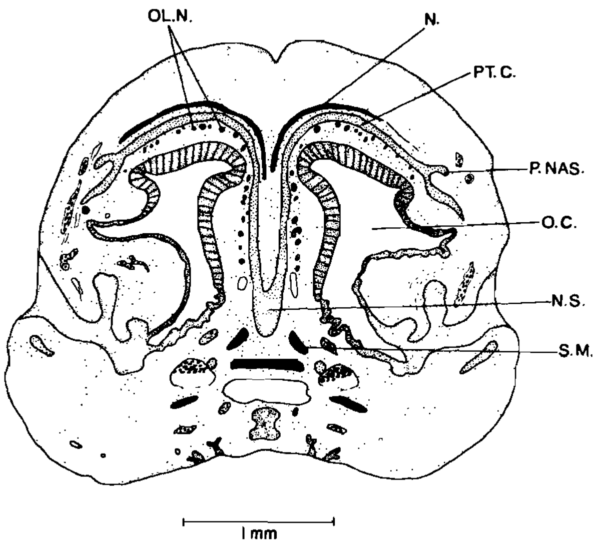

Fig. 7 Transverse section through the nasal capsule of *D. polylepis polylepis* to show the paranasal cartilage. (See Table 1 Key to anatomical drawings.)

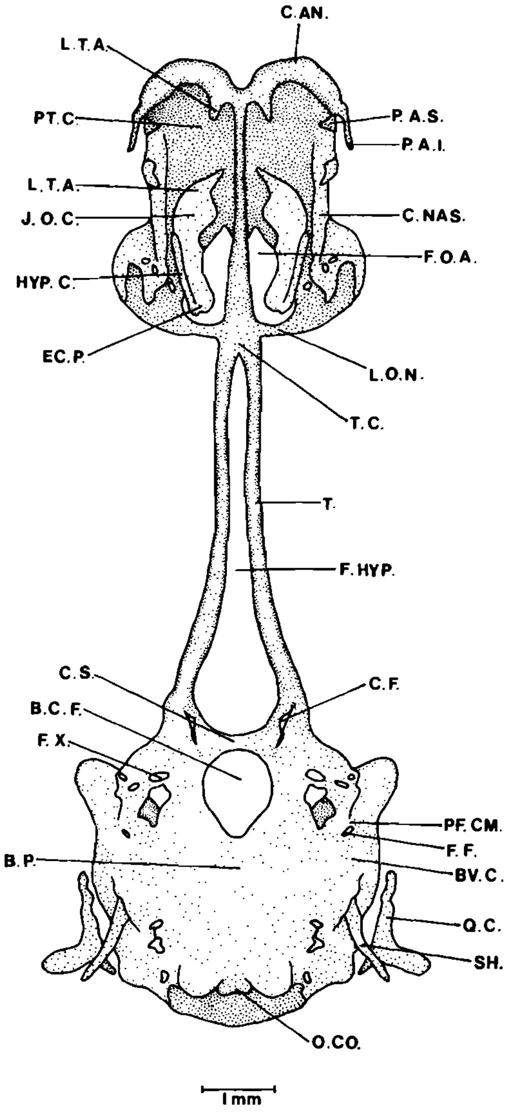

Fig. 8 Graphic reconstruction of the fully formed chondrocranium of *D. angusticeps* as seen in ventral view. (See Table 1 Key to anatomical drawings.)

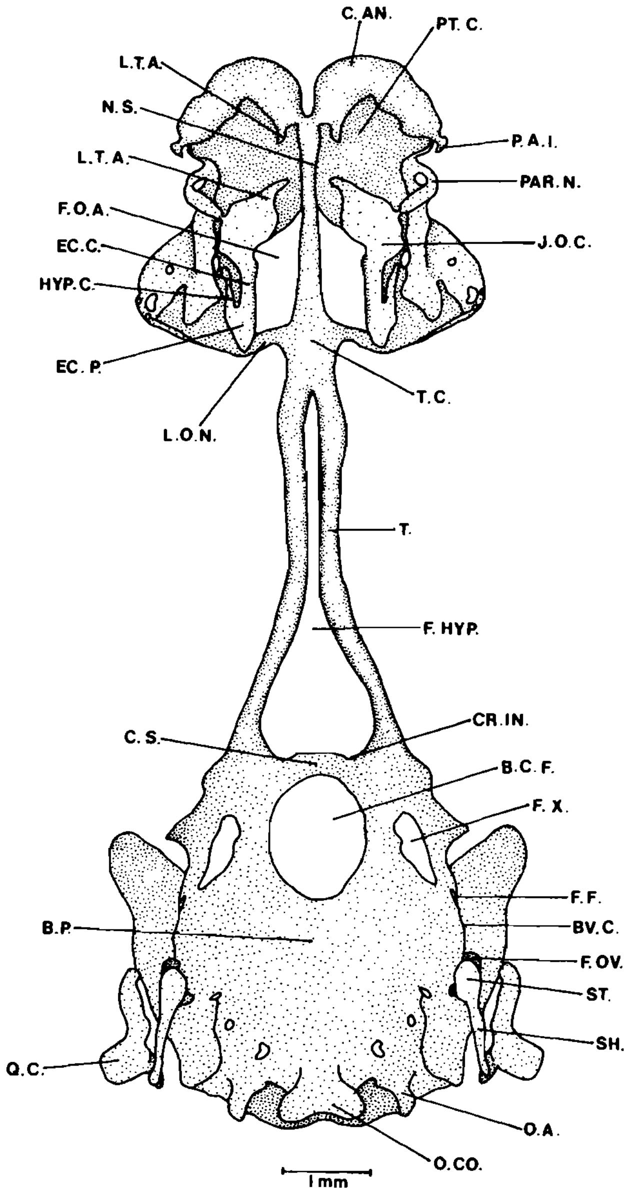

Fig. 9 Graphic reconstruction of the chondrocranium of a 50-day-old embryo of *D. polylepis polylepis* as seen in ventral view. (See Table 1 Key to anatomical drawings.)

with the result that the solum nasi is completely isolated from the roof of the nasal capsule.

