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MALONE, BRIAN SCOTT
THE SYSTEMATICS, PHYLOGENY AND PALEOBIOLOGY
OF THE GENUS ALLIGATOR.

CITY UNIVERSITY OF NEW YORK, PH.D., 1979

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THE SYSTEMATICS, PHYLOGENY AND PALEOBIOLOGY OF THE GENUS *ALLIGATOR*

by

BRIAN MALONE

A dissertation submitted to the Graduate
Faculty in Biology in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy, The City University
of New York.

1979

Brian Malone

This manuscript has been read and accepted for the Executive Committee in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

January 16, 1979
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Max Hecht
Chairman of Examining Committee
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Abstract

THE SYSTEMATICS, PHYLOGENY AND PALEOBIOLOGY OF THE GENUS *ALLIGATOR*

by

Brian Malone

Adviser: Professor Max K. Hecht

This study primarily involved an analysis of the variability patterns that characterize the skulls of both living and extinct alligators. A morphometric analysis of the skull of alligators was conducted by using three growth series which had originated from natural populations of the extant species (*A. mississippiensis* and *A. sinensis*). The growth patterns that were associated with five variables in the skull and one in the lower jaw were investigated. It was determined that intracranial growth involving these characters was mainly isometric. No statistically significant differences were found between the growth patterns of *A. sinensis* and those that characterize a population of *A. mississippiensis* from Florida. However, it was also determined that significantly different patterns of growth do exist between *A. sinensis* and a Texas population of *A. mississippiensis*.

Qualitative morphological characters were used to distinguish between fossil and Recent forms of *Alligator*. Three fossil forms were recognized on this basis. These include *A. prenasalis* from the early and late Oligocene of South Dakota, *A. mcgrewi* from the early Miocene of Nebraska and *A. olseni* from the early Miocene of Florida. Fossil samples that are referred to *A. mississippiensis* are recorded from the early and middle Miocene of Nebraska and Texas, from the late Miocene of Nebraska, from the late Miocene and Pleistocene of Florida.

The theoretical and practical problems surrounding attempts to reconstruct the evolutionary history of organisms are discussed in detail. An hypothesis is proposed concerning the phylogenetic relationships within the genus *Alligator*. This hypothesis is based upon comparisons of the cranial morphology of alligators and related forms. Three lineages were delineated as a result of this analysis (*A. prenasalis* - *A. mcgrewi*, *A. olseni* - *A. mississippiensis* and *A. sinensis*). *A. mcgrewi* is considered to represent a close morphologic

approximation of the common ancestor of the A. sinensis and A. olseni - A. mississippiensis lineages. The major morphologic changes that occurred during the evolutionary history of alligators involved modifications in the biomechanics of feeding.

The present disjunct distribution of alligators (southeastern United States and eastern Asia) is hypothesized to have arisen as a result of vicarious events that occurred during the Miocene. These events appear to be correlated with climatic shifts caused by major tectonic activity in western North America during this period of time.

ACKNOWLEDGEMENTS

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INTRODUCTION

Animals that are referred to the genus Alligator (family Alligatoridae, suborder Eusuchia) can be considered typical members of the order Crocodilia in being semiaquatic predators that achieve large size by growing throughout life. Although they subsist mainly on aquatic and semiaquatic vertebrates, a wide variety of prey appears to be exploited during the life history of an individual (Chabreck, 1972; Fogarty & Albury, 1967; Giles & Childs, 1949; Jackson et al., 1974; Kellog, 1929; McIlhenny, 1935; Valentine et al., 1972).

Alligators show the typical features of the crocodilian skull, such as a flattened dorsal surface, a depressed snout and a dorsal position of the orbits and external nares. Such features appear to be related primarily to their aquatic mode of life. Although there can be considerable variability in snout proportions within other genera of crocodilians (especially in Caiman and Crocodylus), members of the genus Alligator possess extremely broad, short snouts. The dorsal and lateral surfaces of the skull and lower jaw bear the characteristic sculpturing of crocodilians, which develops ontogenetically as a result of the fusion of secondary dermal ossifications (osteoderms) to these surfaces (Iordansky, 1973). Their dentition is pseudoheterodont, i.e. crown size and shape varies along the tooth row. However, sections of the tooth row do appear to be nearly uniform; the most posterior series (generally the last four teeth) in alligators are relatively blunt, laterally compressed and come to lie in a common alevolar groove. The shapes of the teeth are also known to vary ontogenetically (Kalin, 1933a). In occlusion the mandibular tooth rows lie medial to those of the upper jaw, as they do in all other members of the family Alligatoridae. Although tooth placement, which proceeds by alternating waves of replacement from back to front along the tooth row, generally occurs throughout life, the replacement pattern becomes irregular and slows with increasing age (Edmund, 1962, 1969).

Alligator is represented in the Recent fauna by two species. A. mississippiensis (the American alligator) and A. sinensis (the Chinese alligator), which exhibit a large disparity in body size. Individuals of the former species may attain a maximum length of about six meters, while the largest individual of A. sinensis on record has measured about two meters in length (Neill, 1971). A. mississippiensis occupies a variety of habitats in lowland areas of southeastern North America, while A. sinensis inhabits portions of the lower region of the Yangtze River Valley in eastern Asia (Figure 1). The present distribution of Alligator appears exceptional among Recent crocodilians in that it represents the only widespread occurrence of the group in warm temperate regions.

Although the genus has a relatively extensive fossil record from Middle Tertiary to Recent time in North America, fossil remains that can be unequivocally allocated to Alligator are unknown from outside that continent (Figure 2). Five fossil taxa have been previously described and allocated to Alligator: A. prenasalis from the Chadron (Early Oligocene) and Brule Formations (Middle Oligocene) in South Dakota (Barbour, 1926; Higgins, 1971; Loomis, 1904; Mook, 1932; Wilson & Tucholke, 1967), A. mcgrewi from the Marsland Formation (Early Miocene)

Fig. 1. The geographic distribution of the genus *Alligator* during the Recent. In historical times *A. mississippiensis* ranged along the Atlantic Coastal Plain from southeastern Virginia into Florida, along the Gulf Coastal Plain into eastern Texas and up the Mississippi River Valley into Arkansas. *A. sinensis* has been recorded only from a small area in the Yangtze River Valley in eastern Asia but may have also extended into other parts of the Valley (after Neill, 1971).

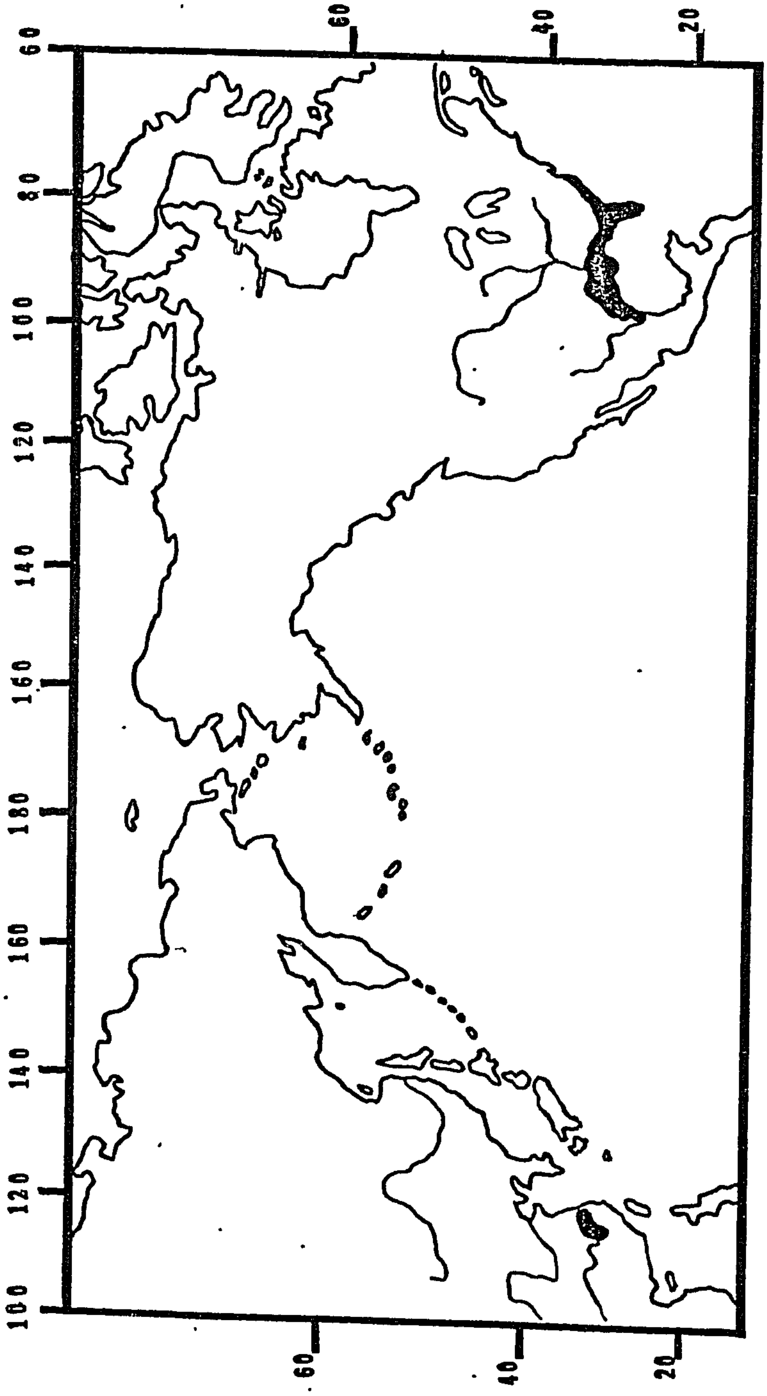
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Fig. 2. The geographic and stratigraphic distribution of fossil alligators. Solid circles refer to geographic localities; numbers place the geographic distribution of fossil forms in a stratigraphic framework according to the North American Land Mammal Ages (Wood et al., 1941). Heavy line represents the northern and western limits of the range of *A. mississippiensis* during the Recent. 1- Chadron Formation (Chadronian), South Dakota; 2- Brule Formation (Orellan), South Dakota; 3- Marsland Formation (early Hemingfordian), Nebraska; 4- Sheep Creek Formation, Nebraska and Hawthorne Formation, Florida (late Hemingfordian; 5- Olcott Formation, Nebraska and Flemming Formation, Texas (early Barstovian); 6- Lower Ash Hollow Formation (early Clarendonian), Texas; 7- Middle Ash Hollow Formation (late Clarendonian), Nebraska; 8- Mixon's Bone Bed (Hemphillian), Florida; 9- McLeod Lime Rock Mine (Irvingtonian), Florida; 10- Ichtucknee River (Rancholabrean), Florida.

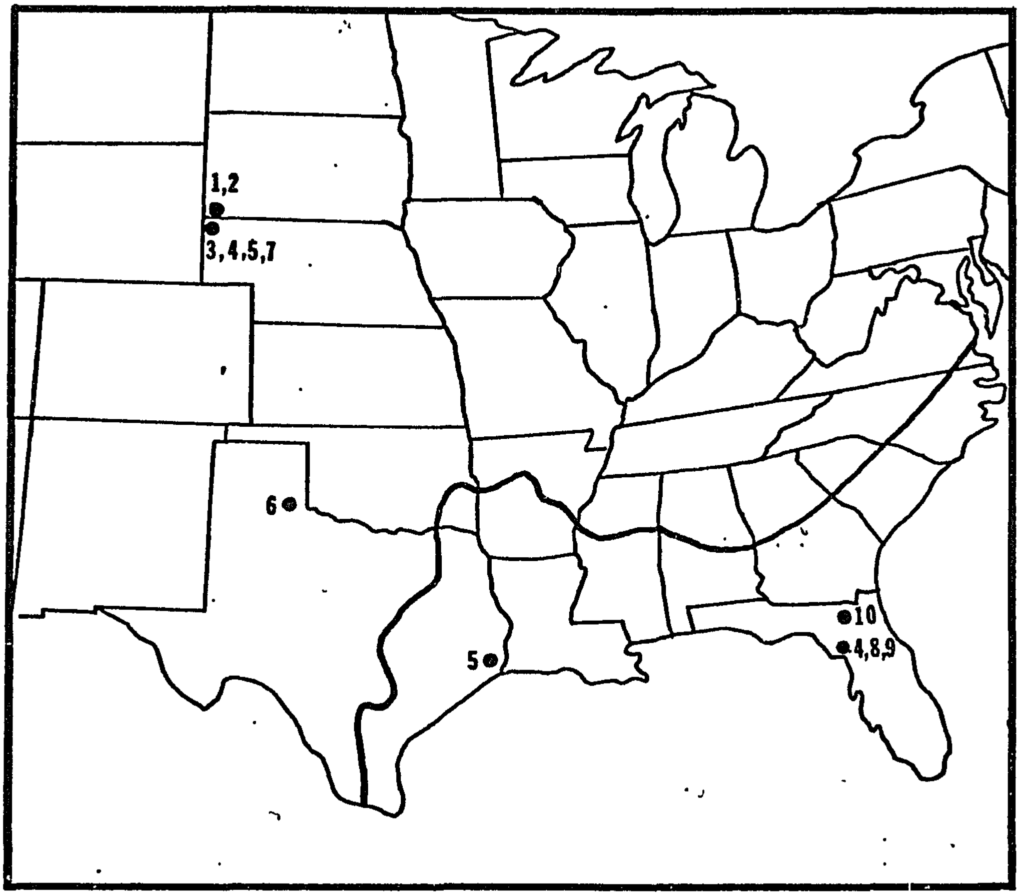


FIG. 2

in Nebraska (Schmidt, 1941), *A. olseni* from the Hawthorne Formation (Early Miocene) in Florida (White, 1942), *A. thomsoni* from the Olcott Formation (Early Miocene) in Nebraska (Mook, 1923b) and *A. mefferdi* from the Middle Ash Hollow Formation (Late Miocene-Pliocene) in Nebraska (Mook, 1946). Fossil material which has been referred to *A. mississippiensis* has been reported from the Pleistocene of South Carolina, Texas and Florida (Hay, 1923, 1929). Although the generic allocation is equivocal because of the fragmentary nature of the material, *Alligator* has also been reported as in the Pleistocene of Maryland (Hay, 1923), the Miocene and Pleistocene of Texas (Holman, 1968, 1969), the Pliocene of Oklahoma (Woodburne, 1959), the Miocene of northern Kiangsu, The People's Republic of China (Chow & Wang, 1964) and the Cretaceous of Mongolia (Konzshukova, 1954). In addition, undescribed fossil material, which can be allocated to the genus, has been recovered from new collecting localities in the Great Plains and in south-central and southeastern United States.

The diagnoses of fossil species within *Alligator* (and within other crocodilian genera in general) rest almost entirely on differences in cranial proportions. However, such criteria have proven unsatisfactory since most studies involving living forms have also shown that there is so much variability in many skull proportions, that considerable overlap exists between closely related species (Iordansky, 1973; Kalin, 1933a). Because of the equivocal nature of taxonomic decisions based on morphometric data, I conducted a comparative morphological analysis of the alligator skull for the purpose of uncovering qualitative characters that could be used to distinguish fossil species of *Alligator*.

Although it is known that much of the observed intraspecific variation in skull proportions of crocodilians is due to differential growth (Dodson, 1975; Kalin, 1933; Kramer & Medem, 1955; Mook, 1921b) nothing is known about the variation that occurs between natural populations of alligators. In order to pursue this, a morphometric analysis of skull variability was carried out on several samples from natural populations of the living species.

An hypothesis concerning the phylogenetic relationships among the delineated species is proposed. This reconstruction of the evolutionary history of the genus is based on a morphological comparison of the skull. However, recent discussions of the methods of phylogenetic reconstruction have created considerable disagreement concerning many of the basic principles. These differences are attributable in part to the different assumptions used in constructing phylogenetic hypotheses. I focus on these fundamental issues in a discussion of the principles of phylogenetic inference before attempting to reconstruct the evolutionary history of Alligator.

Another focal point of the study involves the examination of this evolutionary history with the expressed purpose of uncovering the patterns of morphological change which are associated with the phylogeny of alligators.

Finally, an attempt is made to correlate major geological events and broad-scaled environmental change with the shifting zoogeographic pattern which is associated with the group's evolutionary history.

In summary, then, this study will address the following questions:

1. What skull characters can be used to discriminate different species of Alligator?

2. What are the patterns of variability in skull proportions that occur within and between natural populations of alligators?

3. What methods should be employed in the reconstruction of the evolutionary history of a group of organisms?

4. What has been the evolutionary history of Alligator?

5. What have been the major patterns of morphological change that have occurred during this history?

6. How can the zoogeographic distribution of Alligator be explained?

SELECTION OF CHARACTERS

Most systematic studies involving crocodilians have been based on comparisons of skull variation. The emphasis on skull characters may be largely due to the generally accepted view that the basic design of the crocodilian skull reflects a primary feeding adaptation which is thought to vary to some degree among different groups of crocodilians (see Iordansky, 1973; Langston, 1973 for recent reviews). The reliance on skull characters in crocodilian systematics may also be partly due to the preponderance of skulls in fossil collections. It is not at all clear as to whether this situation is due to the preferential preservation of the skull, or whether it reflects a collecting bias. In any event, postcranial elements of fossil crocodilians (especially Tertiary forms) are relatively uncommon and, when they are present, are usually not found in close association with skull material. Nevertheless, notable exceptions to this pattern are known. For example, several well-preserved, fully articulated skeletons of Alligator prenasalis have been recovered from the Chadron Formation (White River Badlands) of

South Dakota. Evidently, crocodilian remains have been preserved in a variety of depositional environments.

The high degree of variability in cranial proportions that characterizes crocodilian populations is clearly the result of individual differences in the growth pattern of the skull. The variability in these proportions of a population will depend upon the following factors: (1) the variability of the genotypes, (2) the variability of the environments, (3) the variability of the genotype-environment interactions, (4) the variability due to allometric growth.

Although it is difficult to discriminate between the relative contributions of these components, it appears that each may contribute significantly to the total amount of variation that has been observed. There is some evidence which indicates that considerable variation is caused by the first three factors. A gross examination of similar sized individuals of *Alligator mississippiensis* from Alachua County, Florida indicated that there is conspicuous variability in individual growth patterns. This marked variability in growth is also reflected in the observation that growth rates in *Crocodylus niloticus* are so variable that age-size classes are obscured after three years (Cott, 1961). Growth patterns should also vary geographically, especially in a form like *A. mississippiensis* which has ranged from subtropical to warm temperate regions in Recent time (Neill, 1971). Kramer and Medem (1955) discovered differences in skull variation among geographical populations of *Caiman sclerops*, but it is unclear what factors produced the differentiation. That much of the variability of crocodilian skulls results from allometric growth is unequivocal; several studies have shown the strong allometric relationship that exists between some skull variables (Dodson, 1975; Kramer & Medem, 1955). The point of this short discussion of the underlying factors affecting the variability of crocodilian skulls is to indicate the complex nature of the phenomenon and to point out the difficulties which would surround any attempt at interpreting such data.

Many of the studies that have attempted to characterize the variability of crocodilian skulls suffer from several inadequacies. In some cases samples were quite small, consisted of limited size ranges or contained individuals of unknown origin. Similar morphometric studies involving fossil crocodilians have been limited to an even greater degree by extremely small samples (Langston, 1965).

Some of the difficulties surrounding morphometric studies of living forms stem from the paucity of osteological specimens that possess precise locality information. Although a large number of skulls, which also span a considerable range in size, can be assembled by combining specimens from several osteological collections, many specimens generally lack locality records. Assembling a sample of skulls only from individuals which are known to have been derived from natural populations is important for two reasons. First, almost nothing is known concerning the geographical patterns of skull variation in crocodilians. Selection of only those individuals with precise locality records would provide a data base from which geographical patterns of variability could be studied. Second, growth anomalies, which appear to be associated with periods of captivity, are known to occur in crocodilians (Iordansky, 1973; Kalin, 1937; personal observations). Since many individuals that can be found in collections have recorded histories of periods of captivity, the inclusion of them in a sample may produce spurious results.

The other major problem encountered in the study of crocodilian skull variation involves the high degree of variability between individuals of different sizes which results from the allometric relationship that exists between some skull variables (Dodson, 1975; Kalin, 1933a,b; Karmer & Medem, 1955; Mook, 1921b). The use of samples consisting of individuals of a limited size range would preclude the elucidation of patterns of ontogenetic changes in skull proportions and would also lead to an underestimate of the amount of variation that could be found in natural populations. This is especially true for crocodilian skulls, the sizes of which can span an order of magnitude.

Most of the workers who have described new fossil forms of _Alligator_ appear to have been aware of the possible allometric relationships which may have existed between skull variables, and generally were careful to compare specimens of approximately the same size (e.g., see Mook, 1923b). However, even gross examination of similar sized individuals from natural populations of _A. mississippiensis_ indicates that there is a high degree of variation in growth patterns among individuals. The lack of a large number of individuals of approximately the same size precludes any attempt to arrive at precise estimates of the variability of particular size classes.

Because of the problems associated with the data, the standard statistical parameters, which are generally useful in describing the variations of a population, do not appear to be particularly meaningful to the study of crocodilian skull variation. Although studies of the relationships between skull variables have proven to be useful in analyzing some cranial indices in living forms (Kramer & Medem, 1955), the small size and limited size range of fossil samples may preclude this approach.

MATERIALS AND METHODS

Data were obtained by assembling several ontogenetic series of skulls which were recorded as having been derived from natural populations of the two living species of _Alligator_ (see Appendix I for a list of the institutional and anatomical abbreviations used; Appendix II for a complete listing of examined specimens). Four individuals which either lacked locality data or were known to have lived in captivity were included in the skull series of _A. sinensis_ in order to improve the size range of the sample.

One skull series consisted of sixteen osteological specimens of _A. mississippiensis_ from Alachua County, Florida and ranged in size from 52-491 mm (skull length). A second consisted of fourteen osteological specimens of _A. sinensis_, ten of which had been collected from Ahnwei Province, The People's Republic of China, and which ranged in size from 126-310 mm (skull length). A second series of skulls derived from a western population of _A. mississippiensis_ was included in the morphometric analysis of skull variability. This latter sample consisted of thirteen individuals from Victoria County, Texas and ranged in size from 51-360 mm (skull length). It should be noted that the skull measurements of this series were made from alcoholic specimens and preserved skins with intact skulls. Although the nature of these specimens made some of the standard variables impossible to record, it was the only sample consisting of a sufficient number and spanning a significant size range that was available for study.

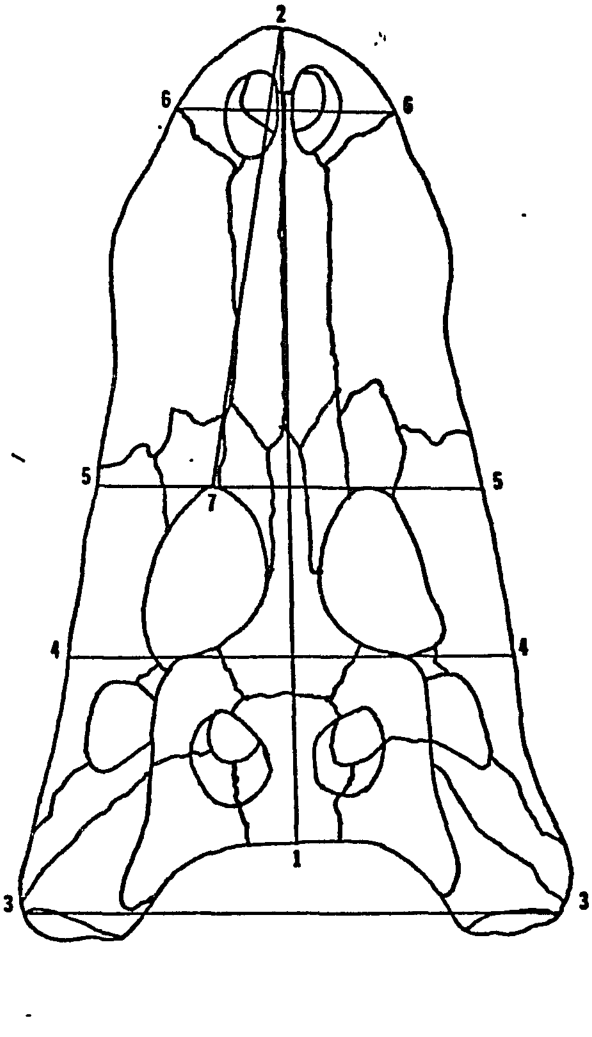
The skull series of A. mississippiensis from Alachua County, Florida and that of A. sinensis was examined in detail mainly for characters that varied in a discontinuous manner. The search for qualitative character differences was conducted by comparing a bone of one species with the corresponding element in the other. Any significant variation within a species was noted and examined for ontogenetic patterns. Fossil forms were compared to the living species and to each other in the same manner. I disregarded variation in the lengths or proportions of different bones and skull openings for the same reasons that I ignored differences in cranial proportions.

QUANTITATIVE CHARACTERS: MORPHOMETRIC VARIABILITY OF THE SKULL OF ALLIGATORS

The morphometric variables used in this study are illustrated in Figure 3. They include some of the standard cranial measurements that have been used by other authors (see for example, Dodson, 1975; Kalin, 1933a; Langston, 1965), as well as an additional variable that appears to reflect functional properties of the alligator skull (length of the mandibular symphysis). Six variables were measured in the skull and one in the lower jaw.

