

## The Evolution of the Crocodylia: A Conflict Between Morphological and Biochemical Data<sup>1</sup>

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**SYNOPSIS.** Recent investigations into the evolution of the living Crocodylia, belonging to the suborder Eusuchia, have revealed that the genus *Gavialis* may be its most primitive living member. New morphological studies have shown that the braincase structure, neural pocket, air sinus systems, jaw adductor mechanisms, pelvic and hindlimb morphology and epaxial musculature of the caudal region of *Gavialis gangeticus* do not correspond to the rest of the living Eusuchia. Contrary to the morphological findings, recent biochemical studies suggest a sister group relationship between *Gavialis gangeticus* and *Tomistoma schlegelii*, another longirostrine eusuchian. Judged by its morphology, *Tomistoma* is merely another member of the genus *Crocodylus* within the Eusuchia. This conflict in data either means that not enough of the genome of both *Gavialis* and *Tomistoma* is known, the shared genome represents the primitive states for these genes or that similar genotypes can give rise to rather different morphologies. As *Gavialis* resembles in some ways a Mesozoic level of organization it is considered to be a surviving eusuchian relict.

### INTRODUCTION

The Crocodylia are the last surviving reptiles of the once numerous subclass, the Archosauria. As such they represent the only surviving relatives of extinct dinosaurs, thecodonts and pterosaurs and the extant birds. For many people, the Crocodylia are familiar amphibious reptiles that occupy most of the tropical and subtropical climates throughout the world. However, the earliest known crocodylians were not aquatic but probably terrestrial in habit (Colbert and Mook, 1951; Walker, 1970; Whetstone and Whybrow, 1983; Hecht and Tarsitano, 1983). These early forms are represented by the Protosuchia and fossils are known from the Late Triassic of South America, South Africa, North America and the Cretaceous of Mongolia (Steel, 1973). The latter three areas may actually be Lower Jurassic in age (Clark, personal communication). An offshoot of the protosuchian lineage, the Notosuchia, is found

in the Upper Cretaceous of Argentina (Gasparini, 1971; Hecht and Tarsitano, 1983). In the Bauplan of the Protosuchia their terrestrial habit is suggested by their relatively long limbs, large preacetabular iliac crest, construction of the dermal armor and most importantly by a locomotory system that uses the dermal osteoderms and epaxial musculature to flex and extend the vertebral column (Frey, 1984, 1988).

At the present time there is little information as to the origin of the modern day crocodylians. Aside from the Protosuchia, the next groups of crocodylians noted in the fossil record are already highly aquatic, such as the marine Jurassic Teleosauridae (Westphal, 1962) and the (probably freshwater or estuarine) amphibious types, the goniopholid, and their kin (Buffetaut, 1982a).

At the present time the Recent and fossil Crocodylia are still represented by a grade classification (Kälin, 1955; Romer, 1956; Steel, 1973) although attempts are being made to determine lineages within this taxon (Ginsburg, 1970; Buffetaut, 1982a, b; Gauthier, 1984; Clark, 1986; Benton and Clark, 1988). Traditionally the Crocodylia

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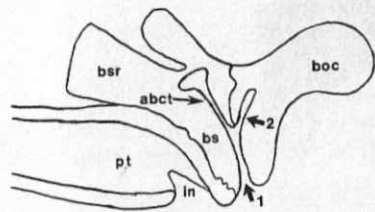


FIG. 2. A midsagittal section through the head of a juvenile caiman showing the verticalization of the braincase floor and the conversion of a diffuse sinus to basicranial tube system. abct = anterior basicranial tube, boc = basioccipital, bs = basisphenoid, bsr = basisphenoid rostrum, in = internal nares, pt = pterygoid, arrow 1 indicates the entrance to the basicranial tube system, arrow 2 indicates the posterior basicranial tube.

braincase (Owen, 1850; Wettstein, 1937; Bellairs and Kamal, 1979). Thus, this dorsally placed sinus also connects together both tympanic cavities.

