

The Higher Level Relationships of the Extant Crocodylia

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ABSTRACT.—The relationships of the three living groups of crocodylians (crocodylids, alligatorids and gavialids) are poorly understood. Recent molecular results favor a sister group relationship between the crocodylid genus *Tomistoma* and *Gavialis*, with this as the sister group to the crocodylids (Densmore, 1983). Buffetaut (1985) has reinterpreted some morphologic evidence as supportive of this viewpoint. This morphologic evidence is examined here using outgroup analysis; it fails to support this hypothesis. Few if any morphological features unambiguously support a *Gavialis* + crocodylid or *Gavialis* + *Tomistoma* relationship. Instead the classic pre-Darwinian phylogeny of Duméril (1806) is corroborated by anatomical evidence. This phylogeny supports a monophyletic crocodylid + alligatorid clade as a monophyletic sister group to *Gavialis*.

The relationships between the major groups of living crocodylians are a debated issue in archosaur systematics (Neill, 1971; Densmore, 1983; Buffetaut, 1985). Traditionally, the relationship of the long-snouted species *Gavialis gangeticus* has been at the crux of the issue. Hypotheses of the gavial's phylogenetic position (with the exception of Kälin, 1933) can be divided into two camps—one advancing the gavial's relationship with the crocodylids (Buffetaut, 1979, 1985; Densmore, 1983) and the other indicating the close relationship of the gavial with all living crocodylians (Duméril, 1806; Duméril and Bibron, 1835; Mook, 1934; Sill, 1968). Below I will comment on these competing views and choose between them on the basis of shared derived characters.

My approach in examining this problem is based on cladistic analysis (Hennig, 1965). Cladistic analysis, as it is employed here, is based on the determination of hierarchically nested sets of evolutionary novelties (Nelson and Platnick, 1981). These evolutionary novelties, or derived characters, are discovered by comparing ingroup character distributions with character distributions in a more general hypothesis of relationship—the outgroup. Because character changes in distant outgroup taxa, beyond an ingroup's first sister taxon, may influence the correct determination of character polarity, the use of several outgroups in a hierarchical outgroup hypothesis is necessary (Maddison et al., 1984). Characters with distributions restricted to subsets of the ingroup are derived within the ingroup and contain phylogenetic information. These phylogenetic patterns can be reduced to three taxon statements that retain all hierarchic information contained in larger cladograms (Gaffney, 1979, 1980). Cladograms are predictive statements about character distributions and

phylogeny, that can be tested by the congruence of additional derived characters.

Here the living crocodylians are considered monophyletic (Clark, 1986). Their closest living sister group is the archosaurian group Aves. The radical difference in morphology between the two groups renders birds an unsatisfactory outgroup for comparison of most morphologic characters. Several fossil taxa provide better indicators of the primitive condition of the Crocodylia. The phylogenetic arrangement of these taxa relative to Crocodylia has recently been examined by Clark (1986; Benton and Clark, 1988). These cladograms suggest that *Bernissartia fagesii* and poorly known species of *Shamosuchus* (= *Paralligator*; Yefimov, 1983) form unresolved sister taxa of the eusuchians (*Crocodylia* + *Stomatosuchus inermis*, *Hylaechampsia vectiana* and species of *Leidyosuchus*). The eusuchians *Hylaechampsia vectiana* and *Stomatosuchus inermis* are the sister taxa of the Crocodylia (sensu Clark [1986], including only those taxa advanced over the closest common ancestor of the living taxa).

Hylaechampsia vectiana is known only from a fragmentary cranium; it is neither completely prepared or described in detail. Although better studied, the only specimen of *Stomatosuchus inermis* was destroyed during World War II. *Leidyosuchus* is a well known taxon represented by many species (Erickson, 1976; Lucas and Sullivan, 1986). It is not demonstrably monophyletic monophyletic, and some of its members may be part of the ingroup, although definitive synapomorphies have not been presented (Clark, pers. comm.). In view of the problems presented by these taxa, following Clark (1986), I consider the better known material of *Bernissartia fagesii* + *Shamosuchus* species (outgroup 1), and species of *Goniopholis* + dyrosaurs + *Eutretauranosuchus delfsi* (outgroup 2) to represent sequential out-

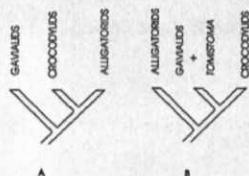


FIG. 1. Two competing hypotheses of higher level relationships within the extant Crocodylia. A. The traditional hypothesis. B. The hypothesis of Densmore (1983) and Buffetaut (1985).

groups of the Crocodylia. *Shamosuchus* material was not examined during this study and is troublesome in light of extensive synonymization and taxonomic problems with many of its species (Yefimov, 1983).