Measurements less than 180 mm were made with a dial calipers to the nearest 0.1 mm; those greater than 180 mm were made with a measuring tape to the nearest 1 mm. Each measurement was made twice, and the average of the two was recorded. Symmetrical variables were measured

Fig. 3. Skull of A. sinensis illustrating the variables employed in the morphometric analysis of the alligator skull: (1-2) length of the skull from the posterior edge of the skull table to the tip of the snout; (3-3) width of the skull at the jaw articulation; (4-4) width of the skull at the postorbital bar; (5-5) width of the skull at the anterior border of the orbits; (6-6) width of the skull at the premaxillary-maxillary suture; (7-2) length of the snout from the anterior border of the orbit to the tip of the snout; (8-9) length of the mandibular symphysis.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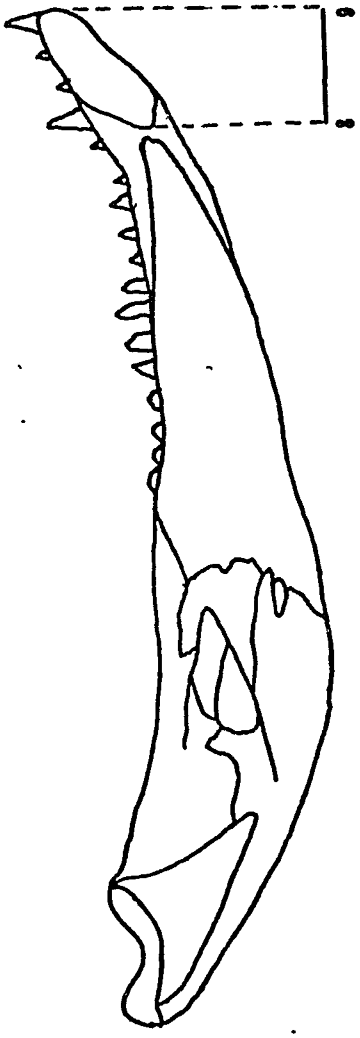
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8

on both sides of the skull and averaged. Appendix III contains a list of the measurements made on each speciman.

It has already been noted that much of the cranial variation that occurs among crocodilian taxa is a consequence of different growth patterns. However, it has also been noted that individuals forming different portions of a growth series may also exhibit differences in the pattern of variation for some characters. This variation may occur because of differential growth involving those parts of the skull. In order to determine whether this pehnomenon is responsible for some of the previously observed differences in cranial proportions among alligators, an analysis of size related differences occurring within and among populations of alligators was conducted.

Skull length (Figure 3) was chosen as the best estimate of the size of an individual, and all other measurements were plotted against that variable. (Dodson (1975) determined that basal skull length grows isometrically with respect to body length in _A._ _mississippiensis_.)

Two series of bivariate plots of these data were made. One series consisted of plots which were based on the actual measurements, while the second consisted of plots based upon the natural logarithmic transformation of the original observations. Only the latter have been included for the purposes of illustration and discussion (Figures 4-9). These plots were also statistically analyzed and compared (Table 1).

BIVARIATE PLOTS

Mere visual examination of the plots of the actual measurements was insufficient to determine whether the variables were related to skull length in a rectilinear or curvilinear fashion. However, plots

Fig. 4. Scatter diagram and relative growth curves of skull width at the jaw articulation plotted logarithmically against the logarithm of skull length in three populations of *Alligator*. Populations are represented by the following symbols: *A. mississippiensis* from Victoria County, Texas (open circles and broken line); *A. mississippiensis* from Alachua County, Florida (solid circles and solid line); *A. sinensis* (triangles and dotted line; open triangles represent individuals lacking locality records or known to have lived in captivity).

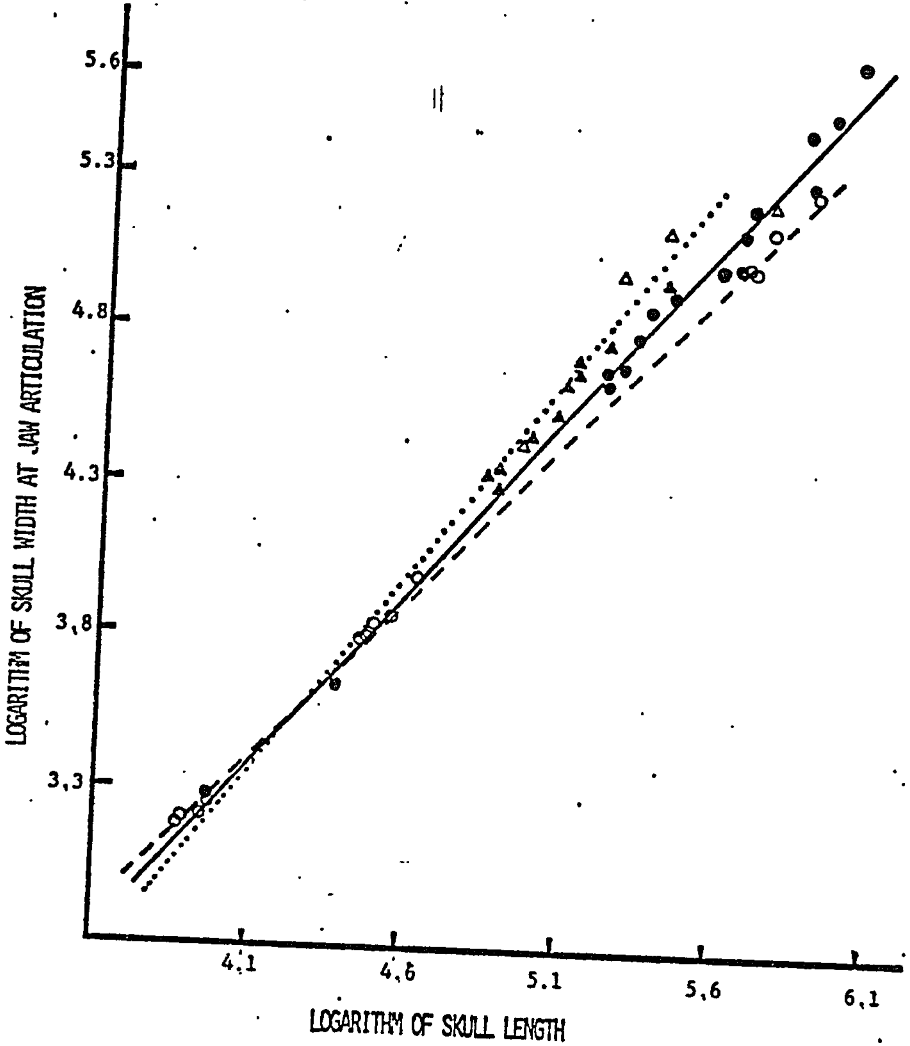
LOGARITHM OF SKULL WIDTH AT JAW ARTICULATION
5.6
5.3
4.8
4.3
3.8
3.3
4.1
4.6
5.1
5.6
6.1
LOGARITHM OF SKULL LENGTH

Fig. 5. Scatter diagram and relative growth curves of skull width at the postorbital bar plotted logarithmically against the logarithm of skull length in three populations of *Alligator*. Symbols as in Fig. 4.

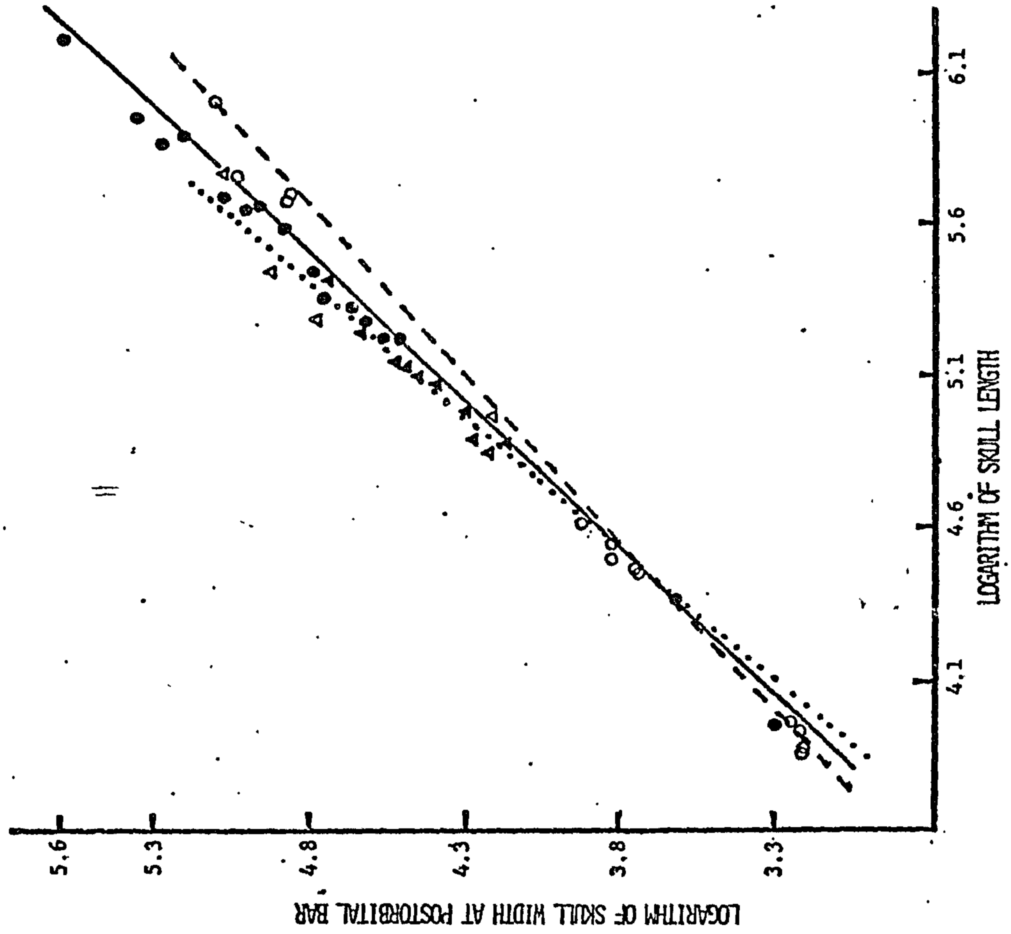
LOGARITHM OF SKULL WIDTH AT POSTORBITAL BAR
5.6
5.3
4.8
4.3
3.8
3.3
LOGARITHM OF SKULL LENGTH
4.1
4.6
5.1
5.6
6.1

Fig. 6. Scatter diagram and relative growth curves of skull width at the anterior border of the orbits plotted logarithmically against the logarithm of skull lengthin three populations of Alligator. Symbols as in Fig. 4.

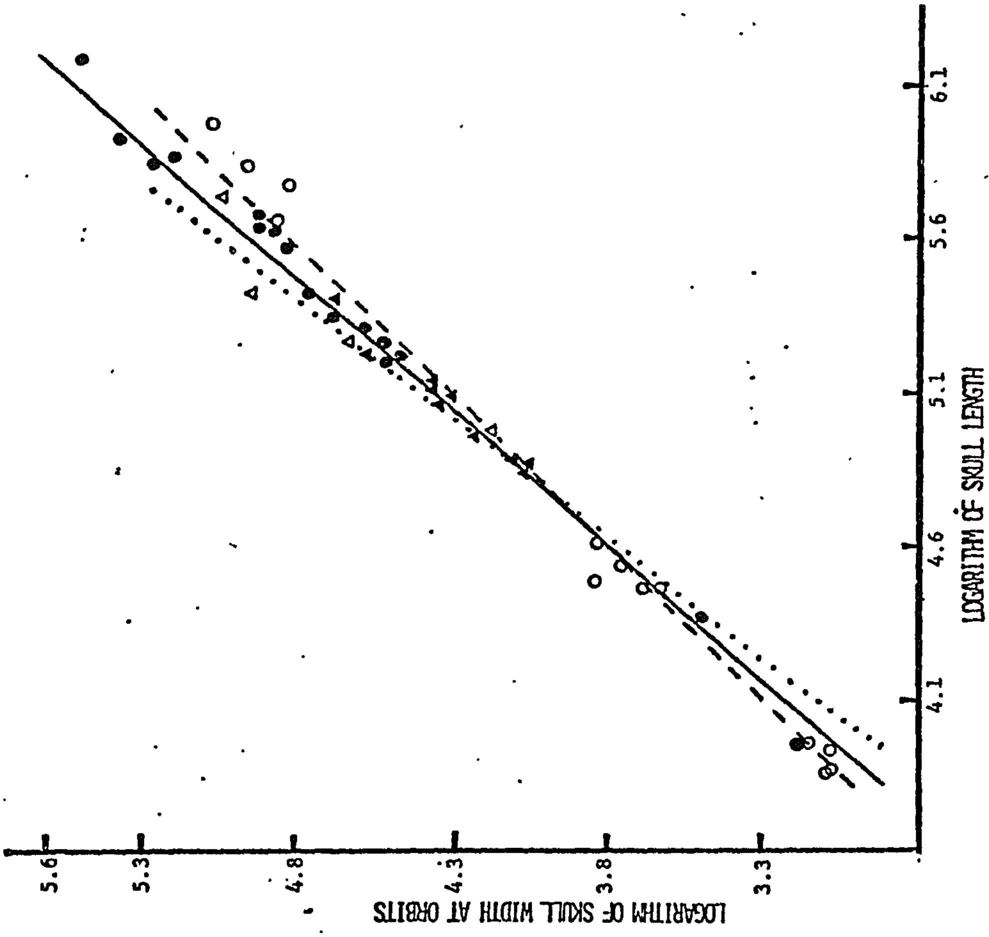
LOGARITHM OF SKULL LENGTH
4.1
4.6
5.1
5.6
6.1
LOGARITHM OF SKULL WIDTH AT ORBITS
3.3
3.8
4.3
4.8
5.3
5.6

Fig. 7. Scatter diagram and relative growth curves of skull width at the premaxillary-maxillary suture plotted logarithmically against the logarithm of skull length in three populations of Alligator. Symbols as in Fig. 4.

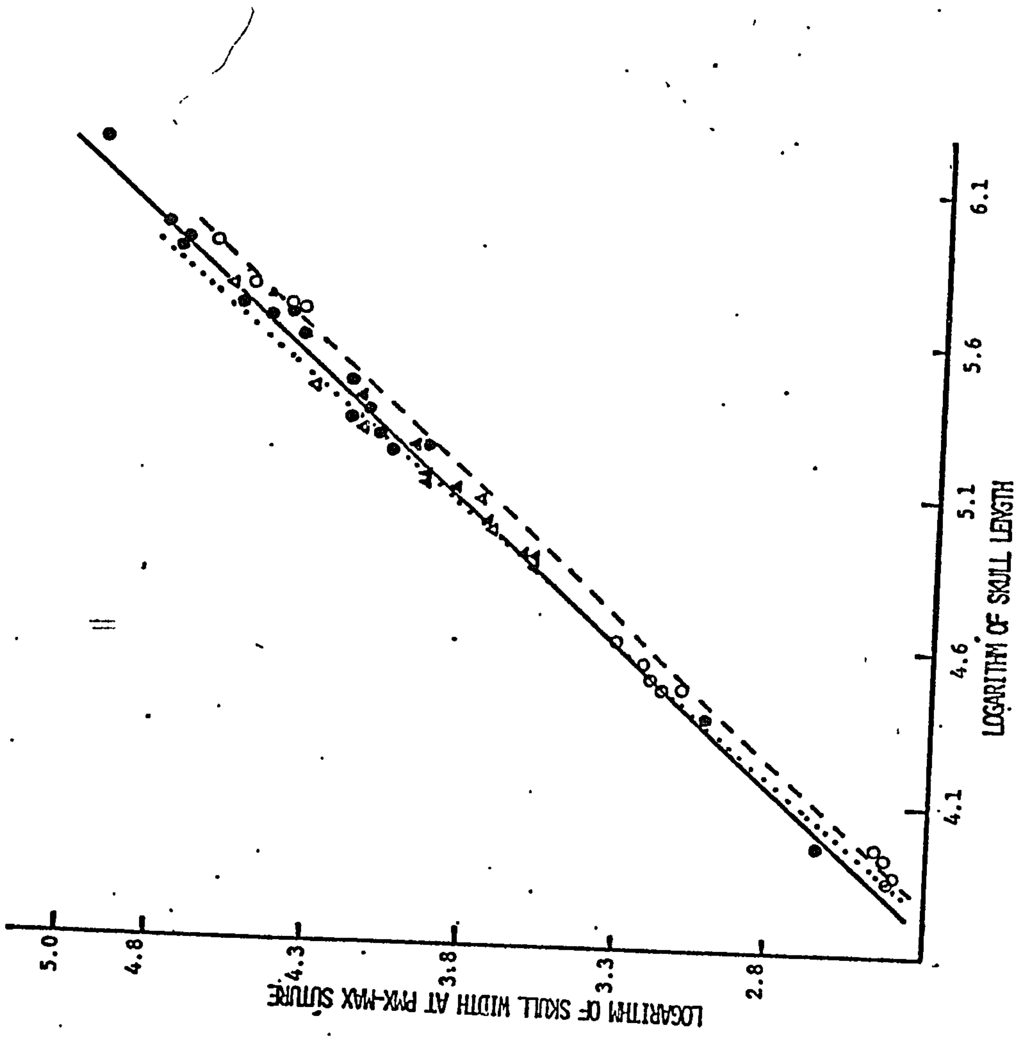
LOGARITHM OF SKULL WIDTH AT PMX-MAX SUTURE
5.0
4.8
4.3
3.8
3.3
2.8
LOGARITHM OF SKULL LENGTH
4.1
4.6
5.1
5.6
6.1

Fig. 8. Scatter diagram and relative growth curves of snout length plotted logarithmically against the logarithm of skull length in three populations of <u>Alligator</u>. Symobls as in Fig. 4.

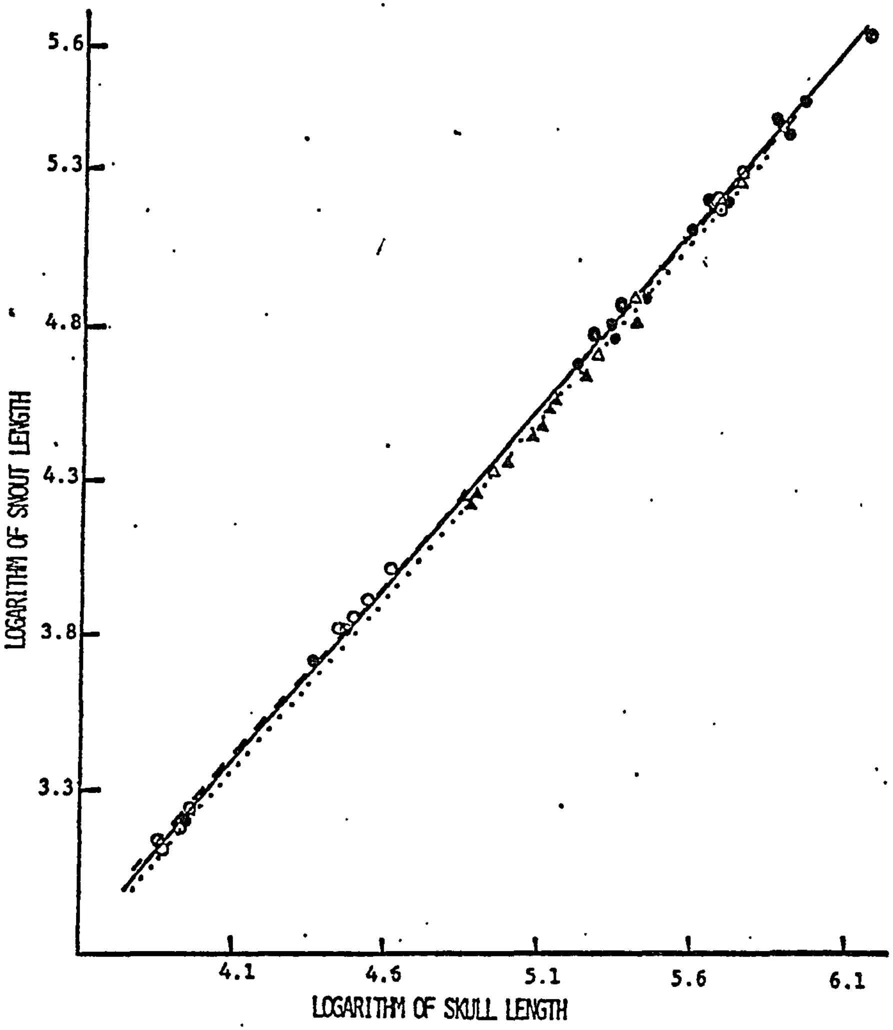
5.6
5.3
4.8
4.3
3.8
3.3
LOGARITHM OF SNOUT LENGTH
4.1
4.6
5.1
5.6
6.1
LOGARITHM OF SKULL LENGTH

Fig. 9. Scatter diagram and relative growth curves if mandibular symphysis length plotted logarithmically against skull length in three populations of <u>Alligator</u>. Symobls as in Fig. 4.

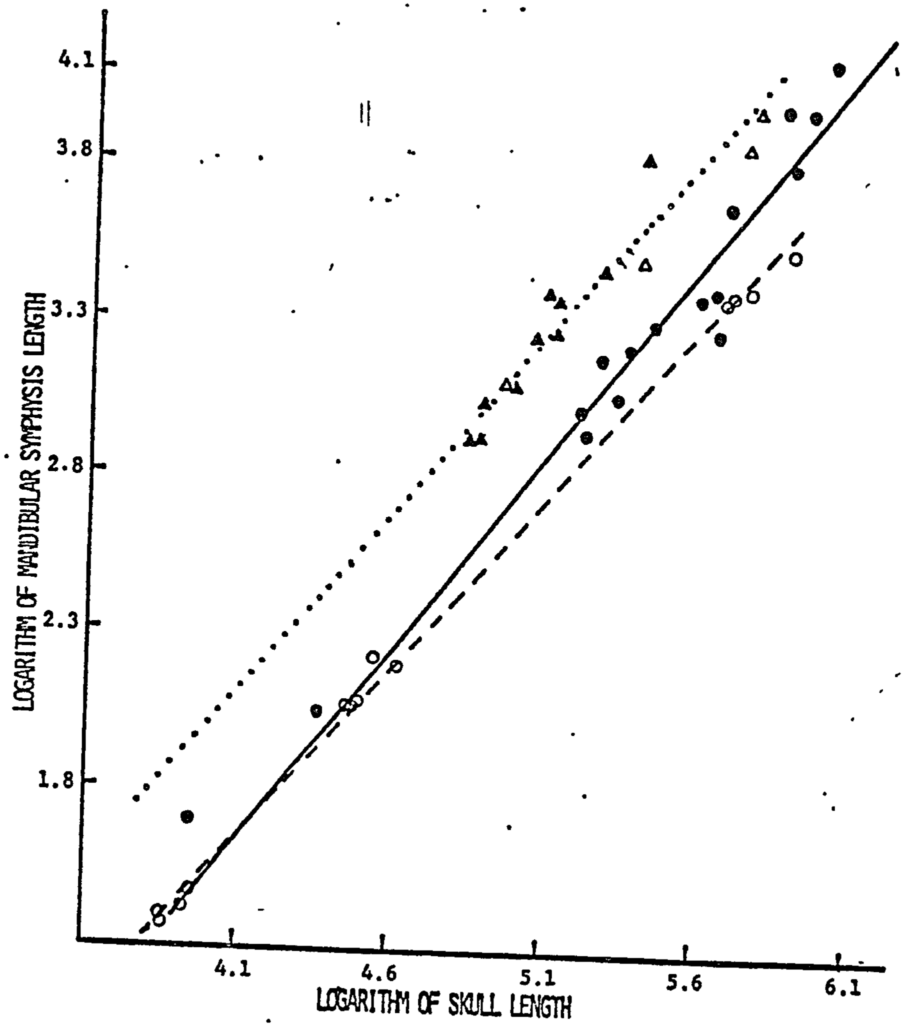
4.1
3.8
3.3
2.8
2.3
1.8
LOGARITHM OF MANDIBULAR SYMPHYSIS LENGTH
4.1
4.6
5.1
5.6
6.1
LOGARITHM OF SKULL LENGTH

TABLE 1

Variables X = skull length Y	N	r_u	r_t	a	b	95% confidence limits for a	95% confidence limits for b	T_0	T_1	T_2
A. mississippiensis (Victoria County, Texas)	13									
skull width at jaw articulation		.999	.996	1.033	-0.819	1.019-1.043	-0.780-(-)0.858	***	ns	***
skull width at postorbital bar		.998	.999	0.947	-0.474	0.937-0.954	-0.447-(-)0.502	***	ns	***
skull width at orbits		.998	.998	0.987	-0.748	0.951-1.011	-0.647-(-)0.850	***	ns	*
skull width at pmx-max suture		.999	.998	1.117	-1.915	1.048-1.162	-1.724-(-)2.106	***	ns	ns
snout length		.999	.999	1.157	-1.338	1.136-1.171	-1.279-(-)1.396	***	ns	ns
mandibular symphysis length		.998	.998	1.087	-2.818	1.050-1.351	-3.068-(-)3.630	***	ns	ns
A. mississippiensis (Alachua County, Florida)	16									
skull width at jaw articulation		.987	.995	1.127	-1.232	1.113-1.137	-1.210-(-)1.254	***	ns	ns
skull width at postorbital bar		.994	.997	1.060	-0.986	1.027-1.085	-0.931-(-)1.040	***	ns	ns
skull width at orbits		.985	.996	1.107	-1.308	1.073-1.131	-1.253-(-)1.362	***	ns	ns
skull width at pmx-max suture		.995	.997	1.102	-1.757	1.077-1.121	-1.717-(-)1.798	***	ns	ns
snout length		.999	.999	1.162	-1.363	1.155-1.168	-1.350-(-)1.375	***	ns	ns
mandibular symphysis length		.967	.985	1.222	-3.349	1.050-1.351	-3.068-(-)3.630	***	ns	ns
A. sinensis										
skull width at jaw articulation	14	.949	.965	1.259	-1.795	1.222-1.286	-1.767-(-)2.858	***	*	
skull width at postorbital bar		.968	.971	1.167	-1.487	1.166-1.167	-1.486-(-)1.487	***	ns	
skull width at orbits		.959	.971	1.254	-2.038	1.201-1.322	-1.985-(-)2.090	***	ns	
skull width at pmx-max suture		.989	.989	1.167	-2.076	1.153-1.178	-2.065-(-)2.086	***	ns	
snout length		.996	.997	1.154	-1.361	1.132-1.182	-2.278-(-)2.635	***	ns	
mandibular symphysis length		.923	.943	1.155	-2.615	0.930-1.326	-2.443-(-)2.787	***	ns	

N = sample size
r_u = correlation coefficient of variable Y with variable X, using actual measurements
r_t = correlation coefficient of variable Y with variable X, using natural logarithms of measurements
a = allomteric coefficient
b = y intercept in the allometric equation
T_0 = test as to whether a differs significantly from zero
T_1 = test as to whether a differs significantly from one
T_2 = test as to whether a values for *A. sinensis* differ significantly from those of *A. mississippiensis*

* $0.05 > p > 0.01$
** $0.01 > p > 0.001$
*** $p < 0.001$
ns not significant ($p > 0.05$)

of the data transformed to their logarithmic form generally yielded higher correlation coefficients than those which were based upon the original arithmetic scale (Table 1).

