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## The Crocodylomorpha at and between geological boundaries: the Baden-Powell approach to change?

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### Summary

Although the Crocodylomorpha spans a time period of over 200 million years, none of its notable morphological transitions appear to coincide with major geological boundaries. The Crocodylomorpha originated before the extinction event at the end of the Carnian Stage (Late Triassic), concomitant with a shift of locomotor pattern from bipedal erect posture to quadrupedal erect posture. With the successive divergence of the Sphenosuchia and Protosuchia the majority of features of the extant Crocodylia became established before the end of the Triassic. The Mesoeucrocodylia may have arisen in the early part of the Early Jurassic. The adoption of a more sprawling posture in the Longirostrine Taxa of the Mesoeucrocodylia was associated with a change of way of life from terrestrial to aquatic, probably immediately after the extinction event at the end of the Pliensbachian Stage (Jurassic). The Eusuchia arose in the Early Cretaceous, being characterized mainly by a complete bony secondary palate and the procoely of all vertebrae. The three extant clades most probably all arose before the Cretaceous-Tertiary boundary. Thus, the patterns of cladogenesis and diversification within the Crocodylomorpha indicate that, at least as currently understood, these taxa were prepared for the major environmental and biotic events that occurred during their history. Baden-Powell's motto of "be prepared" (Maynard 1946), taken from his own initials, appears to be an adequate descriptor of the history of the Crocodylomorpha.

### Introduction

The Crocodylomorpha is one of two extant clades of archosaurs (*sensu* Gauthier 1986). It is taxonomically equivalent to the Crocodylia of traditional usage (including the Protosuchia, "Mesosuchia" and Eusuchia) plus the Sphenosuchia (e.g. Bonaparte 1982)). The Crocodylia of current usage is cladistically restricted to three extant groups: the Alligatoroidea, Crocodyloidea and Gavialoidea (see Clark in Benton and Clark 1988; Norell *et al.* 1994; Brochu 1997). The evolution of the Crocodylomorpha has been the subject of detailed studies for more than a century (e.g. Huxley 1875; Mook 1934; Kälin 1955; Langston 1973; Buffetaut 1982) as this archosaurian lineage has a reasonably complete and continuous fossil record, spanning over 200 million years, back to the late Triassic. However, in nearly all studies prior to the mid-1980s the basis for determining phylogenetic relationships was subjective (relying on overall similarities) and hence no reasonable hypothesis of evolutionary scenarios within the Crocodylomorpha could be made because of the inability to distinguish between homology and convergence. Furthermore, extant crocodylians are often considered to be "living fossils", and as such are portrayed as relics of the Mesozoic "ruling reptiles" that have changed little during their evolution (e.g. Neil 1971; Meyer 1984).

Over the past two decades our knowledge of the Crocodylomorpha has increased significantly due to the discovery of many new taxa, the

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restudy of previously enigmatic taxa, the functional analysis of certain structural systems and, especially, the application of cladistic methodology to phylogenetic studies (e.g. Busbey 1986, 1995; Clark 1986, 1988 (in Benton and Clark), 1994; Wu 1986; Walker 1990; Sereno and Wild 1992; Gasparini *et al.* 1993; Wu and Chatterjee 1993; Norell *et al.* 1994; Wu and Sues 1995; Wu *et al.* 1994a, 1994b, 1995, 1996a, 1996b, 1997; Brochu 1997). This has led to the realization that extant crocodylians are actually highly modified in many respects. The skull is very flat and extremely rigid, an extensive bony secondary palate is present, there are broad scarf joints between the skull roof elements, and there is extensive "fusion" of the quadrate (the mandibular suspensorium) and the braincase wall. The external naris and ear are able to be closed by muscular flaps and they are coplanar with the eye. The postcranium, especially the fore- and hind-limbs, has unique specializations as well.

As a result of these phylogenetic studies it became evident that some of these features first occurred in the most primitive fossil crocodylomorphs, and that others are exclusive to the extant crocodylians and their closest relatives. Yet others show successive modification towards those typical of the extant Crocodylia throughout the history of the group. Phylogenies inferred using cladistic methodology provide a basis for interpreting crocodylomorph evolution.

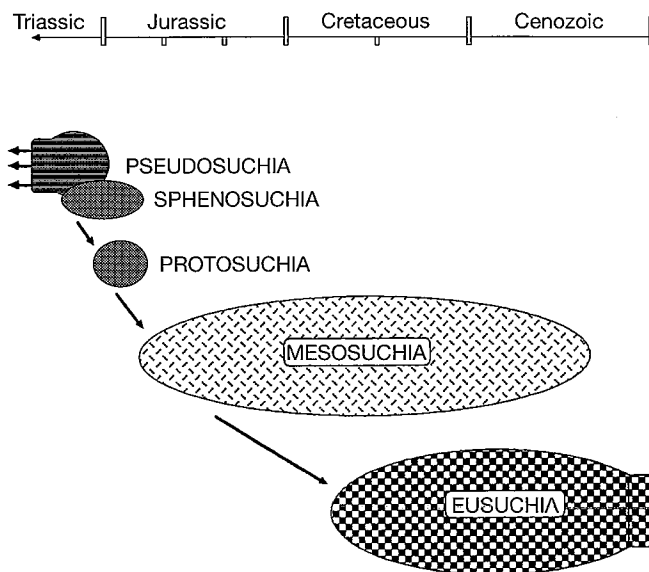
Additionally, our knowledge of crocodylomorph evolution has benefitted from detailed stratigraphic studies on dating, and correlation of the formations in which early crocodylomorphs are found. For example, the Lower Lufeng Formation of southwestern China, the upper Elliot Formation of southern Africa, the upper Newark Supergroup of eastern North America, and the Kayenta Formation of the Glen Canyon Group of the western United States were traditionally considered to be of Late Triassic age (see Young 1951; Romer 1966), but recently they have been reassigned to the Early Jurassic (see Olson and Galton 1984; Luo and Wu 1994; Sues *et al.* 1994). Thus, questions relating to geological boundaries and their association with evolutionary events must be revised as stratigraphic knowledge becomes more refined.

In this paper we begin by summarizing, within a phylogenetic context, the changes in major structural complexes of extant crocodylians that show morphological trends within the Crocodylomorpha as a whole. Then we compare these morphological transitions with geological boundaries passed by the Crocodylomorpha. This leads us to hypotheses about the morphological evolution of the Crocodylomorpha in relation to geological boundaries.