Throughout this paper the three groups of living eusuchians will be referred to with the informal names: alligatorids (including species of *Alligator*, *Caiman*, *Paleosuchus*, and *Melanosuchus niger*); crocodylids (including species of *Crocodylus*, *Osteolaemus tetraspis*, and *Tomistoma schlegelii*) and gavialids (only *Gavialis gangeticus*). These names are used merely for convenience and are not necessarily equivalent in hierarchical or taxonomic rank.

DISCUSSION

Fig. 1 presents two genealogies for the living crocodylian groups. Fig. 1A portrays the gavialids, crocodylids (including *Tomistoma*), and the alligatorids as monophyletic. Fig. 1B suggests a sister group relationship between *Gavialis* and *Tomistoma* with alligatorids as the sister group to other Crocodylia. Other crocodylian phylogenies are unresolved at this level (Mook, 1934; Wermuth, 1953; Steel, 1973), or have considered the Crocodylia as polyphyletic, with the gavialids having thalatosuchian affinities (Kälin, 1933, 1955). This last possibility is rejected for reasons outlined in Clark (1986), who demonstrates that the thalatosuchians are distantly related to the eusuchians.

Molecular and Biochemical Evidence for Relationships within the Crocodylia

Problems and Prospects.—Fig. 1B is a recent departure from the traditionally accepted phylogenetic pattern in Fig. 1A. This phylogeny has been prompted by the recent biochemical and molecular studies of Densmore (1983).

It is not the purpose of this paper to provide a detailed critique of Densmore's molecular data or detailed consideration of the methodological approach on which his study was based. Nevertheless, a few points are relevant to this dis-

ussion. First, much of Densmore's data is phenetic and therefore of limited phylogenetic efficacy because it does not distinguish between primitive and derived character states (see Farris, 1983, 1985, 1986; Patterson, 1987). Densmore (pers. comm.) as well as other workers (Norell, in prep.) are gathering additional molecular data that will be appropriate for numerical cladistic analysis. Second, at the highest level of the analysis, between the crocodylian groups considered here, no outgroup was used to root the phylogenetic trees. This is difficult when closely related living taxa are not available (Rieppel, 1987); outgroups are, however, crucial to the determination of any phylogenetic branching pattern (Nelson and Platnick, 1981). Regardless, it is fair to point out, that the small amount of genetic distance between *Gavialis* and *Tomistoma* is surprising and that no rooting of Densmore's preferred phylogeny will result in phylogeny A (Fig. 1A).

Due to problems in outgroup topology, even discrete (i.e., nonphenetic) molecular sequence information may not further elucidate the higher level relationships among the three groups of extant Crocodylia within a cladistic framework. As indicated above, the closest living outgroup of Crocodylia is birds (which with Crocodylia forms the Archosauromorpha); the second outgroup is the clade Lepidosauromorpha (including lizards, snakes, sphenodontids and amphisbaenians). Both of these clades are very diverse, and since outgroup methodology (Maddison et al., 1984) requires that at least two outgroups are needed to unambiguously determine a character's polarity, detailed study of both is crucial. Choosing a single member of each of these clades as representative of a primitive condition does not suffice. Only detailed comparisons among several members within each clade allows the determination of the primitive clade condition—the condition useful in outgroup analysis.

A second difficulty with molecular results relates to the relative times of divergence of these clades. Crocodylia first appears in the fossil record in the Late Cretaceous. The earliest fossil crocodylomorphs first appear in the Early Triassic (Carroll, 1988) indicating phylogenetic departure from the line leading to birds. The lepidosauromorph-archosauromorph split occurred in the Late or Middle Permian (Carroll, 1988). Crocodylia has thus been separated from its nearest extant sister group for roughly 170 million years and from its second (the Lepidosauromorpha) for 200 million years.