After the first year of life the posthatchling skull undergoes a verticalization process. The basisphenoid and basioccipital grow downward (Romer, 1956) and the diffuse sinus (Fig. 2) becomes transformed into a tube system (Tarsitano, 1984, 1985, 1986, 1987). The verticalization of the basisphenoid requires the posterior end of the pterygoid to also verticalize. It is thought that this process changes the angle of force application of the *M. pterygoideus* and it allows for a larger volume of this muscle (Tarsitano, 1984, 1985, 1986). The double opening into the basicranium (described above) is modified by verticalization into a single tube which opens into the pharynx (Fig. 3). Dorsally the tube bifurcates into an anterior and posterior basicranial tube (Owen, 1850; Wettstein, 1937; Colbert, 1946) situated within the basisphenoid and basioccipital respectively (Fig. 3). Each of these tubes divides into a left and a right fork that proceed to the tympanic cavity. The posterior tube joins with the true eustachian tubes in a sinus, the rhomboidal sinus (Owen, 1850; Colbert, 1946). From this point there is a double opening into the tympanic cavity from the rhomboidal sinus, divided by a postotic strut (Tarsi-

tano, 1985). The tympanic cavity is in turn connected to the pneumatic quadrate (Huxley, 1869). The pneumaticity of the quadrate ends as a siphonium which invades the articular bone (Huxley, 1869; Parker, 1883). The tympanic cavity in turn is connected to the intertympanic sinus dorsally via the upper tympanic recess (Bellairs and Kamal, 1979) and via paraoccipital canals in the posthatchling (Tarsitano, 1985).

This complex pattern of verticalization and pneumatic tube formation is principally similar within the genera *Crocodylus*, *Osteolaemus*, *Alligator*, *Caiman*, *Melanosuchus*, *Paleosuchus* and *Tomistoma*. However, among living crocodylians there are different extremes in the degree of basicranium and palate verticalization (compare Figs. 3-5). For example, *Osteolaemus* has the relatively highest braincase verticalization and thus it appears that crocodylian skulls can be identified on the basis of verticalization morphology. Although *Gavialis* has a similar basicranial tube formation, the verticalization does not correspond to that seen in the adults of other genera. In all of the above genera except *Gavialis*, the basisphenoid and to a lesser degree the basioccipital are highly antero-posteriorly narrowed (Romer, 1956; Iordanski, 1973), the result being a fairly short and vertical braincase floor (Fig. 6). The abbreviated verticalization pattern in gharials results in a low braincase floor that is also elongate (Fig. 5). The degree of braincase verticalization in gharials resembles the verticalization of the *Alligator* braincase when the latter is about 13 cm in length. Based on preliminary measurements, gharials have a braincase floor (measured from the foramen magnum to the anterior edge of the laterosphenoid) that is at least 25% longer than any comparatively sized adult *Tomistoma* and *Crocodylus*, based on American Museum of Natural History material (Fig. 7). In contrast, the dorsal (where the brain actually rests) length of the braincase floor in comparatively sized *Tomistoma* and *Crocodylus* skulls is nearly identical. The braincase construction of *Gavialis* reveals an elongate basisphenoid and basioccipital that appears to have led to a more posterior orientation of the internal nares. In other

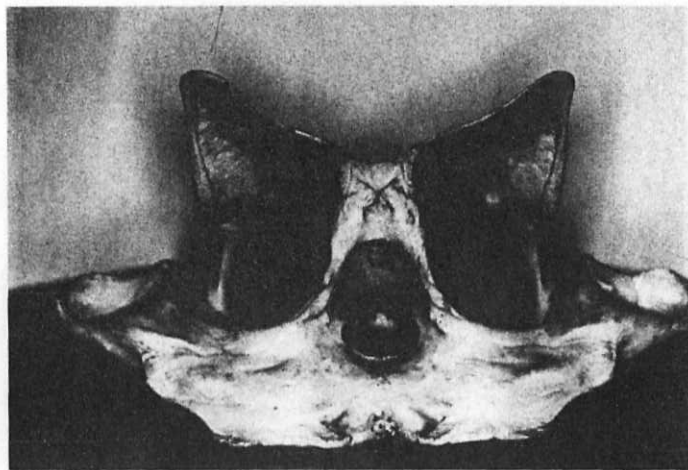


FIG. 3. The posterior view of a skull of *Crocodylus cataphractus* showing the verticalization of the braincase floor.

living crocodylians the internal nares are vertical (Kälin, 1955; Hecht and Malone, 1972). The internal nares of teleosaurs appear vertical, but are placed within the palatines (Westphal, 1962). Early gharials from Colombia (Langston, 1965) already show the elongated and abbreviated, verticalized braincase.

