

8. Archosaur phylogeny and the relationships of the Crocodylia

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Abstract

The Archosauria include the living crocodylians and birds, as well as the fossil dinosaurs, pterosaurs, and basal 'thecodontians'. Cladograms of the basal archosaurs and of the crocodylomorphs are given in this paper. There are three primitive archosaur groups, the Proterosuchidae, the Erythrosuchidae, and the Proterochampsidae, which fall outside the crown-group (crocodylian line plus bird line), and these have been defined as plesions to a restricted Archosauria by Gauthier. The Early Triassic *Euparkeria* may also fall outside this crown-group, or it may lie on the bird line. The crown-group of archosaurs divides into the Ornithosuchia (the 'bird line': Ornithosuchidae, Lagosuchidae, Pterosauria, Dinosauria) and the Crocodylotarsi nov. (the 'crocodylian line': Phytosauridae, Crocodylomorpha, Stagonolepididae, Rausuchidae, and Poposauridae). The latter three families may form a clade (Pseudosuchia s.str.), or the Poposauridae may pair off with Crocodylomorpha.

The Crocodylomorpha includes all crocodylians, as well as crocodylian-like Triassic and Jurassic terrestrial forms. The Crocodyliformes include the traditional 'Protosuchia', 'Mesosuchia', and Eusuchia, and they are defined by a large number of synapomorphies, particularly of the braincase and occipital regions. The 'protosuchians' (mainly Early

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Jurassic in age) and the 'mesosuchians' (mainly Jurassic and Cretaceous) are probably paraphyletic assemblages, representing successive sister-groups to the Eusuchia. The 'Mesosuchia' and Eusuchia, the Mesoeucrocodylia, are defined by the palatine secondary palate, amongst other features. The sequence of branching within the 'mesosuchian' part of Mesoeucrocodylia is uncertain, but *Bernissartia* and *Shamosuchus* seem to be the closest sister-groups of Eusuchia. This latter group includes the poorly-known *Hylaeochampsia* and *Stomatosuchus*, and the Crocodylia, as redefined here, include only crown-group crocodylians.

Introduction

The archosaurs ('ruling reptiles'), if defined cladistically as a monophyletic group, include the living crocodylians and birds, as well as about 1000 genera of dinosaurs, pterosaurs, and 'thecodontians'. There have been numerous attempts in the past 20 years to classify the archosaurs, and a wide range of differing schemes has been published e.g. Romer 1966, 1972a; Reig 1970; Sill 1974; Bonaparte 1975, 1982; Krebs 1976; Thulborn 1980; Chatterjee 1982). These have proved to be inconclusive in many respects because they have generally been based on a search for ancestor–descendent sequences, and there are too many uncertainties involved in that approach.

More recently, several authors have applied cladistic techniques to various fossil groups within the Archosauria (Gardiner 1982; Benton 1983, 1984a,b, 1985, 1986; Padian 1983, 1984; Gauthier 1984, 1986; Norman 1984; Parrish 1984; Paul 1984, 1985; Sereno 1984, 1986; Cruickshank and Benton 1985; Gauthier and Padian 1985; Clark 1986; Benton and Norman 1988). There are a number of major controversial issues in archosaur phylogeny—the relationships of birds and crocodylians amongst living tetrapods, the relationships of the primitive archosaurs (the 'thecodontians'), and the relationships of crocodylians, pterosaurs, dinosaurs, and birds.

Our aims in this chapter are to consider the relationships of the archosaurs as a whole, to outline the relationships of the primitive archosaurs, and to explore the phylogeny of the crocodylians and their early relatives. Relationships of the early archosaurs are reviewed by M.J.B., and relationships of the Crocodylomorpha by J.M.C. (order of authorship is alphabetical). The major groupings within Aves are considered in Chapter 9.

The limits of Archosauria

There are currently two views of what is and what is not an archosaur

The 'traditional' cladistic Archosauria consists of *Proterosuchus* and everything above it in the cladogram. The 'crown-group' (Hennig 1971) Archosauria consists of all the descendants of the closest common ancestor of crocodylians and birds (the Ornithosuchia plus Crocodylotarsi of this study), and excludes Proterosuchidae, Erythrosuchidae, Proterochampsidae, and (doubtfully) *Euparkeria* (Gauthier 1984, 1986). The bounds of this group are hard to define in the fossil forms. Of the four selected hard-part synapomorphies of Archosauria (sensu stricto) noted by Gauthier and Padian (1985, p. 187), only one appears to be valid: the antorbital fenestra set in a prominent fossa is indeed true of *Euparkeria* and later archosaurs. Of the other three, one (ossification of the laterosphenoid) may have been present in *Proterosuchus* (J.M.C., pers. obs.) and *Erythrosuchus* (Cruikshank 1979), and two (deeply arched otic notch, fully thecodont dentition) are true also of proterochampsids.

The traditional view is obviously subjective in that there is no particular reason for selecting the *Proterosuchus* node as the base of the Archosauria. The crown-group interpretation (Hennig 1971) hypothesizes that all fossil archosaurs possessed the soft-part synapomorphies of birds plus crocodylians, as well as the observable hard-part synapomorphies. The authors of this article have elected to disagree on this matter, M.J.B. retaining a traditional interpretation of the content of Archosauria, and J.M.C. applying a crown-group interpretation to the Crocodylia. This question has no effect on the character analyses, of course.

The relationships of birds and crocodylians

Most biologists have assumed, following Goodrich (1930), that the closest living relatives of birds are crocodylians. However, Gardiner (1982) and Løvtrup (1985) gave cladistic arguments that mammals and birds are nearest sister-groups amongst extant tetrapods. They noted about 20 characters shared by birds and mammals, but these have been criticized in part by Devillers and Ricqlés (1984) and Benton (1985), and in more detail by Kemp (1988) and by Gauthier et al. (Chapter 4 of this volume).

The autapomorphies of the traditional Archosauria are (outgroup other diapsids) (Benton 1984a, 1985; Chapter 6 of this volume):

1. possession of an antorbital fenestra;
2. postfrontal is reduced;
3. postparietals are fused or absent;
4. posterior border of the lower temporal fenestra is bowed;

5. presence of a laterosphenoid ossification in the braincase (J.M.C., *pers. obs.*);
6. teeth laterally compressed (teeth lost in extant birds);
7. loss of trunk intercentra;
8. no ectepicondylar foramen;
9. possession of a fourth trochanter on the femur.

Additional autapomorphies of the crown-group Archosauria (based on living Aves plus Crocodylia) are:

10. four-chambered heart (Goodrich 1930);
11. Jacobson's organ present in embryos, but absent in adults (Parsons 1970);
12. adrenal gland tissue is arranged in bands, which in cross-section seem to alternate with the inter-renal cords (Gabe 1970);
13. in the brain, the structure of the anterior dorsal ventricular ridge is characterized by the presence of fairly evenly spread cell clusters, rather than by having a cell cluster zone near the ventricle, as in lepidosaurians and turtles (Clark and Ulinski 1984);
14. presence of the eye lens protein E-crystallin (Stapel *et al.* 1985).

Birds and crocodylians share numerous other hard-part characters that further define the crown-group Archosauria up to the latest split between the crocodylian line and the bird line (Gauthier 1984, 1986; Benton 1984c, 1985). These synapomorphies are detailed below (see Appendix 1).

Molecular data on tetrapod phylogeny are equivocal regarding the relationships of birds and crocodylians. Several analyses of α -haemoglobin sequences pair-off birds and crocodylians as sister-groups (Leclercq *et al.* 1981; Perutz *et al.* 1981; Goodman *et al.* 1982), as do analyses of cytochrome-c sequences (Maeda and Fitch 1981), and eye lens protein α -crystallin sequences (Stapel *et al.* 1984; de Jong *et al.* 1985). However, other protein sequence analyses seems to give almost every other pairing of tetrapod groups that is imaginable (reviewed in Benton 1985, pp. 106-7; and Chapter 2 of this volume).

The relationships of Archosauria

The archosaurs, although formerly regarded as an independent reptilian subclass by Romer (1966), are now placed by nearly all biologists and palaeontologists in the Diapsida (which also includes *Sphenodon*, lizards, snakes, and various extinct forms: see Chapters 4 and 6 of this volume). The archosaurs form part of an archosauromorph branch of the diapsid reptiles, a lineage that includes

Trilophosaurus, Rhynchosauria, and Prolacertiformes as sister groups of Archosauria (Gow 1975; Brinkman 1981; Benton 1983, 1984a, 1985; Evans 1984; Gauthier 1984; and Chapter 6 of this volume).

Other recent theories of archosaur origins have been very different, positing non-diapsid origins: Romer (1966) suggested that they arose directly from captorhinomorphs, while Reig (1970) derived them from varanopseid pelycosaur (mammal-like reptiles). Other authors (e.g. Hughes 1963; Cruickshank 1972; Gow 1975; Carroll 1976) suggested that the ancestor of the archosaurs was a Permian diapsid like *Youngina* but that reptile is now recognized as belonging to the lepidosauromorph branch of diapsids (Currie 1982; Benton 1983, 1984a, 1985; Evans 1984; Gauthier 1984).