Both series of plots, however, did show consistent features. With a single exception, there is so much variability within the two living species of alligators that an individual cannot be unequivocally allocated to either on the basis of a single character. This general pattern indicates what other studies have shown; namely that most skull proportions cannot be used to discriminate between different species of Alligator. The only variable to show a discrete pattern that is associated with the taxonomic origin of the sample is the length of the mandibular symphysis (Figure 9).

STATISTICAL FEATURES OF THE BIVARIATE PLOTS

To express the change in shape of the alligator skull as it increases in size the allometric growth equation, $y = bx^a$, was employed. In this equation x = the size of the organism (skull length in this case), y = the size of a part of the skull, a = the allometric growth constant, and b = a constant which is numerically equal to the size of any skull part when body size equals unity (Gould, 1966). Allometric coefficients were calculated for each ontogenetic series by transforming this exponential equation into its linear logarithmic form, $\log y = \log b + a \log x$. The logarithms of the data were fitted by means of Bartlett's best fit (Kidwell & Chase, 1967; Simpson et al., 1960; Sokal & Rholf, 1969). Bartlett's best fit is a Model II regression technique that permits the application of Model I methods for tests of significance (Sokal & Rohlf, 1969, p. 482).

This method was used to calculate 95% confidence intervals for a and b and to compute three tests of significance. These include the following: (1) a test to determine whether a differs significantly from zero i.e. a test of the significance of the regression (T_0); (2) a test to determine whether a differs significantly from one i.e. whether there is a significant departure from an isometric relationship between variables (T_1); (3) a test to determine whether there is a significant difference in values for a between the living species of *Alligator* (T_2).

Intracranial growth is mostly isometric in alligators (Table 1). Only in *A. sinensis* does the width of the skull at the jaw articulation show a positively allometric relationship with respect to skull length. The allometric coefficients of three variables in *A. sinensis* were found to differ significantly from those that characterize the *A. mississippiensis* growth series from Texas. These include skull width at the jaw articulation, skull width at the postorbital bar, and skull width at the orbits (Table 1). However, these same coefficients did not show a significant difference when compared to the Florida sample of the same species. These conflicting results may be caused by the differences in the respective size range of the samples (Florida growth series: N = 16, size range = 52-491 mm; Texas growth series: N = 13, size range = 51-360 mm). It appears from the results of this analysis that allometric growth is not involved in producing the previously observed differences among alligators of different size classes. These differences probably are a result of the considerable variability in growth processes that occurs among individuals.

Three of the variables used in this study were also examined by Dodson (1975) in his study of relative growth in *A. mississippiensis*.

Table 2 summarizes the results of my analysis of the relative growth of these variables and those of Dodson (1975, Table 3). Dodson found that the width of the skull at the orbits and the length of the snout grew in a positively allometric fashion with respect to skull length; the results of my analysis, on the other hand, indicate isometric growth. These inconsistencies may be related to the different samples used in the two analyses. Although Dodson's sample was not comprised of individuals from a single geographical locality, it did consist of a larger number of individuals and spanned a greater size range than did the samples used in this study.

Dodson's results may have been significantly influenced by his use of zoo specimens and/or by his use of specimens from different geographic populations. Geographic populations of _A_. _mississippiensis_ from Texas and Florida were found to differ in their respective patterns of skull growth, although they did not differ significantly from each other ($p > 0.05$).

These discrepancies could also be explained if the allometric coefficient changes during ontogeny. The samples used in this study did not span as large a size range as the sample used by Dodson. The allometric relationships may not have been detected if allometric growth occurs only in very large individuals which were poorly represented in my samples.

QUALITATIVE CHARACTERS

In the following section I discuss the skull variation of alligators that I observed. Examples of most of the character states that are used in the diagnosis of taxa are illustrated, as are several significant

TABLE 2

VARIABLES	N	SR	a	b	T_1
A. mississippiensis (Dodson, 1975)					
skull width at jaw articulation	39	35 - 632	0.99	0.470	ns
skull width at orbits	39	35 - 632	0.98	0.533	*
snout length	35	35 - 632	1.10	0.311	***
A. mississippiensis (Texas)					
skull width at jaw articulation	13	48 - 360	1.033	-0.819	ns
skull width at orbits	13	48 - 360	0.987	-0.748	ns
snout length	13	48 - 360	1.157	-1.338	ns
A. mississippiensis (Florida)					
skull width at jaw articulation	16	52 - 491	1.127	-1.232	ns
skull width at orbits	16	52 - 491	1.107	-1.308	ns
snout length	16	52 - 491	1.162	-1.363	ns

N = sample size
SR = size range (skull length in mm)
a = allometric coefficient
b = y intercept of the allometric equation
T_1 = test as to whether a differs significantly from one

* $0.05 > p > 0.01$
** $0.01 > p > 0.001$
*** $p < 0.001$
ns not significant ($p > 0.05$)

features that varied in a continuous manner. Characters are referred to by letters (A-G); character states are referred to by numbers (0-3). Subsequent analysis of the characters determined the probable primitive to derived sequence of character states (see section on phylogenetic inference).

The cranial morphology of representative alligators is illustrated in Figures 10-15. All alligators possess relatively short, broad snouts that are more or less uniform in width. In some alligators the lateral margins of the rostrum gradually converge anteriorly (Figures 11a, 13a, 14a); in others they remain more or less parallel (Figures 10a, 12a).

Besides the characteristic sculpturing of the dorsal surface of the skull and lateral surfaces of the lower jaw, crocodilian skulls generally possess a series of bony ridges or crests that often develop around the margins of the skull openings, as well as in the rostral region. In alligators the rostrum generally bears two pairs of longitudinal crests that extend medio-laterally from the anterior border of the orbits to the swellings above the fourth maxillary tooth (also the largest of the series). In some alligators a transverse bony ridge, which is generally located immediately anterior to the orbits, conjoins the longitudinal ridges. Some authors have attempted to use crest patterns to characterize different species of _Alligator_. For example, Iordansky (1973) and Mook (1923a) reported that a transverse crest appears in _A. sinensis_; White (1942) reported a highly developed crest in _A. olseni_; Mook reported a similar development in _A. thomsoni_ (1923b) and _A. mefferdi_ (1946). However, I have found that the

Fig. 10A. Dorsal view of the skull of A. mississippiensis (AMNH 40582). Scale line equals 100 mm.

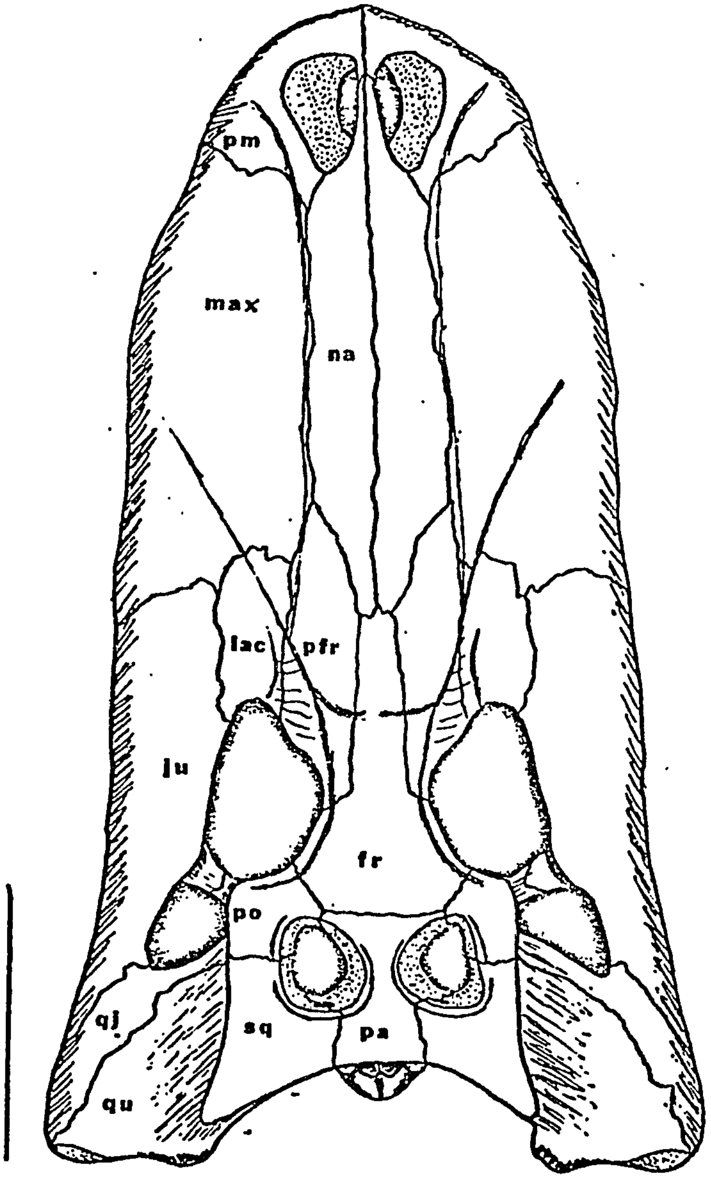
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Fig. 10B. Medial view of the left mandibular ramus of A. mississipiensis (AMNH 40582). Scale line equals 100 mm.

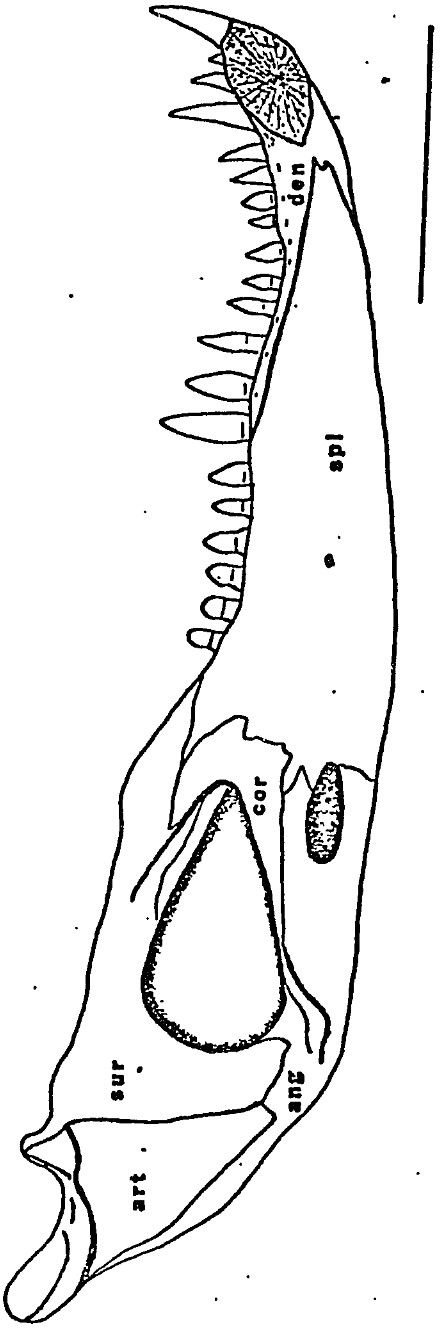
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Fig. 11A, Dorsal view of the skull of *A, sinensis* (UMMCZ S781). Scale line equals 100 mm.

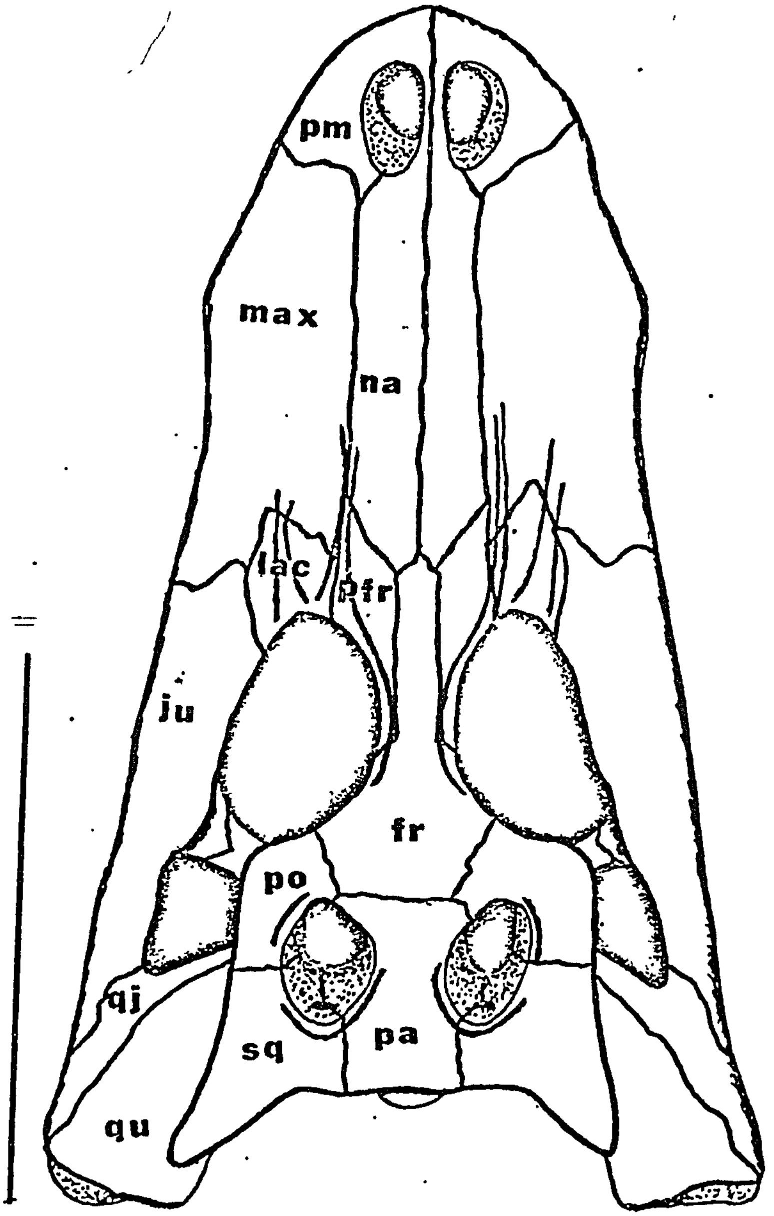
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Fig. 11B. Medial view of the left mandibular ramus of *A. sinensis* (UMMCZ S781). Scale line equals 100 mm.

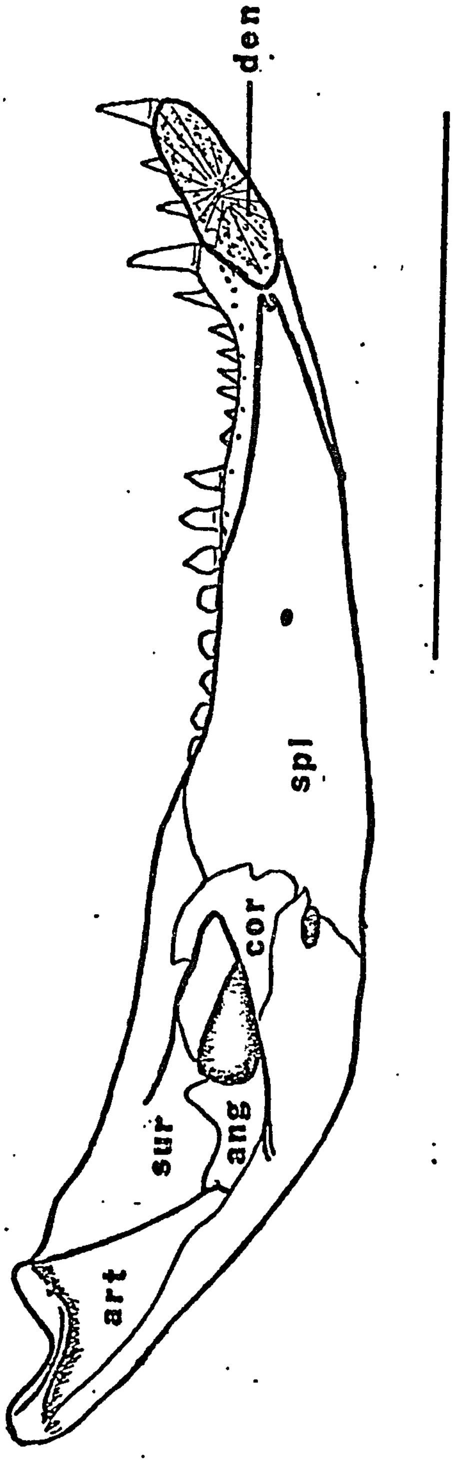
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Fig. 12A. Dorsal view of the skull of *A. olseni* (uncatalogued MCZHU specimen). Scale line equals 100 mm.

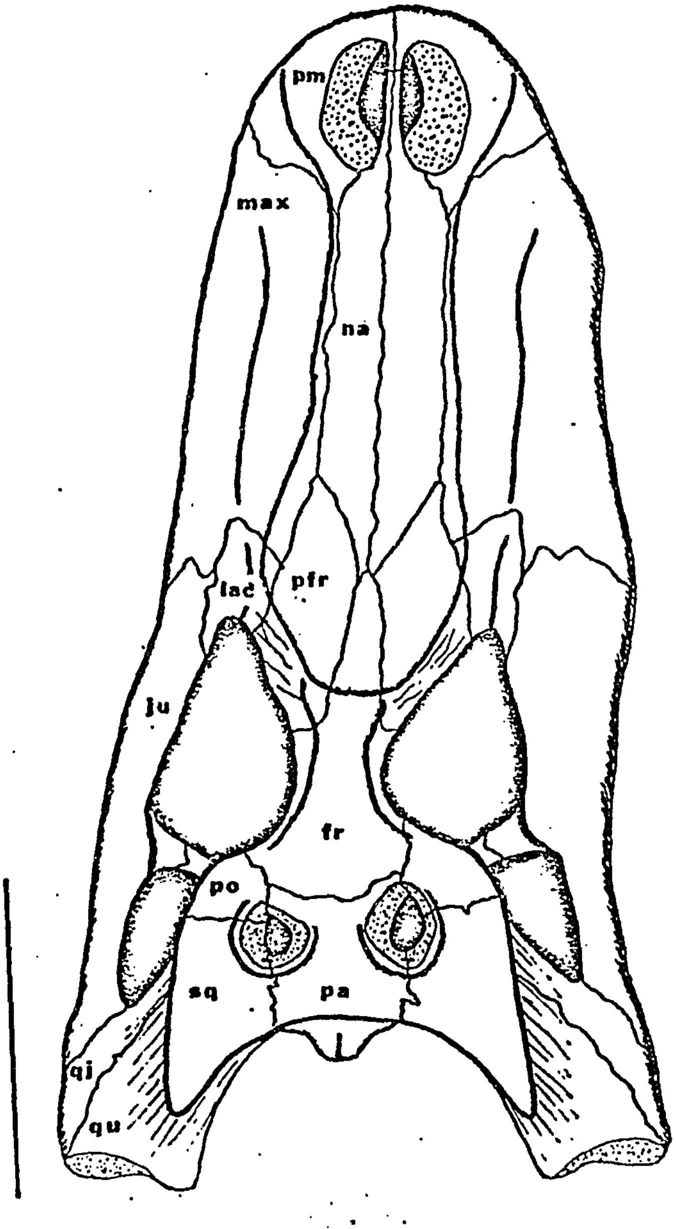
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Fig. 12B. Medial view of the left mandibular ramus of *A. olseni* (MCZHU 1888). Scale line equals 100 mm.

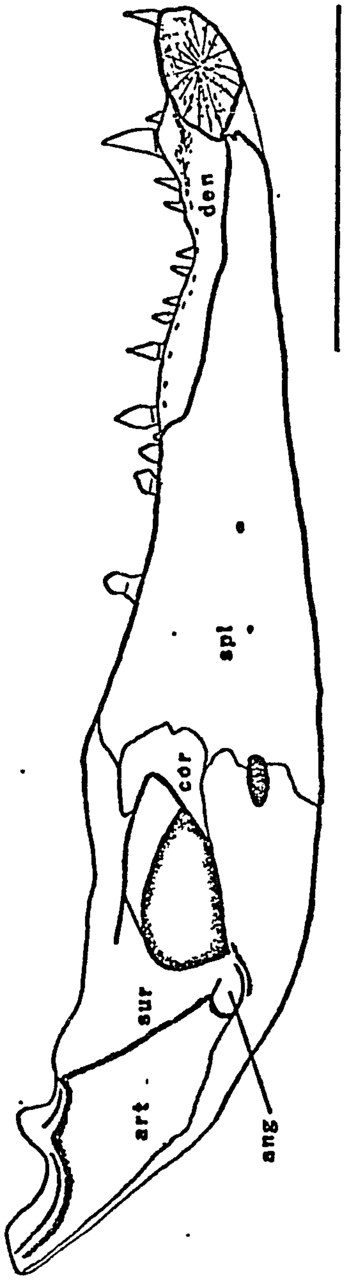
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Fig. 13A. Dorsal view of the skull of *A. mcgrewi* (FMNH P26242). Scale line equals 100 mm.

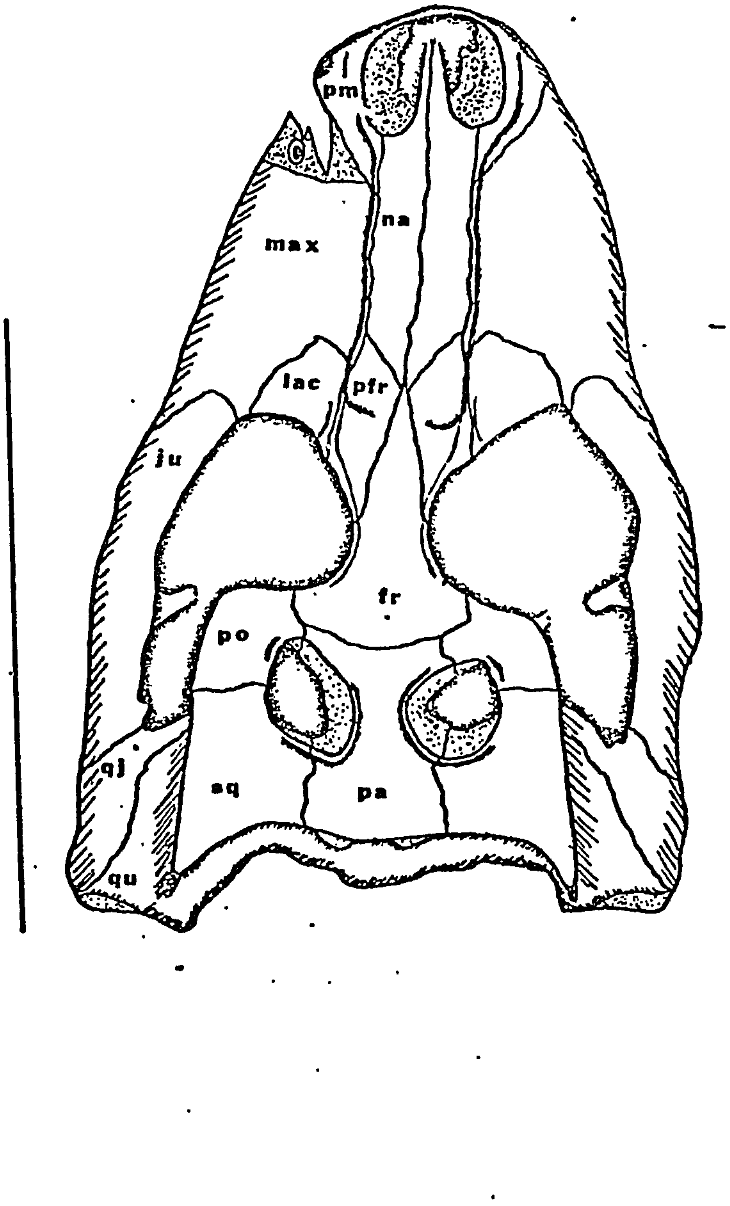
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Fig. 13B. Medial view of the left mandibular ramus of *A. mcgrewi* (FMNH P26242). Scale line equals 100 mm.