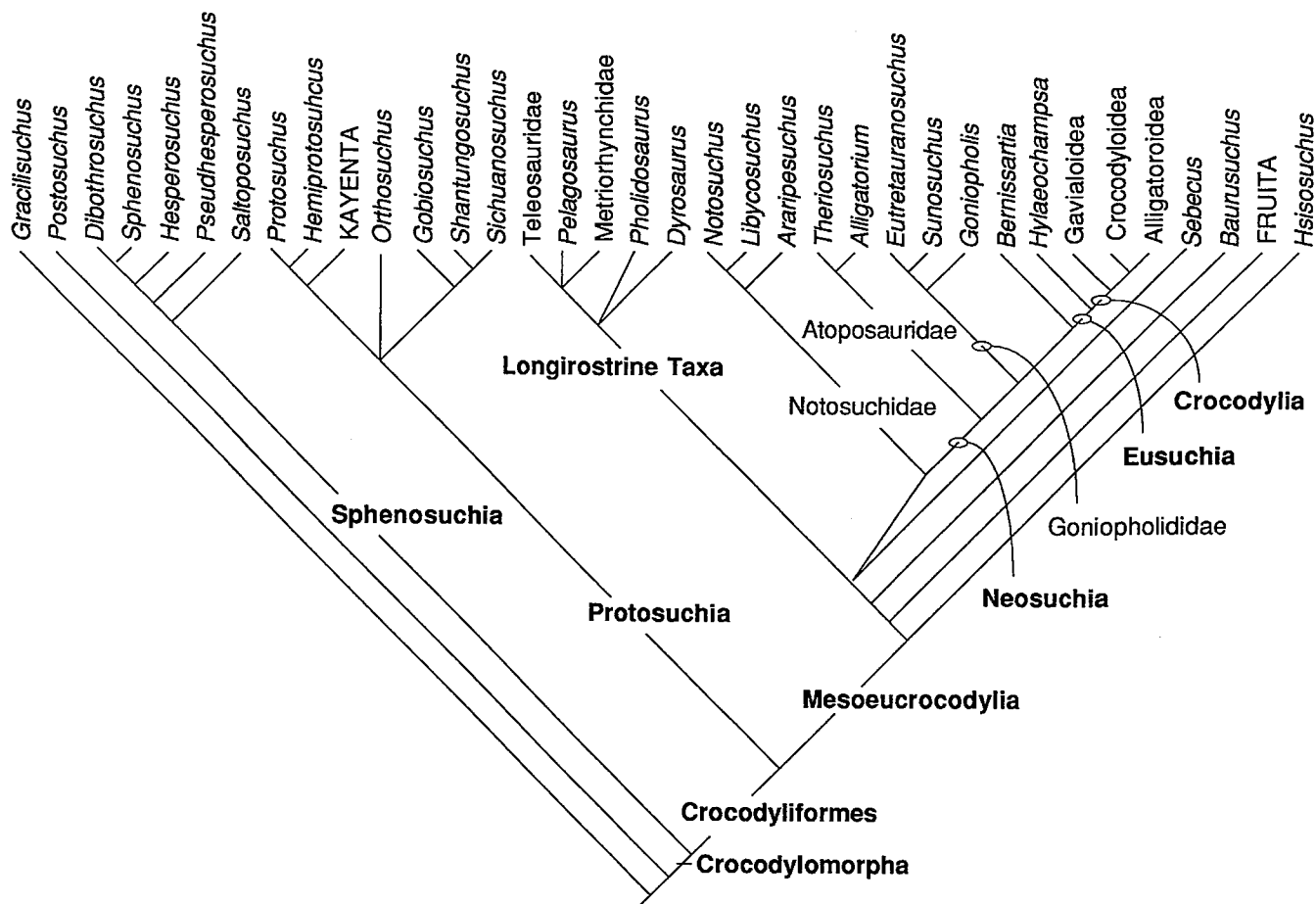
## Results and Discussion

### Crocodylomorph Phylogeny

Traditionally, crocodylomorph evolution has been represented in a gradistic fashion, each grade suggesting a particular level of structural organization. The works of Buffetaut (1982) and Bonaparte (1982), for instance, imply that the Crocodylomorpha has undergone at least four major episodes of evolution, resulting in the attainment of new levels of structural organization (Fig. 1). These are represented by the Sphenosuchia, Protosuchia, "Mesosuchia" and Eusuchia in chronological sequence (even more levels are suggested by Langston [1973]). Clark (1988 in Benton and Clark) concluded that all of these grades, except the Eusuchia, are paraphyletic in a cladistic sense, and the paraphyly of the Sphenosuchia was further supported by the work of Parrish (1991). More recently, however, phylogenetic studies of a number of new taxa demonstrate that the Sphenosuchia (see Sereno and Wild 1992; Wu and Chatterjee 1993) and Protosuchia (see Wu *et al.* 1994a, 1997; Wu and Sues 1995) are monophyletic. The "Mesosuchia", however, remains paraphyletic and consists of a series of successive sister-groups branching from the stem line prior to the Eusuchia. Recently the longirostrine "mesosuchians" (including the Teleosauridae, Metriorhynchidae, Pholidosauridae, and dyrosaurs) have been demonstrated to form a monophyletic clade (Clark 1994; Wu *et al.* 1997). Also from among the "Mesosuchia" *Bernissartia*



**Fig. 1.** Gradistic interpretation of crocodylomorph evolution as implied in the works of Bonaparte (1982) and Buffetaut (1982).



**Fig. 2.** Phylogenetic relationships among major groups of the Crocodylomorpha. This cladogram is derived mainly from Wu *et al.* (1997: Fig. 6), with reference to the work of Wu and Chatterjee (1993) for the Sphenosuchia, Clark (1994) for the Longirostrine Taxa, and Norell (1989) and Brochu (1997) for the Eusuchia and Crocodylia.

(plus *Shamosuchus*), the Goniopholididae and the Atoposauridae form the successive sister-groups of the Eusuchia.

Traditionally, the Atoposauridae has been considered to be the closest relative of the Eusuchia (e.g. Joffe 1967). Within the Eusuchia relationships among the three extant groups are controversial, with some degree of conflict between morphological and molecular data. Morphological data, including that from fossil forms, strongly suggests that the Alligatoroidea and Crocodyloidea are more closely related to each other than either is to the Gavialoidea (Norell 1989; Brochu 1997). This is in contrast to the view yielded by molecular data, in which the Gavialoidea and Crocodyloidea are proposed to be sister-groups (Densmore 1983; Hass *et al.* 1992; Poe 1996). Our cladogram (Fig. 2) depicts the former pattern as it is based upon morphological data. For the purposes of the argument presented herein, the relationships within the Crocodylia have no

bearing on the larger scale patterns within the Crocodylomorpha as a whole.

There is general agreement that the two successive sister-groups of the Crocodylomorpha are the Poposauridae (best represented by *Postosuchus* from the Upper Triassic Dockum Group of Texas [Chatterjee 1985]) and *Gracilisuchus* (from the Upper Triassic Chañare Formation [?Anisian] of Argentina [Romer 1972]) (Fig. 2). Crocodylomorphs can be classified as a nested set of successively less inclusive monophyletic groups (Fig. 2). Although not all of these groups have been named, all of its members may be hierarchically assigned more inclusively to the Crocodylia, Eusuchia, Neosuchia, Mesoeucrocodylia, Crocodyliformes and Crocodylomorpha. The Crocodylia is unequivocally defined by three features, the Eusuchia by six, the Neosuchia by five, the Mesoeucrocodylia by seven, the Crocodyliformes by 14, and the Crocodylomorpha by seven (Wu *et al.* 1997).

## Evolution of the Major Features of Crocodylia

### Binary Transformations

1. Associated with the characterization of the major groups outlined above, there are at least 42 unequivocal features that have been cumulatively established throughout the history of the Crocodylomorpha. Many of these features display a clearly cladogenetic binary pattern of morphological transformation. They are thus most important in establishing the phylogenetic hierarchy of the major groups of the Crocodylomorpha.

The Crocodylomorpha is characterised by at least two cladogenetic features that continue to be possessed by all of its subgroups: the absence of the descending process of the squamosal, and the elongation of the proximal carpals (radiale and ulnare).

At the next level, that of the Crocodyliformes, ten of the cladogenetic features that are involved in characterizing this level are continued through to extant crocodylians. They are (i) a broad postero-ventral process of the coracoid; (ii) an ear flap on the skull table (as suggested by the groove along the lateral side of the table) indicating that the ear could be closed by the flap; (iii) supraoccipital entirely excluded from the foramen magnum; (iv) the basisphenoid rostrum is dorso-ventrally deep; (v) skull surface with a pit and ridge pattern of sculpturing; (vi) the body covered dorsally by osteoderms; (vii) eustachian tubes enclosed by bones; (viii) the ischium with a distinct rod-like pubic process; (ix) the obturator foramen of the pubis closed; and (x) the olecranon reduced.

The Mesoeucrocodylia is characterized by three cladogenetic features that are continued into the extant crocodylians: (i) pterygoids fused posterior to choana; (ii) pubis entirely excluded from the acetabulum; and (iii) pubis with an expanded distal end.

The Neosuchia has one defining feature, the vascular opening on the lateral edge of the dorsal part of the postorbital bar, that is continued through to the extant Crocodylia.

The Eusuchia possess four cladogenetic features that are carried forward to the Crocodylia: (i) first caudal vertebra biconvex, (ii) all vertebrae except for the first caudal procoelous; (iii) cervical vertebrae and the first few dorsals with pronounced hypapophyses; and (iv) the neural spine on posterior cervical vertebrae anteroposteriorly narrow and rod-like.

The Crocodylia is probably unique in that the osteoderms are arranged in a sutural pattern.

### Anagenetic Trends

2. Studies of crocodylomorph evolution have long recognized the existence of anagenetic trends in a

variety of structural complexes. The formation of the bony secondary palate has often been cited as such an example (e.g. Langston 1973; Busbey 1995). Many structural complexes exhibit anagenetic trends within the Crocodylomorpha and appear to approach, in stages, the condition found in extant crocodylians. Most of these are associated with structural modifications associated with the following: increasing rigidity of the skull; gradual flattening of the skull; increasing undulation of the jaw margins; changes in locomotor posture and mode. Each of these character complexes is outlined below and its evolutionary history is traced.

(A) Rigidity of the skull. The skull of extant crocodylians is highly akinetic and inflexible, the condition being achieved primarily by the closure of certain fenestrae and immobilization of certain joints between regions of the skull; the development of extensive "fusion" between elements (especially between the suspensorium [quadrate] and the braincase wall), and the formation of the bony secondary palate (see below). The functional significance of increasing skull rigidity has been considered by a number of authors (e.g. Langston 1973; Busbey 1995).

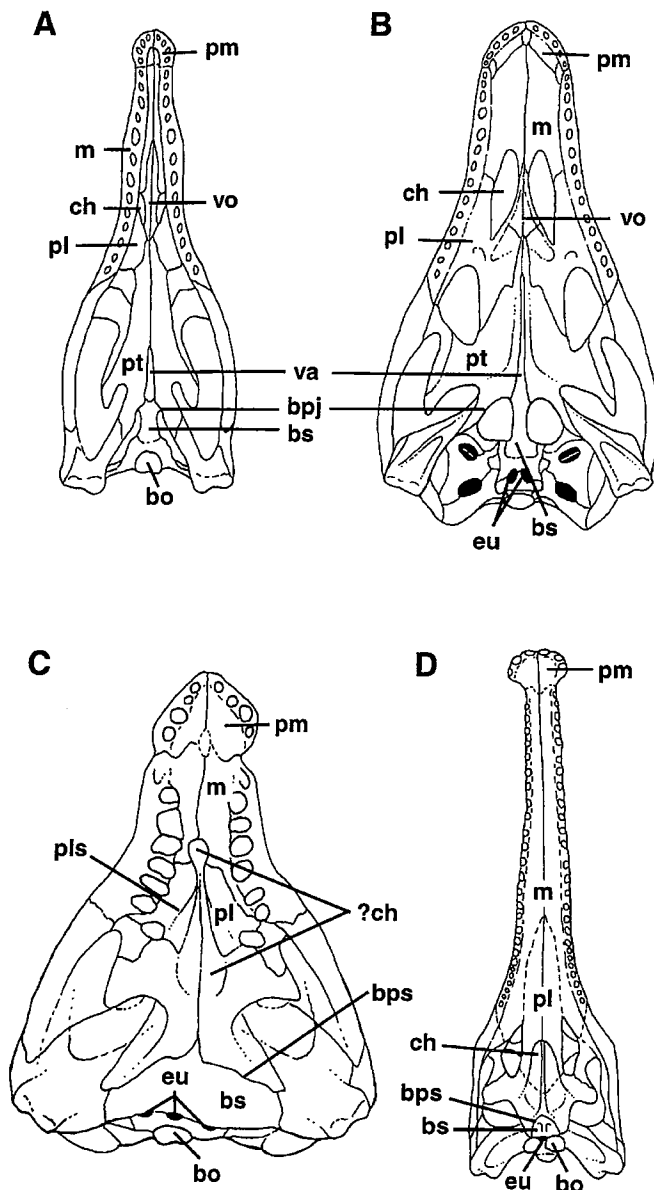
In the Poposauridae (*Postosuchus*), the immediate sister group of the Crocodylomorpha (Fig. 2), the skull is kinetic and very similar in architecture to that of primitive archosaurs. For example, the basiptyergoid joint between the braincase and palate is present, the interptyergoid vacuity between the pterygoids and the antorbital fenestra is still large, the quadrate does not exhibit additional connections with the braincase or roofing bones, and the braincase only loosely contacts the dermal roof elements because of the presence of a post-temporal fenestra and the absence of a firm contact of the paroccipital process with the squamosal and parietal (Figs. 3A, 4A).