Cladistic analysis

The discussion below is based on two analyses of relationships—one of the basal Archosauria by M.J.B., and one of the Crocodylomorpha by J.M.C. The first analysis involved a sample of 17 representative taxa of early archosaurs, and a cladistic analysis of 134 characters. The second analysis was based on a study of 150 characters (excluding autapomorphies and familial synapomorphies) of 33 crocodylomorph taxa (Clark 1986). In the first study, the 17 taxa were as follows: Proterosuchidae, Erythrosuchidae, Proterochampsidae, *Doswellia*, *Euparkeria*, Ornithosuchidae, *Lagosuchus*, Dinosauria, Phytosauridae, *Gracilisuchus*, Stagonolepididae, Ticinosuchus, Saurosuchus, Postosuchus, Terrestrisuchus, Protosuchus, and Crocodylia. In the first study, characters were recorded mainly from the literature, with additional information obtained from original specimens. In the second study, the analysis of crocodylomorphs, nearly all of the named taxa were examined firsthand, as were three undescribed taxa and new material of *Protosuchus richardsoni*. The PAUP program developed by D. Swofford was used to determine global parsimony with multiple outgroups (Maddison et al. 1984). Characters were not weighted, and evolutionary reversal and convergence were assumed to be equally probable. Because of space restrictions, emphasis is placed upon relationships of family or higher-level groups with one another and not on diagnosing lower-level groups i.e. families).

In identifying and scoring characters, a broad latitude has been given to the similarities between taxa, so that somewhat imprecise characters (e.g. 'large supratemporal fenestrae') have been included. For this reason, among others, there is a great deal of homoplasy in the data (consistency indices were 0.5–0.7). Because this is an initial attempt at discovering characters identifying archosaur and cro-

codylomorph clades, this uncritical approach is considered to be preferable to ignoring potential synapomorphies.

The relationships of Triassic Archosauria

'Thecodontians'

The archosaurs radiated extensively during the Triassic, and several distinctive lineages arose. It has been widely accepted that all of the later archosaur groups arose from within the 'Thecodontia', a paraphyletic group since it excludes three or four descendent clades: crocodylians, pterosaurs, dinosaurs, and birds. We will use the informal term 'thecodontian' to refer to all Late Permian and Triassic archosaurs that are not crocodylians, pterosaurs, or dinosaurs.

There is no currently accepted classification of 'thecodontians'. Most authors have favoured a basic tripartite division: Proterosuchia (for Proterosuchidae and Erythrosuchidae, and at times, Rausuchidae and Proterochampsidae), Parasuchia (for Phytosauridae), and Pseudosuchia (for everything else, including some early crocodylomorphs (e.g. Romer 1956; Reig 1970; Krebs 1976)). Others have separated the aetosaurs as Aetosauria (Romer 1966, 1972a; Sill 1974; Bonaparte 1975; Charig 1976; Thulborn 1980), some of the early crocodylomorphs as Sphenosuchia (Bonaparte 1982), ornithosuchids as Ornithosuchia (Chatterjee 1982), and rausuchids and poposaurids as Rausuchia (Chatterjee 1982).

Recent cladistic analyses of the Triassic archosaurs (e.g. Benton 1983, 1984a,c, 1985; Gauthier 1984, 1986; Paul 1984; Cruickshank and Benton 1985; Gauthier and Padian 1985; Benton and Norman 1988) have produced similar cladograms that broadly resemble that shown in Fig. 8.1. However, there are a number of controversial points, which will be highlighted in the discussion below.

The early archosaurs

The three most primitive archosaur taxa in this analysis (Fig. 8.1) appear to be Proterosuchidae, Erythrosuchidae, and Proterochampsidae.

The 'basal' archosaur, Proterosuchus from the Early Triassic of S. Africa (Figs. 8.2A, 8.3A, and 8.4A) and elsewhere, was classed by Cruickshank (1972) with the rhynchosaurs, while Benton (1985) suggested that the proterosuchids shared several characters with the prolacertiforms in general, and with Prolacerta in particular. However, Proterosuchus possesses the archosaur autapomorphies noted above (list

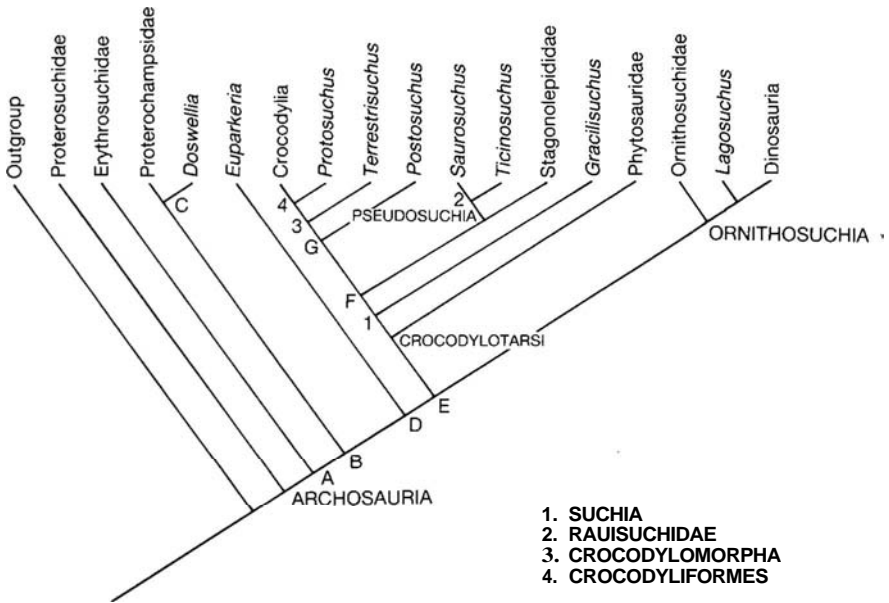


Fig. 8.1. Cladogram depicting phylogenetic relationships of Archosauria, based on a character analysis by PAUP of 17 comparatively well-known taxa. Characters are listed in Appendix 1. The outgroup consists of *Prolacerta*, *Hyperodapedon*, *Trilophosaurus*, and *Youngina*, a cross-section of early non-archosaurian diapsids.

1, Appendix 1; Fig. 8.1), and it has generally been regarded as the most primitive known archosaur.

The Proterosuchidae include about eleven genera of 1.5-m long fish-eating aquatic forms from the Late Permian to the Middle Triassic of most parts of the world (Charig 1976; Benton and Norman 1988). The group is hard to diagnose, but four synapomorphies are: (1) skull relatively long; (2) premaxilla downturned and projects forward beyond the lowerjaw; (3) premaxilla has 6-9 teeth; (4) haemapophyses laterally compressed and broad at the distal end.

Erythrosuchus from the Early Triassic of S. Africa (Figs. 8.2B, 8.3B, and 8.4B) appears to have acquired a number of synapomorphies of the skull and skeleton that are shared with later archosaurs, but are absent in proterosuchids (Fig. 8.1; list 2, Appendix 1). The Erythrosuchidae (Early–Middle Triassic, worldwide) includes seven genera of large archosaurs, which share a number of synapomorphies (Benton and Norman 1988): (1) notch on the lower border of the skull between the maxilla and premaxilla; (2) postparietal projects backwards as a conical peg; (3) cervical vertebrae are extremely short.

Most authors, until recently, classed the Erythrosuchidae with the

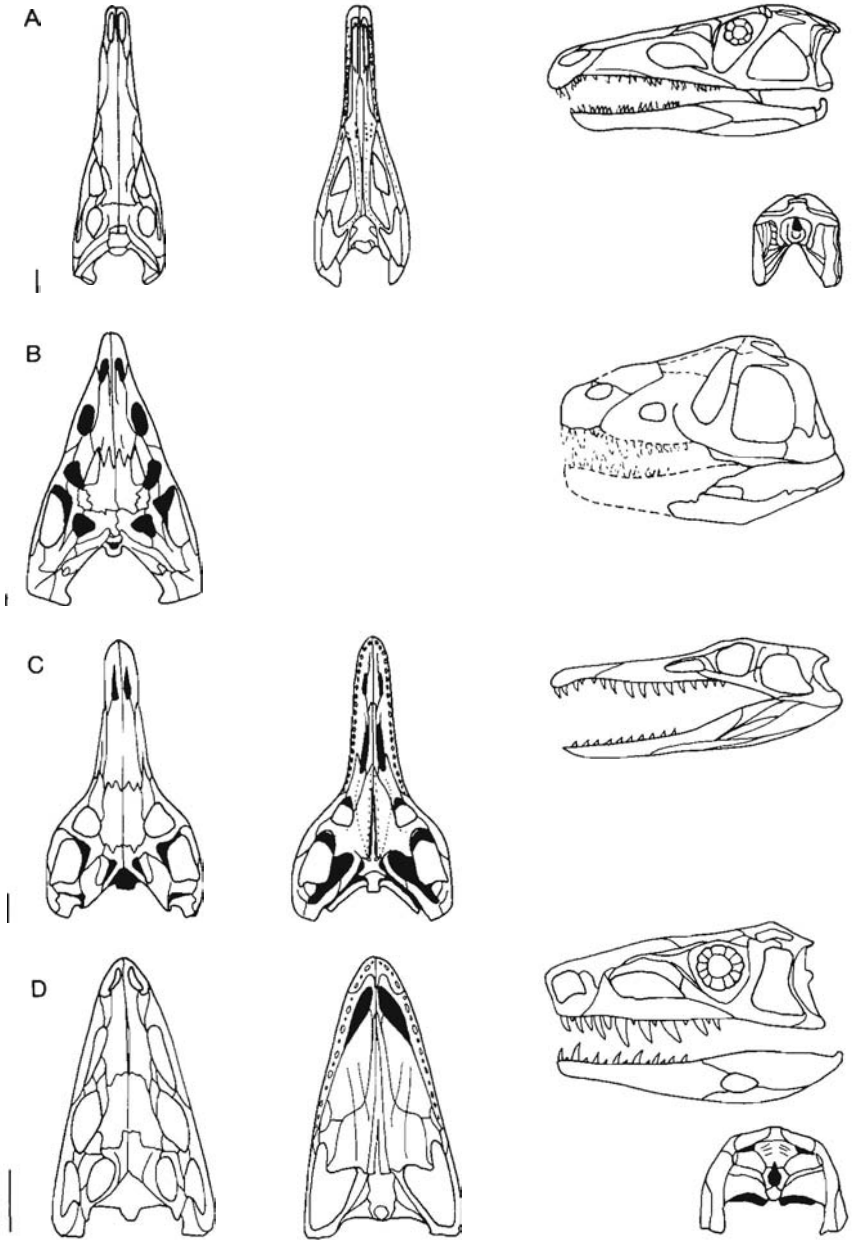


Fig. 8.2. The skulls of A, *Proterosuchus*, B, *Erythrosuchus*; C, *Chanaresuchus*; and D, *Euparkeria*, in dorsal, palatal, lateral and occipital views. The skulls have been drawn to a standard length. Scale bars=20 mm. (A, after Cruickshank 1972; B, after Charig and Sues 1976; C, after Romer 1971a; E, after Ewer 1965.)