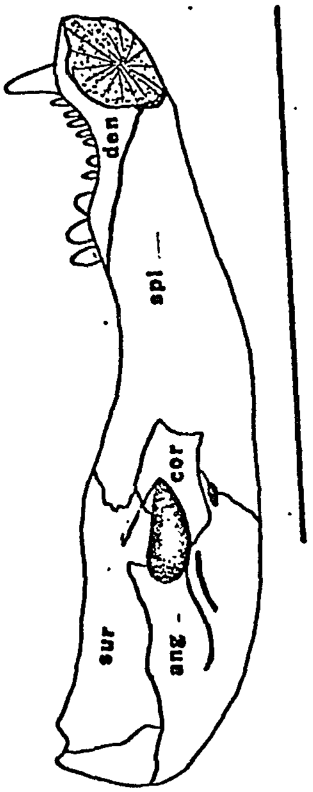
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Fig. 14A. Dorsal view of the skull of *A. prenasalis* (SDSM 6590). Scale line equals 100 mm.

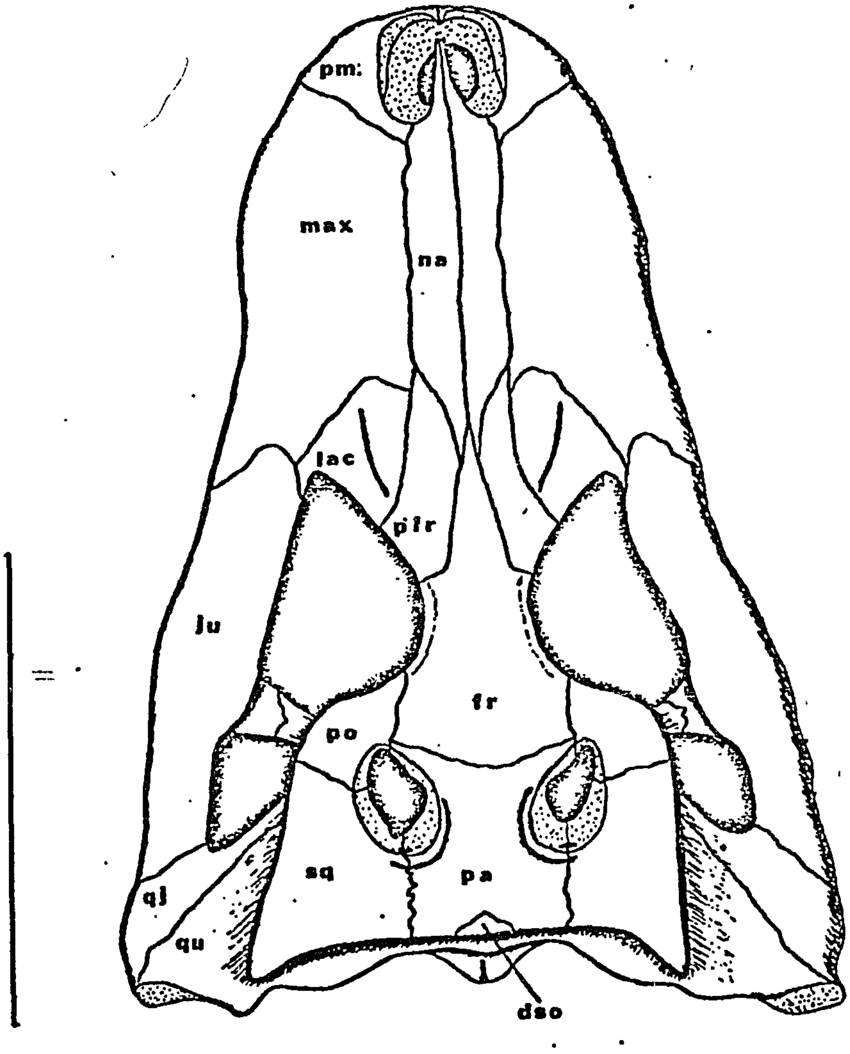
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Fig. 14B. Medial view of the right mandibular ramus of *A. prenasalis* (SDSM 14063). Scale line equals 100 mm.

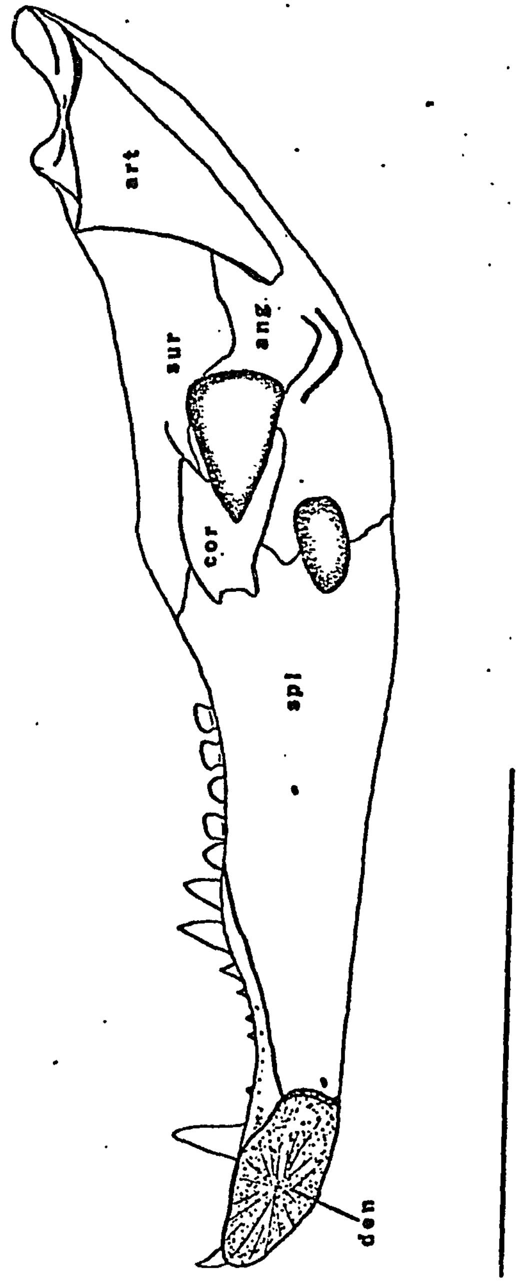
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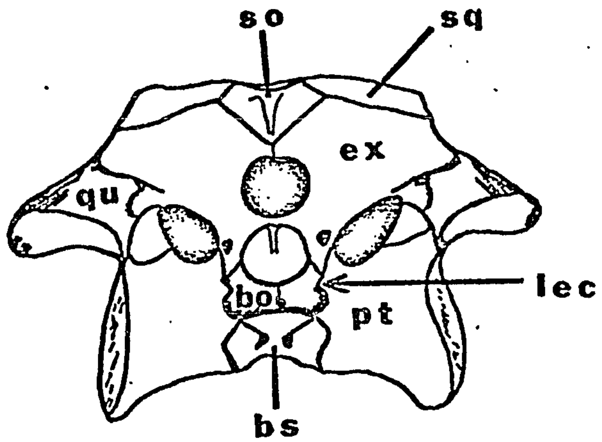
Fig. 15. Posterior view of the occipital region of the alligator skull illustrating the variation in the shape of the basioccipital. A. Basioccipital with lateral processes immediately dorsal to the openings of the lateral Eustachian canals. B. Basioccipital without lateral processes.



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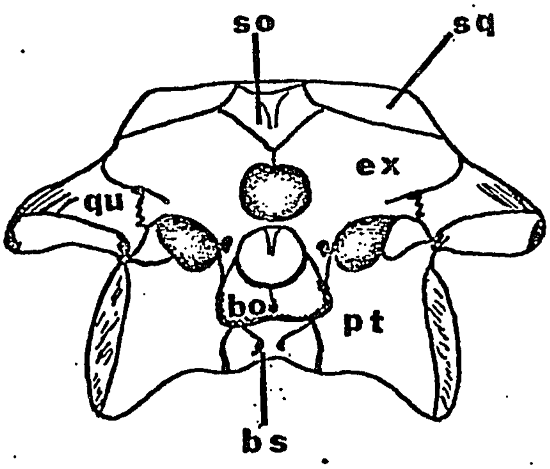


B

development of this crest is quite variable. Even A. mississippiensis, which is supposed to lack this feature, shows variable development of a crest in the orbital region. This crest varies to such a degree in its topographic position, degree of development and completeness, that I was unable to distinguish distinct patterns, outside of one associated with ontogeny. In general, larger individuals exhibit more robust crests than those that are smaller in size.

CHARACTER A: external narial aperture. 1-completely divided by an ossified internarial septum (Figures 10A-14A).

In alligators the external narial aperture, which is located near the anterior tip of the snout, is elevated to variable degrees above the rostrum. Alligators appear to be unique among the Alligatoridae in possessing an ossified internarial septum which completely divides the external narial aperture. This septum is formed by anteriorly directed processes of the nasals which articulate with corresponding posteriorly directed processes of the premaxillaries. Higgins (1971) reported that the internarial septum is complete only in some specimens of A. prenasalis and incomplete in others. Close examination of these latter specimens indicates that this situation is the result of breakage, and that the internarial septum was probably complete in these specimens as well.

CHARACTER B: shape of interorbital region. 0-relatively wide and flat (Figure 14A). 1-relatively narrow with thickened lateral margins which are raised above the surrounding bone (Figures 10A-13A).

As was pointed out above, crocodilian skulls generally possess a series of bony ridges that often develop around the margins of many of the skull openings. Crests are sometimes well developed along the dorsal border of the orbits or are incipiently developed. In such situations the interorbital plate is also relatively narrow. In other forms the interorbital region is relatively wide and lacks the thickened lateral margins.

CHARACTER C: formation of the dorsal surface of skull table along the posterior border. 0-lateral portions formed by paired squamosals with medial portion formed by dermosupraoccipital plus paired processes of parietal (Figure 14A). 1-lateral portions formed by paired squamosals with medial portion formed by parietal only (Figures 10A-13A).

CHARACTER D: medio-posterior border of the external mandibular fenestra. 0-formed by an ascending process of the angular (Figures 11B, 13B, 14B). 1-formed by a descending process of the surangular (Figures 10B, 12B).

CHARACTER E: shape of the bassioccipital. 0-with lateral processes lying above the openings of the lateral Eustachian canals (Figure 15A). 1-without lateral processes (Figure 15B).

Many of the skull and jaw bones of crocodilians are pneumatic and contain cavities which connect with one another to form two systems. One of these is associated with the nasal passages, while the other forms the Eustachian canal system (Iordansky, 1973). The middle ear system opens into the pharynx by a single medial and a pair of lateral

Eustachian canals that lie at the suture of the basioccipital and the basisphenoid. In alligators the openings of the lateral Eustachian canals may lie just beneath lateral processes of the basioccipital, or be obscured by an expanded basioccipital.

CHARACTER F: construction and relative length of the mandibular symphysis. 0-dentaries plus splenials; relatively long, extending posteriorly to a point level with the sixth, seventh or eighth mandibular tooth (Figures 13B, 14B). 1-splenial barely makes contact with the symphysis; relatively short, extending posteriorly to a point level with the third, fourth or fifth mandibular tooth (Figure 12B). 2-dentaries only; relatively short, extending posteriorly to a point level with the third, fourth or fifth mandibular tooth (Figure 10B). 3-dentaries only; relatively short, extending posteriorly to a point level with the fifth or sixth mandibular tooth (Figure 11B).

The length of the mandibular symphysis varies considerably among alligators. In _Alligator mississippiensis_, which has the shortest symphysis among Recent crocodilians, it can extend as far back as the fifth mandibular tooth, while in _A. sinensis_, it can reach back as far as the sixth mandibular tooth.

Not only is there considerable taxonomic variation regarding this character, but there is also significant ontogenetic and individual variation within a species as well. For example, in the ontogenetic series of skulls of _A. mississippiensis_ and _A. sinensis_, which were used in this study, it was observed that the mandibular symphysis increased in length during ontogeny (relative to the mandibular tooth row). It was found that the symphysis extended as far back as the third mandibular tooth in small members of the series of A. mississippiensis (jaw lengths 50-197 mm; N = 4), between the third and fourth mandibular tooth in individuals of intermediate size (jaw lengths 198-445 mm; N = 13), and as far back as the fifth tooth in the largest individuals (jaw lengths 490-570 mm; N = 2). However, there is also some individual variation in this character; occasionally specimens were found that possessed relatively shorter symphyses than smaller individuals of the series. Similar patterns of variation also characterize A. sinensis and fossil forms. In A. sinensis the symphysis extends as far back as the fifth tooth (jaw lengths 153-156 mm; N = 2), between the fifth and sixth tooth (jaw lengths 161-281 mm; N = 12) or as far back as the sixth mandibular tooth (jaw lengths 229-310 mm; N = 2).

Although there are some exceptions, a dentary-splenial mandibular symphysis is generally characteristic of longirostrine crocodilians. A dentary-splenial symphysis also occurs in several forms of Alligator, while in other forms the splenial has lost its contact with the symphysis. In some alligators the splenial bones may barely reach this joint, or they may not contact it at all.

CHARACTER G: palatine bullae. 0-absent. 1-present.

As mentioned above, many of the cranial elements of crocodilians are pneumatic, and the cavities are connected to form systems associated with the middle ear and the nasal passages. This latter system includes cavities within the premaxillaries, maxillaries, palatines, pterygoids and occasionally the prefrontals and vomers

(Iordansky, 1973). Portions of the palatines and/or the pterygoids may expand dorsally to form bullae. In Alligator sinensis, which is the only alligatorid to possess such structures, they are entirely contained within the palatines.

TAXONOMY

Order Crocodilia	Gmelin, 1788
Suborder Eusuchia	Huxley, 1875
Family Alligatoridae	Gray, 1844

Discussion: Current classifications of the order Crocodilia generally recognize five major groups of equal or variable rank; Protosuchia, Mesosuchia, Thalattosuchia, Sebecosuchia and Eusuchia (Kalin, 1955a; Romer, 1956, 1966). These groups more or less correspond to the major radiations that have occurred during the evolutionary history of the group, some of which involved the attainment of new levels of organization (e.g. the Mesosuchia and Eusuchia). All extant crocodilians are assigned to the Eusuchia, which is distinguished from more primitive groups primarily on the basis of the extent of the development of the secondary palate. The secondary palate is effectively lengthened in the eusuchians by the addition of palatal processes of pterygoid bones to those of the premaxillaries, maxillaries and palatines.

Living representatives of the Eusuchia are generally considered to represent three adaptive types, alligators (in the broad sense), crocodiles and gavials, which have been formally recognized at various hierarchical levels in crocodilian classifications (Kalin, 1955a; Kuhn, 1968; Mook, 1934; Romer, 1956, 1966; Steele, 1973; Wermuth, 1953; Wettstein, 1954). I have decided to treat each of these groups as distinct families, since their relationships to each other are still obscure. These groups have been broadly characterized in terms of their relative skull proportions. The Alligatoridae, which contains the Recent South American genera *Caiman*, *Melanosuchus* and *Paleosuchus*, as well as the genus *Alligator*, typically possess relatively broad, moderately elongated snouts. The Crocodylidae, which contains the Recent genera *Crocodylus*, *Osteolaemus* and *Tomistoma*, usually possess longer and more slender snouts. Nevertheless, extensive variation in skull proportions does occur within these assemblages, and some overlap does occur among them. Although the single living gavial (Gavialidae) is characterized by extreme specializations of the longirostrine condition, fossil gavials exhibit considerable variation in skull proportions and superficially resemble the crocodylid genus *Tomistoma* (Hecht & Malone, 1972).

Because of the considerable variation in skull proportions, that occurs in each of these groups, delineation of the major eusuchian groups on the basis of relative skull proportions has proven to be less than satisfactory. These assemblages can be delineated, on the other hand, by reference to the general pattern of tooth occlusion that characterizes each. In alligatorids the mandibular teeth lie medial to the tooth rows of the upper jaw when the jaws are closed; consequently, the mandibular teeth are accommodated by pits running along the palate medial to the tooth row. In contrast, the mandibular teeth in the Crocodylidae and Gavialidae lie outside, or in between, the teeth of the upper jaw (Iordansky, 1973).

Genus *Alligator* Cuvier, 1807

Champsa	Wagler, 1830
Champa	Aggasiz, 1846
Caimanoidea	Mehl, 1916
Caimanoeda	Mehl, 1916
Caimanoideus	Mehl, 1916
Caigator	Deraniyagala, 1947

Type species: *A. mississippiensis* (Daudin, 1801). The generic name *Alligator* Cuvier was originally published as the name for a subgenus of *Crocodylus*. However, Cuvier did not designate or indicate a type species for his subgenus. The first type selection for the genus was made by Stejneger and Barbour (1917) who selected the nominal species *Crocodilus* (*Alligator*) *lucius* Cuvier.

Diagnosis: Alligatorid eusuchians with relatively broad, flat snouts that are more or less uniform in width. Distinguished from all other known alligatorids by the presence of an ossified internarial septum which completely divides the external narial aperture longitudinally. Further distinguished by the exclusion of the dermosupraoccipital bone from the dorsal surface of the skull table (except for *A. prenasalis*). Lacrymals excluded from contact with the nasals by long processes of the prefrontals. Tooth crowns varying in size and shape with the most posterior series (usually the last four) appearing relatively blunt, laterally compressed and lying in a common alveolar groove. Each premaxillary containing 5 teeth; each maxillary 12-15; each mandibular ramus 19-20.

Geographic and geologic range: North America throughout the middle and late Cenozoic (Chadronian to Recent; eastern Asia during the Recent).

Discussion: The reported presence of *Alligator* in Asia during the Miocene by Chow and Wang (1964), which is based upon an isolated tooth, may be premature. Isolated teeth are not sufficiently diagnostic for reference to most crocodilian taxa because of the considerable variability in the size and shape of teeth that occurs among individuals (both along the tooth row and ontogenetically) and within taxa at all hierarchical levels (Edmund, 1962, 1966; Kalin, 1933a).

Alligator mississippiensis Daudin, 1801

Crocodilus mississippiensis Daudin, 1801
Crocodilus lucius Cuvier, 1807
Alligator lucius St. Vincent, 1824
Alligator cuvieri St. Vincent, 1824
Champsa lucia Wagler, 1830
Alligator mississippensis Gray, 1831
Alligator helois Cope, 1865
Alligator thomsoni Mook, 1923. NEW SYNONOMY.
Alligator mefferdi Mook, 1946. NEW SYNONOMY.

Holotype: preserved skin (Natural History Museum, Paris)

Geographic and geologic range: the coastal plains of southeastern United States from Virginia southward into Florida, westward into Texas and northward up the Mississippi River Valley into Arkansas during the Recent; Florida during the Rancholabrean, Irvingtonian and Hemphillian; Nebraska and Texas during the Clarendonian and Barstovian (see below for fossil localities).

Ichtucknee River, Columbia County, Florida (Rancholabrean)

Referred material: right mandibular ramus, FAMNH 7988; complete skulls, FSM 1813, 92757.

McLeod's Lime Rock Mine, Levy County, Florida (early Irvingtonian)

Referred material: incomplete skull and partial left mandibular ramus, FAMNH 7902; incomplete skull, FAMNH 7901; various skull fragments, FAMNH 7912, 7936, 7945; incomplete mandibular rami, FAMNH 7911, 7913, 7914, 7946, 7949, 7915; humeri, FAMNH 7950 A, B, D, E; ulna, 7962 F-H, J-L; fibula, FAMNH 7962 I.

Mixon's Bone Bed, Levy County, Florida (Hemphillian)

Referred material: skulls and mandibles, FAMNH 7903 (partially crushed), 7904 A, 7908, more or less complete postcranial skeleton, FAMNH 7904; incomplete mandibles, FAMNH 7909, 7926, 7930, 7931, 7933; incomplete mandibular rami, FAMNH 7910, 7917, 7918, 7919, 7921, 7922, 7932, 7934 A, 7937, 7938 A, B, 7958, 7959, 7960, 7916, 7920, 7927, 7963, 7934 B, 7957, 7976, 7977, 7978, 7991; many postcranial elements.

Middle Ash Hollow Formation, Cherry County, Nebraska (late Clarendonian)

Referred material: nearly complete skull, mandible and several postcranial elements, FAMNH 7016.

Lower Ash Hollow Formation, Donley County, Texas (early Clarendonian)

Referred material: a nearly complete skull and mandible, FAMNH 7906.

Olcott Formation, Sioux County, Nebraska (early Barstovian).

Referred material: complete skull, AMNH 1736; partial right and left mandibular rami, AMNH 1738, 1730.

Flemming Formation, San Jacinto County, Texas (early Barstovian).

Referred material: an incomplete skull and skull fragments, FAMNH 7907; incomplete mandibular rami, Field Numbers CRO. 17-356, CRO. 22-632.

Diagnosis: An alligator with an extremely broad snout; lateral borders remaining more or less parallel to each other anteriorly. Distinguished from all other known species of the genus by a basioccipital bone in which the lateral margins run uninterrupted and obliquely in the medio-lateral direction to form paired wing-shaped areas. This expansion of the basioccipital bone obscures the openings of the lateral Eustachian canals which lie in the basioccipital-basisphenoid suture. Distinguished from *A. olseni* by a mandibular symphysis that is not met by the splenial bones. Distinguished from *A. sinensis* by a relatively shorter mandibular symphysis, extending as far back as the third, fourth or fifth mandibular tooth, and by a descending process of the surangular which forms the medio-posterior border of the external mandibular fenestra. Distinguished from *A. mcgrewi* and *A. prenasalis* by a descending process of the surangular forming the medio-posterior border of the external mandibular fenestra, by a relatively short mandibular symphysis formed by the dentaries only, and further distinguished from the latter form by a relatively narrow and uprolled interorbital region.

Description: Maximum length attainable approximately six meters; largest skull used in this study measured 491 mm in length, although larger skulls can be found in osteological collections. The characteristic sculpturing of the skull is relatively poorly developed on the jugal and quadratojugal and on the lateral surfaces of the lower jaw. Two pairs of prominent bony crests running longitudinally in the rostral region; an incomplete and varyingly developed transverse crest situated immediately anterior to the orbits. Snout somewhat depressed immediately anterior to the orbits but elevated near the external narial aperture. Lower jaw relatively gracile in form. Each premaxillary containing 5 teeth; each maxillary 14-15, each mandibular ramus 19-20.

Discussion: The original spelling of the specific name applied to this taxon (mississipiensis) was emended by ICZN Direction 97 (Hemming, 1958).

My diagnosis of A. mississippiensis is based upon Recent material. These features exhibit minor variations within the series of skulls examined with one notable exception. It was observed that the relative length of the mandibular symphysis with respect to the mandibular tooth row increases during ontogeny. In small individuals of the series (jaw lengths: 59-197 mm, N = 4) the symphysis extends as far back as the third tooth, from the third to the fourth in individuals of intermediate size (jaw lengths: 198-445 mm, N = 13) and as far back as the fifth mandibular tooth in the largest individuals of the growth series (jaw lengths: 490-570 mm, N = 2). Occasional individual variation in this character was also observed; some specimens possess relatively shorter symphyses with respect to the mandibular tooth row than smaller individuals of the series.

Some of the fossil samples which I have referred to A. mississippiensis exhibit significant variation in some of the diagnostic features of this taxon. Although the Recent samples of A. mississippiensis show insignificant variation in the shape of the basioccipital bone, the samples from McLeod's Lime Rock Mine and Mixon's Bone Bed contain individuals that deviate from this pattern. One individual from the former sample (FAMNH 7901) possesses a typical A. mississippiensis basioccipital, while another (FAMNH 7902) has a basioccipital typical of other Alligator species. In this individual this element bears a pair of lateral processes situated above the openings of the lateral Eustachian canals. The individuals from Mixon's Bone Bed show the same pattern of variation. The single specimen from the Middle Ash Hollow Formation (FAMNH 7016) possesses a basioccipital typical of Recent forms, while those from the Lower Ash Hollow, Olcott and Flemming Formations possess the alternate state. It would appear that while an expanded basioccipital is typical of Recent populations of A. mississippiensis fossil samples contain individuals that possess both types.

Mook (1923b) originally designated a well preserved skull (AMNH 1737) as the type specimen and three mandibular rami as the paratypes of A. thomsoni. Mook considered this taxon sufficiently distinct from previously described forms in terms of its relative skull proportions to warrant its recognition as a new species. Two of these rami (AMNH 1738 and 1739), although fragmentary in nature, are approximately the same size and may belong to the skull. The third ramus (AMNH 1737), which is morphologically distinct from the larger ones, was collected during the following year from the same quarry, but there is no indication in the field notes as to the relative stratigraphic positions of the specimens. In AMNH 1737 the symphysis extends posteriorly to the eighth tooth; in both of the larger specimens it extends back to the fifth tooth. Although the splenial bones are missing in the latter specimens, it is evident that they did not contact the symphysis; in AMNH 1737 the splenial bones actually participate with the dentaries in its formation. I refer this latter specimen to *A. mcgrewi* since it falls within the range of variation of this taxon (see below). I have found that the skull and the two large rami, which belong to the nominal species *A. thomsoni*, to be indistinguishable from *A. mississippiensis* and, therefore, refer them to this taxon.

Mook (1946) also proposed that a single specimen from the Middle Ash Hollow Formation (FAMNH 7016) was sufficiently distinct in terms of its relative skull proportions to also warrant its recognition as a new species. However, the specimen is indistinguishable from *A. mississippiensis* in those features which I consider to be diagnostic of this taxon. I, therefore, refer this specimen to *A. mississippiensis* and also make *A. mefferdi* a new synonym of this taxon.

Alligator sinensis Fauvel, 1879

Alligator chinensis	Gunther, 1889
Alligator sinense	Mook, 1923
Caigator sinensis	Deraniyagala, 1951

Holotype: no type or type series has been designated.

Geographic and geologic range: lower regions of the Yangtze River Valley, The People's Republic of China during the Recent.