Conventional usage of molecular sequence data within phylogenetic systematics relies on the accumulation of substitutions in a defined molecular sequence. If mutation (substitution)

of these sequences is additive, sequence difference should increase over time, eventually causing a near random pattern. Because substitution rates within molecules differ, randomization occurs after different amounts of time. Specific molecules can be classified along a "fast-clock" to "slow-clock" continuum reflecting rates of sequence substitution (Li et al., 1985). Fast-clock molecules are phylogenetically useful in groups that have relatively short divergence times and slow-clock molecules are useful for groups with ancient histories.

The application of molecular sequences to the origin of higher level groups within Crocodylia is hampered by the relatively recent divergence of Crocodylia compared to the ancient diversification of Archosauromorpha. If a slow-clock molecule is examined, it is unlikely that enough phylogenetically informative substitutions will have accumulated since the initial divergence of the higher level clades of Crocodylia. Because sequence substitution in fast-clock molecules occurs quickly, cladistic comparison of fast-clock sequences (which are apt to show differences) with outgroup taxa will be phylogenetically uninformative since these sequences may have progressed to the point of randomization.

The difficulty with using a molecular approach to elucidate relationships within the Crocodylia does not extend to groups less inclusive than the three major clades. For these groups, rooting and outgroup solutions exist in the form of robust higher level hypotheses of relationship developed from morphology (Watrout and Wheeler, 1981). For instance, if the relationship depicted in Fig. 1A is corroborated, a molecular outgroup solution exists for the largely unresolved crocodylid clade. This outgroup solution uses alligatorids and gavialids as outgroups derived from a higher level hypothesis of relationship.

Alligatorids as the Sister Group to Other Crocodylia—Morphologic Evidence

In reconciling the molecular and morphologic data, Buffetaut (1985) reevaluated several anatomical characters and interpreted them as corroborating Densmore's (1983) hypothesis. The features used by Buffetaut in support of this phylogeny were not explicitly listed. The following discussion pertains to evidence presented in Buffetaut's text.

The Quadratojugal Spine.—Buffetaut (1985:77) suggests that the presence of a quadratojugal spine is a shared derived character linking all extant Crocodylia exclusive of the alligatorids (crocodylids + gavialids). The quadratojugal spine occurs on the posterior margin of the infratemporal space in many living and fossil crocodylians. Its morphology varies between taxa

(Kälin, 1933:644); however, when present, it is usually a thin spine directed anteriorly, parallel or diagonal to the lower temporal arcade. The presence of a quadratojugal spine in crocodylids (including *Osteolaemus*; contra Jordansky, 1973), has been used as a diagnostic feature at several hierarchical levels within crocodylids (Miall, 1872; Kälin, 1933; Jordansky, 1973). Buffetaut's interpretation of this feature as a synapomorphy uniting gavialids and crocodylids is inconsistent with outgroup comparison.

A large quadratojugal spine is present in most "mesosuchians" where the region of the skull is preserved, including specimens of *Nanosuchus* in the British Museum, *Bernissartia* from Spain (Buscalioni et al., 1984; Buscalioni, pers. comm.), as well as the type specimen of *Goniopholis felix* (Norell and Storrs, 1989) and specimens referred to *Goniopholis* in the collection of the British Museum. A large quadratojugal spine is, therefore, demonstrably present in both outgroup 1 and 2. A small bump on the quadratojugal is also present in *Protosuchus richardsoni* (Clark, pers. comm.) and a large spine is present on species of *Leidyosuchus* (Erickson, 1976). In *Hyaleochoamps*, an undescribed taxon from the Early Cretaceous of Texas and Montana (Langston, 1973 and pers. comm.), and *Shamosuchus*, all taxa closely related to the Crocodylia, this region of the skull is broken.

Living alligatorids have been considered to lack a quadratojugal spine (Miall, 1872; Jordansky, 1973). However, on close inspection, a small spine is present on all adult alligatorid species except for species of *Alligator* (Kälin, 1933). In *Alligator* a small bump is present in embryos and post-hatchlings (Fig. 2C)—a bump that is identical to the precursor of the large spine in young crocodylids. During ontogeny, this process is eliminated, resulting in a smooth quadratojugal margin of the infratemporal space. The transformation from the more general condition of a "bump" to the less general one of its loss is derived in alligatorids relative to the primitive condition of a large quadratojugal spine. The character of phylogenetic importance is the reduction and loss of the quadratojugal spine in alligatorids, not its primitive presence in any other group.