Organ of Jacobson. In both species of *Dendroaspis*, Jacobson's organ (Fig. 6) is completely closed off from the nasal cavity by its capsule which is partly bony and partly cartilaginous. At the extreme anterior end of the organ, the septomaxillary forms the lateral as well as part of the dorsal wall of the capsule while the vomer forms the medial, as well as parts of the dorsal and ventral walls. The lamina transversalis anterior contributes to the formation of the ventrolateral wall of the capsule of Jacobson's organ in the form of Jacobson's organ cartilage. The cartilaginous ridge of Jacobson's organ cartilage protrudes into the ventral indentation of the organ through the fenestra vomeronasalis. Further posteriad, Jacobson's organ is completely enclosed by the vomer. The duct from this organ runs ventrad, almost vertically, and opens into the buccal cavity. Opening medially into this duct is the duct from the lachrymal gland.

The vomeronasal nerves arise from the epithelial cells of Jacobson's organ and pass dorsad through foramina in the vomer in the roof of the capsule. These nerve bundles then run posteriorly with the branches of the olfactory nerve, alongside the nasal septum, to the olfactory bulb. This organ seems to have an olfactory function since it is innervated by the branches of the olfactory nerve.

Orbitotemporal region

The orbitotemporal region in snakes is of fairly uniform construction, characterized mainly by a reduction of the cartilaginous elements when compared with the lacertilian condition. In this respect, the morphology of this region in *Dendroaspis* is typically ophidian. In both species it consists of two elongate rods of cartilage, the trabeculae cranii, that stretch a little more than one-third the total length of the chondrocranium. They remain separate throughout their entire lengths and enclose a somewhat flask-shaped foramen hypophyseos (Figs. 4 & 5). They fuse anteriorly forming the trabecula communis which is fused to the nasal septum. Posteriorly, the trabeculae cranii fuse with the parachordal plate. The crista sellaris forms the posterior boundary of the foramen hypophyseos. During development, the trabeculae are gradually displaced upwards so that in the

50-day-old embryo of *D. polylepis polylepis*, they have come to lie approximately in the same horizontal plane as the parachordal plate.

The skull in *Dendroaspis* is typically platytrabic; no interorbital septum exists even in early stages.

Paired carotid foramina are present in *D. angusticeps* for the passage of the internal carotid arteries (Fig. 8). In *D. polylepis polylepis*, however, the internal carotid arteries enter the cranium through the posterior corners of the foramen hypophyseos.

Auditory region

With minor variations, the auditory capsules of both species of *Dendroaspis* are similar and they present prominences and cavities similar to those described in other snakes. De Beer (1937) correlates the absence of the crista parotica in snakes with the free rotation of the quadrate during ontogeny.

It is evident from ontogeny that the cochlear portion does not have a separate centre of chondrification but arises from the auditory capsule and chondrifies independently of the parachordal plate. In the 50-day-old embryo of *D. polylepis polylepis* and in the late embryo of *D. angusticeps*, the auditory capsules are attached to the lateral margins of the basal plate by the extensive basivestibular commissure. This commissure extends from the facial foramen to the anterior part of the fissura metotica (Figs. 2 and 3). The fusion between the cochlear portion of the auditory capsule and the parachordal plate takes place early in ontogeny when these structures are still in the mesenchymatous or procartilaginous condition. This is in agreement with the view expressed by De Beer (1937) that the auditory capsules of vertebrates arise quite independently of the parachordal plate but later become attached to it.

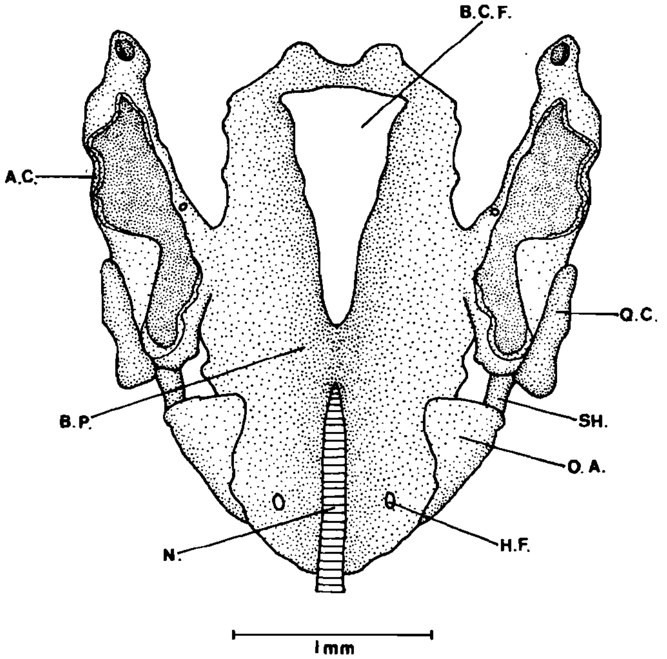

Fig. 10 Dorsal view reconstruction of the basal plate, otic capsules and occipital arches of a 25-day-old embryo of *D. polylepis polylepis. N.B.* Due to extreme cranial flexure the trabeculae lie perpendicular to the basal plate and hence have not been reconstructed. (See Table 1 Key to anatomical drawings.)