A similar anterior-posterior narrowing of the braincase floor during verticalization is also seen in carnososaurs (Tarsitano, 1984) and their ancestor (or sister group which does not denote ancestral relationship), the poposaurid thecodonts (Chatterjee, 1985). In theropods and thecodonts verticalization proceeded without the formation of basicranial sinus tubes so characteristic of living crocodylians. Verticalization is different only in gharials among all living crocodylians. Above the brain cavity of *Gavialis gangeticus* lies a curious structure (Tarsitano, 1986, 1987). There is a large, midsagittal, anterior pocket (Fig. 8) housing supposed neural tissue (histological analysis now pending). There is also a small more posterior pocket that may house tissue or just air. Both pockets lie anterior

to the intertympanic sinus (Tarsitano, 1986, 1987). The anterior pocket communicates with the brain cavity midventrally and retains a meningeal lining and a dural connection to the brain cavity (Fig. 8). It may also communicate via a nerve pathway to the brain itself. The testing of this latter hypothesis is now underway. Within the anterior wall of this anterior pocket is another opening which appears at this time to communicate with possible hemopoietic tissue within the parietal (Fig. 8). The larger anterior pocket lies within the parietal. In the genera *Alligator*, *Caiman* and *Paleosuchus* this pocket (*Melanosuchus* has not yet been examined) has been transformed into an air sinus (Fig. 9), connecting posterolaterally to the intertympanic sinus (Tarsitano, 1985, 1986, 1987). In the genus *Crocodylus* this same alligatorine condition can be found, such as in *C. niloticus*. Some crocodylines have lost the pocket as in *Crocodylus johnstoni*, a longirostrine form. In specimens of *Tomistoma* studied thus far the pockets are not present and are presumed here to have been lost. Thus there is no resemblance whatever to

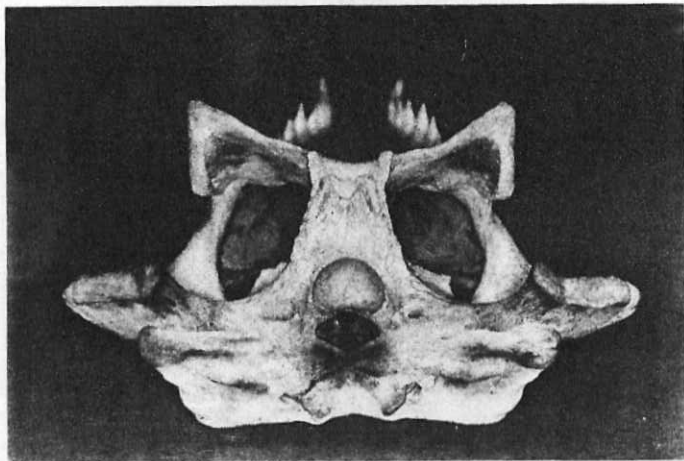


FIG. 4. The posterior view of a skull of *Tomistoma schlegelii*, showing the verticalization of the braincase floor. A comparison with *C. cataphractus* shows how similar *Tomistoma* is to crocodylines whereas a comparison with gavialis shows clear differences in the braincase floor's construction.