Trends towards increasing skull rigidity are evident very early in the history of the Crocodylomorpha, and this is evident in the most primitive clade of the group, the Sphenosuchia. The rigidity of the skull in the Sphenosuchia is exemplified in the following features (Figs. 3B and 4B): (i) The posttemporal fenestra is greatly reduced in size, and is even entirely closed in derived forms of this clade, such as *Dibothrosuchus* (Simmons 1965; Wu 1986; Wu and Chatterjee 1993) and *Sphenosuchus* (Walker 1990); with the reduction of this fenestra, the roofing bones (squamosal and parietal) develop large occipital portions, which, together with enlarged supraoccipital and massive paroccipital processes, form a tightly integrated plate-like occiput, greatly restricting movement between the braincase and skull roof. (ii) The pterygoid ramus of the quadrate (PRQ) and the quadrate ramus of the pterygoid (QRP) are broadened, sheet-like, and extend main-

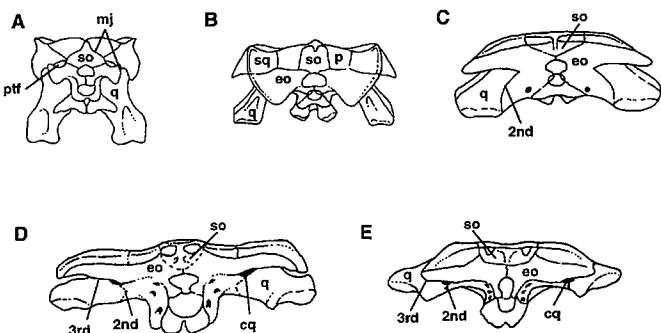
ly dorso-ventrally rather than antero-posteriorly, overlap with one another extensively, and are firmly applied to the anterior wall of the braincase. (iii) The dorsal head of the quadrate is also broadened and

exhibits three processes in *Dibothrosuchus*; these make extensive connection with both the braincase and skull roof. Although (iv) the interpterygid vacuity is reduced to a slit, the ball-and-socket basiptyergoid joint remains. Therefore, the possibility of movement between the braincase and palate remains.

Skull rigidity is greatly increased at the level of the Crocodyliformes. In its most primitive clade, the Protosuchia, there is further enhancement of the above-mentioned features (Figs. 3C and 4C): (i) The posttemporal fenestra is entirely occluded in adults; the occipital portion of the squamosal and parietal become small, and the supraoccipital is entirely excluded by the exoccipitals from the foramen magnum, resulting in the exoccipitals forming the major body of the occiput. (ii) The rami of the PRQ and QRP are "fused" with the braincase wall by way of extensive sutures that cover the prootic and, together with the laterosphenoid, border the lateral aperture of the foramen for the trigeminal nerve. (iii) The quadrate is oblique in orientation, with its dorsal head displaced anteriorly and articulating with the squamosal and prootic. (iv) The interpterygid vacuity is completely closed by the contact of the pterygoids along the midline, and the basiptyergoid joint is replaced by a sutural contact, indicating the abolition of movement between the braincase and palate. In addition, (v) the basisphenoid extends



**Fig. 3.** Skulls of the sister-group and early forms of the Crocodylomorpha in ventral view (not to scale). A, *Postosuchus* (a poposaurid), derived from Chatterjee (1985: Fig. 5b); B, *Dibothrosuchus* (a sphenosuchian), derived from Wu and Chatterjee (1993: Fig. 2B); C, An unnamed protosuchian of the Kayenta Formation, reconstructed based on Clark (1986: Fig. 14); D, *Peipehsuchus* (a longirostrine taxon), derived from Li (1993: Fig. 1). Abbreviations: bo, basioccipital; bpj, basiptyergoid joint; bs, basisphenoid; bps, basiptyergoid suture; ch, choana; ?ch, the functional choana may have opened posteriorly into the fossa in the pterygoids; eu, exits for eustachian tubes; m, maxilla; pl, palatine; pls, palatine shelf; pm, premaxilla; pt, pterygoid; vo, vomer.



**Fig. 4.** Skulls of the sister-group and major groups of the Crocodylomorpha in occipital view (not to scale). A, *Postosuchus* (a poposaurid), derived from Chatterjee (1985: Fig. 5c); B, *Dibothrosuchus* (a sphenosuchian), derived from Wu and Chatterjee (1993: Fig. 3B); C, *Orthosuchus* (a protosuchian), derived from Nash (1975: Fig. 6); D, *Peipehsuchus* (a longirostrine taxon), derived from Li (1993: Fig. 2); E, *Leidyosuchus* (an early alligatoroid), based on No.1903 of the Royal Ontario Museum. Abbreviations: cq, cranio-quadrate canal; eo, exoccipital; mj, mobile joint between the braincase and skull roof; ptf, posttemporal fenestra; q, quadrate; so, supraoccipital; sq, squamosal; 2nd, the second connection of the quadrate with the braincase (i.e., with the ventro-lateral side of the otoccipital); 3rd, the third connection of the quadrate with braincase plus skull roof (i.e., with the paroccipital process and squamosal).

posteriorly and floors the eustachian cavity on the basioccipital, leaving between the basisphenoid and basioccipital a median and a pair of lateral exits for the eustachian tubes; and (vi) the quadrate develops a second connection with the braincase by way of the contact of its medial edge with the broadened posteroventral portion of the otoccipital posterior to the middle ear chamber, which encloses the foramina for cranial nerves IX-XII and the internal carotid artery on the occiput.

In the most primitive members of the Mesoeucrocodylia the rigidity of the skull has almost reached the degree of robustness typical of extant crocodylians. The main difference lies in the involvement of the bony secondary palate and related structures (Figs. 3D and 4D). The most significant additional modification contributing to skull rigidity at the level of the Mesoeucrocodylia is seen (vii) in the development of a third contact of the quadrate with the skull: the posterolateral end of the squamosal and the lateral extremity of the paroccipital process meet the posterodorsal surface of the quadrate, which encloses the cranio-quadrato canal and completes the posterior wall of the middle ear chamber. By this stage the auditory passage is well-formed. Additionally, (viii) the basisphenoid is largely reduced in size on the ventral surface of the palate because of overlap by the posterior shift of the pterygoid (Figs. 4D and 5A).

Further refinements in some of the above-mentioned features are evident in more derived groups, but all are relatively minor in extent except for (viii), the basisphenoid being almost entirely covered by the further posterior displacement of the pterygoid. This is evident at the point at which the Goniopholididae branches (Fig. 5B). Thus, skull rigidity typical of the extant Crocodylia was essentially established as early as the Late Jurassic.

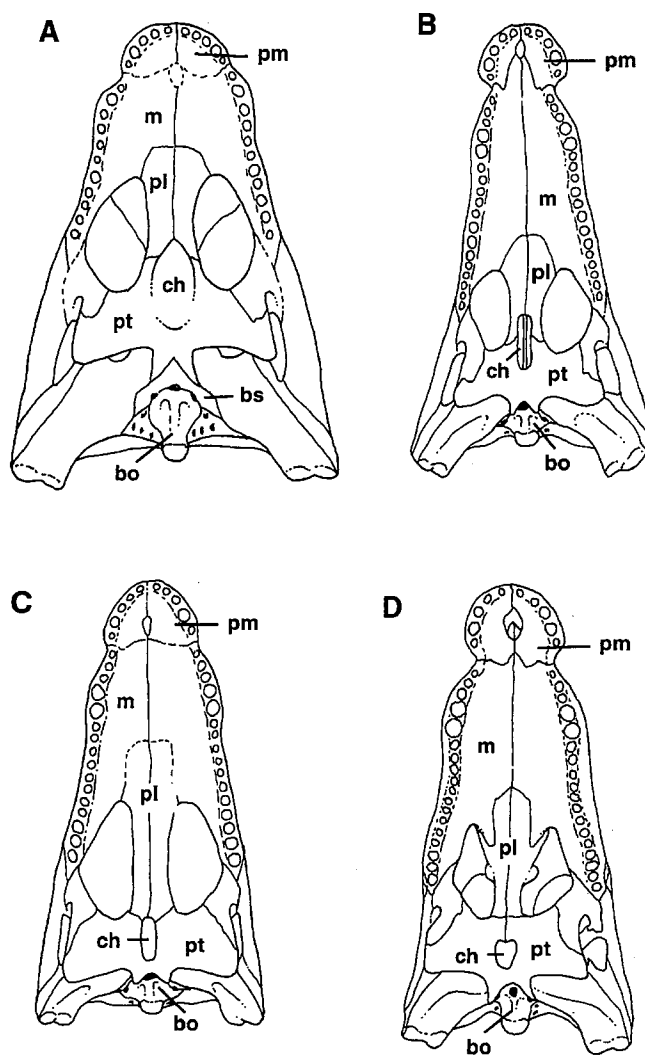
(B) Formation of the bony secondary palate. The secondary palate of extant crocodylians is formed by the palatal shelves of the premaxillae and maxillae, the palatines and pterygoids, resulting in the development of a bony nasal passage (Fig. 5D). During the evolution of the secondary palate, the bony nasal passage is gradually established and the internal choana is simultaneously shifted posteriorly until it is entirely encompassed by the pterygoid. Busbey (1995) recently conducted a detailed functional analysis of the bony secondary palate of crocodylomorphs.

In the Poposauridae palatal structure exhibits the primitive pattern of other archosaurians (Fig. 3A). The vomers are very large and separate the maxillae and palatines along the midline. They are also the major elements bordering the internal choanae.