In the 25-day-old embryo of *D. polylepis polylepis*, the floor and medial wall of the capsule are quite well formed but the roof is incomplete (Fig. 10). The occipital arches also, are widely separated from each other dorsally. Whether the strip of cartilage that connects the auditory capsules and the occipital arches dorsally is the tectum synoticum or the tectum posterius or whether it represents a fusion of both these structures, is a subject of some controversy in the literature on snakes.

Externally, the fully formed auditory capsules of both species of *Dendroaspis* show a number of prominences which indicate internal enlargements for the accommodation of the various parts of the labyrinth. The most conspicuous of these is that of the anterior semicircular canal which is demarcated from the rest of the capsule by two longitudinal depressions or grooves. The prominence of the posterior semicircular canal is not clearly defined. The utricular prominence is quite conspicuous on the medial aspect of the auditory capsule and so is the ridge formed by the lateral semicircular canal. The cochlear prominence is also conspicuous due to its encroachment on the lateral margin of the basal plate (Figs. 2 and 3). There is no sign of a crista parotica on the lateral margin of the auditory capsule.

The interior of the capsule is very similar in both species of *Dendroaspis*. The ductus endolymphaticus leads off from the dorsal surface of the sacculus. It curves below the utriculus and passes upwards through the foramen endolympaticum and ends blindly in the large saccus endolymphaticus. In both *D. angusticeps* and *D. polylepis polylepis* the saccus lies near a large unchondrified area in the medial wall of the auditory capsule (Fig. 11).

The anterior and posterior acoustic foramina, for the branches of the auditory nerve, are present in the medial wall of the auditory capsule. The anterior acoustic foramen lies directly above the facial foramen. In *D. polylepis polylepis* the foramen glossopharyngeum internum is a minute foramen that lies below the foramen endolymphaticum. The glossopharyngeal nerve has a short intracapsular course and then dips downwards through

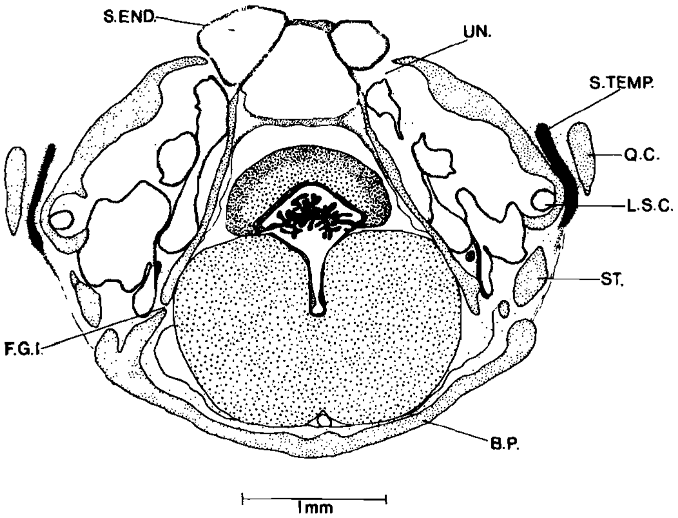

Fig. 11 Transverse section through the auditory capsule of a 50-day-old embryo of *D. polylepis polylepis* to show the relationship between the saccus endolymphaticus and the large unchondrified area on the dorso-medial aspect of the auditory capsule. (See Table 1 Key to anatomical drawings.)

the foramen perilymphaticum and comes to lie in the recessus scalae tympani. It then merges with the vagus ganglion. In *D. angusticeps*, however, the course of the glossopharyngeal nerve is somewhat different from that described above since it does not have an intracapsular course. In the latter snake, the glossopharyngeal nerve passes through a small foramen present in the lateral edge of the basal plate and as in *D. polylepis polylepis*, merges with the vagus ganglion.

The fenestra ovalis lies in the lateral wall of the auditory capsule. In *D. polylepis polylepis* this fenestra is oval whereas in *D. angusticeps* it has an irregular shape. In both species, the footplate of the columella auris fails to occlude the fenestra ovalis completely.

Posterior to the basivestibular commissure, the auditory capsule is separated from the basal plate by the fissura metotica. There is a strip of cartilage that extends downwards from the medial wall of the auditory capsule and comes into very close contact with the lateral margin of the basal plate. This cartilage divides the fissura metotica into the anterior recessus scalae tympani and the posterior jugular foramen.