Diagnosis: An alligator with a moderately broad snout; lateral borders gradually converging anteriorly. Distinguished from all other known species of the genus by the presence of palatine bullae and by a moderately short mandibular symphysis, extending as far back as the fifth or sixth mandibular tooth and formed by the dentaries only. Distinguished from A. mississippiensis and A. olseni by its relatively longer mandibular symphysis and by an ascending process of the angular forming the medio-posterior border of the external mandibular fenestra. Distinguished from A. mcgrewi and A. prenasalis by a relatively shorter mandibular symphysis formed by the dentaries only.

Description: Maximum length attainable approximately two meters; the largest skull used in this study measured 310 mm in length. Dorsal and lateral surfaces of the skull and lower jaw heavily sculptured. Prominent bony crests running longitudinally in the rostral region; an incomplete and varying developed transverse crest situated immediately anterior to the orbits. Snout somewhat depressed immediately anterior to the orbits but elevated near the external narial aperture. Lower jaw moderately robust. Each premaxillary containing 5 teeth; each maxillary 14; each mandibular ramus 19.

Alligator olseni White, 1942

Holotype: MCZHU 1887, complete skull

Hypodigm: MCZHU 1888, left mandibular ramus; MCZHU uncatalogued, several mandibular rami and a nearly complete skull.

Geographic and geologic range: Hawthorne Formation, Gilchrist County, Florida (Hemingfordian).

Diagnosis: An alligator with an extremely broad snout; lateral borders remaining more or less parallel to each other anteriorly.

Distinguished from all other species of Alligator by a relatively short mandibular symphysis, extending as far back as the third, fourth or fifth mandibular tooth but with the splenials barely contacting the symphysis. Distinguished from A. mississippiensis by a basioccipital with lateral processes situated immediately above the openings for the lateral Eustachian canals. Distinguished from A. mcgrewi and A. prenasalis by a descending process of the surangular forming the medio-posterior border of the external mandibular fenestra, and from the latter by a prominently uprolled interorbital region.

Description: Largest skull 334 mm in length. Sculpturing moderately developed. Prominent preorbital transverse bony ridge. Snout strongly depressed anterior to orbits. Each premaxillary containing 5 teeth; each maxillary 14 (?)-15; each mandibular ramus 20.

Discussion: The known ontogenetic series of cranial elements of A. olseni is quite limited in terms of its size range; most of the material represents moderately large individuals (skull length: 286-341 mm, N = 3; jaw length: 320-383 mm, N = 4). As a result, the length of the symphysis in this series does not show a similar range of variation as in an ontogenetic series of Recent forms. The symphysis extends as far back as the fourth or fifth mandibular tooth in specimens that I have referred to *A. olseni*, but probably would extend only as far back as the third tooth in smaller individuals. The mandibular series of *A. olseni* exhibits unusual variation in terms of the manner in which the symphysis is constructed. The splenial bones may barely reach the symphysis in some individuals, or they may not contact it at all. In any event, the splenial bones do not actually participate in the construction of this joint.

Alligator mcgrewi Schmidt, 1941

Holotype: FMNH P26242, a nearly complete skull and mandible.

Hypodigm: FAMNH 7905, complete skull lacking mandible; FAMNH 8700, complete skull and mandible; FAMNH 10316, complete mandible; FAMNH 1741, 1742, 7980, skull fragments; FAMNH 1737, 1740, 7905, 7981, 7997, FAMNH Field Number S112-4282, S115-4397, S115-9269, S128-5009, S140-5870, S173, 9119, S175-9269, S207-1184, S208-1184, S208-11267, S220-12288, complete and fragmentary mandibular rami.

Geographic and geologic range: Marsland Formation, Sheep Creek Formation and equivalents (Hemingfordian) and Lower Snake Creek Formation and equivalents (Barstovian), northwestern Nebraska.

Diagnosis: An alligator with a moderately broad snout; lateral borders gradually converging anteriorly. Distinguished from *A. prenasalis* by the exclusion of the dermosupraoccipital from the dorsal surface of the skull table, by the incipient uprolling of the interorbital region and by laterally compressed posterior teeth. Distinguished from

A. sinensis by a relatively longer mandibular symphysis, extending as far back as the sixth, seventh or eighth mandibular tooth, and formed by the dentaries plus splenials. Distinguished from A. olseni by a relatively longer mandibular symphysis and by an ascending process of the angular which forms the medio-posterior border of the external mandibular fenestra.

Description: Sculpturing on the skull and lower jaw moderately heavy, but somewhat variable; preorbital transverse bony ridge well developed in some individuals (FAMNH 8700). Each premaxillary containing 5 teeth; each maxillary 13-14; each mandibular ramus 19.

Discussion: Because the known specimens which are referred to A. mcgrewi form a limited growth series, the length of the mandibular symphysis does not show the same degree of variation that characterizes Recent Alligator taxa. The series of specimens that are assigned to this taxon represent moderately small individuals (skull length: 138-156 mm, N = 3; jaw length: 203-248 mm, N = 3). The symphysis extends back to the sixth or seventh tooth in these specimens. Presumably the symphysis would extend as far back as the eighth tooth in larger individuals.

Alligator prenasalis Loomis, 1904

Crocodilus prenasalis	Loomis, 1904
Caimanoidea visheri	Mehl, 1916
Caimanoeda visheri	Mehl, 1916
Caimanoideus visheri	Mehl, 1916
Alligator "Crocodilus" prenasalis	Matthew, 1918

Holotype: SDSM 991, anterior fragment of snout and lower jaw.

Hypodigm: AMNH 4994, MCZHU 1014, 1015, PU 13799, 14063, 16273, ROM 1375, SDSM 243, 6590, SMM P73.4.1, FMNH P26881.

Geographic and geologic range: Chadron Formation (Chadronian) and Brule Formation (Orellan), South Dakota.

Diagnosis: An alligator with a moderately broad snout; lateral margins gradually converging anteriorly. Distinguished from all other species of the genus by the presence of the dermosupraoccipital on the dorsal surface of the skull table, by a flat interorbital region lacking elevated margins and by posterior teeth with relatively rounded cutting surfaces. Distinguished from _A. sinensis_, _A. olseni_ and _A. mississippiensis_ by a relatively long mandibular symphysis, extending as far back as the sixth, seventh or eighth mandibular tooth, and formed by the dentaries plus splenials. Further distinguished from the latter two species by an ascending process of the angular forming the medio-posterior border of the external mandibular fenestra.

Description: Heavy sculpturing of the skull and lower jaw. Each premaxillary containing 5 teeth; each maxillary 12-13; each mandibular ramus 19.

Discussion: Because of the fragmentary nature of the type specimen, Mook (1934) designated MCZHU 1015 as the plesiotype. In his review of the crocodilian material from the Badlands of South Dakota, Higgins (1971) synonymized _Allognathosuchus riggsi_ (Patterson, 1934), which is the only other crocodilian known from the White River Badlands, with _A. prenasalis_. This form is represented by a single dentary but is lacking a complete dentition. _Allognathosuchus riggsi_ resembles

A. prenasalis in possessing a relatively long mandibular symphysis, extending back to the sixth mandibular tooth, and formed by the dentaries and splenials. *Allognathosuchus* is generally diagnosed by characteristic low-crowned, globular teeth, several of which generally show signs of considerable wear. This condition is also exhibited by *Albertochampsa* from the late Cretaceous of Alberta, Canada. Since the mandibular ramus of *Allognathosuchus riggsi* lacks its dentition, the taxonomic position of this specimen remains problematical. Higgins (1971) also added *Caimanoidea visheri* (Mehl, 1916), which is also from the White River Badlands, to the synonymy of *A. prenasalis*. Although the type specimen of *C. visheri* has been lost, preventing direct comparisons from being made, it appears from Mehl's description that this form does superficially resemble *A. prenasalis*. Thus, I concur with Higgins (1971) in making *C. visheri* a synonym of *A. prenasalis*.

PHYLOGENETIC INFERENCE

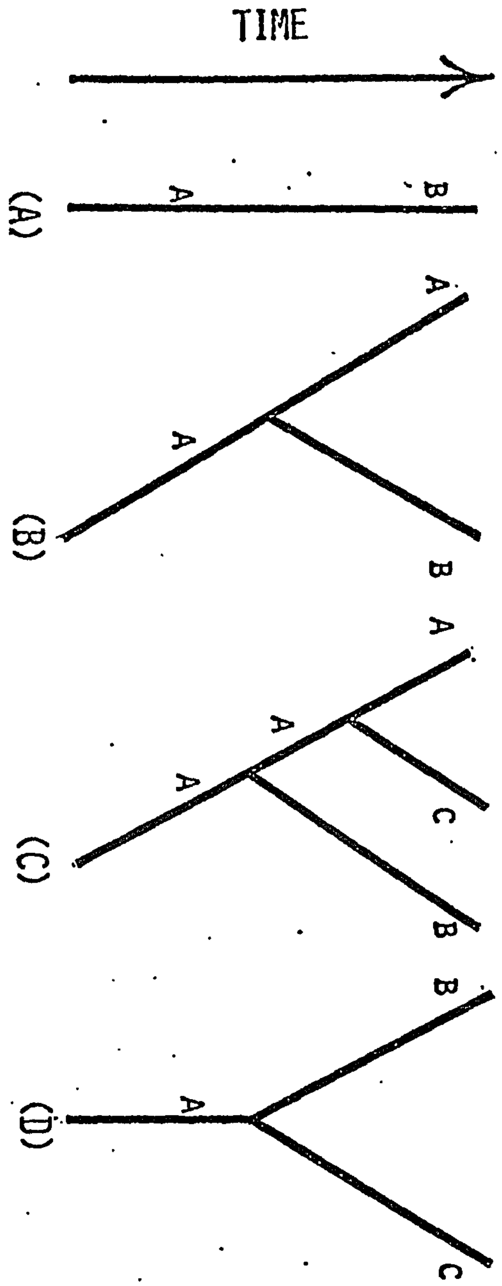
The idea that species represent evolving units, or lineages, which only arise from preexisting species denotes that all species are genealogically (historically) related to each other. This corollary of evolutionary theory is referred to as phylogeny.

Two models of the evolutionary process are thought to be sufficient to explain the origin of new species. According to the speciational (cladogenetic) model, new species arise by the splitting of lineages as reproductive isolation is established between populations which were previously capable of exchanging genes. Under the second model, which has been alternately referred to as phyletic evolution or phyletic gradualism, a morphologically distinct species arises by the gradual transformation of an ancestral species into a descendant species. As a result of the former process, species may share either a relationship of common ancestry (a cladistic relationship) or an ancestor-descendant relationship. Phyletic gradualism, on the other hand, only results in the establishment of an ancestor-descendant relationship. While lineage splitting generates species diversity, no increase in diversity occurs according to the linear model, since "new" species are merely arbitrary subdivisions of an evolving continuum. The postulated relationships (both cladistic and ancestor-descendant) of a series of taxa can be summarized in a diagram known as a phylogenetic tree (Figure 16).

Phylogeny is not directly observable since most species are the result of evolutionary events which have occurred during geologic time. The fossil record, which does provide data at the appropriate time scale, does not "record" phylogeny directly, but does, more or less, provide momentary glimpses of lineages at different points in time and generally within a limited geographic area. The arrangement of delineated taxa in their stratigraphic sequence is not in itself indicative of their phylogenetic relationships. However, the fossil record may provide data which are useful in the evaluation of these relationships if these data are interpreted in the light of evolutionary theory.

Our present understanding of the evolutionary process does provide the underlying basis for approximating the evolutionary histories of organisms. According to the neo-Darwinian Paradigm, the modification of the heritable features of organisms, which accompanies the descent

Fig. 16. Four possible patterns in phylogeny are illustrated in these simple phylogenetic trees (A). Species A evolves directly into Species B in linear fashion; an ancestor-descendant relationship is established between A and B (B). Species B evolves from Species A as a result of speciation, while A persists; an ancestor-descendant relationship is established between A and B (C). Species A splits allochronically into descendant. Species B and C continues to persist; B and C share a relationship of common ancestry, and their common ancestor is A (D). Species A splits isochronically into descendant Species B and C; B and C share a relationship of common ancestry, and their common ancestor is A.


TIME
(A)
A
B
(B)
A
A
B
(C)
A
A
A
C
B
(D)
A
B
C

of populations, generally leads to diverging lineages because they acquire features unique to each. However, it is also known that distinct lineages can acquire similar features independently by parallel or convergent evolution.

Since the differences and similarities between species originate during the course of phylogeny, the evolutionary history of these species can, in theory, be inferred from at least some of the observable features of the organisms themselves. Thus, phylogenetic reconstructions can be considered scientific hypotheses which must be evaluated on the basis of a strictly comparative methodology (Ghiselin, 1972; Nelson, 1970).

At present, there is no consensus regarding the underlying theory, the basic procedures, or the philosophical framework to be employed in phylogenetic inference, and considerable disagreement exists concerning many fundamental issues. In addition, these discussions are often obfuscated by their extension into other realms, notably classification. Some workers employ phylogenetic reconstructions for strictly classificatory purposes and adopt a method of analysis specifically designed with this end in mind (Cracraft, 1974; Hennig, 1950, 1966; Nelson, 1970, 1973). However, classificatory systems can reflect phylogeny to variable degrees, and the determination of phylogenetic relationships can be considered to be a separate problem (Ashlock, 1974; Ghiselin, 1972; Hecht, 1976; Mayr, 1974; Sneath & Sokal, 1973). The present attempt at reconstructing the evolutionary history of the Genus Alligator is made with the expressed purpose of examining this history for patterns in morphological change.

Although it is generally agreed that phylogenetic reconstructions should be concerned with the delineation of monophyletic groups, there is some disagreement and ambiguity as to the exact phylogenetic quality of a monophyletic series of taxa. These different views appear to be rooted in different philosophies of classification. A case in point concerns Simpson's (1961, p. 124) definition of monophyly as "the derivation of a taxon through one or more lineages . . . from one immediately ancestral taxon of the same or lower rank." Accordingly, Simpson allows for different degrees or levels of monophyly, in which case the concept of monophyly becomes an artifact of his classificatory procedure.

Similarly, the definition of monophyly developed by Hennig (1950, 1966) is largely the result of his classificatory procedure. Hennig's definition not only requires that a monophyletic group be derived from a single ancestral species but also requires that all the descendants of a common ancestral species be ascertained. Although this latter requirement may be an ultimate goal of phylogenetic reconstruction, it does not appear to be absolutely necessary in the determination of the interrelationships of a group of organisms. The reconstruction of evolutionary histories may not always be resolvable down to the level of the species, in which case phylogenetic hypotheses will involve supraspecific taxa. Ashlock (1971, 1972) has suggested that the term holophyly be substituted for Hennig's concept of monophyly, so as to distinguish it from the more conventional use of the concept.

Although the ultimate common ancestor of any group of organisms is the population, the species is generally considered to represent the evolving unit is phylogeny. Even though sexually reproducing species are generally considered to be monophyletic in origin, they may occasionally arise polyphyletically as the result of hybridization. However, since this latter mode of origin is considered to be a relatively rare event, species origins will be considered to be strictly monophyletic events, and in this study delineated taxa will be considered to be monophyletic if all share a common ancestral species.

THE NATURE OF THE EVIDENCE

In most phylogenetic studies the procedures which were employed in the construction of the hypothesis are seldom explicitly stated, and a phylogenetic scheme is often merely proposed along with the evidence which is thought to support it. The evidence which has been traditionally used in the determination of relationships has included information concerning (1) the distribution of the taxa in space (biogeographic data), (2) the distribution of the taxa in time (stratigraphic data) and (3) the attributes of the organisms themselves (i.e. their respective characters).

Recently, there has been a reexamination of the significance of these categories of evidence in terms of the role which they should play in the evaluation of phylogenetic hypotheses (Eldredge & Tattersall, 1975; Hecht, 1976; Schaeffer et al., 1972). These authors have argued that the evaluation of phylogenetic relationships should be based only upon the characteristics of the organisms that have a genetic basis (e.g., morphological, karyological, physiological, biochemical and behavioral features), and that the spatial and temporal distributions of taxa are unreliable indicators of these relationships. However, other authors contend that distributional data, at least, can constitute valid criteria for relating organisms (Ghiselin, 1972; Harper, 1976).

Obviously, individual species cannot occur in different geographical areas unless phylogeny occurs. But the distribution of organisms in space is largely the result of geological and ecological events (immigration and extinction) which have occurred during a group's evolutionary history. In fact, it is now recognized that phylogenetic relationships can be obscured by the complex geological and ecological histories which characterize most geographical areas. Biogeographical data, thus, should not be used to form phylogenetic hypotheses, but must be explained in the light of a working phylogenetic hypothesis which is based upon more basic data.

A more fundamental issue, however, involves the exact role of temporal data, i.e. the fossil record, in the reconstruction of the evolutionary history of organisms. The traditional view among paleontologists is that the fossil record provides historical links (transitional or ancestral groups) between taxa, and that the discovery of these links documents the actual course of phylogeny. Patterson (1977) has pointed out that the view that the fossil record provides the key to phylogeny is, at least in part, the result of a taxonomic artifact, since it is often based upon the prospect that the fossil record can demonstrate the polyphyletic origin of higher taxonomic categories.

According to the traditional view, taxa which are hypothesized to be ancestral are recognized, in part, by their precedence to descendant taxa in the stratigraphical record (Harper, 1976; Szalay, 1977). The validity of this principle is vitiated on theoretical grounds since ancestral species can persist without morphological change even after a new lineage has split off from it (Figure 16B and C) (Mayr, 1974, p. 110; Simpson, 1975, p. 6). Harper (1976, p. 189) also acknowledges that the strength of this principle depends upon how well the group is represented in the stratigraphic column. However, there is no apparent method with which to assess objectively the completeness of the fossil record. It would appear that the stratigraphical precedence of a taxon is not a prerequisite for postulating an ancestor-descendant relationship, and that temporal data does not necessarily provide evidence for a specific phylogenetic relationship. Hypothesized ancestor-descendant relationships may be testable by the application of other criteria (see below).

Although the designation of ancestral groups may not be necessary for reconstructing some aspects of phylogeny, nevertheless, temporal data may provide important evidence concerning the directions of evolutionary change for morphological characters (Harper, 1976; Ross, 1974; Simpson, 1975; Szalay, 1977).

METHODOLOGY

Although all the methods which are employed in phylogenetic inference are comparative in nature, they appear to proceed according to two distinct approaches to the problem. According to the phenetic method, relationships are estimated on the basis of some measurement of overall similarity/dissimilarity exhibited by the taxa under consideration. A variety of clustering techniques can be employed to generate a branching diagram (referred to as a phenogram) which is used to express the phenetic relationships among a series of taxa (Sneath & Sokal, 1973). Although the phenetic method of analysis does not attempt to distinguish between similarity due to common ancestry (patristic similarity) and similarity due to parallel or convergent evolution (homoplasy), the confounding effects of the latter, which constitutes phylogenetic "noise," are assumed to be reduced by employing a large number of what pheneticists consider to be "unweighted" characters. It is now generally recognized that this method of analysis will produce inaccurate estimates of phylogenetic relationships if rates of divergence have varied either within or between lineages (Colless, 1970).

Some authors, who advocate this method of analysis, sometimes assume that the degree of morphological resemblance is a reflection of relative genetic similarity (Harper, 1976, p. 187). However, there is some contrary evidence and much theoretical reasoning that suggests that morphological evolution and the evolution of structural genes can proceed at different rates (King & Wilson, 1975; Maxson & Wilson, 1975).

A second approach to the problem of evaluating phylogenetic affinities has attempted to decode the phylogenetic message by identifying what its proponents consider to be phylogenetic "noise" in the phenetic system. Proponents of this approach have explicitly criticized the notion that the relative magnitude of overall similarity among a series of taxa is indicative of their phylogenetic relationships to one another (Nelson, 1970).

This alternative method is based on the concept that two taxa can be considered to be more closely related to each other than either is to a third taxon by virtue of their more recent common ancestry (Hennig, 1950, 1966). Such relationships, which are based upon recency of common ancestry, have been termed cladistic and are expressed in a branching diagram known as a cladogram (Cain & Harrison, 1960). Taxa which are recognized to be related in this manner are referred to as sister taxa or sister groups.

Although this method is also based upon a divergent model of the evolutionary process, it differs significantly from the phenetic characterization of the divergence. According to the cladistic view, lineages generally diverge from each other as a result of the differential modification of their characters. The actual sequential modification of a character into newly evolved conditions, or states, produces what is referred to as a chronocline (Maslin, 1952). The chronocline is said to exhibit polarity in the sense that only one state of the character, which is termed the primitive (ancestral or plesiomorphous) condition, is the one from which all others have evolved. Character states which have evolved from the primitive condition of the chronocline are termed derived (apomorphous) states. The primitive to derived sequence of a chronocline (its polarity), therefore, refers to the sequence of changes which occurred during the evolution of that character.

Since the modifications of a character differentially appear during the course of phylogeny, new lineages, which originate at different points in a group's evolutionary history, will presumably possess unique mosaics of primitive and derived character states. Besides derived states which are unique to a taxon (autapomorphies), taxa will exhibit both primitive and derived character states which are shared by other closely related taxa. Presumably, lineages share at least some of these similar conditions as a result of their inheritance of those conditions from a common ancestor. Hennig (1950, 1966) pointed out that, since primitive conditions can be shared by organisms that are only remotely related, sister groups can be recognized and placed within a cladogram only on the basis of their common possession of derived character states (synapomorphies). If such character states are unique (i.e. if they have not arisen independently by parallel or convergent evolution), they can be used in the recognition of monophyletic groups (Wilson, 1965). Thus, the distinctive feature of cladistic methods vis-a-vis phenetic methods is the assumption that the phylogenetic message can be read by the identification of shared derived character states, and that shared primitive states of a character (symplesiomorphies) are not indicative of the degree of relationship between taxa. Primitive conditions can be used to associate more remotely related taxa if those states are derived relative to other states of the character.

The major problems in cladistic analysis involve the determination of the primitive to derived sequences of characters and the recognition of derived conditions which may have arisen in two or more lineages in parallel or convergent fashion.

Presumably, some or all of the states which appeared in the evolution of a character are differentially represented among the taxa under consideration. These various states of a character can be ordered into what has been alternately termed a morphocline, phenocline or transformation series (Hennig, 1950, 1966; Maslin, 1952; Ross, 1976). Such a series should correspond, at least in part, with the chronocline from which they were derived. It is generally assumed that an analysis of the distribution of the states of a character among a monophyletic group of taxa has the potential to provide some indication as to the sequential order in which they actually appeared.

In order to compare the distribution of character states among a series of taxa, it is usually assumed that these states are homologous. Although the concept of homology generally refers to similarities among taxa that are due to their common ancestry, Bock (1969, 1973) has pointed out the conditional nature of such statements and the necessity of specifying the level of homology.

As defined here, a homologous series of character states are assumed to have been ultimately derived from a single condition which was present in the ancestral species of the group. Operationally, homologous character states are recognized on the basis of topographic, developmental, structural or biochemical criteria.

Although there is no specific rule for determining the primitive to derived sequence of a morphocline, numerous principles have been proposed to resolve this problem (see Hennig, 1950, 1966; Maslin, 1952; Ross, 1976 for a comprehensive listing). Most of these principles involve an analysis of the distributional patterns of character states across taxa. The most commonly employed criterion involves an analysis of the distribution of character states in related taxa which are not descendants of the group under study. The character state which is found to be widely distributed in these related taxa is regarded as the primitive state for the group under study. This has been called the commonality principle (Schaeffer et al., 1972), and is based upon the parsimonious assumption that the state which is distributed in this manner did not evolve more than once. Within this system an hypothesized polarity for a morphocline can be corroborated if it is found to be concordant with hypothesized polarities involving other characters.

A second approach to the problem involves an analysis of the distribution of character states within the group under study and is restricted to groups with an extensive fossil record. According to this principle, the primitive to derived sequence of a character can be determined by the relative positions of the states in time. Thus, a condition which occurs in a taxon which appears later in the fossil record is considered to be derived relative to a state which appears in forms which occur earlier.

However, the use of biostratigraphic data in assessing the direction of evolutionary change of a character has been criticized in that it proceeds on the assumption that older taxa will invariably exhibit primitive states with regard to all characters (Cracraft, 1974; Eldredge & Tattersall, 1975; Schaeffer et al., 1972). It is generally the case that taxa exhibit mosaics of primitive and derived conditions. The use of temporal data in this way has received additional criticism from these authors because of the acknowledged fragmentary nature of the fossil record for most groups of organisms. The oldest known taxon of a group may actually exhibit derived conditions, which would erroneously be considered to be primitive if other forms which possessed the primitive state were unknown.

Some of these objections may be overcome if the analysis of the distribution of character states in time was extended outside the group under study to related taxa which occur earlier in time as suggested by Harper (1976, p. 185).

In this study the morphocline polarities which are determined on the basis of the commonality principle will be compared with those which are determined within a stratigraphical framework. In this way an hypothesized primitive to derived sequence of a character can receive additional support if the resulting polarities correspond to each other.

The other major problem in cladistic analysis involves the confounding effects of homoplasy. Homoplasy refers to similarities shared by organisms that are not due to their common ancestry, but which occur as the result of convergent or parallel evolution. Convergence, which refers to the independent appearance of similar characters in distant lineages, is usually easier to detect than the latter, since an inexact correspondence between the characters is often discovered after close examination. In parallel evolution derived character states evolve independently in separate lineages from an ancestor which possessed a primitive condition for that character (Hecht & Edwards, 1976).

The independent development of derived character states in separate lineages is potentially detectable within the cladistic system when the polarities of independent morphoclines fail to correspond to one another. In fact, the application of this method of analysis has demonstrated that the parallel development of derived character states among closely related lineages is extremely widespread (Hecht, 1976; Hecht & Edwards, 1976, 1977).