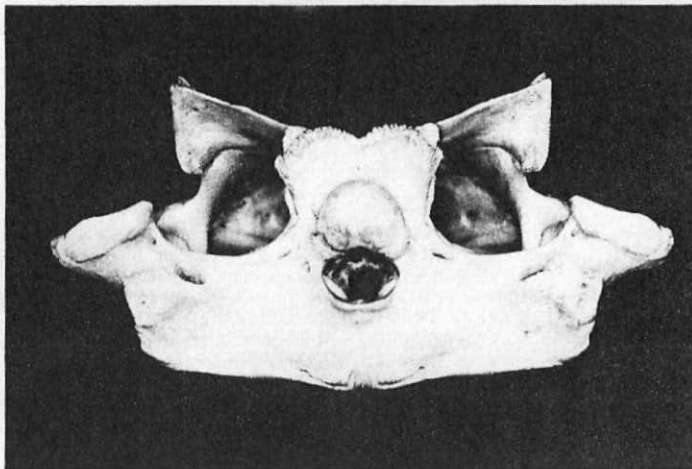


FIG. 5. The posterior view of a skull of *Gavialis gangeticus* illustrating the low verticalization and large basituberal processes as compared to *Tomistoma*.

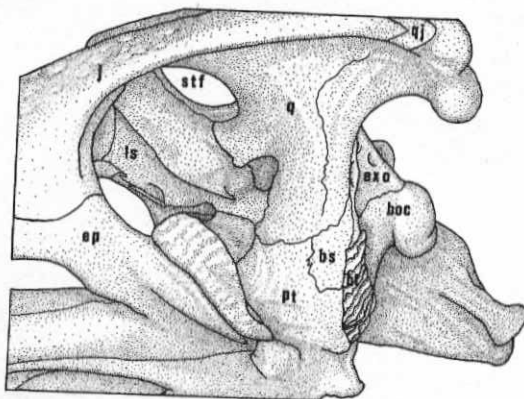


FIG. 6. A lateral view of the braincase of *Tomistoma schlegelii* illustrating the narrow braincase floor construction as compared to gavialis. boc = basioccipital, bs = basisphenoid, ep = epipterygoid, exo = exoccipital, j = jugal, ls = laterosphenoid, pt = pteryoid, q = quadrate, qj = quadratojugal, stf = supratemporal fenestra.

the *Gavialis* condition. In this regard *Tomistoma* again compares identically to one of the crocodyline conditions.

Another character noted by Källin (1955) and Hecht and Malone (1972) is the large

supratemporal fenestra of gharials. These large fenestrae represent a large pseudotemporalis muscle. The sides of the temporal fenestrae in gharials are fairly vertical and a similar though larger temporal

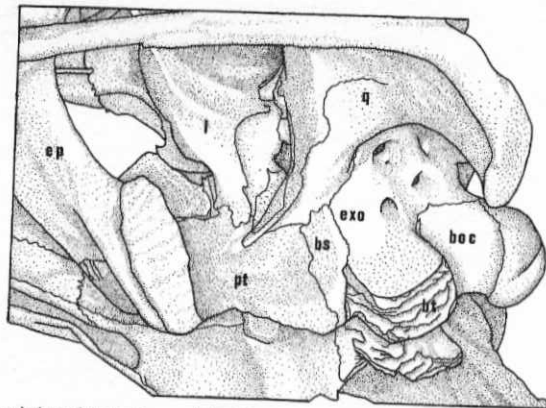


FIG. 7. A lateral view of the braincase of *Gavialis gangeticus* illustrating the elongation of the braincase as compared to *Tomistoma schlegelii*. boc = basioccipital, bs = basisphenoid, bt = basituberal processes, ep = epipterygoid, exo = exoccipital, l = laterosphenoid, q = quadrate.

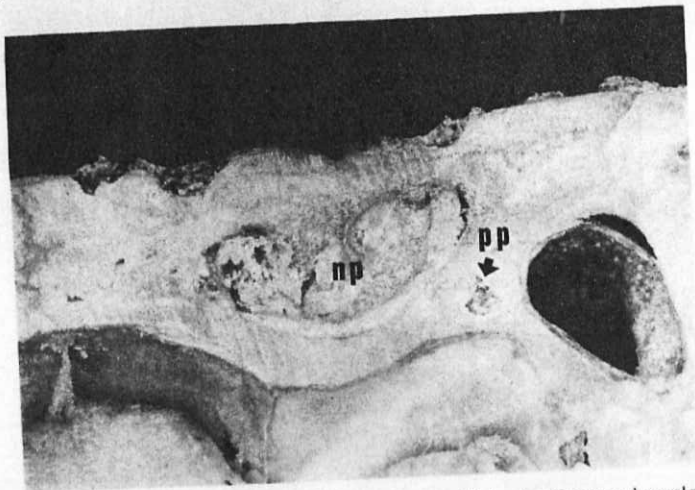


FIG. 8. A slightly parasagittal section through the skull roof of *Gaviialis* showing the supposed neural pocket. its = intertympanic sinus, np = neural pocket, pp = posterior pocket.