Basal plate

In both species of *Dendroaspis*, the basal plate is roughly rectangular, extending from the crista sellaris anteriorly to the occipital condyle posteriorly. The basal plate lies ventral to the notochord. This appears to be a common feature of snakes. De Beer (1937) describes a similar condition in *Tropidonotus* and states that in this respect, snakes resemble *Lacerta* and *Sphenodon*. In both species of *Dendroaspis* a narrow prefacial commissure separates the facial foramen from the widely open prootic incisure (Figs. 2 and 3). The basicranial fenestra in the 50-day-old embryo of *D. polylepis polylepis* is oval in shape and is much larger than the bell-shaped fenestra present in *D. angusticeps*.

There is neither an abducens depression nor an abducens tunnel present in either species of *Dendroaspis* and the abducens nerve passes forward dorsal to the basal plate.

Occipital region

The occipital region is markedly similar in both species of *Dendroaspis*. The occipital arches are continuous with the basal plate and the upper portion of each arch contacts the posterior border of the auditory capsule. The occipital arches extend upwards and unite mid-dorsally to form the tectum posterius. The foramen jugulare is closed off posteriorly and does not communicate with the fissura occipitocapsularis dorsally.

The single occipital condyle is considerably thickened. Two small lateral projections present on the condyle, articulate with the lateral facets present on the atlas vertebra. The notochord is completely embedded in the occipital condyle.

There are four hypoglossal foramina on each side in a 50-day-old embryo of *D. polylepis polylepis* but in *D. angusticeps*, only three hypoglossal foramina could be found.

In both species of *Dendroaspis*, the occipital vein passes out between the basal plate and the atlas vertebra to join the internal jugular vein.

Splanchnocranium

The fully formed splanchnocrania of *D. angusticeps* and *D. polylepis polylepis* are similar and do not show any deviation from the general ophidian pattern.

Mandibular arch. The quadrate and Meckel's cartilage appear very early in ontogeny and in a 15-day-old embryo of *D. polylepis polylepis*, the blastematous rudiments of these two structures are distinct and at no stage in ontogeny do the anterior tips of Meckel's cartilage contact one another. Unlike the condition in lizards, the crista parotica is absent and the quadrate has no connection with the auditory capsule. As in *Hemachatus* (Pringle 1954) the quadrate cartilage is hammer-shaped in both species of *Dendroaspis* (Figs. 2 and 3). This may be a common feature of the members belonging to the family Elapidae. The anterior tips of Meckel's cartilage curve medially and approach each other but the symphysis Meckelii is absent (Fig. 12). Behind the convex articular surface of each ramus, there is a long and somewhat pointed processus retroarticularis (Fig. 12).

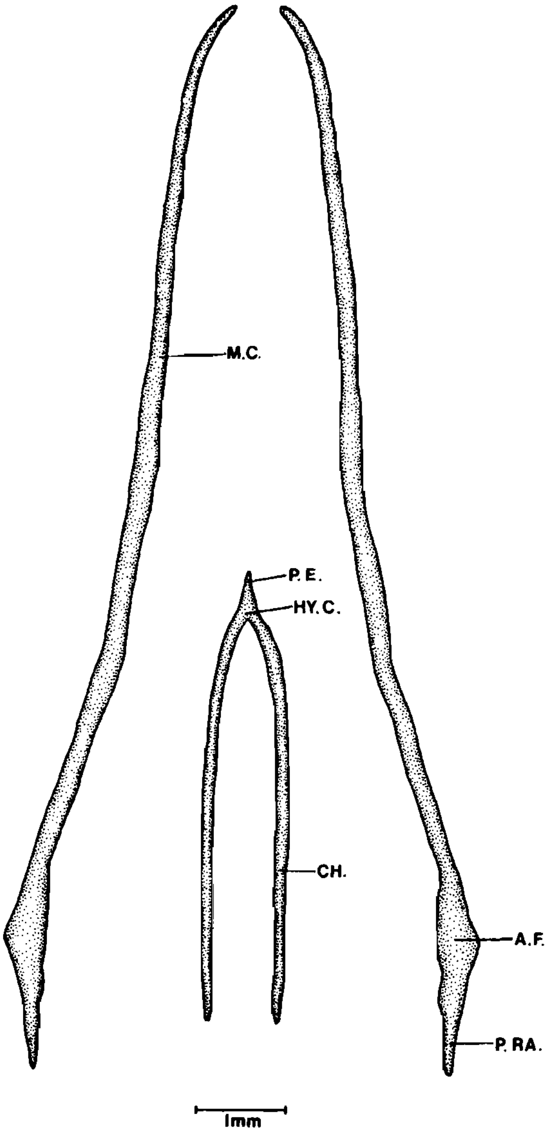

Fig. 12 Graphic reconstruction of the fully formed viscerocranium of *D. angusticeps* as seen in dorsal view. (See Table 1 Key to anatomical drawings.)

Hyoid arch. In both species of *Dendroaspis*, the hyoid arch skeleton is similar and is composed, in addition to the columella auris, of two very elongate ceratohyals, the hyoid corpus and the processus entoglossus (Fig. 12). The ceratohyals lie parallel to each other and have elongated considerably posteriorly.

Columella auris. The columella auris in *Dendroaspis* is typically ophidian. It is a simple structure consisting of a footplate and a distal elongate process or shaft (Figs. 2 and 3). The footplate lies in the fenestra ovalis but fails to fill it completely. The shaft extends slightly outwards from the side wall of the auditory capsule and then inclines postero-ventrally. The distal portion of the shaft extends beyond the posterior margin of the quadrate. There is a dense aggregation of mesenchyme cells at the distal end of the columella auris in a 50-day-old embryo of *D. polylepis polylepis* which later develops into a cartilaginous nodule and fuses with a small posterior projection of the quadrate. In the late embryo of *D. angusticeps* on the other hand, such a nodule could not be identified and the shaft of the columella is not fused but attached by means of ligaments to the quadrate.