However, the problem of how to evaluate parallelisms appears to be handled in two different manners. One approach has been to assume, on the basis of parsimony, that the minimum number of parallelisms and reversals have occurred (Camin & Sokal, 1956; Farris et al., 1970; Kluge & Farris, 1969; Marx & Rabb, 1970, 1972). Hecht (1976) and Hecht and Edwards (1976, 1977) have offered an alternative approach in which an a priori weighting scheme is employed. According to this system, certain categories of evidence are given low weight (e.g. loss of character states) or high weight (e.g. complex innovative states) on the basis of the potential for detecting parallel development of those states.

Although such a system is arbitrary in nature, there may be some validity in its application. Hecht (1976) found that, among the various hypotheses that had been proposed concerning the phylogenetic relationships within the lizard Infraorder Gekkota, the one containing the minimum number of parallelisms was highly improbable, since it involved the parallel development of a biologically complex character state.

Because the cladistic system of analysis is limited to estimating the phylogenetic affinities of a group of taxa only on the basis of the recency of their common ancestry, no attempt is made to specify the exact nature of the relationship (ancestor-descendant or cladistic). Within this system, only the distributional pattern of shared derived character states (synapomorphies) is considered to constitute a valid test of a phylogentic hypothesis (Cracraft, 1974; Engelmann & Wiley, 1977; Nelson, 1970, 1973). Within the logical framework of this system, ancestors are purely hypothetical constructs, and ancestor-descendant relationships are not considered to represent testable hypotheses.

Other systems, which may employ cladistics at some point in the analysis, consider hypotheses concerning ancestor-descendant relationships to be empirically testable (Bock, 1973); Bretsky, 1975; Szalay, 1977). In these systems, phylogenetic relationships are, therefore, considered to be testable at the level of the phylogenetic tree. Platnick (1977) has argued that, in some instances at least, an hypothesized ancestral relationship can never be rejected, since it can be falsified only by what he considers to be negative evidence (failure to detect an autapomorphy).

Most of the arguments that are used against the proposition that ancestor-descendant relationships are testable clearly involve the philosophical question as to what constitutes a valid test of an hypothesis. Most cladists appear to adopt the Popperian view that the only valid tests of scientific hypotheses are those which are potentially falsifiable (Englemann & Wiley, 1977; Platnick, 1977; Wiley, 1975).

In this study I will develop a different philosophical framework in which to test phylogenetic hypotheses. Within this framework, phylogenetic hypotheses will be treated as probability statements which are based upon the distribution of the character states among the taxa under consideration. Ancestor-descendant relationships are viewed as testable hypotheses, but not to the same degree that relationships based upon recency of common ancestry are. The placement of taxa within a cladogram is extremely important, since it illustrates the distributional pattern of derived character states within the group. The common possession of derived character states by taxa indicates a phylogenetic relationship which remains unspecified at this level. Taxa which possess common derived states can be related in either an ancestor-descendant or cladistic manner. These two possible relationships can then be treated as competing hypotheses, one of which will better explain the distribution of primitive and derived character states among the taxa.

In this system an ancestor-descendant relationship between two taxa is hypothesized if one taxon (considered to be the ancestor) conforms, in every detail of the characters used in the analysis, to the hypothesized primitive (ancestral) condition. This hypothesized ancestor-descendant relationship will be rejected if both possess a derived state which is not shared with the other (an autapomorphy). Thus, if taxa can be shown not to be related in an ancestor-descendant fashion according to the aforementioned criteria, they will be considered to share a relationship of common ancestry.

Although the ultimate recognizable ancestor of any group of organisms is the species, the concept of ancestry has actually involved several hierarchical levels; supraspecific taxa are often designated as ancestral to other groups of organisms. Engelmann and Wiley (1977) have rejected the possibility of designating a supraspecific taxon as an ancestor, since they consider traditional higher taxonomic categories to be artifacts of an arbitrary classificatory procedure. However, the designation of supraspecific taxa as an ancestral group may actually involve a problem of resolution. For example, the Genus Hyracotherium can be considered the ancestral group from which all other equids have been derived, although it may not be possible to resolve this ancestry down to the level of the species.

PHYLOGENY AND CROCODILIAN CLASSIFICATION

Before reconstructing the evolutionary history of the genus Alligator, some perfunctory remarks about the relationship between phylogeny and current classifications of the Crocodilia are necessary. As was pointed out in the introduction to the taxonomic section, conventional classifications of crocodilians generally recognize five major groups of equal or variable rank: Protosuchia, Mesosuchia, Thalattosuchia, Sebecosuchia and Eusuchia. All extant members of the group are assigned to the suborder Eusuchia, which is distinguished from more primitive groups primarily on the basis of the extent of the development of the secondary palate. However, it is generally suspected that the eusuchian secondary palate has developed independently in a number of separate lineages within the Mesosuchia (Kalin, 1955a,b; Langston, 1973). Thus, the eusuchians represent a "grade" or level of organization, and, as presently conceived the group must be considered polyphyletic in origin (in sensu Hennig, 1950, 1966). Evidence to support this hypothesis is based on the presence of the overlapping type of tooth occlusion (which distinguishes the Alligatoridae from the other eusuchian groups) in the mesosuchians Theriosychus and Goniopholis (Langston, 1973, p. 280).

The referral of the three assemblages of living eusuchians to specific hierarchical ranks should not be interpreted as indicative of their phylogenetic relationships to each other either, since each may have had a separate origin from within the Mesosuchia. For example, the alligator and corcodile groups are often referred to different subfamilies of the Crocodylidae, while the gavials are placed in their own family (Gavialidae). This procedure appears to be an attempt to characterize the degree of morphological divergence that has occurred between each of these assemblages but may not reflect the actual relationships between the groups.

It has already been stated that there is morphological evidence which indicates that the Alligatoridae does form a monophyletic group. During occlusion in the Alligatoridae the mandibular teeth lie medial to the tooth rows of the upper jaw; consequently the mandibular teeth are accommodated by small depressions located medial to the upper dentition. In contrast, the mandibular teeth in the Crocodylidae and the Gavialidae are situated outside or in between the teeth of the upper jaw.

If one assumes that the alligatorid occlusal pattern has appeared only once in the evolutionary history of the Crocodilia (at the level of the Mesosuchia), it can be interpreted as evidence for the monophyletic origin of the Alligatoridae.

Since the Genus Alligator can be referred to the Alligatoridae on the basis of its possession of the typical occlusal pattern, outgroup comparisons will be restricted to other members of this monophyletic assemblage. Appendix IV contains a listing of the alligatorid taxa which were examined and employed in this segment of the analysis.

PREVIOUS WORK

Mook (1932, 1946) has produced the only previous attempts at reconstructing the evolutionary history of the Genus Alligator. Although his method of analysis was not explicitly stated, it would appear from the way in which his taxa were compared, that his interpretation was based upon a non-numerical phenetic analysis of cranial proportions (Mook, 1923, 1946).

Although Figure 17 presents Mook's interpretation of the phylogenetic relationships within Alligator is essentially unmodified form, one should not interpret this diagram too literally. Even though it may appear from the diagram that Mook only postulated phylogenetic relationships on the basis of recency of common ancestry, he also hypothesized ancestor-descendant relationships between taxa. For example, he stated in his discussion of the phylogenetic affinity of Alligator thomsoni, that "the resemblance of A. thomsoni . . . to A. sinensis is remarkably close, so close that it indicates direct descent."

THE CRANIAL CHARACTERS OF ALLIGATORID CROCODILIANS

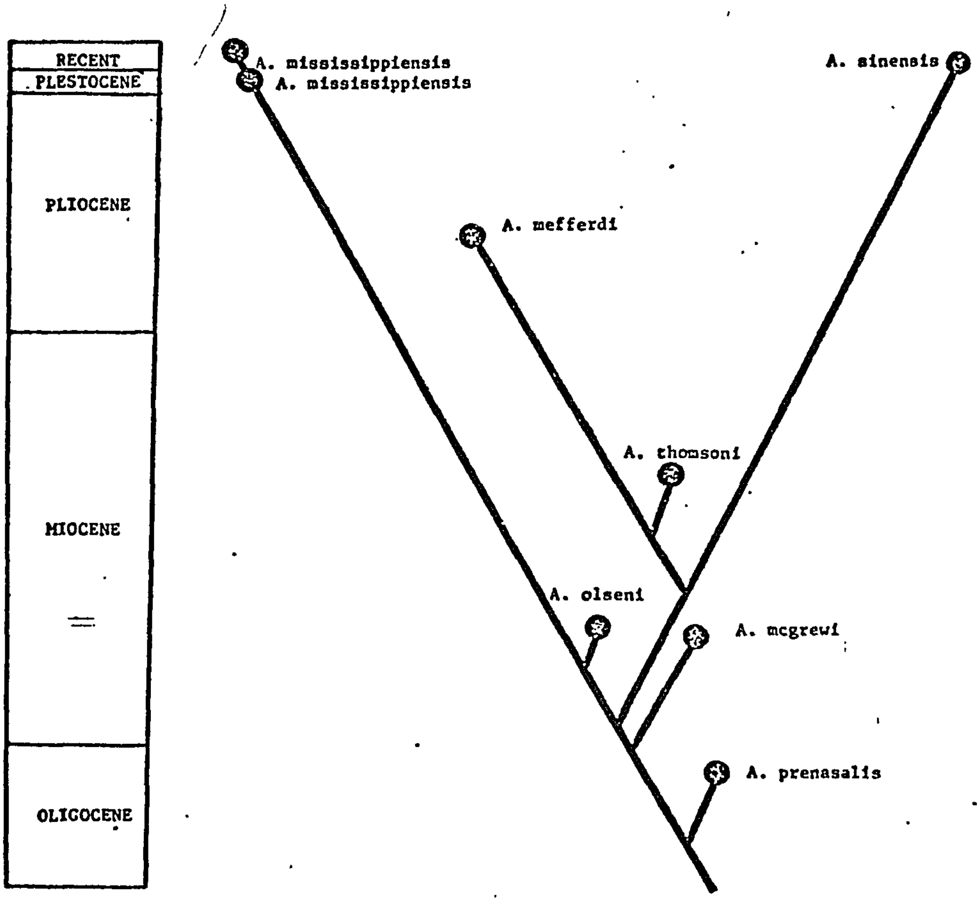
In the following section I discuss the variation in the cranium of alligatorid crocodilians mainly in those characters that occur differentially within the Alligator assemblage. Examples of the character states are illustrated, and their respective distributions among the taxa examined in this study are summarized (Table 3). The character states used in this analysis are described and the numbers (0,1,2,3) listed after each character refer to the different states that are recognized. The number "0" refers to the states which are

TABLE 3

The distribution of character states among species of the genus <u>Alligator</u> and in other alligatorids. The category "other alligatorids" includes both Recent and fossil forms, while "early alligatorids" includes only those forms which occur earlier than the Oligocene. See Appendix IV for a complete listing of the taxa that were examined.

CHARACTER STATES-	OTHER ALLIGATORIDS	EARLY ALLIGATORIDS	ALLIGATOR PRENASALIS	ALLIGATOR MCGREWI	ALLIGATOR SINENSIS	ALLIGATOR OLSENI	ALLIGATOR MISSISSIPPIENSIS
A: external narial aperture 0-undivided 1-divided	0	0	1	1	1	1	1
B: interorbital region 0-broad and flat 1-narrow and uprolled	0 and 1	0	0	1	1	1	1
C: medio-posterior border of skull table 0-parietal plus dermosupraoccipital 1-parietal only 2-dermosupraoccipital only	0 and 2	0	0	1	1	1	1
D: medio-posterior border of external mandibular fenestra 0-angular 1-surangular	0	0	0	0	0	1	1
E: basioccipital 0-with notch 1-without notch	0	0	0	0	0	0	1
F: mandibular symphysis 0-dentary & splenial and long (6-8) 1-splenial barely in contact and short (3-5) 2-dentary only and short (3-5) 3-dentary only and short (5-6)	0, 2 & 3	0	0	0	3	1 & 2	2
G: palatine bullae 0-absent 1-present	0	0	0	0	1	0	0

Fig. 17. Mook's (1946) interpretation of the phylogentic relationships among species of the genus Alligator.


RECENT
PLESTOCENE
PLIOCENE
MIOCENE
OLIGOCENE
A. mississippiensis
A. mississippiensis
A. sinensis
A. mefferdi
A. thomsoni
A. olseni
A. mcgrewi
A. prenasalis

hypothesized to be primitive on the basis of the two out-group comparisons which have been previously described; the numbers "1," "2," and "3" refer to derived states of the characters.

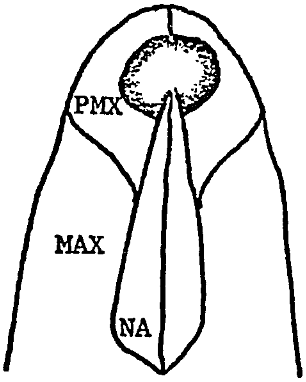
The cranium and its components that are used in this analysis are illustrated in Figures 10-15, 18 and 19. Most alligatorids have relatively broad, moderately elongated snouts; proportions do vary from the relatively broad snouts of *Alligator* and *Caiman latirostris* to the somewhat narrower snouts of *Paleosuchus* and *Caiman crocodilus*. However, the extreme longirostrine conditions, which are exhibited by some non-alligatorids (e.g., *Gavialis* and *Tomistoma*) apparently have never developed within this group.

CHARACTER ANALYSIS

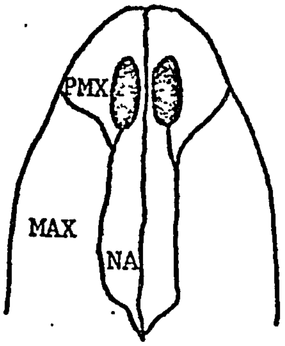
CHARACTER A: external narial aperture. 0-undivided (Figure 18A). 1-completely divided by an ossified internarial septum (Figure 18B).

The shape of the external narial aperture, which in crocodilians is located on the dorsal surface of the snout, near its anterior tip, varies considerably. The aperture is almost completely enclosed by the paired premaxillary bones; the paired nasal bones generally form the medial border of the aperture posteriorly, often with processes that project into the opening. These processes may continue anteriorly as cartilaginous extensions. *Alligator* is unique among alligatorids in that it possesses a completely ossified internarial septum, which is formed by anteriorly directed processes of the nasals which articulate with posteriorly directed processes of the premaxillaries. It has been suggested that its development in *Alligator* is the result

Fig. 18. Dorsal view of the anterior portion of the alligatorid snout illustrating the variation in the external narial aperture. A. External narial aperture undivided. B. External narial aperture completely divided by an ossified internarial septum.

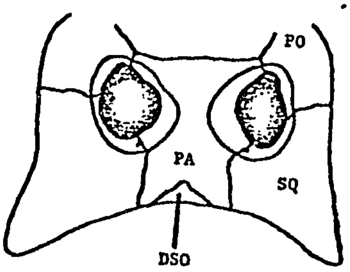


A

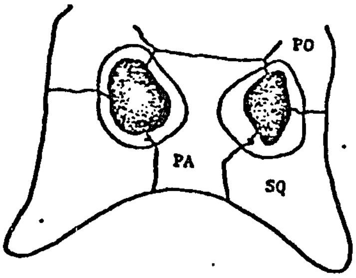


B

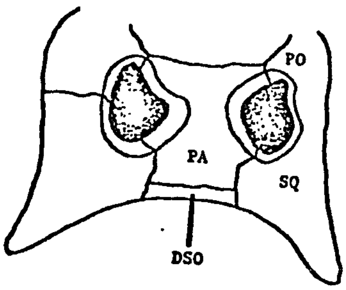
Fig. 19. Dorsal view of the alligatorid skull table illustrating the variation in the construction of its posterior border, A. Medial portion formed by a wedge-shaped dermosupraoccipital with processes of the parietal lying lateral to this element, B. Medial portion comprised only of the parietal, C. Medial portion comprised only of the dermosupraoccipital.



A



B



C

of this form having an extremely broad, flat rostrum, a relatively long external narial aperture and apparent weak sutural relationship between the premaxillary and maxillary bones (Langston, 1973).

It should be noted that a completely ossified internarial septum also occurs in other Recent and fossil crocodilians. This structure appears in the Recent African genus Osteolaemus and in Paralligator from the Cretaceous of Mongolia (Konzshukova, 1954). However, the taxonomic status of these forms remains problematical. Although Osteolaemus is usually allocated to the Crocodylidae, it does exhibit the typical alligatorid type of tooth occlusion. This suggests that either Osteolaemus has been incorrectly referred to this family, or that this form has independently developed typical alligatorid features. Although Paralligator possesses the typical alligatorid bite, Konzshukova (1954) referred the form to the Mesosuchia on the basis of her reconstruction of the secondary palate. This suggests that either the development of the narial septum in Alligator and Paralligator occurred in parallel, or that this character state does not represent a derived condition at the level of Alligator.

Since all other alligatorids, both living and fossil, possess an incompletely ossified internarial septum, it would appear that the condition found in Alligator is unique to this group (Table 3). If so, it can be taken as evidence for the monophyletic origin of Alligator.

CHARACTER B: interorbital region. 0-relatively wide and flat (Figure 14A). 1-relatively narrow with thickened lateral margins which are raised above the surrounding bone (Figures 10A-13A).

Besides the characteristic sculpturing of the dorsal surface of the skull and lateral surfaces of the jaw, crocodilian skulls generally possess a series of bony ridges and crests which often develop around the margins of the skull openings, as well as in the rostral region. These ridges and crests appear to be the response of bone to the patterns of stress that are exerted on the skull and jaws during their normal functions (Coldiron, 1974). As indicated in Table 3, *Alligator* prenasalis possesses a flat interorbital region, while all other taxa within *Alligator* exhibit the alternate condition. Both of these conditions, however, are widely distributed among the other alligatorids examined, although the former condition is characteristic of early forms (i.e. *Albertochampsa* (Late Cretaceous), *Allognathosuchus* (Paleocene and Eocene) and Arambourgia (Eocene)). The presence of a flat, relatively broad interorbital region in these early alligatorid taxa is assumed to indicate that it represents the primitive condition for *Alligator*, and that the narrow, uprolled interorbital region represents the derived state of this character.

CHARACTER C: posterior border of the skull table. 0-medial portion comprised of a wedge-shaped dermosupraoccipital with processes of the parietal forming the border lateral to this element (Figure 19A). 1-medial portion comprised only of the parietal (Figure 19B). 2-medial portion comprised only of the dermosupraoccipital (Figure 19C).

The posterior border of the crocodilian skull table is comprised of a variable number of elements. In all forms the lateral portions are formed by the paired squamosal bones. Medially, this border can be formed by single or dual elements. In some forms a small wedge-shaped ossification, the so-called "dermosupraoccipital," can be found on the dorsal surface of the skull table with processes of the parietal forming the borders between this element and the squamosals (Figure 19A). In all alligators, with the exception of *A. prenasalis*, which exhibits the condition just described, the dermosupraoccipital bone excludes the parietal from participation in the formation of this border. As the name implies, the dermosupraoccipital is dermal in origin and appears as a separate ossification during late development (Miall, 1878). Its appearance has been described in *Alligator mississippiensis* (Mook, 1921) and in *Crocodylus proosus* (Deranlyagala, 1939). According to Mook (1921) this ossification eventually fuses with the parietal in *A. mississippiensis*. It would appear that the variable states of this character within the alligatorids are the result of different fusion patterns which occur with respect to the dermosupraoccipital, supraoccipital and parietal bones.

As indicated in Table 3, states C-0 and C-1 can be found within *Alligator*; C-0 and C-2 are distributed in the outgroups. State C-0 is also characteristic of the non-alligatorid eusuchians. It would appear from this distribution that the presence of the wedge-shaped dermosupraoccipital on the dorsal surface of the skull table represents the primitive condition for the alligators. State C-1, which is restricted to some forms of *Alligator*, can be considered a derived condition, as can state C-2, which is only found in the Recent South American forms, *Caiman* and *Melanosuchus*. I interpret this distribution of character states to indicate that the morphocline for this character exhibits dual polarity in that there is a single primitive state, C-0, from which two derived conditions, C-1 and C-2, have evolved.

CHARACTER D: medio-posterior border of the external mandibular fenestra. 0-formed by an ascending process of the angular (Figures 11B, 13B and 14B). 1-formed by a descending process of the surangular (Figures 10B and 12B).

The medio-posterior border of the external mandibular fenestra, which is present in all Recent crocodilians, is formed by two elements; the dorsal portion is formed by the surangular, while the ventral element is usually referred to as the angular bone. Liem and Smith (1961) have presented circumstantial evidence that this latter element may actually originate as the result of the fusion of two centers of ossification. One of these centers may represent the prearticular (which is generally considered to be absent in crocodilians), while the other may represent the actual homologue of the angular.

These two character states, which have been found to be differentially represented in species of Alligator, are the result of different patterns of growth involving the angular and surangular. The surangular forms the medio-posterior border of the external mandibular fenestra as a result of it growing over the ventrally located angular bone. This condition is considered to represent the derived state for this character within Alligator, since only the alternative state has been found to be distributed in both outgroups (Table 3).

CHARACTER E: shape of the basioccipital. 0-with lateral processes lying above the openings of the lateral eustachian canals (Figure 15A). 1-without lateral processes (Figure 15B).

In alligators the openings of the lateral Eustachian canals may lie just beneath lateral processes of the basioccipital, or they may be obscured by an expanded basioccipital. Since this latter condition is restricted to a single sepcimen, _A. mississippiensis_, and has not been found in any of the other alligatorids that were examined, it will be considered to represent an autapomorphy.

CHARACTER F: construction and relative length of the mandibular symphysis. 0-dentaries plus splenials; relatively long, extending posteriorly to a point level with the sixth, seventh or eighth mandibular tooth (Figures 13B and 14B). 1-splenial barely makes contact with the symphysis; relatively short, extending posteriorly to a point level with the third, fourth or fifth mandibular tooth (Figure 12B). 2-dentaries only; relatively short, extending posteriorly to a point level with the third, fourth or fifth mandibular tooth (Figure 10B). 3-dentaries only; relatively short, extending posteriorly to a point level with the fifth or sixth mandibular tooth (Figure 11B).

The length of the mandibular symphysis varies considerably among crocodilian species. In _Alligator mississippiensis_, which has the shortest symphysis among Recent crocodilians, it can extend as far back as the fifth mandibular tooth, while in _Gavialis gangeticus_, which possesses the longest symphysis, it can reach back as far as the 24th mandibular tooth.

Not only is there considerable taxonomic variation regarding this character, but there is also significant ontogenetic and individual variation within a species as well. This pattern of variation has already been described in some detail previously.

Although there are some exceptions, a dentary-splenial mandibular symphysis is generally characteristic of longirostrine crocodilians. However, a dentary-splenial symphysis also occurs in several species of _Alligator_, as well as some short-snouted Early Tertiary alligagorids (Table 3). In other forms of _Alligator_ the splenial has lost its contact with the symphysis, although in _A. olseni_ the condition can vary from individual to individual. In this latter form the splenial bones may barely reach the symphysis, or they may not contact it at all. The incorporation of the splenial into the symphysis is generally interpreted as resulting in the strengthening of this joint.

Since several of the character states are widely distributed in other alligatorids, the condition exhibited by the Early Tertiary forms is postulated as being primitive for _Alligator_. These forms are characterized by relatively long, dentary-splenial symphyses, the length of which can sometimes extend as far back as the seventh mandibular tooth (e.g., _Allognathosuchus_). The relatively short symphyses without the splenial contact are considered to be derived within the group.

It should be pointed out that the condition in _A. olseni_ is particularly significant in the analysis of this morphocline. This form is characterized by a relatively short symphysis which may be contacted by the splenial bones in some specimens. The symphysis in this form reaches as far back as the third, fourth or fifth mandibular tooth, as it does in A. mississippiensis. However, in A. mississippiensis the splenials are never found in contact with the symphysis. It would appear that this condition was derived from that exhibited by A. olseni, since this condition is identical to that in some specimens of this species. This interpretation would indicate that the relatively short mandibular symphysis of A. sinensis (although longer than those of the A. olseni--A. mississippiensis assemblage), which also lacks the splenial contact, has been independently derived from the more primitive condition exhibited by A. mcgrewi and A. prenasalis. This interpretation is corroborated by the postulated polarities of other transformation series (Table 3).

CHARACTER G: palatine bullae. 0-absent. 1-present.

As mentioned above, many of the cranial elements of crocodilians are pneumatic, and the cavities are connected to form systems associated with the middle ear and the nasal passages. This latter system includes cavities within the premaxillaries, maxillaries, palatines, pterygoids and occasionally the prefrontals and vomers (Iordansky, 1973). Portions of the palatines and/or the pterygoids may expand dorsally to form bullae. In Gavialis these bullae are formed entirely by the pterygoids, while in Osteolaemus, Tomistoma and some species of Crocodylus they are formed by portions of the palatines and pterygoids. In Alligator sinensis, which is the only alligatorid to possess such structures, they are entirely contained within the palatines. It would appear from this data that the palatine bullae of A. sinensis is a uniquely derived character state both within Alligator and the Alligatoridae.

THE PHYLOGENETIC RELATIONSHIPS WITHIN THE GENUS *ALLIGATOR*

In this section an hypothesis is proposed concerning the phylogenetic relationships among species of the genus *Alligator*. The proposed hypothesis is considered to be the most probable statement that can be made concerning the relationships of the taxa under consideration and is based upon the distribution of primitive and derived character states which were described and analyzed in the previous section (summarized in Table 3). The primitive to derived sequence of a character was determined on the basis of the methods described earlier.

Selected cladograms which illustrate alternate hypotheses concerning the cladistic relationships among recognized taxa are presented in Figures 20-22. The common possession of derived conditions by taxa is assumed to indicate close phylogenetic affinities, although the exact nature of the relationship remains unspecified at this level of the analysis.