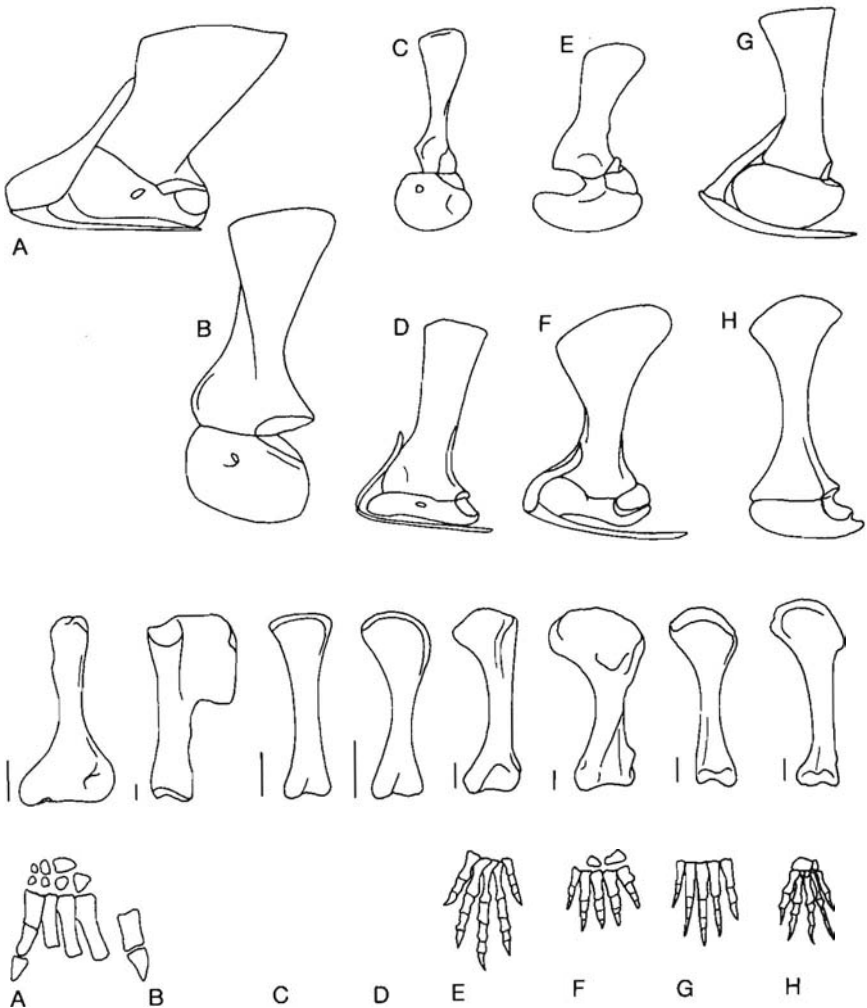


Fig. 8.3. The pectoral girdle (left, lateral view), humerus (left, dorsal view), and hand (left, dorsal view) of A, *Proterosuchus*; B, *Erythrosuchus*; C, *Chanaresuchus*; D, *Euparkeria*; E, *Parasuchus*; F, *Stagonolepis*; G, *Ticinosuchus*; and H, *Postosuchus*. The humeri have been drawn to a standard length, and the pectoral girdles and hands have been drawn to scale for each genus. Scale bars = 10 mm. The hands of *Erythrosuchus*, *Chanaresuchus*, and *Euparkeria* are too poorly known for reconstruction. (A, after Cruickshank 1972; B, after Charig and Sues 1976; C, after Romer 1972c; D, after Ewer 1965; E, after Chatterjee 1978; F, after Walker 1961; G, after Krebs 1965; H, after Chatterjee 1985.)

Proterosuchidae in the Suborder 'Proterosuchia', which is a paraphyletic group with no evident synapomorphies. Bonaparte (1984) established a Suborder *Erythrosuchia* for erythrosuchids, proterochampsids, and raiusuchids. These he defined in terms of their

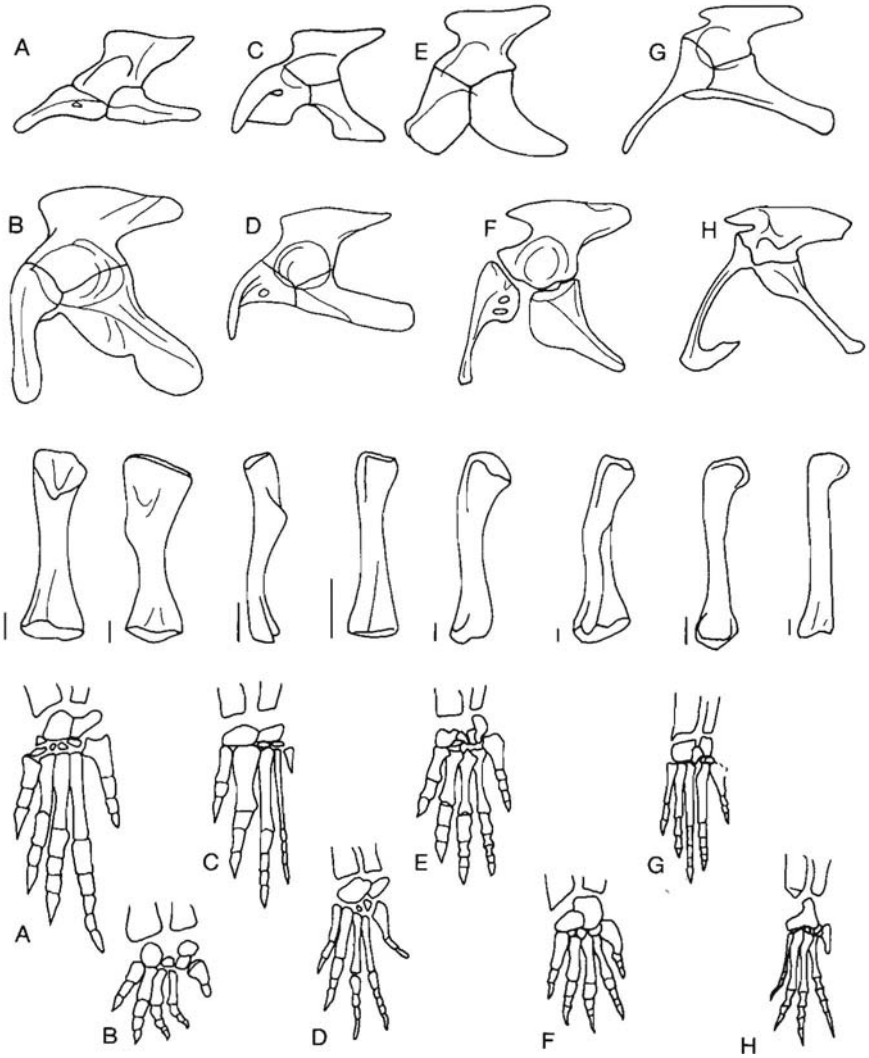


Fig. 8.4. The pelvis (left, lateral view), femur (posterolateral view), and foot (dorsal view) of *A*, *Proterosuchus*; *B*, *Erythrosuchus*; *C*, *Chanaresuchus*; *D*, *Euparkeria*; *E*, *Parasuchus*; *F*, *Stagonolepis*; *G*, *Ticinosuchus*; and *H*, *Postosuchus*. The femora have been drawn to a standard length, and the pelvic girdles and feet have been drawn to scale for each genus. Scale bars=20 mm. (Sources as for Fig. 8.3.)

generally large size, large fenestrated skull, and keyhole-shaped orbit, as well as some other points. However, these characters are outweighed by the synapomorphies that rauisuchids share with other pseudosuchians (see below; Fig. 8.1). Paul (1984) also classed erythrosuchids with rauisuchids, and possibly also with phytosaurs, on the

basis of their supposedly shared erect gait, a view that we do not accept.

Chanaresuchus from the Middle Triassic of Argentina (Figs. 8.2C, 8.3C, and 8.4C) falls next on the line to more advanced archosaurs, just above the Erythrosuchidae, on the basis of seven synapomorphies (Fig. 8.1; list 3, Appendix 1). It is a member of the Proterochampsidae, a family of superficially crocodylian-like animals from the Middle and Late Triassic of S. Africa (five or six genera), which may be characterized by at least eight synapomorphies (Benton and Norman 1988), including: (1) the very low skull; (2) slit-like external nares; (3) small posteriorly placed antorbital fenestra; (4) loss of postfrontals; (5) V-shaped occipital crest; (6) huge lateral mandibular fenestra; (7) pes digits III and IV are thin, and II is heaviest; (8) metatarsal V is reduced to a nubbin with no phalanges.