fenestral condition is paralleled in teleosaurs (Westphal, 1962). In both gharials and teleosaurs the large temporal fenestrae cause the squamosal to nearly overlap the quadrate (Mook, 1921a; Kälin, 1955; Westphal, 1962; Hecht and Malone, 1972). The overlapping of the squamosal is primitive for crocodylians, but in the case of most teleosaurs and *Gaviialis* it requires the frontal bone to be widened. The other living crocodylians all reduce the skull table width. In the case of teleosaurs the enlargement of the supratemporal fenestrae coincides with a flattening of the skull, an adaptation to a largely aquatic existence (Westphal, 1962). *Gaviialis* also has a low skull but its significance and just how flattened it is compared to other living crocodylians is still under investigation. Comparison of temporal fenestrae and the width of the skull table in tomistomines and other crocodylines and alligatorines shows a different method of housing the *M. pseudo-temporalis*. The skull table in these forms is noticeably narrower as noted above and the *M. pseudo-temporalis* extends posteriorly within the temporal fenestra along

a pulley or trochlear surface (Lakjer, 1926; Schumacher, 1973). In this way the *M. pseudo-temporalis* is elongated posteriorly in most eusuchian genera (except adult *C. porosus*) including *Tomistoma* whereas in gharials the *M. pseudo-temporalis* muscle is thickened by expanding the volume of the supratemporal fenestrae. Thus, *Gaviialis* uses a different strategy than other eusuchians. The same is true for the *M. pterygoideus*. Even though *Tomistoma* has an extreme longirostrine condition, the insertion points of this muscle, the retroarticular processes (Poglayen-Neuwall, 1953; Iordanski, 1964), remain small and are comparable in size to that of crocodylines and alligatorines. This is not the case for gharials and teleosaurs. In both taxa the retroarticular processes are elongated (more so in *Gaviialis*). This shifting of the origin of the *M. pterygoideus* posteriorly apparently required the posterior elongation of the retroarticular processes in gharials. This would also serve the functioning of the *M. depressor mandibulae* (Clark, personal communication).

In front of the eye in the gharial lies a

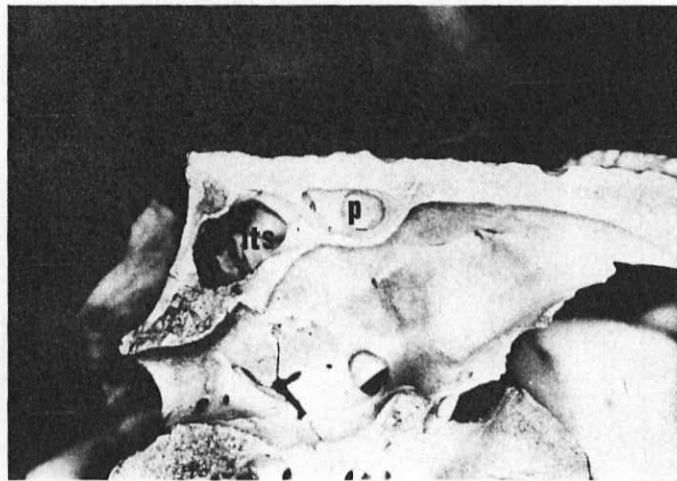


FIG. 9. A midsagittal section through the braincase of *Alligator mississippiensis* illustrating the probability that the neural pocket has been transformed to an air sinus connected to the intertympanic sinus. its = intertympanic sinus, p = air sinus derived from the neural pocket.

sack-like structure which is connected to a duct that extends the length of the snout. The sack does not appear at this time to be glandular in nature. We are now investigating the occurrence of this structure in other crocodylians. In casual dissections of the snout we have never seen such a structure. If gharials are demonstrated to be the sole possessors of this structure among living crocodylians then this structure is further testament to the uniqueness of the Indian gharial.