The most significant of the modifications of the palate at the point of origin of the Crocodylomorpha is the development of broad palatal shelves of the

maxilla. These meet along the midline and form, together with the premaxilla, the anterior portion of the bony secondary palate, as seen in sphenosuchians (Fig. 3B). In contrast to the condition seen in the Poposauridae, the palatines are markedly enlarged and approach the midline. The vomers are reduced, forming only one-third of the choanal border. The choanae are narrowly separated and their anterior borders are entirely formed by the maxillae.

In most members of the Protosuchia from the Upper Triassic-Lower Jurassic, palatal morphology differs little from that of the Sphenosuchia. In an unnamed late Early Jurassic Kayenta Form (Clark



**Fig. 5.** Skulls of late crocodylomorphs in ventral view (not to scale). A, *Theriosuchus* (an atoposaurid), reconstructed based on Clark (1986: Fig. 16); B, *Goniopholis* (a goniopholidid), reconstructed based on Mook (1942: Fig. 1C [*Amphicotylus*]); C, *Bernissartia*, reconstructed based on Norell and Clark (1990: Fig. 2B) and Buscalioni and Sanz (1990: Fig. 2); D, *Leidyosuchus* (an early alligatoroid), based on No. 96.12.47 of the Royal Tyrrell Museum of Palaeontology. Abbreviations as in Figure 3.

1986) and in two further genera from the Upper Jurassic-Lower Cretaceous of China (Wu *et al.* 1994a, 1997), however, the palatine displays a ventral shelf, thus forming an incipient secondary palate. This shelf does not, however, meet its mate of the opposite side, and thus leaves a ventral, slit-like opening of the nasal passage (Fig. 3C) which continues posteriorly from the original choanal aperture of sphenosuchians and other archosaurians. A fossa posterior to the palatine is formed along the midline of the pterygoids (as mentioned above, the pterygoids meet along the midline to close the vacuity between them). The internal choana is superficially single and may have opened posteriorly into the fossa on the pterygoids, although the nasal passage is not entirely closed ventrally by bone (it may have been covered by soft tissue in life).

At the level of the Mesoeucrocodylia the anterior portion of the bony nasal passage is completed by the contact of the ventral shelves of the palatines along the midline. These form the anterior border of the internal choana (Figs. 3D and 5A–C). In most early mesoeucrocodylian clades the choana is strongly demarcated only around its anterior margin (Figs. 3D and 5A). Not until the level at which the Goniopholididae branched (the Late Jurassic), is the posterior portion of the choana well-demarcated (Fig. 5B). At this phylogenetic level the derived condition of the basisphenoid being nearly covered by the pterygoids is encountered. The most highly derived state of the secondary palate and choana within non-eusuchians is reached at the level of the *Bernissartia-Shamosuchus* clade, at which point the palatines have extended further posteriorly and carried the choana backwards, almost entirely into the pterygoid (Fig. 5C). Such a condition of the secondary palate and choana is also convergently present in dyrosaurs among the Longirostrine Taxa.

The final stage of the development of the secondary palate is attained by the pterygoids completing the posterior portion of the nasal passage, resulting in the choana being entirely surrounded by the pterygoids (Fig. 5D). This occurs concurrently with the origin of the Eusuchia in the Early Cretaceous.

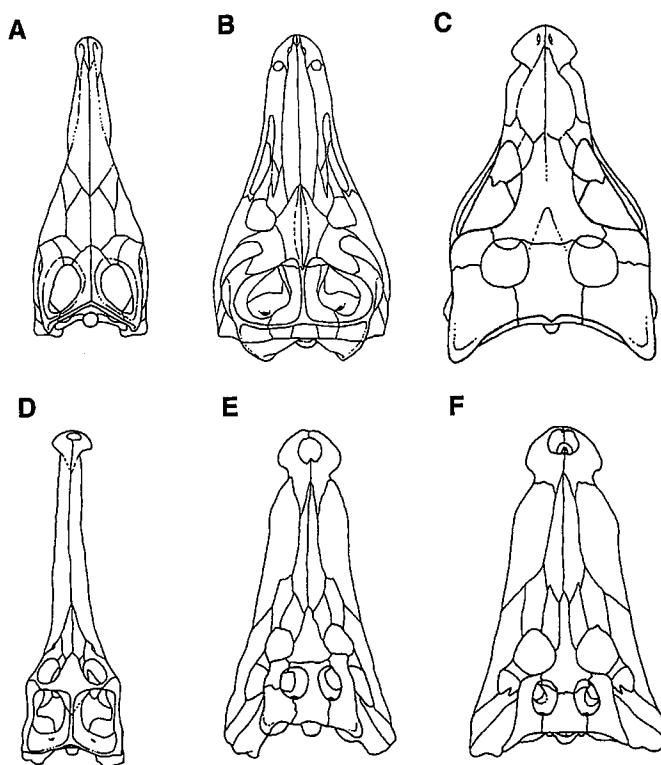
(C) Skull flattening. Skull flattening is one of the most striking cranial modifications within the Crocodylomorpha. Its functional implications (along with those of the bony secondary palate) have most recently been considered by Busbey (1995). The flattening typical of the skull of the extant Crocodylia has been achieved by passing through at least three stages.

In the Poposauridae and most other archosaurians the rostrum is higher than wide (the oreinirostral condition *sensu* Busbey [1995]) and the skull dis-

plays a laterally compressed morphology (Figs. 6A and 7A).

In the sphenosuchian and protosuchian clades the rostrum is slightly wider than high (with the antorbital fenestra being reduced in size in the latter), but the skull, as a whole, still displays an oreinirostral condition, as suggested by the nearly vertical premaxilla and maxilla (Figs. 6B,C and 7B,C). The skull of protosuchians is widened posteriorly in association with the posterolateral shift of the obliquely oriented quadrate (Figs. 6C and 7C).

Snout flattening is first encountered in the tubular or subtubular (the tubular platyrostral shape of Busbey [1995]) rostrum of the Longirostrine Taxa of the Mesoeucrocodylia (Fig. 6D). This has been interpreted as being a modification in aquatic forms for piscivory. True snout flattening (the narrow or broad platyrostral shape of Busbey [1995]), however, occurs initially at the neosuchian level, with the di-



**Fig. 6.** Skulls of the sister-group and major groups of the Crocodylomorpha in dorsal view (not to scale). A, *Postosuchus* (a poposaurid), derived from Chatterjee (1985: Fig. 5a); B, *Dibothrosuchus* (a sphenosuchian), derived from Wu and Chatterjee 1993: Fig. 2A); C, *Sichuanosuchus* (a protosuchian), reconstructed based on Wu *et al.* (1997: Fig. 1A); D, *Peipehsuchus* (a longirostrine taxon), derived from Li (1993: Fig. 1); E, *Goniopholis* (a goniopholidid), reconstructed based on Mook (1942: Fig. 1A [*Amphicotylus*]); F, *Leidyosuchus* (an early alligatoroid), based on No. 1903 of the Royal Ontario Museum.



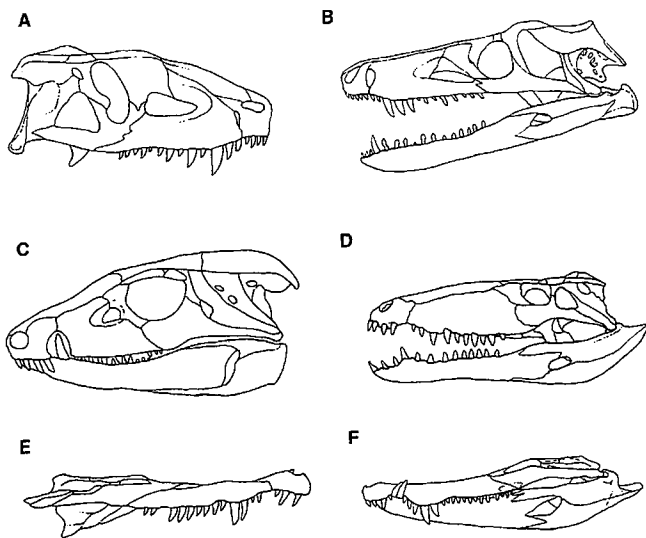
chotomy of the Atoposauridae in the Late Jurassic. It is fully developed in more derived neosuchian clades (Figs. 6E,F and 7E,F). In the Atoposauridae the snout is much broader than high, but the postrostral portion of the skull of some of its taxa (e.g. *Alligatorium* [Wellenhofer 1971]) is still quite high. In taxa displaying true flattening, the snout is firmly anchored to the remainder of the skull by way of extensive overlapping scarf joints, and the antorbital fenestra is entirely closed. Skull flattening is associated with skull strengthening required to resist the forces generated during subduing and dismembering prey by the rolling of the body, both in water and on land (Busbey 1995).

It is notable that the morphological patterns of the snout discussed above convergently reoccur in some later forms (e.g. the tubular snout of the Gavialoidea), although to a lesser degree than postulated by Langston (1973).