The Proterochampsidae have been classified as ancestral crocodylians (Reig 1970) or as ancestral phytosaurs (Walker 1968). However, most of the crocodylian-like or phytosaur-like characters of the proterochampsids are primitive for archosaurs in general, and one of the more convincing shared characters, the secondary palate, differs from that of crocodylians in detail. Other authors have classified the proterochampsids as 'Proterosuchia' (Romer 1972a; Cruickshank 1979; Bonaparte 1982), 'Pseudosuchia' (Bonaparte 1971a), or 'Thecodontia incertae sedis' (Chatterjee 1982).

Doswellia from the Late Triassic of Virginia, USA, was classified originally (Weems 1980) as a representative of a new suborder of Archosauria, while Bonaparte (1982) classed it as an aetosaur. However, in the cladistic analysis here, it was placed as a possible sister-taxon of Chanaresuchus on the basis of one synapomorphy, the loss of the postfrontal, and one reversal (Fig. 8.1; list 4, Appendix 1). Doswellia is incompletely known (no details of the anterior part of the skull, forelimb, or foot are known), and it could share some of the other proterochampsid autapomorphies enumerated above.

Euparkeria

Euparkeria from the Early Triassic of S. Africa (Figs. 8.2D, 8.3D, and 8.4D) has generally been regarded as close to the ancestry of later archosaurs, sharing a number of synapomorphies with them (Fig. 8.1; list 5, Appendix 1). Turfanosuchus from China may be related to Euparkeria in the Euparkeriidae, on the basis of three synapomorphies (Benton and Norman 1988): (1) naris is approximately square in side-view; (2) palatines meet in the midline in the palate (?); (3) presence of two foramina in the pubis (but also in Stagonolepis and Riojasuchus).

Several authors (e.g. Hughes 1963; Ewer 1965) placed Euparkeria in the Erythrosuchidae on the basis of its primitive characters, while

Cruickshank (1979) suggested that it was in fact more primitive than *Erythrosuchus*, particularly in terms of its ankle. This view has been contradicted (Thulborn 1980; Brinkman 1981; Chatterjee 1982) and these authors have argued that *Euparkeria* clearly had a more advanced ankle which permitted some movement between the astragalus and the calcaneum—a form of 'crocodilian' ankle that was typical of later archosaurs (Cruickshank and Benton 1985).

Euparkeria has been classified by other authors (e.g. Reig 1970; Romer 1972a; Krebs 1976; Bonaparte 1982) with the advanced 'theodontians', in the *Pseudosuchia*, and it has been interpreted as the sister-group of these later forms, which is the view taken here. An alternative view is that *Euparkeria* had a 'crocodile-reversed' (CR) ankle, as seen in ornithosuchids, and that *Euparkeria* is a close relative of these Late Triassic forms (Bonaparte 1975; Cruickshank 1979; Brinkman 1981; Chatterjee 1982; Gauthier 1984, 1986; Gauthier and Padian 1985). In support of its placement in the dinosaurian line, Gauthier (1986, p. 43) lists six postulated synapomorphies of *Euparkeria* and other ornithosuchians:

1. squamosal reduced and descending ramus gracile;
2. centra steeply inclined in at least the first four postatlantal cervicals;
3. modifications in the hindlimb and girdle, correlated with semierect gait;
4. ventral flange of astragalus absent;
5. crocodile-reversed (CR) ankle joint, with peg on calcaneum and socket on astragalus;
6. pedal digit V with fewer than four phalanges.

Character (2) is not clear in *Euparkeria* and early ornithosuchians, and character (3) is not precisely enough defined: according to Parrish (1986), the hindlimb and girdle of *Euparkeria* is primitive in most respects. We do not accept that *Euparkeria* has a CR ankle (5) (Cruickshank and Benton 1985). There is a slight peg on the calcaneum, and a socket on the astragalus, but these are very different from the ornithosuchid condition. The ankle of *Euparkeria* is modified from that of *Proterosuchus* (Cruickshank and Benton 1985), which has the 'primitive mesotarsal' (PM) condition, but it is not closely comparable with either the CR or the 'crocodile-normal' (CN) forms. Character (6) is primitive, being true of *Proterosuchus*, *Erythrosuchus* (?), *Chanaresuchus*, and others. The squamosal character (1) and the astragalular flange character (4) stand as possible synapomorphies of *Euparkeria* and *Ornithosuchia*, although it is arguable whether the squamosal of *Ornithosuchus* or *Riojasuchus* is truly 'gracile'.

In opposition to the placing of *Euparkeria* within the *Ornithosuchia*, it appears to lack the four postulated synapomorphies of advanced

archosaurs listed below (list 6, Appendix 1). Some of these characters could be explained away by the suggestion that the known specimens of *Euparkeria* are juveniles (Gauthier 1986, p. 43), but present evidence seems to be equivocal on its correct placement in the cladogram.

The Crown-group Archosaurs

None of the four primitive families of archosaurs, the Proterosuchidae, Erythrosuchidae, Proterochampsidae, and *Euparkeriidae*, seems to have given rise to further lineages. All of the remaining archosaurs fall into a single monophyletic group, equivalent to Gauthier's (1986) Archosauria (*sensu stricto*). This group is characterized by four autapomorphies (Fig. 8.1; list 6, Appendix 1):

1. parietals send posterior processes into the occiput, which meet the supraoccipital;
2. discrete postparietal and exoccipitals are absent beyond juvenile stages of development (postparietals are variably developed in crocodylians);
3. pterygoids meet medially in the palate;
4. palatal teeth are absent.

The crown-group Archosauria split into two lineages at the end of the Early Triassic, one of which led to the crocodylians, the other to the dinosaurs. The crocodylian line includes phytosaurs, aetosaurs, raiisuchids, and poposaurids, and it is termed here **Crocodylotarsi** (literally 'crocodyle ankles'). The dinosaur line includes ornithosuchids, dinosaurs, birds, and probably pterosaurs, termed collectively the Ornithosuchia (Gauthier and Padian 1985; Gauthier 1986).

The PAUP analysis initially gave a most-parsimonious tree that placed the ornithosuchians within the Crocodylotarsi as sister-group of *Postosuchus* plus *Crocodylomorpha*. This was because of the larger number of apparent synapomorphies shared by the erect-gaited ornithosuchians and early crocodylomorphs, such as *Terrestrisuchus* and the poposaurid *Postosuchus*, and a large number of reversals are necessary (many of the characters in lists 7, 8, 9 and 10, Appendix 1). The cladogram presented here (Fig. 8.1) is only slightly less parsimonious but, we believe, more likely.

The Crocodylotarsi (new taxon)

The Crocodylotarsi (=Pseudosuchia *sensu lato*, Gauthier and Padian 1985; Gauthier 1986) includes the phytosaurs, the aetosaurs (*Stagonolepididae*), the raiisuchids, the poposaurids, and the cro-

codylomorphs. The Crocodylotarsi are characterized by several autapomorphies (Fig. 8.1; list 7, Appendix 1: Gauthier 1986; Benton and Norman 1988):

1. crocodile-normal (CN) tarsus, in which the astragalus forms a distal peg that fits into a deep socket on the calcaneum, and the two elements can rotate about this joint;
2. large posterior calcaneal tuber;
3. cervical ribs are short and stout;
4. deltopectoral crest extends less than one-quarter of the way down the humerus (a reversal of the condition in the archosaurs so far described, and in Ornithosuchia).

The Phytosauridae

The Phytosauridae (=Phytosauria, Parasuchia) is a distinctive clade of up to 40 genera of long-snouted 2–4-m-long animals that lived almost exclusively in the Late Triassic, in central Europe and N. America in particular. One of the most fully known is *Parasuchus* from India (Chatterjee 1978) (Figs. 8.3E, 8.4E, and 8.5A). They share at least 16 synapomorphies in comparison with other archosaurs (Benton and Norman 1988): very long snout; snout is made up on all sides by the premaxillae; tip of the snout is spoon-shaped, and bears two or three extra large teeth; external nares lie well back in the posterior half of the length of the skull; external nares are elevated on a crater-like bump; external nares are surrounded by the nasals and septomaxillae; nasal often enters the dorsal border of the antorbital fenestra; orbit lies high; upper temporal fenestra is reduced to a roughly triangular shape; postfrontal does not border the upper temporal fenestra; prootics meet in the floor of the braincase; very long symphysis of the lower jaw between the dentaries; anterior tip of the lower jaw is bulbous and bears three or four large teeth; coronoid is reduced to a tiny element; emargination on the anterior edge of the coracoid; coracoid has a large anteroventral process below an anterior notch.