The Postorbital Bar.—The small spine present on the anterior surface of the postorbital bar in *Gavialis* and juvenile *Tomistoma* (Aoki, 1976) is also considered a synapomorphy uniting these taxa by Buffetaut (1985:710). Buffetaut suggests that the presence of a spine (the *Tomistoma* juvenile condition) in adult *Gavialis* represents a pedomorph. An almost identical spine is found on the postorbital bar of outgroup 1 (*Bernissartia fagesii* [Norell and Clark, in rev.]) and outgroup 2 (*Goniopholis felix* and *Goniopholis simus*). The

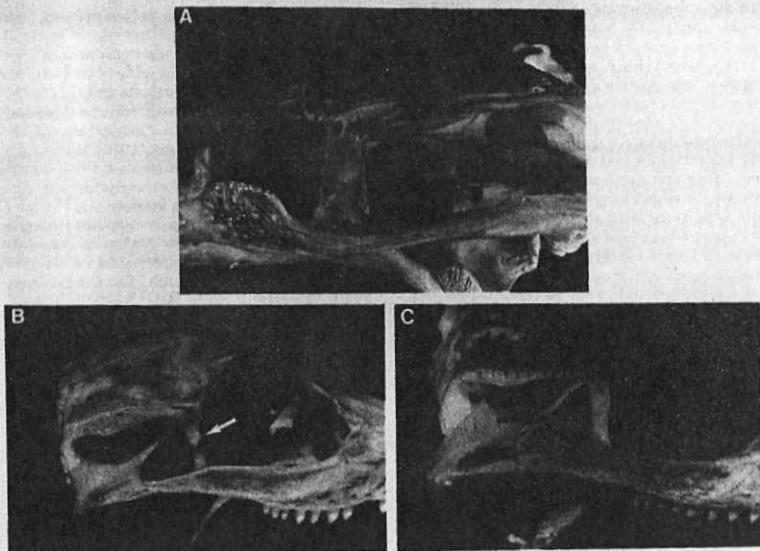


FIG. 2. A. The large, thick postorbital bar of *Gavialis gangeticus*. B. The postorbital bar of hatchling *Alligator mississippiensis* showing presence of an anterior spine. C. The vestigial infratemporal spine of alligatorids indicated by arrow in juvenile *Caiman crocodylus*.

presence of a spine on the postorbital bar in embryos and post-hatchlings of other eusuchians (Fig. 2B)—a spine which disappears during ontogeny—suggests that the shared presence of a spine in juvenile *Tomistoma* and *Gavialis* is a primitive feature; the reduction of this feature in crocodylids and alligatorids is derived. Additionally, the massive postorbital bar found in *Gavialis* (Fig. 2A) is reminiscent of the condition in *Bernissartia* and dyrosaurs (outgroup 1) and unlike other living crocodylians. The condition of this feature in outgroup 2 is ambiguous, since both conditions occur in *Goniopholis*. However, in *Hylaeochampsia* the postorbital bar is relatively wider than in living non-gavialid Crocodylia. In *Stomatosuchus* the postorbital bar is massive. The narrow postorbital bar seen in non-gavialid eusuchians (including *Leidyosuchus canadensis* [Erickson, 1976] and other *Leidyosuchus* species [pers. obs.]) can be provisionally regarded as a derived condition; however, this character requires more detailed study to determine its polarity at the level of this analysis.

The Nasopharyngeal Duct.—Referring to the architecture of the nasopharyngeal duct Buffetaut suggests (citing the work of Müller, 1967) that "Comparison of the differentiation of the

ductus nasopharyngeus and of the cranial base in *Crocodylus* (*sic*) and *Gavialis* shows that in both cases the difference between *Gavialis* and *Crocodylus* (*sic*) is smaller than that between *Alligator* and *Crocodylus* (*sic*)" (Buffetaut, 1985:713). During ontogeny, the eusuchian nasopharyngeal duct undergrows the basisphenoid plate, eventually exiting just anterior to the basisphenoid-basioccipital suture (Müller, 1967). A relatively long posterior excursion of the nasopharyngeal duct and a posteriorly directed choanal opening are characteristic of many crocodylids and *Gavialis*. In alligatorids the choanal aperture opens posteroventrally. Müller (1967:285) indicates (in reference to *Alligator*) that "Dieser Formzustand ist dem Späteumyonalen von *Crocodylus* ähnlich" (this form is like that of the late embryo of *Crocodylus*).