Figure 20 represents a cladogram based upon Mook's hypothesis concerning the phylogenetic relationships of the taxa recognized by him. According to this hypothesis the *A. thomsoni*--*A. mefferdi* lineage is considered to be more closely related to *A. sinensis* than to any other taxon. This hypothesis requires three parallel developments of derived character states in the *A. thomsoni*--*A. mefferdi* and the *A. olseni* lineages (conditions D-1, E-1 and F-2).

According to the second hypothesis (Figure 21) *A. sinensis* and *A. mississippiensis* are considered to be more closely related to each other than to any other taxon. This arrangement requires the

Fig. 20. A cladogram based upon Mook's (1946) hypothesis concerning the phylogenetic relationships of *Alligator* taxa recognized by him. The alphabetic-numeric code refers to the character states discussed in the text (see Table 3 for a complete listing). The horizontal bars indicate the distribution of derived character states among the taxa.

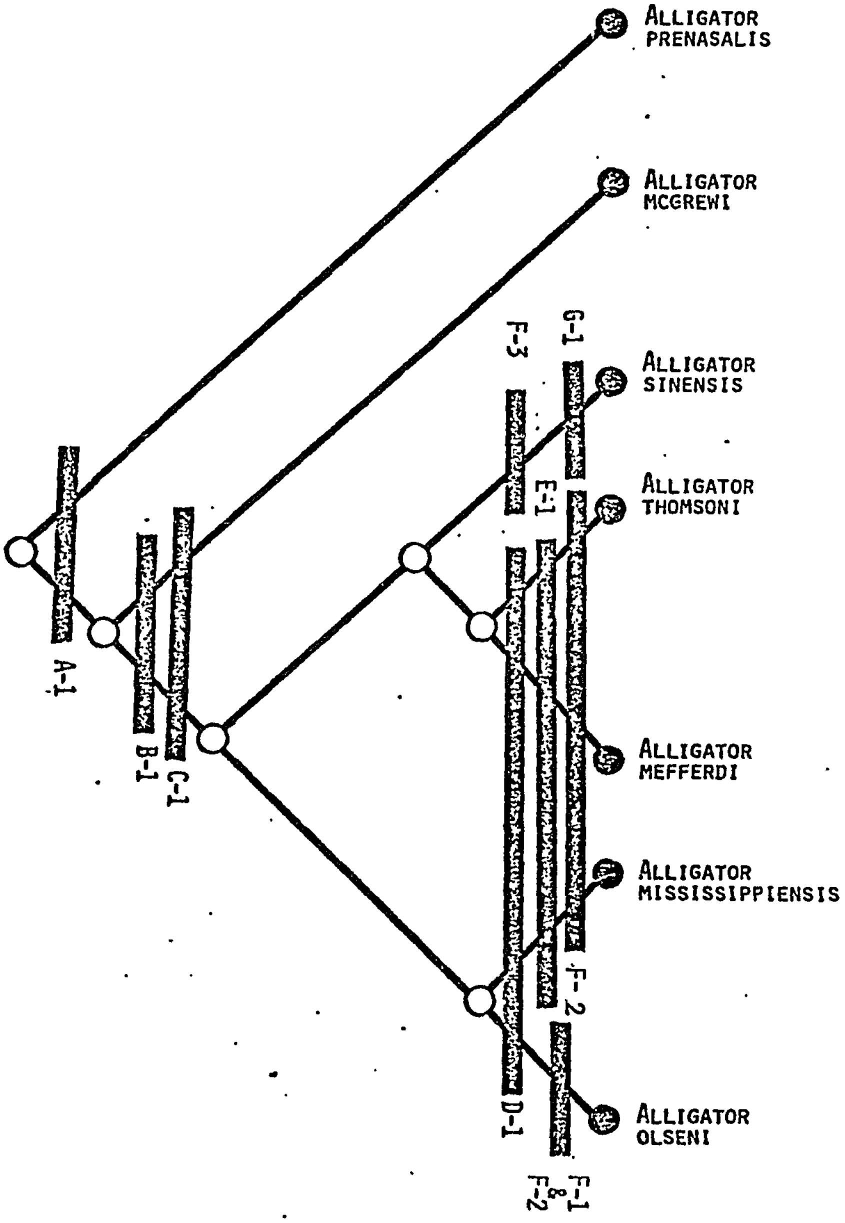

ALLIGATOR PRENASALIS
ALLIGATOR MCGREWI
ALLIGATOR SINENSIS
ALLIGATOR THOMSONI
ALLIGATOR MEFFERDI
ALLIGATOR MISSISSIPPIENSIS
ALLIGATOR OLSENI
A-1
B-1
C-1
D-1
E-1
F-1 & F-2
F-2
F-3
G-1

Fig. 21. A cladogram in which _A._ _mississippiensis_ and _A._ _sinensis_ are postulated as being more closely related to each other than to any other taxon. Symbols as in Fig. 20.

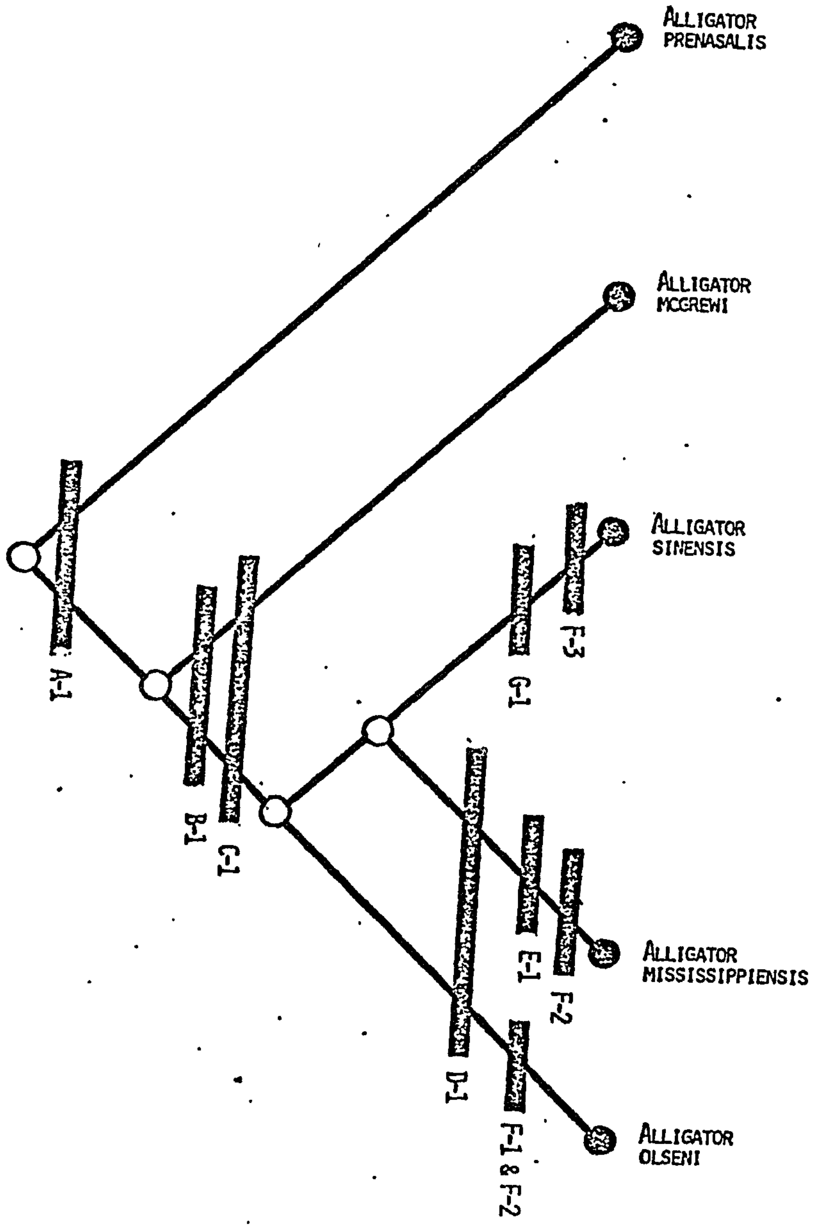
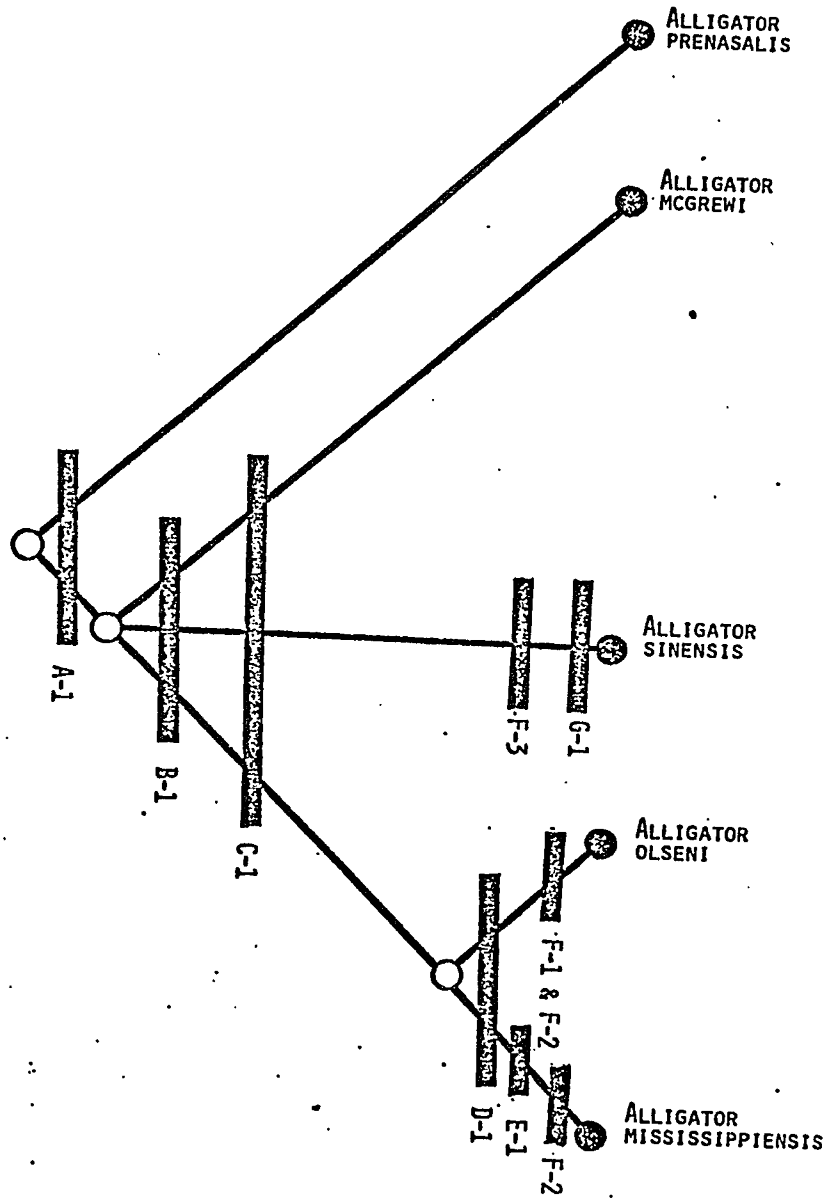

ALLIGATOR PRENASALIS
ALLIGATOR MCGREWI
ALLIGATOR SINENSIS
ALLIGATOR MISSISSIPPIENSIS
ALLIGATOR OLSENI
A-1
B-1
C-1
D-1
E-1
F-1 & F-2
F-2
F-3
G-1

Fig. 22. A cladogram in which *A. mississippiensis* and *A. olseni* are postulated as being more closely related to each other than to any other taxon. Symbols as in Fig. 20.


ALLIGATOR PRENASALIS
ALLIGATOR MCGREWI
ALLIGATOR SINENSIS
ALLIGATOR OLSENI
ALLIGATOR MISSISSIPPIENSIS
A-1
B-1
C-1
F-3
G-1
F-1 & F-2
D-1
E-1
F-2

independent development of character states D-1 and F-2 in *A. olseni* and *A. mississippiensis*.

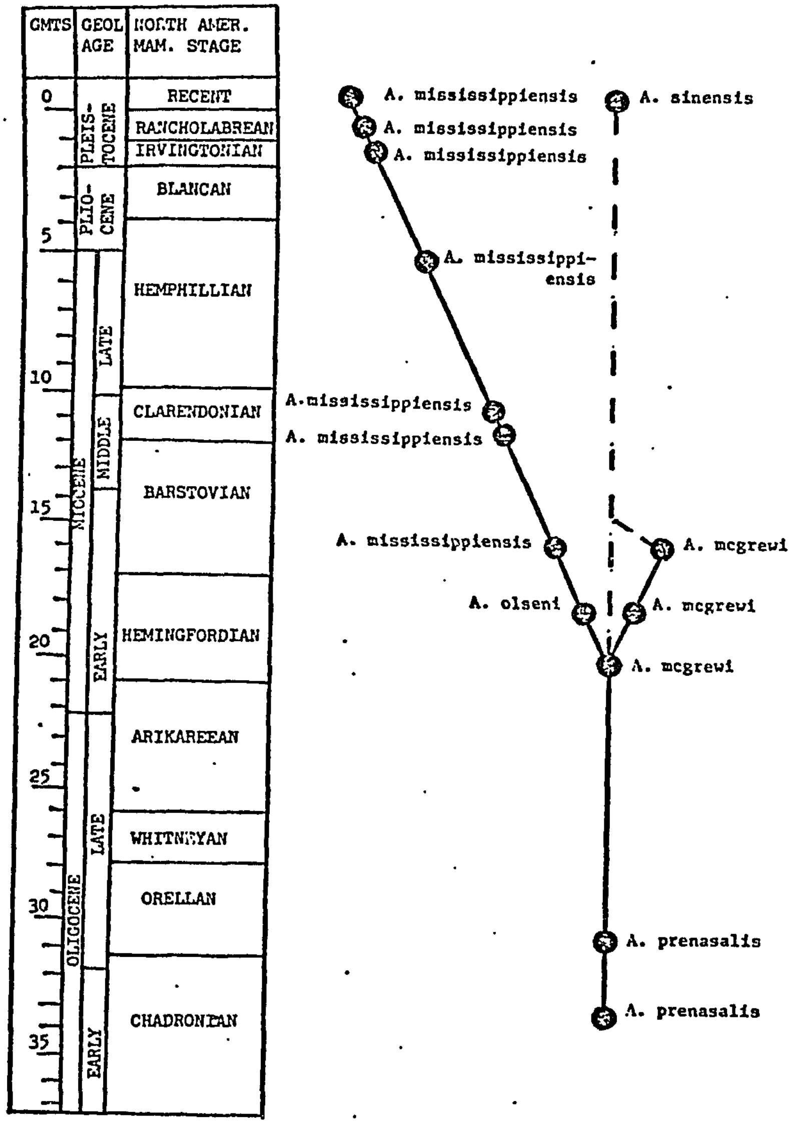
In Figure 22 taxa are arranged within the cladogram such that *A. olseni* and *A. mississippiensis* are postulated as being more closely related to each other than to any other taxon. Note that this last arrangement does not also postulate the parallel development of derived character states in independent lineages.

The first hypothesis is considered to have the lowest probability of the three since it requires three parallelisms. In fact, *A. thomsoni* and *A. mefferdi* are considered to be indistinguishable from *A. mississippiensis* and are considered here to be synonyms of the latter taxon. The second hypothesis also involves the independent development in distinct lineages of the same character states, while the last requires none. Therefore, this last cladogram (Figure 22) is considered the most probable hypothesis on the basis of the distribution of character sets that have been analyzed.

Specific ancestor-descendant and cladistic relationships are hypothesized for taxa within the *Alligator* assemblage according to the criteria developed in the section dealing with phylogenetic methods. According to the criteria developed there, an ancestor-descendant relationship between two taxa is hypothesized if the taxon, which is hypothesized as being ancestral to the other, exhibits the primitive condition for every character used in the study. A cladistic relationship between two taxa is hypothesized if both possess a derived state of a character which is not shared with the other.

Figure 23 presents the hypothesized phylogenetic relationships within the Genus *Alligator* within a stratigraphical framework. This

Fig. 23. The hypothesized evolutionary history of Alligator placed in a stratigraphic framework. The broken lines connecting *A. mcgrewi* with *A. sinensis* are to indicate an ancestor-descendant relationship between the two forms, although a minimum age for the *A. sinensis* cannot be estimated. Correlations between the Geomagnetic Time Scale (GMTS), Geologic Ages (Geol. Age) and North American Land Mammal Stages (North Amer. Mam. Stage) after Berggren and van Couvering (1974).


GMTS
GEOL AGE
NORTH AMER. MAM. STAGE
0
5
10
15
20
25
30
35
PLEIS-TOCENE
PLIO-CENE
MIOCENE
OLIGOCENE
LATE
MIDDLE
EARLY
LATE
EARLY
RECENT
RANCHOLABREAN
IRVINGTONIAN
BLANCAN
HEMPHILLIAN
CLARENDONIAN
BARSTOVIAN
HEMINGFORDIAN
ARIKAREEAN
WHITNEYAN
ORELLAN
CHADRONIAN
A. mississippiensis
A. sinensis
A. mississippiensis
A. mississippiensis
A. mississippiensis
A. mississippiensis
A. mississippiensis
A. mississippiensis
A. mcgrewi
A. olseni
A. mcgrewi
A. mcgrewi
A. prenasalis
A. prenasalis

hypothesis contrasts somewhat with Mook's (1946) interpretation (Figure 17). More specifically, the hypothesis developed here differs from that of Mook's concerning three points. First, the nominal form of _A. mefferdi_, which Mook considered to be related to the _A. sinensis_ lineage, has been referred to _A. mississippiensis_ since it falls within the range of variability of this taxon. Second, _A. thomsoni_, which Mook considered to be directly ancestral to the living _A. sinensis_, is also considered to be a synonym of _A. mississippiensis_. Third, _A. mcgrewi_, whose relationship to other forms was not explicitly stated by Mook, is considered to be the common ancestor of the _A. sinensis_ and the _A. olseni_--_A. mississippiensis_ lineages. _A. prenasalis_ and _A. olseni_ are postulated as the ancestral taxa to _A. mcgrewi_ and _A. mississippiensis_ respectively. Mook also proposed these relationships for these forms.

THE MORPHOLOGY AND PALEOBIOLOGY OF ALLIGATORS

Variation in the cranial anatomy of alligators has already been described in some detail. In the following discussion I refer only to those morphologic features of the skull that show patterns associated with the hypothesized evolutionary history of _Alligator_ (Figure 23).

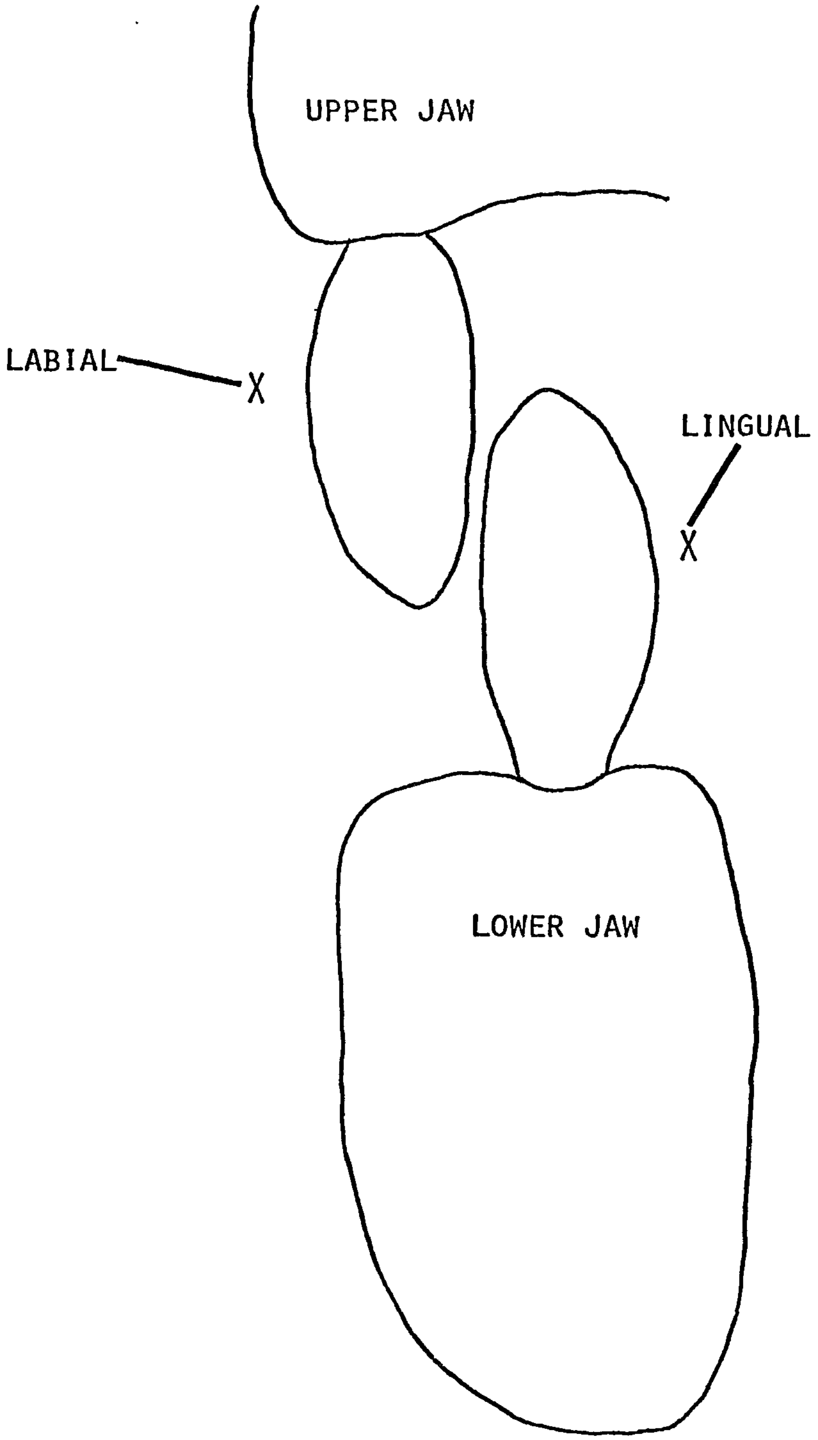
The characteristic features of the crocodilian skull and the structural variation among living (Iordansky, 1973) and extinct crocodilians (Langston, 1973) have been recently surveyed. The basic features of crocodilian head musculature and the variation occurring among living species has also been recently reviewed (Schumacher, 1973). These studies indicated that the design of the typical crocodilian skull primarily reflects an adaptation to an aquatic mode of feeding, although the skull is also indirectly involved in thermoregulatory (Johnson, 1973, 1974), social (Garrick & Lang, 1977) and nesting behaviors (Herzog, 1975; Kushlan, 1973).

The morphologic features of the skull that arose during the evolutionary history of Alligator developed as part of an integrated form--functional complex and appear to be primarily related to shifts in the biomechanics of feeding. However, an analysis of the sequence of these changes, as they occurred in this evolutionary history, indicate that some changes preceded others. Early stages in the sequence involved morphologic changes in the posterior dentition, which were then followed by changes in the design of the mandibular symphysis. There were also concurrent modifications in the pattern of cranial sculpturing and in the size and shape of the skull.

The most prominent feature of the dental pattern of alligators involves the regional differentiation of the dentition and implies some degree of functional specialization along the tooth row. While the anterior dentition appears to be responsible for the seizing, holding and manipulation of prey, the way in which the flattened surfaces of the posterior dentition oppose each other in the upper and lower jaws suggests that these teeth provide an effective shearing mechanism.

Figure 24 illustrates the spatial relationship between posterior teeth that oppose each other when the jaws of an alligator are closed. Note that it is the lingual surface of the upper teeth and the labial surface of the lower teeth that are flattened to form potential shearing surfaces. Although there is usually a narrow space between opposing teeth, occasionally there is tooth on tooth contact depending upon the

Fig. 24. A diagram illustrating the spatial relationship between the posterior teeth of the opposing upper and lower dentitions in alligators when the jaws are closed. Note that occasionally there is tooth on tooth contact depending upon the stage of replacement of the teeth involved. Also note that it is the lingual surfaces of the upper teeth and the labial surfaces of the lower teeth that are flattened to form potential shearing surfaces.


UPPER JAW
LABIAL
X
LINGUAL
X
LOWER JAW

stage of replacement of the teeth involved. This shearing mechanism does not conform to the one typical of mammals, in which relatively efficient shearing forces are supplied by precise tooth on tooth contact.

All alligators conform to this pattern with the exception of the most primitive member of the group, *A. prenasalis*. This form is characterized by a posterior dental series with slightly more rounded cutting surfaces than is typical for the genus. These teeth appear to be morphologically intermediate between the highly compressed teeth of more advanced alligators and the rounded (almost circular in cross section), low-crowned teeth that characterize *Albertochampsa* and *Allognathosuchus*. Although several of these teeth in the latter forms generally show signs of heavy wear, there is no consistent pattern regarding the relative position of the wear facets. It is generally thought that the heavy wear on these teeth indicates a durophagous habit (Langston, 1973). However, my superficial examination of these forms indicates that it is not at all clear as to whether the wear pattern was due to tooth on tooth contact, or whether it was produced by food abrasion. If my interpretation of this morphological pattern is correct, it indicates that the genus *Alligator* initially developed as a result of a shift from the *Albertochampsa*-*Allognathosuchus* type of dentition to an effective shearing dentition.