The affinities of the Phytosauridae have so far been shrouded in mystery. Walker (1968) suggested an origin from *Proterochampsa* on the basis of various shared characters, while Reig (1970), Romer (1972a), Thulborn (1980), Bonaparte (1982), and others simply regarded the phytosaurs as descendants of 'proterosuchians' (the basal archosaurs) that had evolved completely independently of all other archosaur groups. Other authors (e.g. Westphal 1976; Chatterjee 1978) have regarded the question of phytosaur origins as unsolved. Recently, it has been shown that phytosaurs had a CN ankle joint (Chatterjee 1978; Parrish 1986), and Chatterjee (1982) made phytosaurs the sister-group

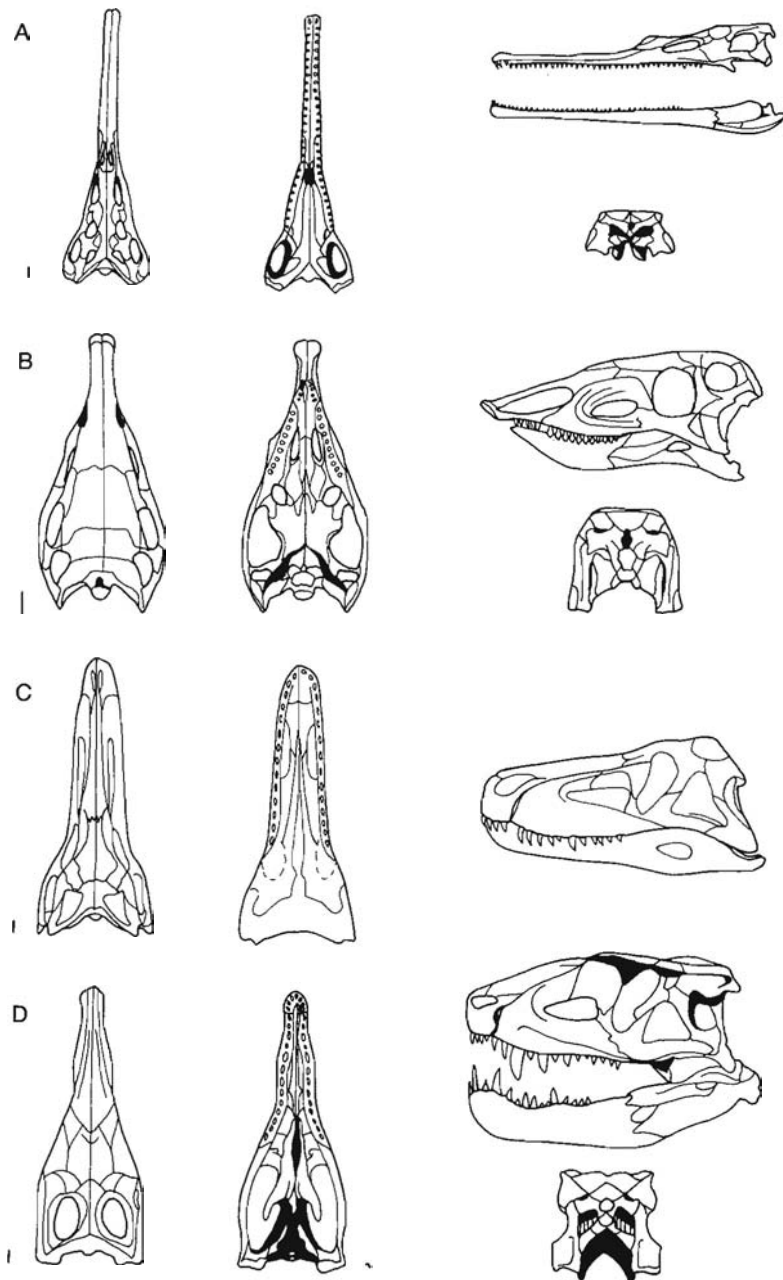


Fig. 8.5. The skulls of A, *Parasuchus*; B, *Stagonolepis*; C, *Luperosuchus* (dorsal, palatal) and *Saurosuchus* (lateral); and D, *Postosuchus*, in dorsal, palatal, lateral, and occipital views. The skulls have been drawn to a standard length. Scale bars=20 mm. (A, after Chatterjee 1978; B, after Walker 1961; C, after Romer 1971b; Bonaparte 1981; D, after Chatterjee 1985.)

of (aetosaurus plus rausuchians) on the basis of ankle structure, the view that we take here.

The Phytosauridae appear to be the most primitive group of the Crocodylotarsi (Gauthier and Padian 1985; Gauthier 1986) (Fig. 8.1). They lack several characters of the pelvis and hindlimb, in particular, which are characteristic of all crocodylomorphs and pseudosuchians. The ankle of phytosaurs, although CN, shows various features that are intermediate between the PM and CN conditions: the peg and socket are not so pronounced as in the fully CN condition, there is still some sliding between the calcaneum and the fibula, and the rotation about the astragalus-calcaneum joint is less than in crocodilians and pseudosuchians (Chatterjee 1982; Parrish 1986).

It could be argued that phytosaurs and crocodilians are sister-groups, and that these two form a distinctive lineage separate from the Pseudosuchia. In the early and middle 19th century (e.g. Huxley 1875), phytosaurs were commonly classified as early crocodilians because of their apparent similarities. For example, they both generally have very long snouts, low skulls, a quadratic skull table, a long posterior overhanging process of the squamosal, a reduced dorsally placed upper temporal fenestra, and a well-ossified braincase with the laterosphenoid enclosing the passages for cranial nerves II–V. Many of these features, however, are clearly not homologous upon closer examination. For example, the long snout of phytosaurs is made up largely from the premaxillae, while in crocodilians it is formed from the maxillae. The low skull and long jaws also give a similar overall appearance to many other features of the head skeleton.

Certain phytosaurs have shown characters that would suggest a more primitive position in the cladogram (Fig. 8.1). A parietal foramen has been noted in one form (reversal of character a at node B), and interparietals and 'tabulars' in the occiput in another (Camp 1930). These features were observed only in a small number of juveniles, and they are absent in adults and in all other phytosaur genera (Westphal 1976; Chatterjee 1978). We do not regard their appearance in phytosaurs as sufficient evidence for a different placing in the cladogram.

The Suchia

The *Suchia*, a name introduced by Krebs (1974, 1976), includes the advanced 'thecodontians' (Pseudosuchia) and the crocodylomorphs, which are characterized by several synapomorphies (Fig. 8.1; list 8, Appendix 1: Benton and Norman 1988):

1. septomaxilla is absent;
2. lower temporal fenestra is reduced in size and has a triangular shape

- with a dorsal point. The quadratojugal slopes forwards towards the postorbital;
3. axial diapophysis is reduced or absent;
 4. no pubo-ischiadic plate. The pubis and ischium are long and narrow. The pubis expands distally into a broad forward-facing plate. There is no broad plate-like union between the pubis and ischium in side-view;
 5. long distal process of the pubis is bent down into a subvertical orientation;
 6. pubis is longer than the ischium. The lengths are about equal in phytosaurs, and the pubis is shorter than the ischium in more primitive thecodontians (not true of *Ticinosuchus*);
 7. proximal head of femur is turned inwards at about 45°;
 8. fully developed CN tarsus. This tarsus is capable of a rotation of 60–70°, compared to only 30° or so in phytosaurs (Parrish 1986).
 9. digit V in the foot is reduced in length, being shorter (pseudosuchians) or much shorter (crocodilians) than digit I.

Gracilisuchus from the Middle Triassic of Argentina, originally classed as a primitive ornithosuchid (Romer 1972b), actually has a CN ankle (Brinkman 1981) and other suchian characters. It falls in the cladogram (Fig. 8.1) below the pseudosuchians plus crocodylomorphs, since it apparently lacks several of their synapomorphies (list 9, Appendix 1), but more complete material of *Gracilisuchus* might move some of these characters.

The remaining suchians appear to divide into a clade consisting of Stagonolepididae plus Rausuchidae (termed here Pseudosuchia), and another consisting of Crocodylomorpha plus Poposauridae (Fig. 8.1). The position of the Poposauridae and the Rausuchidae is hard to determine.

The Poposauridae, represented by *Postosuchus* from the Late Triassic of N. America (Chatterjee 1985) (Figs. 8.3H, 8.4H, and 8.5D) and by numerous other fragmentary remains, have been hard to classify. *Poposaurus* was described variously as an ornithopod dinosaur, a stegosaur, a phytosaur, a carnosaur, a form related to the rausuchids, a pseudosuchian, a rausuchid (Bonaparte 1981), and a rausuchian directly ancestral to tyrannosaurid dinosaurs (Chatterjee 1982, 1985). *Postosuchus* shows a number of very crocodilian-like characters that are apparently not present in rausuchids or aetosaurs. It has the 'crocodilian otic notch' in which the quadratojugal runs anterodorsally to meet the postorbital, a possible maxillary–vomere secondary palate, a reduced quadrate foramen (lost in crocodylomorphs), no clavicle (?), and pedal digit V with no phalanges, amongst others (list 12, Appendix 1). The Crocodylomorpha, and the relationships of *Postosuchus*, are discussed further below.

Gauthier and Padian (1985) and Gauthier (1986) have argued that the Rausuchia (Podosauridae plus Rausuchidae) as a whole is the sister-group of Crocodylomorpha, on the basis of their joint possession of the following characters:

1. enlarged pneumatic basiptyergoid processes;
2. atlas intercentrum much longer than wide;
3. axial diapophysis reduced or absent;
4. pubis more than three times the length of the acetabular width;
5. fewer than four phalanges in pedal digit V;
6. presence of an anterolateral process on parasagittal osteoderms.

Of these six characters, no. 6 was dropped by Gauthier (1986) since the osteoderms of rausuchians are not clearly homologous with those of crocodylomorphs. The remaining characters are hard to assess because many of them are known in only one or two rausuchian genera, or the data are equivocal. The enlarged pneumatic basiptyergoid processes (1) are a feature of Crocodylomorpha, but they have only been reported (Zawiskie, pers. comm.) in *Heptasuchus* (=Podosaurus) and they are apparently not present in *Postosuchus* (Chatterjee 1985). The elongated atlas intercentrum (2) is not clear in rausuchians: in two genera at least (*Stagonosuchus*, *Postosuchus*), the atlas intercentrum appears to be short, the primitive condition (Huene 1938; Chatterjee 1985). The pubis of advanced rausuchians and early crocodylomorphs is indeed very long (4), but that of the early rausuchid *Ticinosuchus* (Krebs 1965) is no longer than that of the aetosaur *Stagonolepis* (Walker 1961), both then showing the primitive condition. Most crocodylomorphs have no phalanges on pes digit V (5), although *Terrestriusuchus* does, and this is the case in *Postosuchus*. *Ticinosuchus* has three, the same number reported in the aetosaur *Typhothorax* (Sawin 1947), while *Stagonolepis* has four, the last two being very tiny (Walker 1961). As noted earlier, the possession of less than four phalanges in pedal digit V may be a primitive character, being present in *Proterosuchus*, *Erythrosuchus* (?), *Chanaresuchus*, and *Ornithosuchia*. Only the reduced axial diapophysis character (3) seems to be valid, being shown clearly by the rausuchians *Ticinosuchus*, *Fasolasuchus*, and *Postosuchus*, but it may refer to a more inclusive taxon, the *Suchia* (list 8, Appendix 1).