The posterior migration of the crocodylian choana during the evolution of the Eusuchia was considered evidence for the Victorian notion of progressive evolution (Huxley, 1875). It is difficult to assume that an anterior position of the choana represents a eusuchian primitive condition. Unfortunately, outgroups are not very informative, since no outgroup possesses a state directly comparable with that of the in-

group. Ontogenetic arguments are also troublesome since no detailed analysis of *Gavialis* has been completed.

Adding to the confusion, a survey of the variety of choana shapes and positions in Källin (1955, Fig. 53) shows that the difference in choana position between many crocodylid species and *Alligator* is not as extreme as the difference reported by Müller (1967) for *Alligator* and *Crocodylus niloticus*. In many alligatorids such as *Caiman latirostris* and *Melanosuchus niger* the choana lies posteriorly under the middle of the braincase, approximating the general crocodylid condition. Moreover, within alligatorids, derived characters influence the anterior position of the choanal opening relative to some crocodylids and gavialids. In *Alligator* and other alligatorids (although not as developed) there is an extreme development of the pterygoid sinus (Fig. 3). This sinus begins development early in ontogeny and its occurrence anterior to the basisphenoid and anterodorsal to the braincase floor influences the position of the choana.

Another piece of evidence commented on by Buffetaut refers to Müller's (1967) description of three ontogenetic trajectories of choanal development relative to the braincase. These trajectories share no components and the ontogeny of outgroup taxa in relation to this feature is unknown. Buffetaut interprets the small amount of difference between the gavialid and crocodylid trajectories as evidence for relationship without discussing the primitive ontogeny. Until detailed developmental analysis of gavialid ontogeny can be combined with outgroup analysis the amount of difference among these ontogenies should not be construed to indicate phylogenetic information.

Buffetaut's use of the ontogenetic argument to suggest phylogenetic relationship is problematic. In most cases primitive ontogenies cannot be differentiated from secondarily shortened ones (Fink, 1982) unless the developmental information is used in conjunction with outgroup analysis (DeQueiroz, 1985). Outgroup analysis was not explicitly included within Buffetaut's (1985) study.

The Braincase Wall.—Two similarities of the braincase between gavialids and *Tomistoma* are striking and provide some of the only evidence suggestive of phylogenetic relationship between these taxa. In gavialids and *Tomistoma* the basisphenoid and prootic are broadly exposed on the lateral wall of the braincase (lordansky, 1973, fig. 10). This condition is primitive for the Crocodylia (Clark, 1986); however, if reversal to the primitive state occurred within the ingroup it may be indicative of phylogenetic relationship.

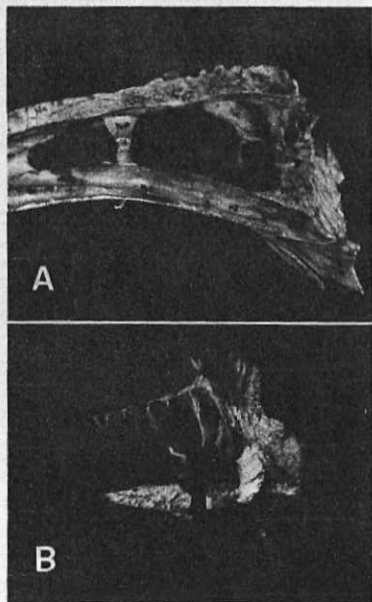


FIG. 3. The choanal passage shown in hemisected skulls of (A) *Crocodylus acutus* and (B) *Alligator mississippiensis*. Notice the elaborate air sinus anterodorsal to the choana in *Alligator mississippiensis*.

The prootic of crocodylians usually surrounds the posterior wall of the foramen ovale. In most eusuchian taxa the prootic is hidden inside the foramen, only slightly visible on the lateral braincase surface (lordansky, 1973, fig. 10). In *Tomistoma* and *Gavialis* the prootic is broadly exposed posterior to the foramen ovale; occasionally in *Gavialis* the prootic also forms the anterior wall of the foramen ovale. Ontogenetic factors may influence this similarity. In juvenile and embryonic crocodylians the prootic is exposed on the braincase wall, becoming overgrown by the opisthotic and laterosphenoid during growth. In *Tomistoma* the ontogeny of the braincase wall stops short of that in some other non-gavialid Crocodylia, as indicated by basisphenoid exposure and the lack of a well developed laterosphenoid bridge anterior to the foramen ovale. These features occur late in ontogeny of all other Crocodylia (except *Osteoleaemus* and some *Crocodylus cataphractus*). If other characters indicate that *Tomistoma* and *Gavialis* are phylogenetically separate, this similarity can

TABLEAU SYNOPTIQUE DES ESPÈCES DE CROCODYLIENS,

DISTRIBUÉS EN TROIS SOUS-GENRES



FIG. 4. A cladogram for living crocodilians proposed by Dumeril (1806). The cladogram for the higher level groups is presented at top.

be explained by truncation of the *Tomistoma* ontogeny at the primitive condition.