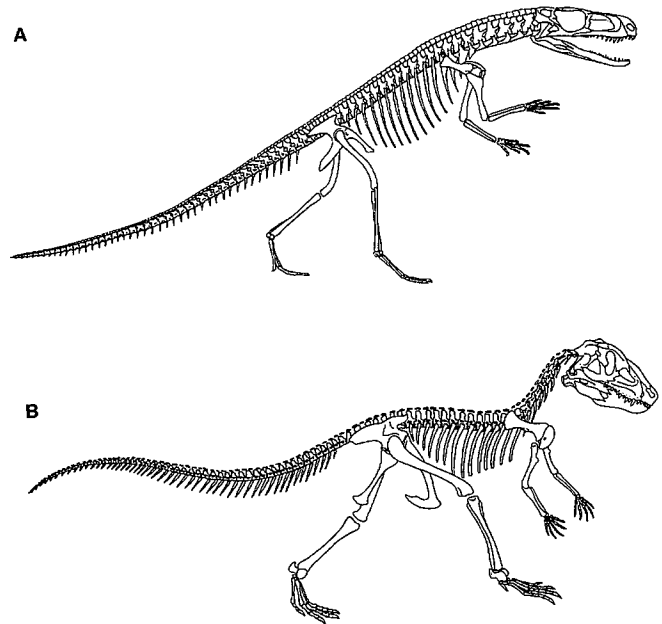
(D) Undulation of the jaw margins. In the Crocodylia (except for the longirostral Gavialoidea) both upper and lower tooth rows consist of heterodont (in size) teeth, forming two dental "waves". These waves match the convexo-concave lateral margins of the maxilla and dentary (Fig. 7), resulting

in the upper and lower tooth rows, as a whole, being integrated as two large, mutually matched "serrated blades". This is functionally significant for holding prey and/or tearing flesh from prey. The completeness of the two dental waves is evident as far back as the origin of the Goniopholididae in the Late Jurassic (Fig. 7E), and is coincident with the beginnings of the true flattening of the skull. In more recently derived clades the two dental waves are further emphasized (Fig. 7F). In primitive mesoeucrocodylian clades there is only a single dental wave, such as is found in *Hsisosuchus* (Young and Chow 1953; Li *et al.* 1994) and the Sebecidae (Fig. 7D). In the Protosuchia and Sphenosuchia, both the maxilla and dentary bear a straight dental margin, a state shared with most other archosaurians (Fig. 7B,C).

(E) Evolution of locomotor mechanisms. Extant crocodylians have two types of locomotory posture: sprawling (the belly walk or swimming gait) and erect (the high walk and juvenile gallop of some species) (Zug 1974; Webb and Gans 1982). Morphological analyses of the tarsus, pelvic girdle, hindlimb and pes indicate that early crocodylomorphs, such as sphenosuchians and protosuchians, had an erect posture (Walker 1970; Brinkman 1980; Parrish 1987), and phylogenetic studies suggest that the erect posture is primitive and is shared with the closest relatives of the Crocodylomorpha



**Fig. 7.** Skull and mandibles of the sister-group and major groups of the Crocodylomorpha in lateral view (not to scale). A, *Postosuchus* (a poposaurid), derived from Chatterjee (1985: Fig. 2); B, *Dibothrosuchus* (a sphenosuchian), derived from Wu and Chatterjee (1993: Fig. 3A); C, *Protosuchus* (a protosuchian), derived from Clark (1986: Fig. 8); D, *Sebecus* (a sebecid), derived from Colbert (1946: Fig. 22B) and Busbey (1986: Fig. 4); E, *Goniopholis* (a goniopholidid), reconstructed based on Mook (1942: Fig. 2B [*Amphicotylus*]); F, *Leidyosuchus* (an early alligatoroid), based on No. 1903 of the Royal Ontario Museum.



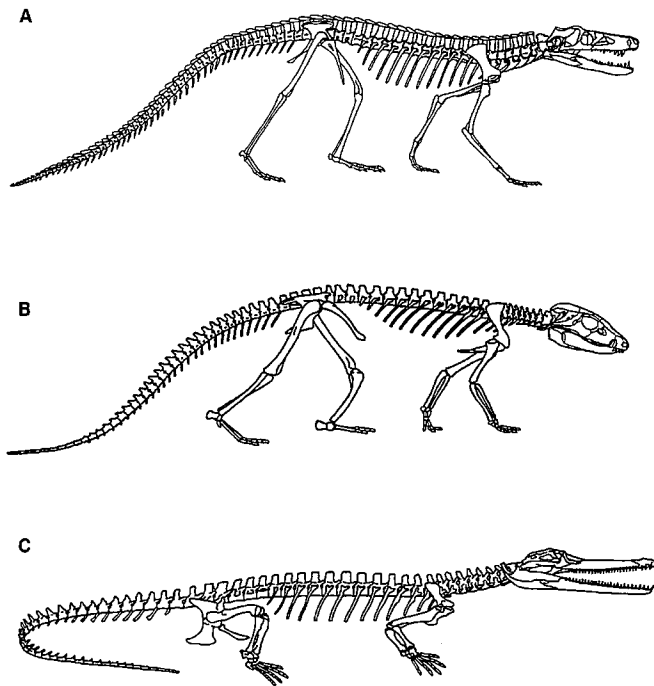
**Fig. 8.** Skeletons of two sister-groups of the Crocodylomorpha in lateral view (not to scale), showing erect bipedal posture. A, *Gracilisuchus* (the second sister-group), modified from Romer (1972: Plate 1); B, *Postosuchus* (the first sister-group), modified from Chatterjee (1985: Fig. 19).

(Gauthier 1986; Parish 1987; Benton and Clark 1988; Sereno 1991). However, at the crocodylomorph level the erect posture is quadrupedal rather than bipedal (Figs. 8 and 9A,B), and as such represents a derived or an apomorphic reversed state. Consequently, the demonstrably sprawling posture of more phylogenetically derived clades of the Crocodylomorpha is a further derived character-state (Fig. 9C). This is superimposed upon the more primitive quadrupedal erect posture.

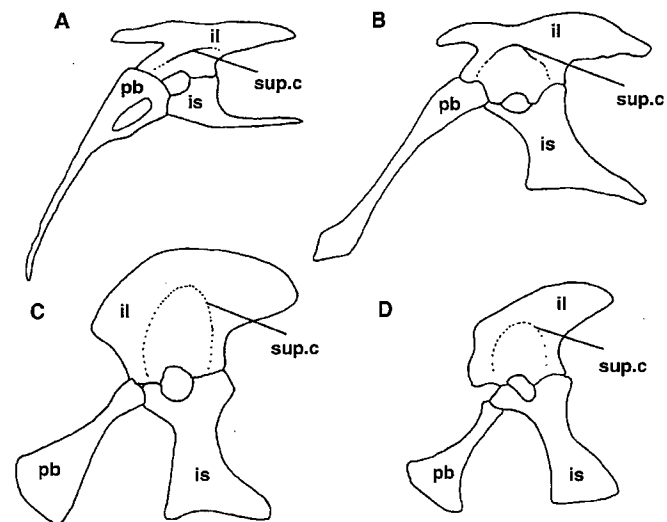
The pelvic girdle, hindlimb, tarsus and pes of the Sphenosuchia and Protosuchia are basically similar in morphology to those of the Poposauridae and the more primitive archosaurs with a bipedal, erect posture. The ilium has a deep and perforated acetabulum which is overhung by a prominent supraacetabular crest (Fig. 10A,B). The femur bears a prominent, medially-directed head (Fig. 11A,B,D) that fits tightly into the acetabulum and is braced dorsally by the supraacetabular crest. As a result, the hip joint is osteologically constrained and restricts abduction of the femur, which moves primarily in a parasagittal plane. The ilium also bears an elongate anterior process that carries the origin of the ilio-femoral muscle group anteriorly and increases its mechanical advantage for protraction of the

femur. The pubis and ischium are expanded ventrally (the former being longer than the latter), thus shifting the origins of the femoral protractors and retractors further from the hip joint, increasing their mechanical advantage. In extant crocodylians the acetabulum is very shallow and the dorsal supraacetabular crest is greatly reduced (Fig. 10D). This imposes fewer osteological constraints on femoral movement than is the case in the Sphenosuchia and Protosuchia. Furthermore, the anterior process of the ilium is reduced to a knob-like tuberosity, the pubis is short and projects ventrally to the same level as the ischium, and the pubic process of the ischium extends further anteriorly and excludes the pubis entirely from contact with the ilium.

The femur of the Sphenosuchia and Protosuchia lacks the adductor fossa but possesses a fourth trochanter on the posterior surface (Fig. 11A,B,D). This is indicative of a massive caudofemoralis longus. The femur also has a prominent, posteriorly directed tibial condyle and a fibular condyle at its distal end. These match the two sloping facets on the proximal end of the tibia, forming a tight, stable, and hinge-like knee articulation. In extant crocodylians the morphology of the femur differs little from this, although the fibular condyle is smaller



**Fig. 9.** Skeletons of some crocodylomorphs in lateral view (not to scale), showing quadrupedal locomotor postures. A, *Dibothrosuchus* (a sphenosuchian), modified based on Wu and Chatterjee (1993: Fig. 15); B, *Protosuchus* (a protosuchian), modified from Colbert and Mook (1951) and Clark (1986: Fig. 8); C, *Gavialis* (an extant gavialoid), after Steel (1973: Fig. 3).



**Fig. 10.** Pelvic girdles of major groups of the Crocodylomorpha in lateral view (not to scale), *Saltoposuchus* (a sphenosuchian), derived from Crush (1984: Fig. 8C [*Terrestriisuchus*]); B, *Protosuchus* (a protosuchian), derived from Colbert and Mook (1951), C, *Sunosuchus* (a goniosphenonid), reconstructed based on Wu *et al.* (1996a: Fig. 15A-C); D, *Alligator sinensis* (an extant alligatoroid), based on dissected specimen 2 of the Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica. Abbreviations: il, ilium; is, ischium, pb, pubis; sup.c, supraacetabular crest.