A careful search for the connection between the ceratohyal and the columellar shaft was made in early embryos of *D. polylepis polylepis*. In a 15-day-old embryo, where the chondrocranium appears in a blastematous condition, the columella auris is quite distinct from the wall of the auditory capsule. The blastematous rudiments of the columella auris appear as a rather dense aggregation of mesenchyme but no ligamentous attachment could be traced from the ceratohyal to the columellar shaft. A dense mesenchymatous strip, however, could be seen extending upwards from the ceratohyal but disappearing shortly afterwards. If such an attachment between the distal end of the columella and the ceratohyal exists at all, then it must occur very early in the ontogeny. In a 25-day-old embryo of *D. polylepis polylepis*, the columella auris is clearly discernible (Fig. 13). The fenestra is beginning to form as a result of the resorption of cartilage cells. In this embryo also, no connection between the ceratohyal and columella auris could be found.

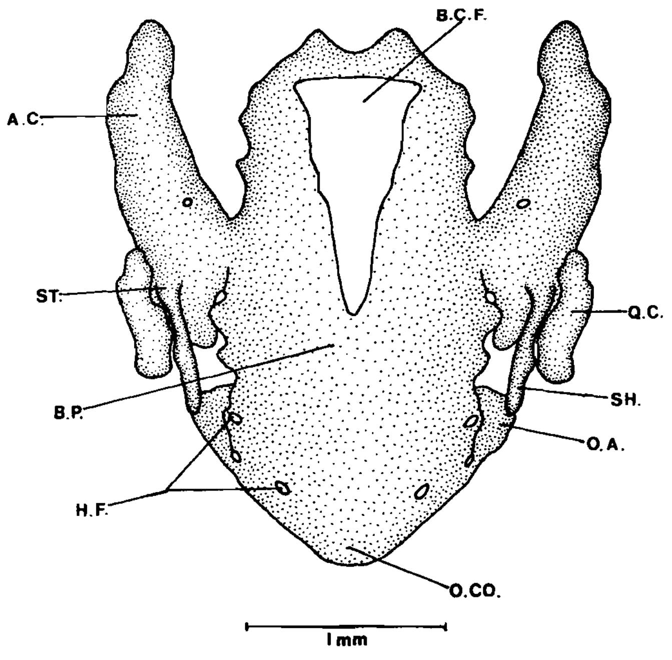

Fig. 13 Ventral view reconstruction of the basal plate, auditory and occipital regions of a 25-day-old embryo of *D. polylepis polylepis*. The trabeculae have not been reconstructed because they lie perpendicular to the basal plate. (See Table 1 Key to anatomical drawings.)

In both species of *Dendroaspis*, the hyomandibular branch of the facial nerve passes backwards over the shaft of the columella auris. It then gives off the chorda tympani which runs antero-ventrally below the shaft to the medial aspect of Meckel's cartilage. The head vein passes over the shaft of the columella auris.

Discussion

The chondrocrania of both species of *Dendroaspis* do not show any marked deviation from the general ophidian pattern. This investigation has revealed that both species are closely related and show a number of specialized features. The marked reduction in the size of the solum nasi, the absence of orbitosphenoid cartilages, posterior maxillary and basitrabecular processes in both species are specializations which suggest that the Elapidae is an advanced ophidian family since the abovementioned structures are present in lizards and some primitive snakes.

Although there are no significant differences between the chondrocrania of the two species of *Dendroaspis* certain features appear to be sufficiently distinctive to warrant separation at species level. Rudimentary paranasal cartilages are present in the nasal capsule of *D. polylepis polylepis* whereas no such structures could be identified in *D. angusticeps*. Also present in the nasal capsule of *D. polylepis polylepis* is a narrow strip of cartilage that connects the floor of the nasal capsule to the paries lateralis nasi. In contrast to this, the solum nasi of *D. angusticeps* is completely isolated from the rest of the nasal capsule.

An interesting difference in the orbitotemporal region is the presence of a pair of carotid foramina in *D. angusticeps* for the passage of the internal carotid arteries. In *D. polylepis polylepis*, on the other hand, carotid foramina are absent and the internal carotid arteries enter the cranium through the carotid incisures.

Other minor variations in the auditory and occipital regions also tend to set the species apart.

Ethmoid region

An important and advanced feature in the ethmoid region is the marked reduction in the size of the solum nasi. Brock (1929) correlates the exceptionally light framework with the extreme mobility of the jaws.