The Pseudosuchia

The Pseudosuchia, as defined here, includes two families of Middle and Late Triassic archosaurs, the stagonolepidids (aetosaurs) and the rausuchids. The Pseudosuchia is normally interpreted to include a varied assortment of advanced thecodontians (Romer 1966, 1972a; Krebs 1976; Chatterjee 1982). It is restricted here to the two families

just noted: the Pseudosuchia was originally established (Zittel 1887-90) for a few aetosaurs, and we consider that the present usage is closer to the original sense than the broader view of Gauthier and Padian (1985) and Gauthier (1986), which would include crocodylians in a group named for 'fake crocodylians'.

The Pseudosuchia are characterized by several autapomorphies (Fig. 8.1; list 10, Appendix 1):

1. The dorsal centra are very constricted in ventral view.
2. The acetabulum is horizontal and faces downwards, so that the femur fits directly into it. This gives pseudosuchians a kind of erect gait, which is termed here the 'pillar-like' erect condition, which differs from the erect gait of dinosaurs, birds, and some early crocodylomorphs (Bonaparte 1984). In these latter forms, the acetabulum is subvertical, and the proximal head of the femur fits into it from the side: this is termed here the 'buttress-like' erect condition. This is not clear in *Stagonolepis* or *Ticinosuchus*.
3. The iliac blade is oriented subhorizontally, rather than vertically.
4. The iliac blade is low and long, and turned slightly outwards.
5. The pubis attaches to an anteroventral face on the ilium.

The Stagonolepididae (or Aetosauridae) are a well-defined group of archosaurs that are restricted to the Late Triassic, and had a virtually worldwide distribution. Aetosaurs (Figs. 8.3F, 8.4F, and 8.5B) were about 1–3 m long, with heavily armoured bodies and tails, and they have the distinction of being the first herbivorous archosaurs. They are defined by at least 13 synapomorphies (Benton and Norman 1988): skull is relatively small; snout is blunt and 'shovel-like'; external naris is large and long; lower temporal fenestra is much reduced in size; upper temporal fenestra is laterally placed; parietal enters upper part of the sloping occiput; maxilla enters the border of the naris; premaxilla lacks teeth at the front; anterior end of the lower jaw is toothless, and the dentary has only 6–10 teeth in the dentary; mandible is 'boat-shaped' with a pointed anterior end; teeth are small, compressed, and constricted near the base; pubis has two openings; heavy dorsal, lateral, and ventral armour over back, neck, and tail.

The Rauisuchidae were a widespread group that lived in the Middle and Late Triassic, and typical forms are *Ticinosuchus* (Figs. 8.3G and 8.4G), *Luperosuchus* (Fig. 8.5C), and *Saurosuchus* (Fig. 8.5C). They were large animals (2.5–5.0 m long), and they were apparently the top carnivores in their respective faunas. The Rauisuchidae are distinguished from other archosaurs by several autapomorphies (list 11, Appendix 1).

The Rauisuchidae have been treated as 'proterosuchians' by some authors — direct descendants of the erythrosuchids (e.g. Hughes 1963;

Romer 1966, 1972a; Bonaparte 1982; Paul 1984)—but they are clearly pseudosuchians. The Rausuchidae were paired with the Poposauridae in the Rausuchia by Chatterjee (1982, 1985) and Benton (1984d, 1986) on the basis of a number of apparent synapomorphies. *Postosuchus* has the extra slit-like antorbital fenestra between premaxilla and maxilla, the movable joint between maxilla and premaxilla, the main antorbital fenestra is low in front, the tall orbit with a 'stepped' postorbital/jugal bar behind, and the lacrimal forming a heavy ridge over the orbit of Rausuchidae, and possibly the subhorizontal acetabulum of Pseudosuchia, but these potential synapomorphies are outweighed by the nine that pair *Postosuchus* with the Crocodylomorpha (list 12, Appendix 1).

The Ornithosuchia

The Ornithosuchia, which includes Ornithosuchidae, *Lagosuchus*, Pterosauria, and Dinosauria (including Aves), is defined by numerous autapomorphies (list 14, Appendix 1). A number of the modifications of the limbs and girdles that relate to the acquisition of erect gait appear to be parallelisms with suchians, and with certain early crocodylomorphs in particular.

The Ornithosuchidae, known from the Late Triassic of Scotland and Argentina (Bonaparte 1975), are characterized by several synapomorphies (Benton and Norman 1988): premaxillae form a bulbous snout that extends well forward of the anterior tip of the dentaries, gap in tooth row between maxilla and premaxilla, lacrimal and prefrontal form a shelf-like projection, subsidiary postpalatine fenestra between pterygoid and palatine, three or four sacral vertebrae, coracoid has a posterior projection beneath the glenoid, crocodile-reversed (CR) tarsus. In the CR ankle joint, the calcaneum has a peg that fits into a socket on the astragalus, the opposite of the CN ankle of crocodylotarsans (see above).

Lagosuchus, a slender long-limbed form from the Middle Triassic of Argentina, is a close sister-group of Pterosauria (not considered here) and Dinosauria (Gauthier and Padian 1985; Gauthier 1986), forming the Ornithodira, which is defined by numerous autapomorphies (list 15, Appendix 1). Ornithodirans have an advanced mesotarsal (AM) ankle joint, in which there is no hinge between the astragalus and calcaneum, but only between these and the distal tarsals. This is apparently similar to the PM condition of *Proterosuchus* and non-archosaur diapsids, but the astragalus is a mediolaterally elongated hemicylinder with an ascending dorsal process to lock the tibia into place. The calcaneum is reduced or absent and lacks the 'heel' seen in all other archosaurs.

The Dinosauria, according to all recent cladistic analyses, form a monophyletic group (e.g. Benton 1984b,c, 1986; Gauthier 1984, 1986; Paul 1984; Cruickshank and Benton 1985; Gauthier and Padian 1985), defined by numerous autapomorphies (list 16, Appendix 1). Dinosaurian polyphyly used to be the standard view (e.g. Romer 1966, 1968, 1972a; Reig 1970; Charig 1976; Thulborn 1980; Bonaparte 1982). Some authors (Cruickshank 1979; Chatterjee 1982, 1985) have distinguished two states of the AM ankle: 'advanced mesotarsal normal' (AM-N) and 'advanced mesotarsal reversed' (AM-R). The former is said to be present in coelurosaurs, ornithischians, prosauropods, and tyrannosaurids, while the latter is present in sauropods and megalosaurs. This has been used as evidence of dinosaur polyphyly, on the assumption that the AM-N tarsus evolved from the CN, and the AM-R from the CR, independently of each other. We do not accept that view, since all dinosaurs share numerous synapomorphies and are, we believe, a monophyletic group. Further, the AM ankle is so different from any 'thecodontian' ankle, and the calcaneum is often such a tiny element, that it is not certain that the tiny 'pegs' and 'sockets' in AM ankles are direct homologues of the large structures seen in the CN and CR ankles (Cruickshank and Benton 1985).

The relationships of Crocodylomorpha

The Crocodylomorpha

The Crocodylomorpha ('sphenosuchians' and crocodyliforms) are diagnosed by characters in list 1 (Appendix 2). This synapomorphy list is slightly larger if poposaurids are not the sister-group of crocodylomorphs. The poorly-known *Trialestes* (Reig 1963; Bonaparte 1982) is apparently related to the Crocodylomorpha because it has elongated carpal bones, but it is too poorly known to determine its precise relationships. There is some uncertainty as to whether specimens referred to this taxon that have a mesotarsal ankle indeed belong to *Trialestes*. Because *Trialestes* is so poorly known, aetosaurs, poposaurs, and rauisuchids have been used as outgroups in diagnosing the Crocodylomorpha.

Pseudhesperosuchus Bonaparte (1971b) and *Saltoposuchus* are the two most primitive crocodylomorphs (Fig. 8.6), but *Pseudhesperosuchus* may be the more primitive of the two. *Terrestriusuchus gracilis* (Crush 1984) is apparently synonymous with *Saltoposuchus connectens* (Huene 1921) because the characters cited by Crush to differentiate the two taxa do not appear to be valid; even if valid, there is little reason to consider the two species to represent different genera. Most 'sphenosuchians'

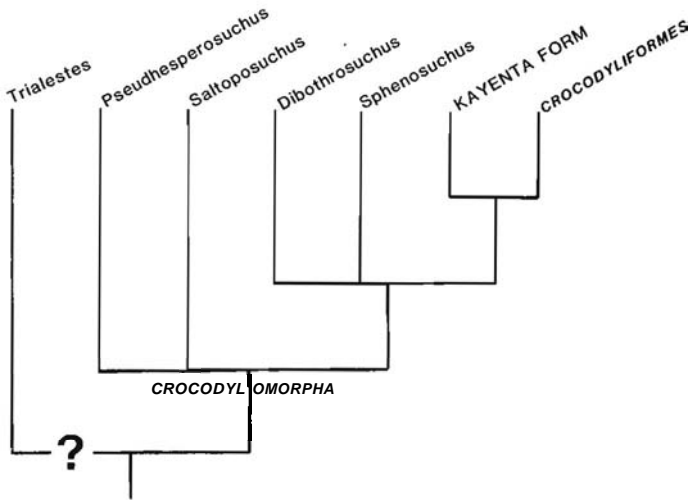


Fig. 8.6. A hypothesis of relationships for primitive crocodylomorphs. Characters are listed in Appendix 2.

apparently held their hind limb erect (Walker 1970; Parrish 1986), with the possible exception of *Pseudhesperosuchus*.