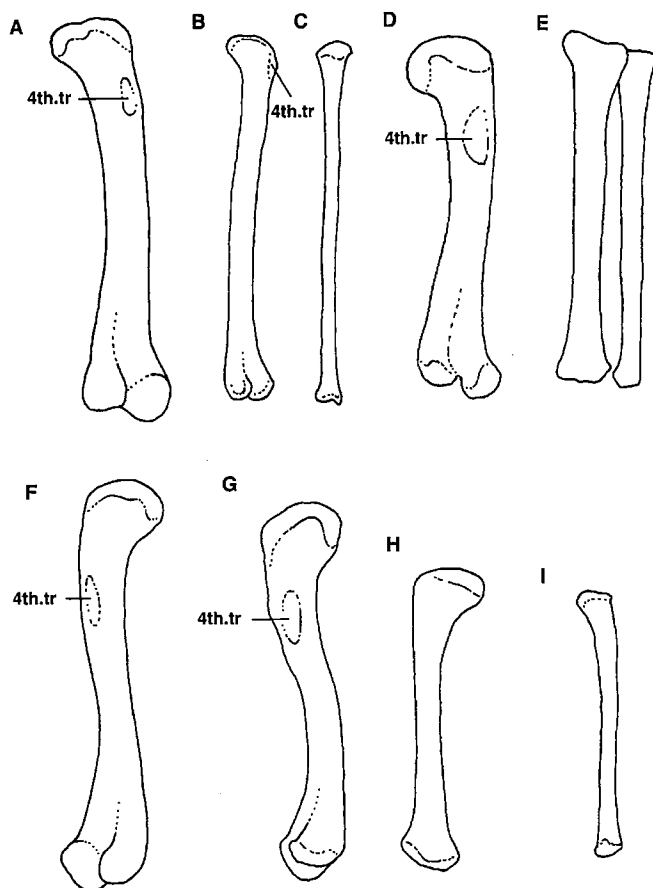
than that of the early crocodylomorphs (Fig. 11G).

Locomotory gait is also reflected by tarsal mechanics, which is closely associated with the three joints within the ankle (see Parrish 1987): the upper joint (UAJ) between the astragalus + calcaneum and the tibia + fibula; the middle joint (MAJ) between the astragalus and calcaneum; and lower joint (LAJ) between the astragalus + calcaneum and the distal tarsal rows (Fig. 12A,B).

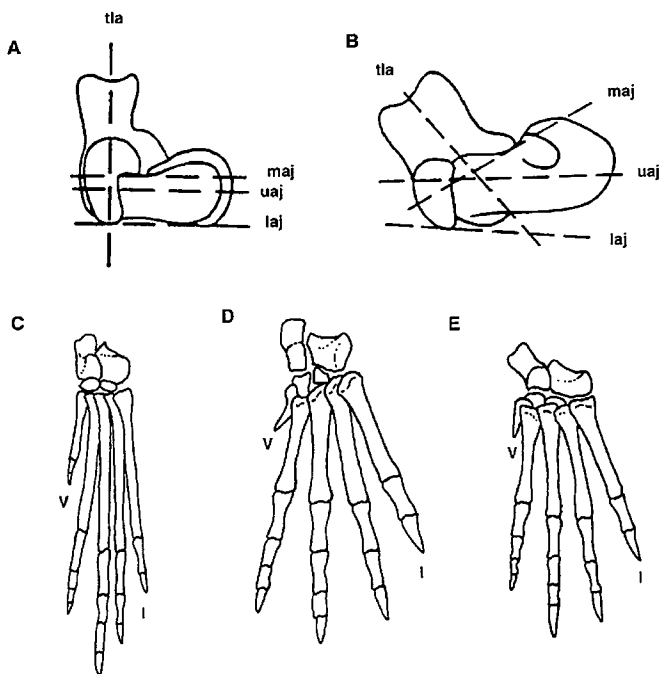
In the Sphenosuchia and Protosuchia the distal facet on the tibia is saddle-shaped, and corre-

sponds with the tibial facet on the astragalus to form an immobile joint between these two bones. The joint between the astragalus and fibula is tight, but is slightly more flexible and ligamentous than the former. The calcaneal facet on the distal end of the fibula is planar or concave, and, together with the hemicylindrical fibular facet on the calcaneum, forms a mobile fibular-calcaneal joint. The latter is a required concomitant of the mobile joint developed between the astragalus and calcaneum. In addition, the long axes of the three ankle joints are parallel, as they are in erect-limbed archosaurs, favouring a simple, hinge-like motion in the parasagittal plane (Fig. 12A).

In extant crocodylians the proximal end of the tibia is flat and its distal end is slightly saddle-shaped. These modifications, as seen in sprawling



**Fig. 11.** Hindlimb elements of major groups of the Crocodylomorpha (not to scale, but B and C, D and E, and G-I scaled with respect to each other). A, right femur of a sphenosuchian in postero-medial view, reconstructed based on Parrish (1991: Fig. 9B); B and C, right femur and left tibia of *Saltoposuchus* (a sphenosuchian) in postero-medial view, derived from Crush (1984: Fig. 9A,B [*Terrestri-suchus*]); D and E, right femur and left tibia and fibula of *Orthosuchus* (a protosuchian) in postero-medial view, separately derived from Nash (1975: Figs. 16B, 17A); F, left femur of *Sunosuchus* (a goniopholidid) in postero-medial view, derived from Wu *et al.* (1996a: Fig. 15F); G-I, left femur, tibia, and fibula of *Alligator sinensis* (an extant alligatoroid) in postero-medial view, based on dissected specimen 2 of the Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica. Abbreviations: 4th.tr, fourth trochanter.



**Fig. 12.** Ankle joint and pedes of major groups of the Crocodylomorpha (not to scale). A, Schematic of the ankle joint of sphenosuchians and protosuchians (see text for details); B, Schematic of the ankle joint of extant crocodylians (see text for details); C-E, pedes with ankle elements of a sphenosuchian *Saltoposuchus* (= *Terrestri-suchus* Crush, 1984), a protosuchian *Protosuchus*, and an extant alligatoroid *Alligator sinensis*. A and B, derived from Parrish (1987: Fig. 9 C,D); C, derived from Crush (1984: Fig. 10E); D, reconstructed based on Nash (1975: Fig. 17D); E, based on dissected specimen 2 of the Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica. Abbreviations: laj, lower joint between the astragalus + calcaneum; maj, middle joint between the astragalus and calcaneum; tia, long axis of the tuber calcanei; uaj, upper joint between the astragalus + calcaneum and the tibia + fibula; I and V, the first and fifth digits.

archosaurs, result in simplification of the knee and ankle joints, and permit the wide range of movement associated with the diversity of gaits employed by extant crocodylians. This is also demonstrated by the fact that the UAJ and MAJ joints are not parallel in orientation (Fig. 12B).

In the Sphenosuchia and Protosuchia the pes is also distinct in morphology. The fifth digit is reduced and the remaining digits form a bilaterally symmetrical foot. The proximal ends of the metatarsals overlap significantly. These specializations allow the foot to act as a flexion-extension lever in a single plane (Fig. 12C,D). In extant crocodylians the pes shows no significant changes, although the overlap of the proximal ends of the metatarsals is reduced (Fig. 12E). As has been suggested by Parrish (1987), it is possible that extant crocodylians evert the fourth digit as a pivot for pedal rotation during sprawling posture, in much the same way that the fifth digit is employed in lizards.

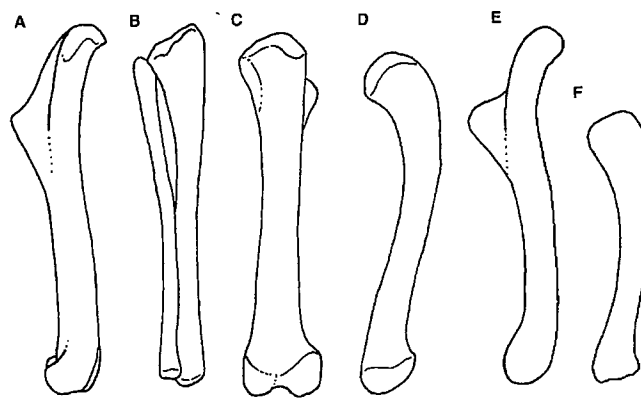
As suggested by the phylogenetic relationships of the three extant groups (Fig. 2), the locomotor patterns of the Crocodylia must have appeared before the Cretaceous-Tertiary boundary. Sphenosuchians and protosuchians have been widely interpreted as being terrestrial, as have most early archosaurs (e.g. Colbert 1952; Colbert and Mook 1951; Walker 1970; Crush 1984; Wu 1986; Parrish 1987), including the two successive sister-groups of the Crocodylomorpha. Therefore, an erect locomotor pattern seems primarily to be restricted to terrestrial animals, as was suggested by Charig (1972). Extant crocodylians, such as *Alligator* and *Crocodylus*, use an erect stance when walking on land, but a sprawling posture when entering or travelling in the water (Cott 1961). It is most parsimonious to conclude that the quadrupedal erect gait and posture are patterns retained from the Sphenosuchia and Protosuchia, whereas the more sprawling gait and posture are derived and are most probably associated with secondarily aquatic adaptations (Parrish 1987).

The Longirostrine Taxa, one of the early clades of the Mesoeucrocodylia, constitute the first clearly semiaquatic or aquatic group of the Crocodylomorpha. If the more sprawling posture of extant crocodylians is reflective of secondarily aquatic adaptation, then such a trend was also established in the Longirostrine Taxa as early as the late Early Jurassic. On the other hand, the "Sebecosuchia" (= Sebecidae plus Baurusuchidae of this paper) and the "Notosuchia" (Notosuchidae in this paper), have often been considered to be terrestrial on the basis of a laterally compressed skull (Buffetaut 1979; Busbey 1986). Within the Atoposauridae, both terrestrial (with erect posture) and semi-aquatic (with more sprawling posture) modes of life have been suggested (Wellnhofer 1971; Buscalioni *et al.*

1990). *Hsisosuchus* from the Upper Jurassic has a laterally compressed skull with serrated, knife-like teeth. It may also have been terrestrial, retaining an erect posture. However, well-preserved postcranial remains of early mesoeucrocodylians are rare, and/or no adequate study of known postcrania has been undertaken, thus rendering the description of transitions to a more sprawling posture from an erect posture unsubstantiated.