In both species of *Dendroaspis*, the lamina orbitonasalis is imperceptibly fused with the nasal septum. A similar fusion also occurs in the nasal capsule of *Vipera aspis* (Peyer 1912), *Leptodeira hotamboia* (Brock 1929), *Lamprophis, Dasypeltis* and *Hemachatus* (Pringle 1954) and *Cerastes vipera* (Kamal & Hammouda 1965a). Such a fusion, however, does not occur in *Tropidonotus* (Bäckström 1931), *Xenopeltis* (Bellairs 1949a), *Typhlops* (Smit 1949), *Vipera russelii* (Srinivasachar 1955) and *Eryx* (Kamal & Hammouda 1965b). In *Lacerta* (Gaupp 1900) the lamina orbitonasalis is separated from the nasal septum by a very narrow cleft. Gaupp (1900) regards the detached lamina orbitonasalis as the primary condition since it is of common occurrence in lizards. From an investigation of early embryos of *D. polylepis polylepis* it is evident that the fusion of the lamina orbitonasalis with the nasal septum is a secondary condition. Brock (1929, p.319) also states: 'It might be a secondary attachment, an adaptation correlated with the delicate nature of the skeletal framework in the nasal region'. This view is further strengthened by the fact that the lamina orbitonasalis is widely separated from the nasal septum in *Eryx* which belongs to the primitive family Boidae (Kamal & Hammouda 1965b). Kamal and Hammouda (1965b) believe that this lamina has no separate centre of chondrification but originates directly from the parietotectal cartilage. Hence there is both ontogenetic and comparative anatomical evidence to support the secondary nature of the attachment of the lamina orbitonasalis to the nasal septum.

In neither species of *Dendroaspis* is there a maxillary process on the lamina orbitonasalis. The processus maxillaris posterior is present in *Lacerta* (Gaupp 1900) and is absent in most snakes described so far, exceptions being *Typhlops* (Smit 1949) and *Eryx* (Kamal & Hammouda 1965b). The occurrence of the processus maxillaris posterior in snakes is a primitive feature since it is present in lizards.

Kamal and Hammouda (1965a) report the presence of a cartilaginous projection from the hind wall of the concha nasalis in *Cerastes vipera*, similar to the condition in both species of *Dendroaspis*. They consider this structure in *Cerastes* as representing the posterior process of the concha nasalis. Pringle (1954) has also illustrated and described a similar process in *Dasypeltis*, extending from the posterior end of the concha nasalis but could not homologize this structure with the posterior maxillary process because it was not attached to the lateral margin of the capsule. He regarded this cartilaginous process to be a primitive feature in *Dasypeltis* and suggested that it might be the paranasal cartilage. From the position and orientation of the paranasal cartilage in lizards (Gaupp 1900) it is doubtful whether Pringle's interpretation is correct. As in *D. polylepis polylepis*, the paranasal cartilage is present in *Cerastes vipera* (Kamal & Hammouda 1965a) and contributes to the formation of the concha nasalis. Since this cartilage is present in lizards, its occurrence in snakes indicates a primitive feature.

In both species of *Dendroaspis* there is a small cartilaginous process from the floor of each anterior cupola close to the nasal septum (Figs. 8 and 9). Pringle (1954) describes a similar process in *Lamprophis* as well as in *Hemachatus* and considers it to be the lamina transversalis anterior. He suggests that this lamina represents part of the connection between the floor of the anterior cupola and Jacobson's organ cartilage.

As in practically all snakes, paraseptal cartilages are absent in both species of *Dendroaspis*. The paraseptal cartilage is present in *Lacerta* (Gaupp 1900) and appears to be of common occurrence in lizards. Bellairs (1949a) reports the presence of a rudimentary paraseptal cartilage in *Xenopeltis*. De Beer (1937) considers the slender cartilaginous process that forms a reduced floor of the capsule in *Tropidonotus natrix* to be the lamina transversalis anterior. From the position and orientation of the paraseptal cartilages it is very likely that the so-called anterior paraseptal cartilage described by Bäckström (1931) in *Tropidonotus natrix* actually represents a part of the lamina transversalis anterior which has still retained its attachment with the floor of the anterior cupola. The absence of the paraseptal cartilages in snakes appears to be in line with the general process of reduction of the skeletal framework in the nasal region. This can be interpreted as an adaptation to give extreme mobility to the jaws.

Orbitotemporal region

In both species of *Dendroaspis*, the orbitotemporal region conforms to the platytrabic ophidian type with the trabeculae cranii widely separated from each other. There is no trace of an interorbital septum even in early stages. An interorbital septum is present in *Lacerta* (Gaupp 1900 & De Beer 1937) in contrast to the platytrabic type of skull present in snakes. De Beer (1937) correlates the platytrabic and tropitrabic types of skulls with the relative sizes of the eyeballs and of the brain in the region of the eyes. Gaupp (1906) mentions the presence of an interorbital septum in *Tropidonotus* which, however, does not chondrify. He considers the skull in *Tropidonotus* to be tropitrabic although the trabeculae do not fuse. Peyer (1912) also reports the presence of an interorbital septum in *Tropidonotus* but could not find it in the viper. The majority of investigators have been unable to confirm Peyer's observation.

Although orbitosphenoid cartilages could not be detected in *Dendroaspis*, Parker (1879) reported the presence of a pair of unfused orbitosphenoids in an embryo of *Tropidonotus*. These were situated above the trabeculae in the orbital region. Peyer (1912) in *Vipera aspis*, Brock (1929) in *Leptodeira hotamboia* and Bäckström (1931) in *Tropidonotus natrix* have denied the presence of orbitosphenoid cartilages. Parker's discovery, however, has been confirmed by Bellairs (1949b) who described orbitosphenoid cartilages in *Vipera berus* and *Python molurus*. These cartilages are also present in *Causus* (Pringle 1954 and Sülter 1962), *Vipera russelii* (Srinivasachar 1955), and in *Eryx* (Kamal & Hammouda 1965b). Pringle (1954) is of the opinion that these cartilages in *Causus* are of spasmodic occurrence. Kamal and Hammouda (1965b), however, do not agree, for in *Eryx* they discovered orbitosphenoid cartilages in embryos obtained from three different females. As to the homology of these cartilages, both Bellairs (1949b) and Pringle (1954) suggest that they represent rudiments of the orbital cartilages of lizards. Their occurrence in snakes could be interpreted as a primitive feature since they occur in *Python* and in *Eryx*, both belonging to primitive families, namely Pythonidae and Boidae respectively.