Dibothrosuchus (Simmons 1965; Wu 1986), *Sphenosuchus* (Walker 1972), and an unnamed form from the Kayenta Formation of Arizona, USA (Clark 1986) are more closely related to crocodyliforms than are *Pseudhesperosuchus* and *Saltoposuchus* (list 2, Appendix 2). *Hallopus* (Walker 1970), and perhaps *Hesperosuchus*, may belong to this clade but they are very poorly known.

An unnamed taxon from the Kayenta Formation of northeastern Arizona, described in Clark (1986), is the sister-taxon of the Crocodyliformes (list 3, Appendix 2). It shares with them two features, including a groove on the squamosal to which the dorsal ear-flap muscle originates in living crocodylians (Shute and Bellairs 1955).

The Crocodyliformes

The group including 'protosuchians', 'mesosuchians', and eusuchians, which has often been considered to correspond to the Crocodylia (but see Romer 1972a and Crush 1984), has been termed the Crocodyliformes by Clark (1986), an emendation of a term initially coined by Hay (1930) for a more restricted group. It is defined by a large number of autapomorphies (list 4, Appendix 2), many of which are unique. (Because the new Kayenta form is as yet incompletely prepared, the diagnosis of the Crocodyliformes includes features that are currently

unknown for this form but which are known for *Sphenosuchus* or *Dibothrosuchus*).

An intriguing ambiguity exists regarding the phylogenetic position of the *Thalattosuchia*. The most-parsimonious hypothesis is that *thalattosuchians* are the sister-group of *dyrosaurs* and *pholidosaurs* (Fig. 8.10B). However, this hypothesis is based mainly upon features that are directly associated with *longirostry* (e.g. large supratemporal fenestrae; list 20, Appendix 2), and when these characters are considered to be correlated, this hypothesis is rejected. *Thalattosuchians* lack six crocodyliform synapomorphies (k–p in list 4, Appendix 2), suggesting that they may be the sister-group of other crocodyliforms (Fig. 8.7A). One of the most striking of these features is the position of the postorbital in *thalattosuchians* lateral to the jugal on the postorbital bar; the postorbital is anterior to the jugal primitively and is medial to it in all other crocodyliforms. However, it is more parsimonious to consider *thalattosuchians* to be the sister-group of all other mesoeucrocodylians (Fig. 8.7B), and they will be discussed with that group below.

The 'Protosuchia' currently includes over a dozen named species, but most of these are not valid (Clark 1986). This group includes the most primitive crocodyliforms, and is most parsimoniously considered to be paraphyletic (contrary to Hecht and Tarsitano 1983), with some taxa being more closely related to mesoeucrocodylians than to other 'protosuchians' (Fig. 8.7B). Only if the *Thalattosuchia* are the sister-group of other crocodyliforms is the Protosuchia monophyletic (Fig. 8.7A), because most would then be united by their loss of mesoeucrocodylian synapomorphies found in *thalattosuchians* and *Gobiosuchus*.

Protosuchus, and its junior synonyms *Lesothosuchus* Whetstone and Whybrow (1983) and *Baroqueosuchus* Busbey and Gow (1984), is allied in the Protosuchidae with *Hemiprotosuchus* Bonaparte (1971b) and an unnamed form from the Kayenta Formation of Arizona, USA (similar to *Edentosuchus tienshanensis*; Young 1973). Protosuchids share several striking features, including an accessory mandibular articulation with the braincase (Clark 1986). *Eopneumatosuchus* (Crompton and Smith 1980; Clark 1986) may be a protosuchid, but it is too poorly known to be certain (it may also be the sister-taxon of *thalattosuchians*, as suggested by its large supratemporal fenestrae; Busbey and Gow 1984).

Orthosuchus (Nash 1975) shares with crocodyliforms other than protosuchids several features (list 5, Appendix 2), including a broad contact between the quadrate and otoccipital (Busbey and Gow 1984; Clark 1986). The type specimen of *Orthosuchus* has been distorted by vertical compression, so that, for example, the antorbital fenestra is not a sinuous groove but is instead a round fenestra, like that of *Protosuchus*.

Gobiosuchus (Osmolska 1972; Efimov 1983) is more closely related to mesoeucrocodylians than are other 'protosuchians' (list 6, Appendix 2).

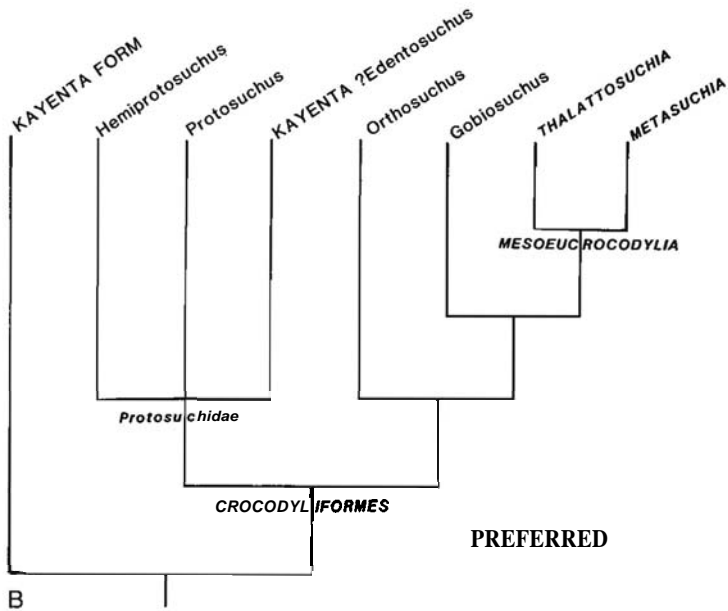
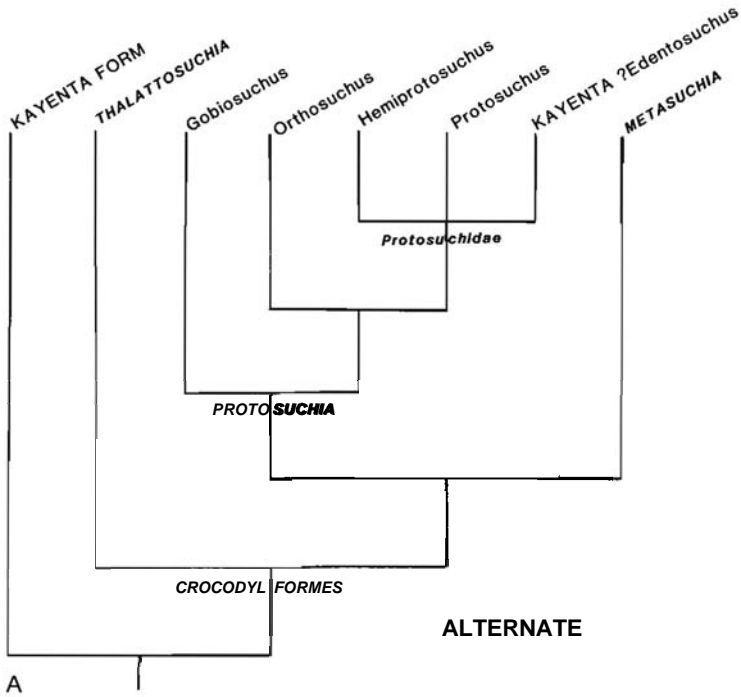


Fig. 8.7. Two hypotheses of relationships for primitive crocodyliforms. A, Alternative, less-parsimonious hypothesis; B, preferred hypothesis. See Fig. 8.10 for an alternative hypothesis of thalattosuchian relationships.

It has not yet been fully described, and so several mesoeucrocodylian features have not been looked for in *Gobiosuchus*.

The Mesoeucrocodylia

Because the traditional group Mesosuchia (Huxley 1875) is clearly paraphyletic, Whetstone and Whybrow (1983) erected the Mesoeucrocodylia for the 'Mesosuchia' plus Eusuchia. It is diagnosed by numerous features (list 7, Appendix 2; Clark 1985, 1986), including three cited by Huxley (a, c, e). An argument can be made in support of the exclusion of thalattosuchians from this group (see above), but otherwise the group is well supported.

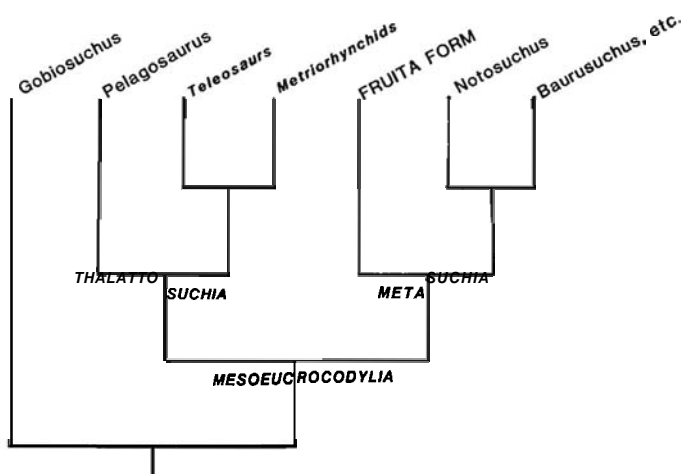


Fig. 8.8. A hypothesis of relationships for primitive mesoeucrocodylians. See Fig. 8.10 for an alternative hypothesis of thalattosuchian relationships.