The distribution of this feature in outgroup taxa is difficult to examine since few braincases are well enough preserved or adequately prepared to examine the braincase wall. Clark's (1986 and pers. comm.) work suggests that a large prootic exposure (as well as a large exposure of the basisphenoid) are primitive characters near the level of Crocodylia.

The occurrence of a large basisphenoid surface on the braincase wall in *Gavialis* and *Tomistoma* has been overstated (Iordansky, 1973). Large basisphenoid exposures also occur in several adult crocodylids. The similarity between the general crocodylid and gavialid morphology is not compelling. In *Gavialis* the exposure of the basisphenoid is semicircular and similar to the pattern seen in outgroup 1. In *Tomistoma* the basisphenoid has a more crocodylid-like appearance.

In summary, support for hypothesis B (Fig. 1) is limited to the possible similarity of the prootic and basisphenoid on the braincase wall (primitive characters at the level of Eusuchia, which must reverse within the ingroup to show relationship), the overall longirostrine nature of the skull (a similarity that occurs independently in several crocodylid groups), and the amount of difference between ontogenies of the basisphenoid plates (a feature that is incompletely studied and difficult to reconcile with outgroup analysis).

Gavialis as the Sister Group to Other Crocodylia

A competing hypothesis (Fig. 1A) places *Gavialis* as the sister group to all other extant crocodylids. This phylogeny was originally presented by Dumeril in 1806 and Dumeril and Bibron in 1835 (Fig. 4), although they did not consider *Tomistoma*. This classification is typical of many pre-Darwinian classifications in that it included evidence (in the form of character data) in support of the recognition of natural groups (Gaffney, 1984). Although this phylogeny has been favored by several subsequent authors, supporting characters have not been presented.

Acceptance of this phylogeny hinges on the presence of synapomorphies between alligatorids and crocodylids, and the inclusion of *Tomistoma* in a monophyletic crocodylid group. Several morphological features serve as evidence for these suggestions.

Baur (1888) indicated that a small diapophysis occurs on the axial centrum of *Gavialis*. A diapophysis occurs in no other living crocodylian, including *Tomistoma*. The axis is unknown in most outgroup taxa; nevertheless, it is present in the type specimen of *Bernissartia fagesii* (outgroup 1) (Norell and Clark, in rev.), other fossil crocodylids (outgroup 2) (Clark, pers. comm.) and in other reptiles.

Several features indicate a monophyletic group of alligatorids and crocodylids (including *Tomistoma*) that is derived over gavialids. In

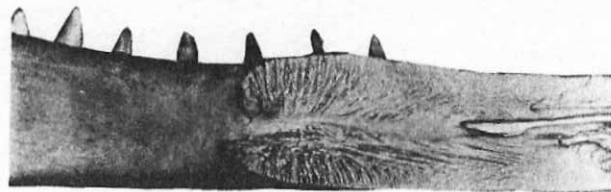


FIG. 5. The mandibular symphysis in *Gavialis gangeticus* (top) and *Tomistoma schlegelii* (below). Notice the presence of an intermandibular foramen in the splenial of *Gavialis gangeticus*, and its absence in *Tomistoma schlegelii*.

most reptiles the foramen intermandibularis oralis perforates the splenial's medial surface. The branches of the ramus mandibularis of cranial nerve V leave Meckel's canal through this foramen. Alligatorids possess this condition, and it is known in both outgroup 1 and 2 (although in some taxa this feature is not preserved). The condition in *Gavialis* is difficult to examine because much of the splenial is incorporated into the mandibular symphysis (Fig. 5). In disarticulated mandibles a small splenial perforation lies within the mandibular symphysis in the identical alligatorid position. The splenials of crocodylids (including the disarticulated rami of *Tomistoma*) are imperforate and cranial nerve V leaves Meckel's canal anteriorly. A small canal is present anteriorly in crocodylids, apparently housing cranial nerve V. The loss of the splenial perforation in crocodylids is a derived feature.