The ilium of the Upper Jurassic goniopholidid *Sunosuchus junggarensis* (Wu *et al.* 1996a) is very similar to that of extant crocodylians in that its anterior process is short and its acetabulum faces laterally, is shallow, and lacks the prominent dorsal supraacetabular crest (Fig. 10C), suggesting that a more sprawling posture could be attained in this taxon during the belly walk. Furthermore, the fourth trochanter of the femur in this taxon is lower in position (Fig. 11F), as it is in extant crocodylians (Fig. 11G), than it is in sphenosuchians and protosuchians (Fig. 11A,B,D), indicating a strong but slow walking phase. In addition, the tibia and fibula are relatively much shorter in extant forms (Fig. 11H,I) than in sphenosuchians and protosuchians (Fig. 11C,E) when compared with the femur. The transition between the erect stance and the more sprawling posture of extant crocodylians took place within the Jurassic, and that true terrestrial and fully aquatic forms coexisted during the Late Mesozoic.

Although no anatomical analyses of the pectoral girdle and forelimb have been conducted in connec-



**Fig. 13.** Forelimb elements of major groups of the Crocodylomorpha (not to scale, but A and B, C and D, and E and F are scaled with respect to each other). A and B, right humerus and right radius and ulna of *Dibothrosuchus* (a sphenosuchian) in postero-medial view, separately derived from Wu and Chatterjoc (1993: Figs. 12D, 13C); C and D, left humerus and ulna of *Orthosuchus* (a protosuchian) in antero-medial and lateral views, respectively, separately derived from Nash (1975: Fig 13B,E); E and F, right humerus and ulna of *Stangerochampsia* (an early alligatoroid) in antero-medial view, separately derived from Wu *et al.* (1996b: Plate 2: Figs. 6, 9).

tion with attempts to elucidate the evolution of the locomotor patterns of crocodylomorphs, the morphology (especially the proportional lengths of elements) of the pectoral girdle and forelimb is clearly different in erect forms and those with a more sprawling posture (see Buscalioni *et al.* 1995). In those sphenosuchians and protosuchians in which the forelimb is preserved, the antebrachium is relatively longer than it is in more sprawling forms, being at least 90% of humeral length. In the sphenosuchians *Dibothrosuchus* and *Saltoposuchus* (= *Terrestriusuchus* [Crush 1984]) the ulna is effectively equal (about 98%) in length to the humerus (Fig. 13A,B). This ratio is slightly smaller in the Protosuchia: ulna length is about 93-95% of humeral length in the Early Jurassic *Orthosuchus* (Fig. 13C,D) and the Late Jurassic-Early Jurassic *Shantungosuchus* (Wu *et al.* 1994a). The ulna reaches about 92% of humeral length in the Mesoeucrocodylian *Hsisosuchus*, which has been interpreted as an erect form (see above). Within the three species of the Atoposauridae (sensu Wellnhofer 1971) the ulna is negatively allometric when compared to the humerus: in *Alligatorellus* the ulna is moderately long, attaining on average about 84% of the length of the humerus. If *Atoposaurus* and *Alligatorellus* are synonyms of *Alligatorium* (Clark 1986), then this ratio is only 76% in the largest specimen of these taxa. This is in contrast with the situation seen in the two basal clades of the Crocodylomorpha, each of which is characterized by erect posture.

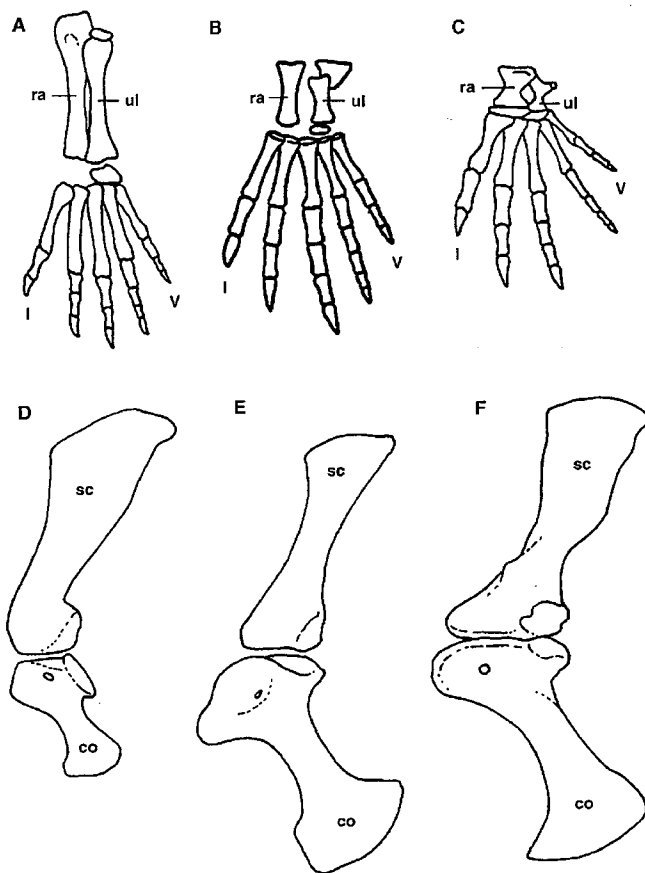
The antebrachium is markedly shorter than the humerus in the Longirostrine Taxa, the ulna being, for example, about 73% of humeral length in *Pelagosaurus* and the teleosaurid *Stenosaurus* (Westphal 1962). The Late Cretaceous alligatoroid *Stangerochampsia* (Wu *et al.* 1996b), has a similar ratio, about 75% (Fig. 13E,F).

In the members of the Sphenosuchia and Protosuchia in which the carpals and manus are preserved, the proximal carpals are more slender and relatively longer than those of more sprawling forms (Fig. 14A,B). The radiale is consistently longer than the longest metacarpal in *Dibothrosuchus*, the Jurassic-Early Cretaceous protosuchian *Sichuanosuchus* (Wu *et al.* 1997), *Orthosuchus*, and the Early Jurassic *Protosuchus* (Nash 1975). In *Alligatorium* (sensu Clark 1986) the radiale is also clearly longer than the longest metacarpal. In contrast, the proximal carpals are generally short and massive in the taxa with a more sprawling posture. The radiale is shorter in length than the longest metacarpal in extant crocodyllans (Fig. 14C).

In those protosuchians in which the pectoral girdle is known, the coracoid is relatively small, being about half the length of the scapula (Fig. 14D). In the basal mesoeucrocodylian *Hsisosuchus* the coracoid is similarly proportioned. In those taxa with

a more sprawling posture the coracoid is relatively larger, being about the same in length as the scapula in the Longirostrine Taxa (where the two elements are known) and in extant crocodyllans (Fig. 14E,F).

Whether the foregoing discussion of morphological differences attributed to the pectoral girdle and forelimb of erect and sprawling taxa are universally true cannot be definitely stated, because the relevant elements are not preserved in many of the taxa. It is, however, noteworthy that current evidence seems to support this general hypothesis of differential limb and girdle element proportions.



**Fig. 14.** Pectoral girdles, wrists, and manus of major groups of the Crocodylomorpha (not to scale). A, *Dibothrosuchus* (a sphenosuchian), derived from Wu and Chatterjee (1993: Fig. 13E,F); B, *Protosuchus* (a protosuchian), derived from Nash (1975: Fig. 37A); C, *Alligator sinensis* (an extant alligatoroid), based on dissected specimen 2 of the Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica. D, *Orthosuchus* (a protosuchian), derived from Nash (1975: Fig. 36C); E, *Steneosaurus* (a longirostrine taxon), derived from Steel (1973: Fig. 5[2]); F, *Alligator mississippiensis* (an extant alligatoroid), derived from Steel (1973: Fig. 5[4]). Abbreviations: co, coracoid; ra, radiale; sc, scapula; ul, ulna; I and V, the first and fifth digits.

## Crocodylomorphs at and between Geological Boundaries

During a period of existence of more than 200 million years, crocodylomorphs transgressed three major geological boundaries (Triassic-Jurassic [T-J], Jurassic-Cretaceous [J-K], and Cretaceous-Tertiary [K-T]) and survived the extinction events experienced by other groups at these boundaries (Fig. 16). The extinctions at the T-J and K-T boundaries have often been considered to be major or global events. Two other extinction events are recognized (Raupe and Sepkoski 1986) within periods, the Pliensbachian-Toarcian (middle Early Jurassic), and Cenomanian-Turonian (earliest Late Cretaceous) although they are minor events for terrestrial amniotes (Benton 1988). The Crocodylomorpha are examined at these major and minor geological boundaries to determine their correlated pattern of crocodylomorph evolution and morphological change.

1. Triassic-Jurassic Boundary. The earliest record of the Sphenosuchia is probably from the late Triassic (Carnian Stage), as exemplified by *Hesperosuchus* from North America (Colbert 1952; also see Parrish 1991; Benton 1994). Prior to the T-J boundary, at least two additional genera had arisen, one known from Europe and one from South America. The Sphenosuchia survived the T-J boundary transition and is known from the Early Jurassic of southern China, North America, and South Africa. At least two extinction events have been documented from the Late Triassic (Benton 1986). The earlier of these occurred at the end of the Carnian Stage, and its extent was greater in terrestrial amniotes than that which occurred at the T-J boundary ("Rhaetian") (Benton 1986, 1988). Based on current evidence, the Crocodylomorpha arose prior to the first of these Triassic extinction events.

The earliest known member of the Crocodyliformes is *Hemiprotosuchus*, probably from the Latest Triassic (Bonaparte 1972; Clark 1986; Benton 1994), establishing the Protosuchia before the T-J boundary, but about 15 million years later than the origin of the Sphenosuchia. With the origin of the Protosuchia, the Crocodyliformes was characterized by at least ten unique features associated with the skull, the pectoral girdle, the pelvic girdle and dermal armour (see above). It is clear that beyond the T-J boundary the Protosuchia became more prevalent than the Sphenosuchia, and persisted for almost the entire remainder of the Mesozoic. More than five protosuchians are known from the Early Jurassic of China, North America, and South Africa, but most of them are either fragmentary or incompletely described (see Clark 1986; Wu and Sues 1995, 1996a,b; Sues *et al.* 1994). Currently most protosuchians can be referred to one of two clades (Fig. 2).