From the above description of the skull it is clear that the method of attainment of the longirostrine condition and braincase construction is not the same in *Gaviialis* and *Tomistoma*. *Tomistoma* is constructed as a typical *Crocodylus*. The pterygoid bones extensively overlap the basisphenoid in *Tomistoma* in a pattern characteristic of the *Eusuchia* (Mook, 1921a, b; Wettstein, 1937; Romer, 1956; Crompton and Smith, 1980). In gharials, the pterygoids do not reach as far posteriorly and therefore the basisphenoid is exposed in lateral view and the bas-

ioccipital is antero-posteriorly elongate. Braincase elongation is primitive for crocodylians and it is seen in posthatchling eusuchians before verticalization occurs. In *Gaviialis* braincase construction and placement of the jaw adductor muscles differ from those of all other living crocodylians. What is interesting is that the only character states similar to *Gaviialis* are to be found among teleosaurs such as *Steneosaurus*. While I was in Tübingen last summer at The Institute and Museum for Geology and Paleontology a braincase of *Steneosaurus* was expertly sectioned by Herr. Riess for us under the direction of Prof. Frank Westphal. Although there was no pocket above the braincase there was seen a low profile to braincase floor, the verticalization height being comparable to *Gaviialis* as was to a lesser degree the braincase elongation (compare Figs. 10 and 11). However, Westphal (1962) in his classic study on teleosaurs listed a number of characters that would bar these marine forms from an ancestor-descendant relationship with



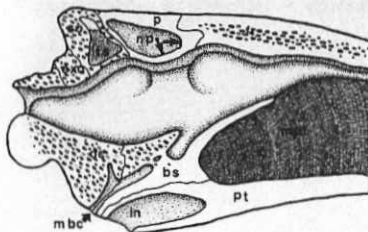


FIG. 10. A diagrammatic representation of a nearly midsagittal section through the cranium of *Gavialis*, illustrating the elongation of the braincase, low verticalization and neural pocket (posterior pocket not seen in this diagram). bs = basisphenoid, exo = exoccipital, in = internal nares, its = intertympanic sinus, mbc = median opening to the basicranial tube system, mpt = M. pterygoideus, np = neural pocket, oc = basioccipital, p = parietal, pt = pterygoid, so = supraoccipital, arrow 1 = entrance to brain cavity, arrow 2 = entrance to supposed hemopoietic tissue in the parietal.

gharials. We agree. However, *Gavialis* shows the same jaw adductor strategy (large pseudo-temporalis muscle and more posterior elongation of the retroarticular processes) and the gharial braincase floor elongation resembles that seen in teleosaurs. The resemblance of the braincase floor is blurred somewhat by the more extensive secondary palate development in gharials. Furthermore, the basituberal development is similar to that in teleosaurs (Kälin, 1955), but may be considered a parallelism (Langston, 1973). The question arises then as to why *Tomistoma* lacks pendulous basituberousities if it is the sister taxon to gharials. The few similarities between gharials, tomistomines and teleosaurs can be attributed to parallelism due to the attainment of a longirostrine condition (Westphal, 1962). Because the braincase of *Tomistoma* is similar to the living members of the genus *Crocodylus*, it appears that *Tomistoma* must have evolved after the modern verticalization pattern was established.

#### POSTCRANIAL CHARACTERS

Concordant with the cranial characters which separate *Gavialis* from the other living crocodylians are those of the postcra-

nia musculature and skeleton. Frey (1982, 1984, 1988) investigated the epaxial and hypaxial musculature of living crocodylians except *Melanosuchus*, a caiman. He has shown that only *Gavialis* among the living Crocodylia lacks a *M. caudofemoralis brevis* and that the epaxial musculature is also different in the caudal region. In all crocodylians except *Gavialis* the *M. longissimus* expands as it enters the tail which in turn reduces the size of the *M. tendino-articularis* muscle. Likewise the *M. tendino-articularis* is not reduced until the tail tapers. In the hindlimb the *M. adductor femoris* muscle in the gharial alone is modified (Tarsitano, 1981, 1986). Instead of two heads that insert down the length of the femur as in other living crocodylians (Romer, 1923), the *M. adductor femoris* parts 1 and 2 insert into a pit just below the fourth trochanter (Tarsitano, 1981). Finally, the calcaneum is reduced (Hecht, personal communication) compared to that of all living crocodylians. This latter character is in need of morphometric examination.