Gavialis and alligatorids possess a large posterior process of the ectopterygoid on the medial surface of the jugal (Fig. 6). This condition is not found in living crocodylids and is present in outgroup 1 and outgroup 2, and more distant crocodylians such as *Therapsuchus*. The lack of a posterior ectopterygoid process is a derived feature uniting all living crocodylids. This feature transforms to an independently derived state in *Alligator* and the primitive condition is not apparent. In some very large *Tomistoma* a small ectopterygoid process is present; however, its

morphology is not consistent with the alligatorid, outgroup or gavialid condition.

The posterior angle of the infratemporal space in crocodylids occurs at juncture of the quadratojugal when viewed medially. No anterior overlapping extension of the quadratojugal occurs anteriorly below the infratemporal fenestra. Variation is seen in this feature, yet the crocodylid condition is never as extreme as in alligatorids. In alligatorids, *Gavialis* and outgroups 1 and 2, an anterior process of the quadratojugal forms the posterodorsal angle of the infratemporal space (Fig. 6), and an anterior process of the quadratojugal overlaps the jugal's dorso-medial surface. The condition in *Tomistoma* is not as extreme as in most alligatorids and *Gavialis*. In *Tomistoma* the jugal-quadratojugal suture passes through the angle of the infratemporal fenestra or occasionally in very large individuals just anterior to it. Although in these cases the quadratojugal forms the posteroventral angle of the infratemporal fenestra, no anterior process of the quadratojugal overlays the medial surface of the jugal as in the primitive condition.

Alligatorids, *Gavialis* and *Bernissartia* possess a distinct posterior process of the postorbital that usually contacts the quadratojugal. When the dorsal process of the quadratojugal is extensive the quadratojugal is isolated from the perimeter of the infratemporal space. The condition of a posterior process is primitive for Crocodylia and is

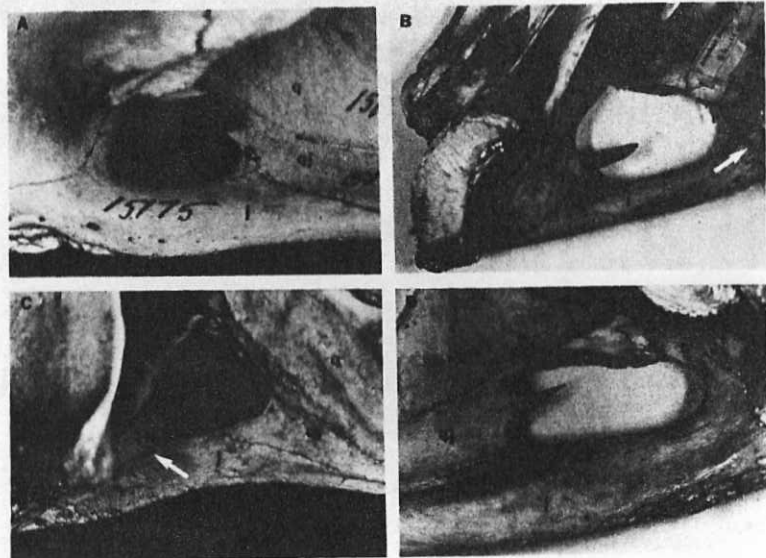


FIG. 6. The ventromedial surface of the infratemporal arcade in (A) *Crocodylus acutus*, (B) *Gavialis gangeticus*, (C) *Alligator mississippiensis*, and (D) *Tomistoma schlegelii*. C and B show postero-medial processes of the ectopterygoid (indicated by arrows) and anterior process of the quadratejugal ventral to the infratemporal fenestra. q, quadrate; qj, quadratejugal; j, jugal.

lacking in *Tomistoma* and other crocodylids except for *Osteoleaemus* where a small posterior postorbital process is present in large individuals.

Gavialids lack hypapophyses on the anterior cervical vertebrae. Hypapophyses are a derived feature near the level of Eusuchia (Clark, pers. comm.). Nevertheless, small hypapophyses are present on the anterior cervical vertebrae of *Bernissartia fagesii* (Norell and Clark, in rev.). All living crocodylians except *Gavialis* have cervical hypapophyses. The polarity of this feature at the level of Crocodylia is equivocal since its distribution within distant outgroup taxa contradicts the polarity determined by the first outgroup.