2. Pliensbachian-Toarcian (P-T) Boundary. No record of the Sphenosuchia is currently known from a stratum younger than the Sinemurian Stage (see Benton 1994). Therefore, the extinction of the Sphenosuchia likely took place before the Pliensbachian Stage. In the Protosuchia, one of its two clades, consisting mostly of Late Triassic-Early Jurassic taxa, became extinct along with the Sphenosuchia. The other clade, however, comprised mainly of later taxa, survived the extinction at the end of the Pliensbachian, although a gap in the fossil record exists between this boundary and the Late Jurassic (Fig. 15).

Although the three primitive clades of the Mesoeucrocodylia have a later stratigraphical occurrence, the origin of this group may have taken place prior to the P-T boundary. The earliest Mesoeucrocodylia, early *Steneosaurus* from Europe (see Hau and Buffetaut 1997) and probably *Peipehsuchus* from China (Li 1993) are members of the Longirostrine Taxa, of Toarcian age. This suggests that the origin of the Longirostrine Taxa most likely occurred immediately after the P-T boundary. As a group, the Longirostrine Taxa were the most successful non-eusuchian clade, and extended well into the Cenozoic. Evolutionary patterns of the Longirostrine Taxa are not fully understood, however, because of unresolved relationships among its members (Fig. 2).

3. Jurassic-Cretaceous (J-K) Boundary. Extinctions at the end of the Jurassic (Tithonian Stage) were only minor in the Crocodylomorpha. Two small early mesoeucrocodylian clades (*Hsisosuchus* and the Fruita Form), each represented by only a single genus, failed to survive this extinction event. However, no major clade became extinct at this boundary, and no major clade emerged immediately thereafter (see Fig. 15). All major clades of the Longirostrine Taxa passed through the J-K boundary. Two early neosuchian clades (the Atoposauridae and Goniopholididae) originated in the Late Jurassic and survived this extinction event. The origin of the more derived *Bernissartia* + *Shamosuchus* clade, and the origin of the Eusuchia are not correlated with this event, as the earliest fossil record for these two clades is from the Barremian Stage, about 20 million years later.

4. Cenomanian-Turonian (C-T) Boundary. The extinction event at the end of the Cenomanian Stage affected the Crocodylomorpha in a modest way. The Pholidosauridae of the Longirostrine Taxa is the only large clade that failed to survive this boundary. Other non-eusuchian clades became extinct during the Early Cretaceous before, rather than at, this boundary. The Teleosauridae and Metriorhynchidae of the Longirostrine Taxa became extinct at the end of the Valanginian Stage and the end of the Hauterivian Stage (Hau and Buffetaut 1997), re-

spectively, while the Atoposauridae and Goniopholididae probably died out later, but still prior to this boundary. No new clades originated immediately after this event. The youngest clade of the Longirostrine Taxa, the dyrosaurs, occurs in the fossil record in the Cenomanian Stage, before this boundary (Hau and Buffetaut 1997). The earliest members of the Notosuchidae have been retrieved from Aptian or Albian deposits in China and South Africa (Clark *et al.* 1989; Wu *et al.* 1995; Wu and Sues 1996a,b). Thus, both the fossil record and phylogenetic relationships indicate that the Notosuchia originated at least 20 million years before the extinction event at the Cenomanian-Turonian boundary. As indicated by the fossil record, the origin of the three extant crocodylian clades took place about 10 million years later than the J-K boundary (probably in the early Campanian Stage).

5. Cretaceous-Tertiary (K-T) Boundary. The extinction event at the K-T boundary eliminated many terrestrial and marine animals, especially dinosaurs. Although the Protosuchia, Notosuchidae, and *Bernissartia* + *Shamosuchus* became extinct during the Late Cretaceous, all were extinct before, not at, the K-T boundary. The latest occurrence of the Protosuchia is from the Campanian Stage; Notosuchidae died out around the Coniacian Stage (Bonaparte 1991); the *Bernissartia* + *Shamosuchus* clade became extinct within the Campanian Stage. Some members of the Crocodylia became extinct at the K-T boundary (see Brochu, 1997), but no major clades disappeared entirely nor was there a significant decline in diversity across this boundary.

6. Cenozoic Boundaries. A number of extinction events have been documented for the marine animal fossil record during the Cenozoic, such as those in the Late Eocene, Early Oligocene, and Late Miocene (see Raup and Sepkoski 1986). The extinction of the remaining non-eusuchian clades may have been separately associated with such events in the Late Eocene (Baurusauridae and dyrosaurs) and in the Late Miocene (Sebecidae).

## Conclusions

### 1. Relationships Between Major Crocodylian Features and Geological Boundaries.

The history of the Crocodylomorpha shows no evidence that primitive clades became extinct at particular geological boundaries and were replaced immediately afterwards by new and more derived clades. This is in contrast with the previous view that the Protosuchia became extinct first and was then substituted by more advanced grades following the T-J extinction event (e.g. see Figure 1 in Langston 1973).

The Crocodylomorpha attained the level of the extant Crocodylia in its major structural features about 125 million years ago (Barremian Stage), when *Hylaeochampsia* evolved (Fig. 15). Prior to the Eusuchia, the Crocodylomorpha had experienced three extinction events (at the T-J, P-T, and J-K boundaries). Except for the Longirostrine Taxa (Mesoeucrocodylia) the original major clades, prior to the Eusuchia, are not related to these three events. Thus, the appearance of significant features of the Crocodylomorpha and transitions of each stage are not correlated with geological boundaries. The Crocodylomorpha appears to have been "prepared" to survive such events (hence the reference to Lord Baden-Powell, founder of scouting and originator of the slogan "Be Prepared", fashioned on his initials - Maynard 1946). In most clades, continuous, relatively gradual change of structural systems over the span of their existence has resulted in a non-dramatic pattern of taxic evolution throughout the entire history of the Crocodylomorpha. The small extinction event at the end of Pliensbachian Stage (Jurassic) was the most crucial of such events, because it is associated with a transition of locomotor pattern from an erect posture to a more sprawling posture.

The origin of the Crocodylomorpha was associated with the transition from bipedal erect posture to quadrupedal erect posture. This occurred before the extinction event at the end of the Carnian Stage (middle Late Triassic). This transition may have been associated with the tendency for the Crocodylomorpha to occupy new terrestrial niches separate from those of other carnivorous archosaurs.

After their successive origin in the Late Triassic, the Sphenosuchia and Protosuchia both survived the T-J boundary and coexisted for about 15 million years. All known protosuchians were small, terrestrial animals, less than one metre in length. They acquired many crocodylian (derived) features, reaching a more derived level of structural organization. This clade survived all extinction events prior to the Campanian Stage (before the K-T boundary).

The origin of the Longirostrine Taxa is associated with an environmental shift from a terrestrial to a semiaquatic, then to an aquatic existence, immediately following the extinction event at the end of the Pliensbachian Stage (early Jurassic). The sprawling posture of the Longirostrine Taxa is a derived condition within the Crocodylomorpha, associated with the shift to an aquatic way of life. This transition to a sprawling posture, was very important during their radiation in the marine environment of the Mesozoic. Members of the Longirostrine Taxa are the only known crocodylomorphs with a fossil record from both marine and terrestrial deposits in the late Early Jurassic through the entire Middle Jurassic.

The more sprawling posture found in most clades of the Neosuchia may represent a retained character-state from more primitive clades, and shared with the Longirostrine Taxa, rather than being of separate origin. However, most members of the Neosuchia were/are amphibious and they have been the dominant crocodylomorphs of the later history (from the Late Jurassic to the present) of the Crocodylomorpha (Fig. 15). Most clades within the Neosuchia arose sequentially, partially overlapping each other in geological occurrence.

## 2. The Evolutionary Pattern of Crocodylomorpha.

Extrapolating from patterns observed in extant populations (e.g. Huxley 1875), the history of the Crocodylomorpha has long provided an example of the "gradual and progressive pattern of large-scale, long-term evolution" as hypothesized by Darwin (1859). In the first edition of his book "On the Origin of Species" Darwin illustrated a continuous and essentially isotropic distribution of radiating lineages and a similar range of evolutionary rates over all time scales (see Carroll 1997). However, new information on the Crocodylomorpha appears to render such an interpretation less adequate than previously thought.

The origin of the Crocodylomorpha and the divergence of its early clades took place much more rapidly than did that of its later clades. The first two clades, the Sphenosuchia and Protosuchia, arose within approximately 15 million years, in the Late Triassic. Three early clades of the Mesoeucrocodylia probably originated within the next 15 million years, in the Early Jurassic (Fig. 15). After the divergence of the Sphenosuchia, Protosuchia, and the early clades of the Mesoeucrocodylia, most features characterizing the extant Crocodylia had become established. This suggests that the latter part of the crocodylomorph evolution as pattern proceeded at a much slower rate than its early part. It is evident from current information that the Crocodylomorpha took about 100 million years first to reach the structural level of the Eusuchia, and then about 140 million years to reach the structural level of the extant Crocodylia. Further the Crocodylomorpha has changed relatively little in both morphology and way of life for about 120 million years from the origin of the Eusuchia during the Early Cretaceous to the present. Certainly modifications in both morphology and way of life have occurred, but these changes are minor and none of them played a significant role in the subsequent history of the Crocodylomorpha.

Although overall changes were minor, some character complexes evolved more rapidly than others (Fig. 16). The completion of the bony secondary palate took more than 95 million years, while the establishment of the two waves along the lateral jaw margins and the flattening of the skull took considerably less time, about 65 million years. The shift in

locomotor pattern from a bipedal erect posture through a quadrupedal erect posture to a more sprawling posture was relatively rapid, approximately 40 million years.

As the fossil record yields more material the interpretations expressed here will no doubt change. Just as the past twenty years have allowed us to further understand and clarify the evolutionary history and patterns of the Crocodylomorpha, the next two decades will no doubt permit further refinements and reassessments.

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