The basitrabecular process is of common occurrence in lizards (Gaupp 1900 and De Beer 1937) but is absent in practically all snakes investigated including *Dendroaspis*. Versluys (1912) stated that the basitrabecular process is present in the python and forms a movable joint with the pterygoid (Brock 1941). Kamal and Hammouda (1965b) recognized a basitrabecular process which was fused with the posterior part of the trabecular rod in an early embryo of *Eryx*. An unusual feature observed by these authors was the complete separation of these processes from the trabeculae cranii in late embryos. The occurrence of the basitrabecular process in snakes is a primitive feature since it is present in *Lacerta* (Gaupp 1900 and De Beer 1937) and in some primitive snakes, such as *Eryx*

(Kamal & Hammouda 1965b).

Basal plate and Occipital region

In the early stages in the ontogeny of *D. polylepis polylepis*, the paired nature of the parachordal plate is quite clearly discernible. This is in agreement with the view expressed by De Beer (1937) that the parachordals throughout the vertebrate series, from the cyclostomes to man, appear as paired structures and that their fusion to form a median basal plate is a secondary condition. Kamal and Hammouda (1965b), however, are not inclined to agree with this view as they did not observe the paired origin of the parachordal plate in very early embryos of *Eryx* and *Cerastes* where the plate was still in a blastematous condition.

From an investigation of the early embryos of *D. polylepis polylepis*, it is evident that the basicranial fenestra (Figs. 4 and 5) represents a region in the basal plate which remains unchondrified similar to the condition described by Gaupp (1900) in *Lacerta* and by De Beer (1937) in *Tropidonotus natrix*. Kamal and Hammouda (1965a), however, are of the view that the basicranial fenestra in *Cerastes* appears by a process of resorption of pre-existing cartilage. According to these authors, the basicranial fenestra also appears in a similar manner in early embryos of *Eryx*. This also contradicts the view held by Pringle (1954) who has found that there is no evidence of any cartilaginous resorption in the embryos of those South African snakes studied by him. Kamal and Hammouda (1965a) are fully convinced that both the basicranial fenestra and fenestra X (Figs. 4 and 5) are formed as a result of the resorption of pre-existing cartilage.

In *D. angusticeps*, there is in addition, a large unchondrified area in the basal plate just posterior to fenestra X (Fig. 3). A similar gap in the basal plate was also observed by Brock (1929) in *Leptodeira*. According to her, this gap in *Leptodeira* was situated in the lateral margin of the basal plate, ventral to the trigeminal incisure and posterior to the crista sellaris. Gaupp (1902) discovered a similar gap in the lateral margin of the basal plate in *Tropidonotus*. Brock (1929) was unable to assign any significance to this opening but added that it could very well be a part of the general process of reduction of the cartilaginous wall of the snake skull.

In *Dendroaspis*, a separate tectum synoticum could not be distinguished from the tectum posterius. The strip of cartilage that connects the auditory capsules and the occipital arches has been identified as the tectum posterius. In *Lacerta* (Gaupp 1900 and De Beer 1937) the occipital arches are dorsally interconnected by the tectum posterius which is anteriorly fused to the tectum synoticum. These two structures, however, remain distinct from each other. In *Tropidonotus*, the occipital arches fail to unite dorsally with the result that there is no tectum posterius and the auditory capsules are interconnected by the tectum synoticum (De Beer 1937). Brock (1929) in *Leptodeira* and Pringle (1954) in *Lamprophis, Dasypeltis, Causus* and *Hemachatus* recognize only a tectum posterius. Kamal and Hammouda (1965b) do not distinguish between a tectum posterius and a tectum synoticum. They regard the single broad structure in *Eryx* and *Cerastes*, that dorsally connects the auditory capsules and the occipital arches, as the tectum synoticum.

Splanchnocranium

As in *Causus* and *Hemachatus* (Pringle 1954) the basihyal is absent in both species of *Dendroaspis*. The presence of the basihyal has, however, been reported by Peyer (1912) in *Vipera* and De Beer (1937) in *Tropidonotus*. The fully formed hyoid arch skeleton in *Eryx* (Kamal & Hammouda 1965b) differs from the condition described in most snakes. According to these authors, the ceratohyals are relatively short and are not fused anteriorly with the result that the hyoid corpus and the processus entoglossus are missing.