Character Analysis

A list of characters pertaining to this discussion is provided in Appendix 1 and their distributions plotted in Table 1. Character polarities at the level of Crocodylia were determined by the sequential outgroup procedure outlined in Maddison et al. (1984). In some cases (i.e., character 12) the polarity at the basal ingroup

node indicated by the first outgroup was modified by character distributions in a more general outgroup hypothesis. Buffetaut's reliance on outgroup analysis was not apparent, and may have influenced his polarity decisions (i.e., his determination of the quadratejugal spine as a derived feature within Crocodylia). This and other methodological considerations may be part of the reason for the difference between the conclusions presented here and those of Buffetaut (1985).

Fig. 7 portrays a cladogram with characters of the Crocodylia and its near outgroups. This genealogy requires 18 steps to explain the distribution of characters in Table 1. This phylogeny had a consistency index of 0.72 indicating relatively small amounts of homoplasy. The monophyly of a group including alligatorids and crocodylids and the monophyly of crocodylids including *Tomistoma* are both supported by three unambiguous synapomorphies. A hypothesis indicating gavialid, *Tomistoma* monophyly (Fig. 1A) as the sister group to the crocodylids requires 25 steps to explain the character distribution in Table 1. Such a tree has a low

TABLE 1. Distribution of character states in Appendix 1 in selected crocodylian taxa.

	1	2	3	4	5	6	7	8	9	10	11	12
Gavialids	0	0	0	2	0	0	0	0	0	0	0	0
Crocodylids	0	1	1	1,2	1	0,1	1	1	0,1	1	1	1
Alligatorids	1	1	1	1	1	1	1	0	0	0	0	1
<i>Tomistoma</i>	0	1	1	2	0	0	1	1	1	1	1	1
Outgroup 1	0	0	0	0	?	0	0	0	0	0	0	1
Outgroup 2	0	0	0,1	0	0	0	0	0	0	0	0	0

consistency index of 0.52, indicating the presence of extensive homoplasy in the data. Although evidence supporting an alligatorid, crocodylid clade is not plentiful, the notion of *Tomistoma*, gavialid monophyly is contrary to six characters.

CONCLUSIONS

I agree with Buffetaut's (1985) suggestion that Densmore's (1983) evidence is the best (in the sense that it is the most resolved) approximation of crocodylian phylogeny yet presented. However, as with all hypotheses of relationship, Densmore's hypothesis should be open to scrutiny from both comparative anatomists and molecular systematists. In some cases (e.g., eutherian mammals) cladistic analysis of morphological data using parsimony and outgroup procedures are less ambiguous and better supported than similar hypotheses derived from molecular data (Wyss et al., 1986). Or, as in the case of higher primate phylogeny, different styles of analysis and different molecular data sets have resulted in incongruent results (Sibley and Ahlquist, 1984; Nei and Tajima, 1985; Templeton, 1985).

Molecular analysis of crocodylians is not without problems. Because living crocodylians have no close living outgroups their higher level phylogeny is probably outside the range of the rigorous application of many molecular techniques (i.e., allozymes and DNA hybridization).

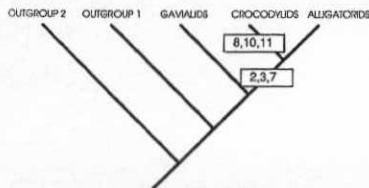
More conservative techniques (e.g., techniques that sample molecular characters with slow evolutionary transformation rates) may not be informative at this level either, since they may lack requisite variation. Likewise, as indicated by Patterson (1987), it is too early to reinterpret all morphologic data to fit hypotheses developed from molecular data, since molecular analyses suffer from many of the same pitfalls as traditional ones.

The question of the relationships of the three extant crocodylian groups is not decisively settled. The morphologic data is standing at odds with molecular phylogenies. This conflict between data sets indicates the need for further work in this area. Nevertheless, the hypothesis of a sister group relationship between the crocodylids and alligatorids originally proposed by Duméril in 1806, is currently best supported by the morphological evidence. It awaits testing by the accumulation of additional molecular and morphologic data.

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APPENDIX 1

Numerical List of Characters

- 1) Quadratorogal spine; present 0, absent 1.
- 2) Anterior spine on postorbital bar; present 0, absent 1.
- 3) Postorbital bar; massive 0, thin 1.
- 4) Choana position; anterior 0, medial 1, posterior 2.
- 5) Prootic exposure; extensive 0, small 1.
- 6) Basisphenoid exposure; extensive 0, small 1.