Gharials do share synapomorphic characters with eusuchians. For example, gharials have a subdermal postorbital bar (Mook, 1921*b*), an overhanging squamosal contacting the quadrate (Crompton and Smith, 1980), tetra-serial osteoderms (Frey, 1984), paravertebral shield where the epaxial musculature originates (Frey, 1988), internal nares within the pterygoids, an incisura otica (Hecht and Tarsitano, 1983) and procoelus vertebrae (Mook, 1921*a, b*; Romer, 1956; Steel, 1973). The formation of a subdermal postorbital bar requires minor changes from the teleosaur condition. An out-turning of the jugal is required which forces the postorbital bar internally to remain as a vertical strut. To do otherwise would invite a collapse of the skull table or jugal (Langston, 1973). It is interesting to note that in the teleosaur *Anglosuchus geoffroyi* the skull table is anteriorly squared off using the postorbit as in eusuchians. The postorbital bar in this form is at least dorsally subdermal (Mook, 1942). Gharials have a eusuchian squamosal-quadrate contact which posteriorly closes off the tympanic cavity. This only requires

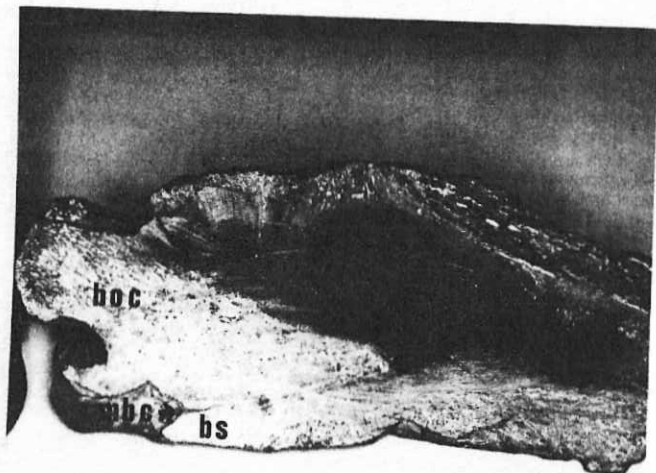


FIG. 11. A nearly midsagittal section through the skull of the teleosaur, *Steneosaurus bollensis* illustrating the low verticalization and an elongated braincase. bc = brain cavity, boc = basioccipital, bs = basisphenoid, mbc = median opening to the basicranial tube system.

a down growth of the squamosal. The primitive condition of the osteoderm covering in archosaurs and crocodylians is to have a biserial paravertebral shield: one row on each side of the vertebral column. In early crocodylians (such as the Protosuchia) the rows are broad and angled which restricts the lateral undulation of the vertebral column (Frey, 1988). In all eusuchians there is a tetra-serial paravertebral shield which most probably is an autapomorphy of the group (Frey, 1988). Finally, procoely is one of the characteristics of the Eusuchia (in contrast to other crocodylians). Eusuchian hatchlings appear at the present time to retain a more primitive amphiplatyan central condition perhaps due to lack of ossification. If their vertebrae were found in the fossil record we would assume them to be of mesosuchian grade and the same would be true of their braincase morphology. How a great difference in classification one year of growth can make! For this reason procoely is not a strong character. It has evolved many times within the Reptilia (Romer, 1956)

and might be more of a functional character rather than a systematically useful one.