The second stage that occurred in the evolution of the skull of alligators involved changes in the design of the mandibular symphysis. As a result, alligators exhibit considerable variability in the construction and length of this joint. Alligators which exhibit the advanced conditions (A. sinensis, A. olseni and A. mississippiensis) possess relatively weak symphyseal joints that are relatively short and formed by the dentaries only. In A. sinensis the symphysis is relatively longer than in the A. olseni-A. mississippiensis lineage (Table 3).

This relatively weak symphysis permits some rotational movement at the joint and also allows some degree of independent movement of the mandibular rami. Differentiation of the mandibular adductor system in crocodilians permits complex movements (protraction, retraction and medial traction) of the mandibular rami as well as strong adduction (Schumacher, 1973). This bone-muscle complex involving the construction of the intermandibular joint and the actions of the mandibular adductors represents an integrated system that allows for rotational movement around the vertical, horizontal and longitudinal axes of the jaw in advanced alligators.

In contrast to this situation in the advanced group of alligators, the primitive A. prenasalis-A. mcgrewi lineage is characterized by a relatively strong symphyseal joint. This joint is relatively longer in these forms and is further strengthened by the incorporation of the splenials in its formation. The strong symphyses of primitive alligators would have prevented both rotational and independent movements at the joint. During this early stage in the evolutionary history of alligators the mandibular rami evidently could not move independently.

Although this latter type of joint is characteristic of longirostrine forms, it is also known to occur among other fossil alligatorids. Although this feature is only known to occur in Allognathosuchus, it may have also characterized *Albertochampsa* (the mandible of this form is unknown). This can be postulated on the basis of the similar type of dentition that is exhibited by these two forms. Once gaian, the evidence seems to indicate the derivation of the *Alligator* lineage from the *Albertochampsa*-*Allognathosuchus* group. I have been unable to resolve the relationships of these taxa to each other to a finer degree because of the apparent lack of derived character states that are shared by two of the taxa and not the third.

The pattern of change involving the design of the mandibular symphysis contrasts with the one that involved the dentition. Although *A. prenasalis*-*A. mcgrewi* lineage had modified its dentition by the latter stage to become more like advanced alligators, *A. mcgrewi* retained the primitive type of mandibular symphysis. The modification of the mandibular symphysis can be interpreted as indicating fundamental changes in the biomechanics of feeding. These changes involved a shift from a mandible that was relatively immobile at the symphyseal joint to one that allowed rotational and independent movement of the mandibular rami.

Alterations in the biomechanics of feeding during the evolutionary history of alligators is also reflected in the modification of the patterns of cranial sculpturing. It has already been pointed out that the skull ornamentation of crocodilians develops in response to the patterns of stress that are exerted on the bones of the skull and lower jaw (Coldiron, 1974). It follows that any biomechanical changes will be reflected by corresponding changes in the ornamentation pattern. Primitive alligators (*A. prenasalis* and *A. mcgrewi*) are characterized by heavier and more extensive sculpturing and by robust lower jaws, while advanced alligators (*A. sinensis*, *A. olseni* and *A. mississippiensis*) exhibit lighter ornamentation and relatively gracile mandibles. The incipient development of elevated borders in the interorbital region in *A. mcgrew* also suggests subtle biomechanical changes within this lineage.

Although there is considerable intraspecific variability in skull shape in alligators, some species are characterized by snouts in which the lateral margins remain more or less parallel (*A. olseni* and *A. mississippiensis*), while others possess snouts in which the lateral borders gradually converge anteriorly (*A. prenasalis*, *A. mcgrewi* and *A. sinensis*).

Although there is no way to determine the maximum size attained by fossil alligators, the considerable size differences between the two living species (*A. mississippiensis* attains a maximum size of about six meters, while *A. sinensis* may only reach two meters in length) indicates that body size has also varied during this evolutionary history.

In summary, this analysis of the patterns of morphologic change involving the skull has shown that the major changes that occurred during the evolutionary history of alligators involved fundamental changes in the biomechanics of feeding. Substantial changes in body size also inferred to have occurred during this evolutionary history.

THE BIOGEOGRAPHY OF *ALLIGATOR*

The observed geographic distribution of related groups of organisms (populations or taxa) can be explained by referring to their ecological restrictions and to the events which have occurred during their evolutionary history. Organisms become confined to specific geographic areas when physical barriers or environmental factors begin to restrict the dispersal of individuals, or when environmental change leads to the extinction of local populations. Related groups of organisms may become endemic to different geographic areas either as a result of dispersal events or by vicariance. Dispersal hypotheses explain disjunctions by the movement of ancestral groups across pre-existing barriers, while vicariance hypotheses explain them by the appearnace of barriers that fragment the ranges of ancestral groups (Platnick & Nelson, 1978).

Recent alligators are found in a variety of aquatic habitats in subtropical and warm-temperature lowlands of southeastern North America (_A. mississippiensis_) and eastern Asia (_A. sinensis_) (Figure 1). The floras in these regions are characterized by either broad-leaved evergreens, or by a broad-leaved deciduous vegetation, depending on local climatic conditions. It would appear from this general distribution pattern that humidity and temperature interact to restrict the distribution of Recent alligators. Their dependence on aquatic environments is not only related to their method of prey capture but may also reflect an important mode of temperature regulation (Johnson, 1974; Lang, 1976) and nesting behavior (Chabreck, 1975). During periods of environmental stress due to seasonal fluctuations in the water table, alligators are known to modify their environments by excavating basin-like dens in order to conserve an available water supply (Neill, 1973). Their dependence on similar aquatic environments appears to have persisted throughout their evolutionary. All fossil alligators, that have been recovered so far, have been associated with aquatic depositional environments (sinkhole, channel and floodplain deposits).

Fossil alligators are sometimes used as an indicator of mild winter climates (Voorhies, 1971; Woodburne, 1959). This interpretation is based primarily on an analysis of the Recent distribution of A. mississippiensis. The northern limit of the range of this form corresponds moderately well with the 7 degree (C) isotherm of average January temperatures, and even better with the -9 degree (C) isotherm of average minimum temperatures (Neill, 1973, p. 193). Although they do not correspond exactly, the geographic ranges of A. mississippiensis and Sabal palm (an indicator of wild winter climate) are quite similar (Axelrod & Bailey, 1976, Figure 7). This implies a similar temperature regime for alligator and palm. Axelrod and Bailey (1976) determined that the northern boundary of palm averages 212 days with a mean annual temperature warmer than 14.5 degrees (C), and that the annual range of temperature is 20 degrees (C) with 2-3% of the hours of the year with frost. However, the temperature regimes that characterize the areas in which living taxa are found should not be applied too literally to fossil forms, which may have lived under different temperatures. For example, Axelrod and Bailey (1976) also demonstrated that fossil palms have lived under temperatures that are not as warm as those which palms live under today. Although living alligators are known to excavate and retreat to burrow-like dens during extended periods of extreme cold (Neill, 1973), it is not at all clear as to whether fossil alligators possessed the same ability.

In any event, there is geologic evidence from some of the sediments that have yielded alligators and vegetational evidence from fossil floras which indicates that fossil alligators have also been restricted to regions that were characterized by wild winter climates. Lithologic features of some of the sediments of the Chadron Formation in southwestern South Dakota, which have produced specimens of A. prenasalis, indicate a paleoenvironment characterized by abundant but highly seasonal rainfall, and by temperatures such as occur in the southeastern United States today (mean annual temperatures 15.5 - 18 degrees (c) and rare frost) (Clarke et al., 1967). This contrasts sharply with the present climate of the region, which can be characterized as cool-temperate and semiarid. Simialr lithologic features of the Brule sediments, which have also produced A. prensalis, implies a similar climate for southwestern South Dakota during the Orellan (Higgins, 1971).

The Kilgore Flora situation in northwestern Nebraska has sub-tropical elements (Cedrela, Cordia, Meliosma) and evergreen sclerophylis (Quercus) implying mild winters for this region during the Barstovian (MacGinitie, 1962). Alligators (A. mcgrewi and A. mississippiensis) from fossil quarries of the Olcott Formation in northwestern Nebraska (Skinner et al., 1977) are essentially contemporaneous with this flora. Such a temperate regime also appears to have characterized areas to the south during the same time interval. The presence of fossil palm in the Skull Ridge Member of the Tesque Formation near Santa Fe, New Mexico is indicative of a mild winter climate (Axelrod & Bailey, 1976). These deposits are essentially contemporaneous with

Trinity River Pit No. 1 (upper part of the Flemming Foundation) in north-central Texas (Galusha & Blick, 1971) which has yielded fossil forms of *A. mississippiensis*. The local extinction of alligators in these areas which were formerly occupied (southwestern South Dakota, northwestern Nebraska and north-central Texas) are clearly related to the dramatic climatic changes which were associated with major tectonic events that occurred in these regions during the late Tertiary. There is ample evidence which indicates that the humid tropical climates at these latitudes during the Early Tertiary were replaced by subhumid, warm-temperature climates during the Middle Tertiary, which were, in turn, replaced by dry, cool-temperate conditions during Late Tertiary time (Dorf, 1960).

The present disjunction of the genus *Alligator* (southeastern United States-eastern Asia) is only explicable in terms of the events which have occurred during its evolutionary history; purely ecological explanations cannot account for the present distributional pattern. The hypothesized evolutionary history of the genus is illustrated in Figure 23 and provides an historical context in which to analyze the distribution of alligators. For the purposes of this discussion I will differentiate between three major lineages which were revealed as a result of the proposed phylogenetic hypothesis. The *A. prenasalis*--*A. mcgrew* lineage has been recorded only from a small area in western United States (southwestern South Dakota and northwestern Nebraska) during the Chadronian, Orellan, Hemingfordian and Barstovian. The *A. olseni*-*A. mississippiensis* lineage now exhibits a more extensive fossil record in terms of both its stratigraphic and geographic distribution. A. olseni has been recorded from a single locality in southeastern United States during the Hemingfordian. While most fossil forms of A. mississippiensis occur within the present range of the living species in the Barstovian, Hemphillian, Irvingtonian and Rancholabrean, extinct members of this taxon also occur in northwestern Nebraska during the Barstovian and late Clarendonian and in north-central Texas during the early Clarendonian.

Platnick and Nelson (1978) have proposed a method for distinguishing between disjunct distributions that have occurred as a result of dispersal, and those that are due to vicariance. This method is based on an ability to place both taxa and land areas in which the taxa are distributed into a dichotomous cladogram. The method of analysis involves converting the hypothesis about the cladistic relationships of the taxa under consideration to an hypothesis about the relationship among the different land areas in which the taxa are distributed. Correspondence of biogeographic patterns among different test groups results in a general pattern which can be translated to a statement of the relative recency of the interconnections among the areas. Geologic evidence may indicate the exact nature of these interconnections. However, the trichotomous arrangement involving A. mcgrewi, A. sinensis and A. mississippiensis in the Alligator cladogram (Figure 23) may preclude this approach, since trichotomous cladograms are only significant as testable hypotheses if the cladograms for all test groups are trichotomous (Platnick & Nelson, 1978, p. 10).

The Recent distribution of Alligator represents a classic disjunction pattern that is also known to occur among other closely related taxa. The floristic affinities between eastern United States and eastern Asia have been recognized for a long time and have been well documented (see Graham, 1972 for a recent review). Vegetational and floristic studies of Tertiary floras in North America indicate that there was a floristic continuity between eastern North America and eastern Asia during the Early and Middle Tertiary (Wolfe & Leopold, 1967). There is compelling geologic and biogeographic evidence which supports the existence of a Beringian Land Connection between northwestern North America and Asia throughout this same period of time (Hopkins, 1967).

Vegetational analyses of Tertiary floras in western United States (Leopold & MacGinitie, 1972) and Alaska (Wolfe, 1972) indicate dramatic climatic shifts in these regions which appear to be associated with local tectonic activity. While the vegetation of Eocene floras is indicative of tropical climates, Middle Tertiary and Late Tertiary floras indicate, respectively, warm-temperate and cool-temperate temperature regimes for the same regions.

The close taxonomic resemblance in the warm-temperate, broad-leaved deciduous vegetation (the Mixed Mesophytic Forest) of Middle Tertiary floras is thought to indicate a biotic continuity between eastern Asia and eastern North America as late as the Middle Miocene (Wolfe & Leopold, 1967). This implies that some of the present disjunctions involving components of the Mixed Mesophytic Forest may have developed as a result of the barriers fragmenting the range of ancestral taxa. However, because of the complex histories of Tertiary floras, it is doubtful that all transpacific disjunctions can be explained by the same patterns in regard to both time and place (e.g., see MacGinitie, 1972). The fragmentation of this once continuous biota initially involved the submergence of the land connection across Beringia during the Late Miocene (Hopkins, 1967). Even though the Bering land bridge was reestablished during Hemphillian and Blancan time, warm-temperate taxa remained in disjunction because of the shift to cool-temperate to subarctic climates at northern latitudes (Dorf, 1960).

The fact that a warm-temperate vegetation characterized Middle Tertiary floras in western North America and Alaska indicates that other warm temperate groups could have attained a trans-Pacific distribution by way of Beringia by late Miocene. I have already discussed the evidence that suggests that alligators represent an element of this Middle Tertiary, warm-temperate biota.

As illustrated in Figure 23 the *A. olseni*--*A. mississippiensis* and *A. sinensis* lineages are postulated as having been independently derived from the *A. prenasalis*--*A. mcgrewi* lineage (*A. mcgrewi* is the portion of this lineage which actually conforms to the hypothetical morphological ancestor). The known fossil record of *A. olseni* and *A. mississippiensis* suggests that this lineage has generally been restricted to the southeastern United States during most of its evolutionary history. However, the occurrence of this lineage in northwestern Nebraska during the Early Barstovian and the Late Clarendonian and in north-central Texas during the Early Clarendonian indicates that such has not always been the case.

The known geographic distribution of *A. mcgrewi* overlaps that of *A. mississippiensis* in northwestern Nebraska during the Early

Barstovian. Although both forms have been recovered from the small fossil deposit (Trojan Quarry), the sympatric occurrence of these two forms during this period of time remains problematical. Although *A. mcgrewi* has been recorded from only a small area in North America (northwestern Nebraska) its postulated phylogenetic relationship to *A. sinensis* (ancestor-descendant) suggests that it may have achieved a trans-Pacific distribution by the Late Miocene. In any event, there is no evidence for major physical or climatic barriers that would have prevented this form from attaining such a distribution along with other elements of the Middle Tertiary, warm-temperate biota. The reported prescence of alligators in eastern Asia during the Miocene (Chow & Wang, 1964), although problematical because of the fragmentary evidence, does suggest that alligators had achieved such a distribution prior to the development of major barriers in Beringia in the Late Miocene. This scenario implies that the present disjunction involving living species of *Alligator* represents a relict of the distribution of their common ancestral taxon (*A. mcgrewi*) which was fragmented as a result of the major geologic and climatic events that took place in northwestern North America during the Late Tertiary.

CONCLUSIONS

Based upon the comparative morphological analysis of the alligator skull that I conducted, I have arrived at the following conclusions:

1. An examination of five cranial measurements as they relate to skull length showed that samples drawn from natural populations of *A. mississippiensis* and *A. sinensis* generally overlap to the same degree as samples drawn from different geographic populations of

A. mississippiensis. However, one variable (length of the mandibular symphysis) did show a discrete pattern of variability which was associated with the taxonomic origin of the sample. Individuals belonging to *A. sinensis* possess relatively longer mandibular symphyses than do those of *A. mississippiensis* of a similar size.

2. Statistical analyses of bivariate plots of these data indicated that intracranial growth of the alligator skull is primarily isometric. Only skull width at the jaw articulation in *A. sinensis* grew in a positively allometric fashion. This contrasts with the results of a similar study (Dodson, 1975) which showed that skull width at the orbits and snout length are positively allometric in *A. mississippiensis*. These inconsistencies may be due to differences in the nature of the samples employed. Intracranial growth was generally found not to differ significantly between *A. mississippiensis* and *A. sinensis*, although exceptions to this pattern were observed to occur. It was demonstrated that intracranial growth involving some characters was significantly different in *A. sinensis* and a Texas population of *A. mississippiensis*, but there was no statistically significant difference in the growth of these characters in A. sinensis and a population of *A. mississippiensis* from Florida. These discrepancies may also be due to the nature of the samples used in the analysis.

3. The known fossil material of *Alligator* was assigned to four taxa: *A. mississippiensis*, *A. olseni*, *A. mcgrewi* and *A. prenasalis*. The nominal species *A. mefferdi* and *A. thomsoni* are considered to be synonymous with *A. mississippiensis*. Taxonomic decisions were primarily based upon qualitative morphologic characters. Similar ontogenetic patterns for some of these features were observed for both living and fossil species.

4. The evolutionary history of alligators was reconstructed on the basis of a cladistic methodology. Theoretical and practical problems associated with this method were discussed. The history of the group involved three principal lineages: *A. prenasalis* - *A. mcgrewi*, *A. olseni* - *A. mississippiensis* and *A. sinensis*. *A. mcgrewi* is postulated as the common ancestor of the *A. olseni* - *A. mississippiensis* and *A. sinensis* lineages.

5. The major modifications of the skull that occurred during the evolutionary history of alligators involved changes in the biomechanics of feeding.

6. It is also concluded that the present disjunct distribution of alligators (southeastern North America and eastern Asia) is related to a vicariant event that occurred during the group's evolutionary history. This event, which probably occurred during the late Miocene, fragmented the once continuous distribution of alligators. Local extinction of alligators was caused by the dramatic climatologic shifts which occurred in western United States as a result of local tectonic activity during this time period.

APPENDIX I

ABBREVIATIONS

INSTITUTIONS

AMNH, American Museum of Natural History
BMNH, British Museum (Natural History)
CM, Carnegie Museum
FAMNH, Frick Collection, American Museum of Natural History
FMNH, Field Museum of Natural History
FSM, Florida State Museum
MCZHU, Museum of Comparative Zoology, Harvard University
PU, Princeton University
ROM, Royal Ontario Museum
SDSM, South Dakota School of Mines
SM, Senckenberg Museum
SMM, Science Museum of Minnesota
UCMVZ, University of California, Museum of Vertebrate Zoology
UMMCZ, University of Michigan, Museum of Comparative Zoology

ANATOMICAL

ang, angular
art, articular
bo, basioccipital
bs, basisphenoid
co, coronoid
den, dentary
dso, dermosupraoccipital
ex, exoccipital
fr, frontal
ju, jugal
lac, lacrymal
lec, lateral Eustachian canal
max, maxillary
na, nasal
pa, parietal
pfr, prefrontal
pm, premaxillary
po, postorbital
pt, pterygoid
qj, quadratojugal
qu, quadrate
so, supraoccipital
spl, splenial
sq, squamosal
sur, surangular

APPENDIX II

RECENT SPECIMENS EXAMINED

All Recent specimens that were examined are listed below. Locality references are provided within parentheses. Unless otherwise noted specimens belong to osteological collections.

Alligator mississippiensis (Alachua County, Florida): AMNH 7128, 7127, 40580, 43314, 40585, 40583, 40581, 40587, 7142, 9112, 8058, 43316, 40579, 43315, 40582, FSM 9225; (Black Bayou, Victoria County, Texas): CM 4113 (alcohol), 4106 (alcohol), 4104 (alcohol), 4107 (alcohol), 4118 (alcohol), 4122 (alcohol), 4120 (alcohol), 4119 (alcohol), 4108 (alcohol), 6395 (preserved skin), 6394 (preserved skin), 6393 (preserved skin), 6396 (preserved skin).

Alligator sinensis (Ahnwei Province, The People's Republic of China): AMNH 23907, 23899, 23901, 23900, BMNH 1954.1.7.30 (no locality data), FMNH 197941 (zoo specimen), MCZHU 17550, SM 49685, 40071, 8126, 35149, 30003 (zoo specimen), UCMVZ 67884 (zoo specimen), UMMCZ S781.

APPENDIX III

Data set upon which the morphometric analysis of the alligator skull was based. Variables; X = skull length; Y1 = skull length at the jaw articulation; Y2 = skull width at the postorbital bar; Y3 = skull width at the orbits; Y4 = skull width at the premaxillary-maxillary suture; Y5 = snout length; Y6 = mandibular symphysis length. All measurements are in mm.

<u>Alligator</u> <u>mississippiensis</u> (Victoria County, Texas)

	X	Y1	Y2	Y3	Y4	Y5	Y6
CM 4113	~~47.7~~	~~24.3~~	~~24.7~~	~~21.8~~	~~11.0~~	~~23.1~~	~~4.0~~
CM 4108	48.1	24.5	24.7	21.6	10.9	22.6	3.9
CM 4107	50.9	24.8	25.0	21.6	11.2	24.1	4.1
CM 4106	~~52.5~~	~~25.7~~	~~25.9~~	~~23.0~~	~~11.6~~	~~25.8~~	~~4.3~~
CM 4118	86.3	44.8	41.9	37.0	23.1	46.2	7.9
CM 4119	86.5	44.9	42.1	39.3	21.7	46.2	7.9
CM 4120	~~89.1~~	~~46.6~~	~~45.5~~	~~46.2~~	~~24.0~~	~~48.1~~	~~8.0~~
CM 4122	93.7	47.9	45.8	42.0	24.7	50.9	9.2
CM 4104	100.7	52.2	50.5	46.0	27.1	56.4	9.0
CM 6396	~~289.~~	~~151.5~~	~~130.7~~	~~126.5~~	~~77.9~~	~~187.~~	~~29.4~~
CM 6395	295.	151.2	129.0	121.7	80.5	182.	27.0
CM 6393	315.	171.5	153.5	139.9	90.7	202.	30.0
CM 6394	~~360.~~	~~195.~~	~~163.4~~	~~156.2~~	~~102.3~~	~~237.~~	~~34.6~~

APPENDIX III (cont.)

Alligator mississippiensis (Alachua County, Florida)

	X	Y1	Y2	Y3	Y4	Y5	Y6
AMNH 7128	52.1	26.7	27.0	23.6	13.9	24.6	5.4
AMNH 7127	78.5	38.3	36.9	32.6	20.1	41.2	7.8
AMNH 40580	183.	104.0	96.0	89.5	57.9	109.0	20.4
AMNH 43314	185.	106.5	90.5	65.8	51.6	112.4	19.0
AMNH 40585	195.	109.8	101.8	90.7	60.2	119.4	24.3
AMNH 40583	204.	119.8	105.5	96.9	66.2	124.0	21.7
AMNH 40581	210.	130.9	115.5	106.5	63.1	128.7	25.0
AMNH 40578	227.	137.0	120.7	114.2	65.8	135.0	27.0
AMNH 8058	266.	149.3	131.1	122.5	77.4	167.2	29.8
AMNH 7142	282.	150.5	134.2	127.8	86.2	184.	30.3
AMNH 43316	283.	169.2	143.3	134.2	80.7	181.	26.5
AMNH 40579	293.	183.	158.7	148.2	94.2	188.	40.2
AMNH 43315	352.	238.	195.	188.	115.4	236.	54.5
AMNH 40582	359.	198.	181.	176.6	113.6	239.	45.6
FSM 9112	380.	249.	210.	210.	121.9	255.	54.6
FSM 9225	491.	296.	265.	237.	150.2	340.	63.7

APPENDIX III (cont.)

Alligator sinensis (Ahnwei Province, China)

	X	Y1	Y2	Y3	Y4	Y5	Y6
AMNH 23901	~~126.2~~	~~76.6~~	~~68.9~~	~~58.2~~	~~36.0~~	~~70.8~~	~~18.8~~
AMNH 23907	130.0	72.9	65.0	57.2	36.0	70.0	18.9
AMNH 23899	131.7	78.5	71.5	60.3	37.2	71.4	21.3
UCMVZ 67884	~~143.2~~	~~83.9~~	~~67.6~~	~~66.6~~	~~41.5~~	~~78.0~~	~~22.5~~
AMNH 23900	145.6	87.0	73.8	64.3	42.0	80.0	22.1
SM 49685	157.4	93.1	80.5	76.6	43.5	86.2	26.3
FMNH 38235	~~163.0~~	~~103.0~~	~~85.3~~	~~73.3~~	~~47.2~~	~~89.1~~	~~30.4~~
SM 40071	167.6	110.6	90.3	76.3	51.6	94.8	26.5
FMNH 38234	168.2	106.2	91.9	77.9	51.8	96.1	29.5
SM 8126	~~186.~~	~~116.6~~	~~102.5~~	~~94.6~~	~~53.5~~	~~105.8~~	~~28.3~~
FMNH 197941	195.	145.1	117.5	101.2	63.6	111.7	32.4
SM 35149	220.	142.8	114.2	107.2	64.2	125.5	33.4
SM 30003	~~221.~~	~~168.5~~	~~135.6~~	~~134.8~~	~~73.4~~	~~134.5~~	~~46.5~~
BMNH 1954.1.7.30	310.	184.	159.6	148.2	97.7	199.	47.8

APPENDIX IV

The alligatorid taxa that were compared to alligators are listed below. Except for Recent forms, taxa are only referred to a currently recognized genus. The known stratigraphic and geographic distribution of each taxon is provided within the parentheses.

Albertochampsa (late Cretaceous; Alberta, Canada)
Allognathosuchus (Paleocene and Eocene ; North America and Europe)
Arambourgia (Eocene; France)
Brachychampsa (late Cretaceous; Montana)
Caiman latirostris (Recent; Central America)
Caiman crocodilus (Recent; South America)
Ceratosuchus (Paleocene; Colorado)
Diplocynodon (Eocene; North America and Europe, Pliocene; Europe)
Eocaiman (Eocene; Patagonia)
Hispanochampsa (Oligocene; Spain)
Melanosuchus niger (Recent; South America)
Paleosuchus palpebrosus (Recent; South America)
Paleosuchus trigonatus (Recent; South America)
Procaimanoidea (Eocene; Utah)
Prodiplocynodon (late Cretaceous, Wyoming)

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