The origin and homology of the columella auris and its components is a subject of much controversy in the literature on snakes. In the 50-day-old embryo of *D. polylepis polylepis*, a small nodule arises from the distal end of the shaft and fuses with a posterior projection of the quadrate. It is for this reason that Pringle (1954) considers the end of the columella to be usually bifid in snakes. A cartilaginous nodule is also present in *Leptodeira* (Brock 1929), in *Cerastes, Eryx* and *Psammophis* (Kamal & Hammouda 1965a, 1965b and 1965c) and *Hemachatus* (Pringle 1954). Parker (1879) regards this nodule as the stylohyale while Möller (1905) considers it to be part of the extracolumella. Peyer (1912) and Bäckström (1931) homologize it with the processus internus of the lacertilia. In a 50-day-old embryo of *D. polylepis polylepis*, this procartilaginous nodule is histologically distinct from the quadrate which is already well chondrified. This suggests that the nodule originates from the columella auris as reported by Möller (1905) and Brock (1929) and secondarily fuses with a process of the quadrate.

The course of the chorda tympani in relation to the columella auris and its components is exceedingly uniform and is an important factor in determining the homologies of these structures. The chorda tympani, in both species of *Dendroaspis* as in other snakes, in passing under the shaft, exhibits an interesting variation from the general condition present in lizards. Brock (1929) states that since the chorda tympani in *Leptodeira* passes under the distally bent end of the columella auris, it cannot be an extracolumella. De Beer (1937) also denies the presence of an extracolumella in *Tropidonotus natrix*. The degeneration of the extracolumella in snakes presumably permits the chorda tympani to slip into a more ventral position.

It is generally accepted that the proximal part of the columella ossifies whereas the distal portion or extracolumella remains cartilaginous. There is some evidence of perichondral ossification of the distal shaft in a late embryo of *D. angusticeps* and this weighs against the recognition of an extracolumella in snakes. Smit (1949) finds that the terminal portion of the columella remains cartilaginous in *Typhlops* and considers it to be homologous with at least a part of the extracolumella of lizards.

Since the shaft of the columella distally lies in the loop of the chorda tympani and hyomandibular nerves and lateral to the head vein, it may be homologized with either the processus dorsalis or the processus internus. Brock (1929), De Beer (1937) and Kamal and Hammouda (1965c) homologize it with the former and consider the cartilaginous nodule to represent the intercalare of other reptilian forms. Brock (1929) suggests that with the backward rotation of the quadrate, the intercalare loses its connection with the otic capsule and becomes attached to the quadrate. The minute nodule from the distal shaft of the columella in the 50-day-old embryo of *D. polylepis polylepis* probably represents the intercalare. This structure is, however, absent in the late embryo of *D. angusticeps* with the result that the shaft of the columella is not fused to the quadrate but is attached to it by means of ligaments. Möller (1905) and Okajima (1915) claim a capsular origin for the columella auris. De Beer (1937), however, found a very faint ligament connecting the distal end of the columella to the rudiment of the ceratohyal in a 5,3 mm head-length embryo of *Tropidonotus natrix*. No ligamentous attachment, however, could be traced from the ceratohyal to the columellar shaft in early embryos of *D. polylepis polylepis*.

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Table 1 Key to anatomical drawings

A.C.	auditory capsule
A.F.	articular facet
A.S.C.	anterior semicircular canal
B.C.F.	basicranial fenestra
B.P.	basal plate
BV.C.	basivestibular commissure
C.AN.	cupola anterior
CAV. CN.	cavum conchale
C.F.	carotid foramen
CH.	ceratohyal
C. NAS.	concha nasalis
C. PROM.	cochlear prominence
CR. IN.	carotid incisure
C. R.	cartilaginous ridge
C. S.	crista sellaris
EC. C.	ectochoanal cartilage
EC. P.	ectochoanal plate
F. EN.	foramen endolymphaticum
F. EP.	foramen epiphaniale
F.F.	facial foramen
F. G. I.	foramen glossopharyngeum internum
F. HYP.	foramen hypophyseos
F. MET.	fissura metotica
F. N.	fenestra narina
F.O.A.	foramen olfactorium advehens
F.O.C.	fissura occipitocapsularis
F. OV.	fenestra ovalis
F.X.	fenestra X
H.F.	hypoglossal foramen
HY. C.	hyoid corpus
HYP. C.	hypochoanal cartilage
IN. PR.	incisura prootica
J.O.	Jacobson's organ
J.O.C.	Jacobson's organ cartilage
L.O.N.	lamina orbitonasalis
L.P.Q.C.	lateral projection of quadrate cartilage
L.S.C.	lateral semicircular canal
L.T.A.	lamina transversalis anterior
MAX.	maxilla
M.C.	Meckel's cartilage
N.	notochord
N.B.	nasal bone
N.S.	nasal septum
O.A.	occipital arch
O.C.	olfactory chamber
O.CO.	occipital condyle
OL.NN.	olfactory nerves
P.A.I.	processus alaris inferior
PAR.N.	paries lateralis nasi
P.A.S.	processus alaris superior
P.E.	processus entoglossus
PF. CM.	prefacial commissure
P. NAS.	paranasal cartilage
P.P.C. NAS.	posterior process of concha nasalis
P. RA.	processus retroarticularis of Meckel's cartilage
PT.C.	parietotectal cartilage
Q.C.	quadrate cartilage
R.L.N.	ramus lateralis nasi
S. END.	saccus endolymphaticus
SH.	shaft of columella auris
S.M.	septomaxilla
ST.	stapes
S.TEMP.	supratemporal bone
T.	trabeculae
T.C.	trabecula communis
T.P.	tectum posterius
UN.	unchondrified area
V.N.NN.	vomeronasal nerves
VO.	vomer

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