#### DISCUSSION

From the above data it seems that *Gavialis gangeticus*, though it is a eusuchian, is clearly separable from the rest of the living crocodylians including *Tomistoma*. Gharials repeatedly offer different functional adaptations in the braincase, jaw adductor systems, pelvic and hindlimb morphology and epaxial musculature. In the braincase structure (which is masked in gharials by the secondary palate development) gharials parallel teleosaurs of the Jurassic (Fig. 8). It is clear from Westphal's (1962) studies that gharials are not direct descendants of the teleosaur lineage. However, it does appear that *Gavialis* may have departed from the eusuchian lineage before the modern eusuchian verticalization pattern was developed. This would also account for the differences seen in the other functional systems. However, recent biochemical investigations (Densmore, 1983; Dens-

more and Dessauer, 1984) have shown that, based on blood protein antigen-antibody reactions, *Gavialis gangeticus* and *Tomistoma schlegelii* share the greatest number of similarities in biochemical terms. These results are fascinating as the morphology is completely at odds with such biochemical data. This conflict in data may in time lead to the heart of the matter as to how genes are utilized in the manufacturing of organisms. Completion of further investigations into the mitochondrial proteins (Densmore and Owen, 1989 and personal communication) may bring the biochemical data in line with the morphological conclusions. It may be that the portion of the genome studied thus far represents retained primitive states in both taxa and thus is not a true indication of relationship. If the biochemical data still indicate a sister group relationship between these two taxa then the biochemical data will have great significance as it would suggest that similar operational DNA (excluding introns) would be able to manufacture very different organisms. This might be accomplished perhaps by similar means as the immune system's ability to manufacture myriads of antibodies from a relatively small gene pool or differential gene expression. Thus crocodilian evolution may reflect the much larger problem namely the control of structural genes and their mechanisms of expression.

#### CONCLUSION

Although the data from the morphological investigations concerning the relationships of the living Crocodilia are incomplete, studies on different functional systems have shown that the Indian gharial, *Gavialis gangeticus*, morphologically stands apart. Such diverse aspect as the braincase, cranial sinus systems, jaw adductor systems, pelvic and hindlimb morphology and epaxial musculature demonstrate that *Gavialis* is unique among the living Crocodilia. Even a typological phylogenetic analysis indicates problems with assigning gavials to the Crocodylinae. Osteological synapomorphies linking gharials to eusuchians minimally include 1) "procoely," 2) tetra-serial osteoderms,

3) subdermal postorbital bar, 4) posterior closure of the tympanic cavity, 5) incisura otica and 6) internal nares enclosed within the pterygoids (characters used by Mook, 1921a, b; Wettstein, 1937; Wermuth, 1953; Källin, 1955; Romer, 1956; Steel, 1973; Crompton and Smith, 1980; etc.). Characters where gharials parallel teleosaurs include: 1) elongated braincase, 2) enlarged and pendulous basitubular processes, 3) low verticalization of the basicranium, 4) elongate retroarticular processes, 5) pterygoid not verticalized, 6) enlarged supratemporal fenestrae and 7) broad frontal bones. Other possible characters shared with the teleosaur lineage may include: A) broad skull table overlapping the quadrate (a sympleiomorphy at the eusuchian level), B) reduction of the limbs and tarsus and C) posteriorly directed internal nares. It seems clear at this time that the characters shared with teleosaurs are either sympleiomorphies or have been derived in parallel due to the piscivorous diet of both groups.

For many of the above characters we are not certain of the time of their development due to the gaps in the fossil record at this time. However, armed now with more characters we can ascertain relationships between eusuchians and metamesosuchians. In terms of crocodilian evolution the morphological data indicate that the suborder Eusuchia is monophyletic, but that the genus *Gavialis* apparently is a primitive member of this assemblage. It appears that since *Gavialis* has a different verticalization and basicranial morphology, a different means of attaining a longirostrine condition and a different epaxial musculature, gharials may have arisen earlier than the modern Eusuchia. This conclusion is only superficially in conflict with the biochemical data which was interpreted as indicating a sister group relationship between *Gavialis* and *Tomistoma* among the living Crocodilia. According to new studies on the morphology of *Tomistoma* this taxon is nothing more than a *Crocodylus*, having attained the longirostrine condition earlier in their evolution than other living crocodylines. The conflict between morphological and biochemical data may indicate an even deeper problem

than the systematics of the Crocodilia. It appears likely that *Gavialis* is a surviving member of an early eusuchian radiation and diverged from this lineage before complete verticalization of the braincase was established.

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