The Thalattosuchia includes *Pelagosaurus*, Teleosauridae, and Metriorhynchidae (Fig. 8.8), and is diagnosed by 26 autapomorphies (see Clark 1986). Buffetaut (1979) has argued that *Pelagosaurus* is a primitive metriorhynchid; although there is some evidence for this, *Pelagosaurus* is most parsimoniously considered to be the sister-taxon of the other thalattosuchians (Clark 1986).

The Metasuchia (new taxon)

An unnamed, gracile mesoeucrocodylian from the Late Jurassic Morrison Formation of Fruita, Colorado, USA (Clark 1985) is more closely related to other mesoeucrocodylians than are thalattosuchians (list 8,

Appendix 2, Fig. 8.8). We erect the name **Metasuchia** (meta, Gr.-near; suchos, Gr.-crocodile) for this group, comprised of non-thalattosuchian mesoeucrocodylians. Even if the Thalattosuchia were the sister-group of all other crocodyliforms, the monophyly of the Metasuchia would not be in question. However, the Metasuchia would include the thalattosuchians, and would thus be redundant with the Mesoeucrocodylia if the longirostrine characters are considered to place them with pholidosaurs and dyrosaurs.

Notosuchus, Uruguaysuchus, Araripesuchus, and often Libycosuchus, have been considered to form the Notosuchia (Gasparini 1971; Buffetaut 1982). However, the features cited in support of this group are nearly all found in 'protosuchians' and the Fruita form, whereas some members share derived features with more advanced mesoeucrocodylians. (The two possible notosuchian synapomorphies are a

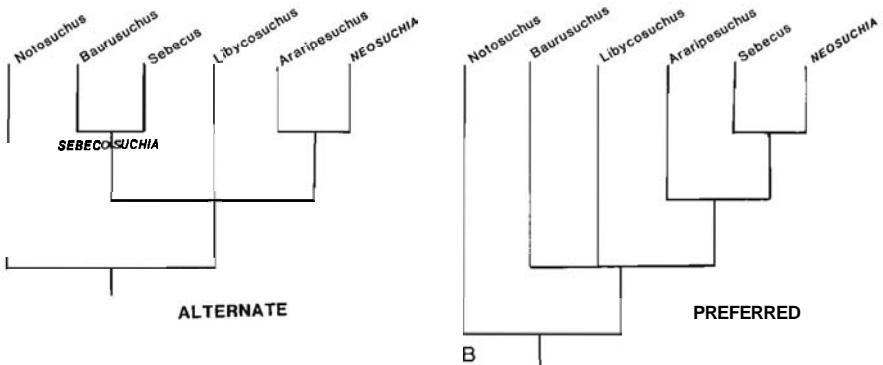


Fig. 8.9. Two hypotheses of relationships for primitive metasuchians. A, Alternative, less-parsimonious hypothesis; B, preferred hypothesis.

peculiar anterolateral-facing edge on the postorbital, shared with Baurusuchus and unknown for Sebecus, and a peculiar posteroventrally directed, paddle-shaped retroarticular process, unknown for Araripesuchus and present in Baurusuchus and Sebecus.) Hecht and Taritano (1984) have argued that the notosuchians belong to a separate monophyletic group, along with 'protosuchians'. This hypothesis is, again, based upon primitive crocodyliform characters retained in some notosuchians', and is therefore untenable. The present analysis suggests that Notosuchus is more advanced than the Fruita form (list 9, Appendix 2), but it is the most primitive of the paraphyletic 'notosuchians'. Notosuchus is very peculiar in having had an articular that allowed for significant longitudinal movement of the mandible (J. F. Bonaparte, pers. comm.; Clark 1986). The poorly-known Spha-

gesaurus (Price 1955) is almost certainly related to *Notosuchus*, and *Uruguaysuchus* may also be related (Clark 1986).

Although they are more advanced than *Notosuchus* (list 10, Appendix 2), the precise relationships of *Libycosuchus* (Buffetaut 1976), *Sebecus* (Colbert, 1946), *Baurusuchus* (Price 1945), and *Araripesuchus* (Price 1959; Buffetaut 1981) are obscured by a puzzling pattern of character distributions (Fig. 8.9). *Sebecus* and *Baurusuchus* have traditionally been included in the *Sebecosuchia* (e.g. Buffetaut 1982), and there is a great deal of apparently derived similarity (list 11, Appendix 2). If this group is valid, then *Araripesuchus* would be more closely related to the *Neosuchia* than *Sebecus* (Fig. 8.9A). However, there are a substantial number of conflicting characters suggesting that *Sebecus* is more closely related to the *Neosuchia* (list 13, Appendix 2; Fig. 8.9B). (The shared synapomorphies of *Araripesuchus*, *Sebecus*, and the *Neosuchia* are found in list 12, Appendix 2). A more refined hypothesis of relationships must await a detailed description of *Baurusuchus*.

The Neosuchia (new taxon)

We erect here the name **Neosuchia** (neos, Gr.-new; *souchos*, Gr.-crocodile) for the *Atoposauridae*, *Goniopholidae*, *Pholidosauridae*, *Dyrosauridae*, *Bernissartia*, *Shamosuchus*, and eusuchians. This is essentially the paraphyletic *Metamesosuchia* (Hulke 1878) as conceived by Buffetaut (1982), with the addition of the *Eusuchia* (except that dyrosaurs were excluded from the *Metamesosuchia* by Buffetaut). The group is diagnosed by several features if *Sebecus* is a *sebecosuchian*; however, because many of these are shared with *Sebecus*, there are only a few that would diagnose the group (unless *Sebecus* was considered its most primitive member). *Atoposaurs* are more advanced than *Araripesuchus* (list 14, Appendix 2) but, contrary to recent opinion (Joffe 1967; Buffetaut 1982), *atoposaurs* are not the sister-group of eusuchians (Fig. 8.10A). Clark (1986) restricts the *Atoposauridae* to two species: *Theriosuchus pusillus* (Owen 1879) and *Alligatorium meyeri* (Wellnhofer 1971), but *Montsechosuchus* (*Alligatorium*) *depereti* (Buscalioni 1986) is apparently also included. Included within *A. meyeri* are several taxa that form a growth series (several species and subspecies of *Atoposaurus* and *Alligatorellus*).

Goniopholids, *pholidosaurs*, and *dyrosaurs* are more closely related to eusuchians than are *atoposaurs* (list 15, Appendix 2). However, their relationships are ambiguous, and the monophyly of all of the *goniopholids* is questionable (*Eutretauranosuchus* may be more distantly related to eusuchians). The incomplete secondary palate of some forms (*Eutretauranosuchus* and *Sunosuchus*; Buffetaut 1986) is most parsimoniously interpreted as a reversal rather than as a retained primi-

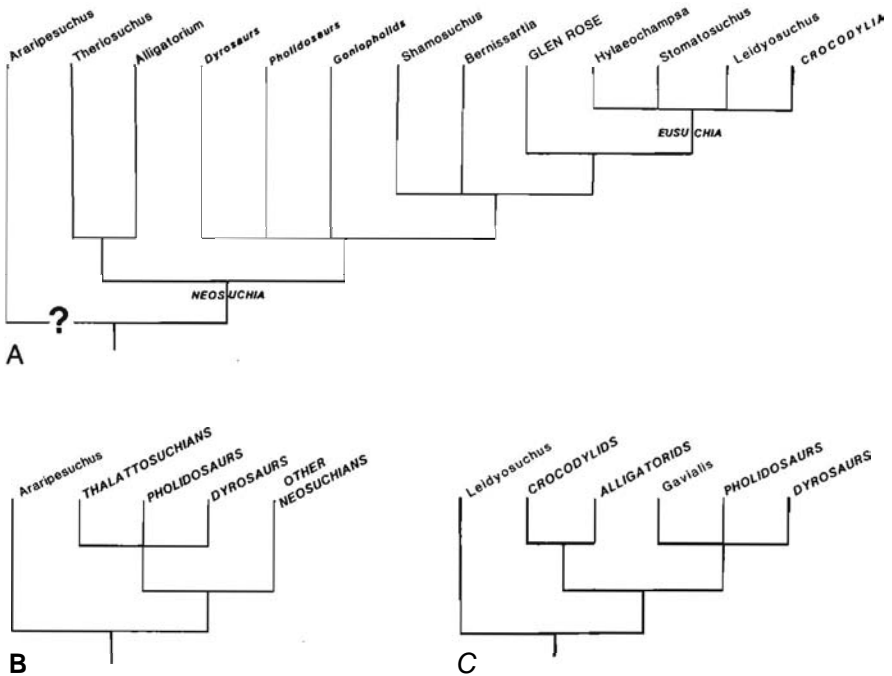


Fig. 8.10. Three hypotheses of relationships for neosuchians. **A**, Preferred hypothesis that is most parsimonious if characters associated with longirostry are correlated; **B**, alternative hypothesis that is most parsimonious if characters are independent; **C**, alternative hypothesis that is less parsimonious than **B**, but more parsimonious than **A**, if characters are independent.

tive feature. Dyrosaurs are a well-defined monophyletic group, and *Sokotosuchus* appears to be the most primitive member of the clade (Buffetaut 1979). Dyrosaurs were considered to be very primitive mesoeucrocodylians by Buffetaut (1982), but this was based upon their peculiar specializations and not upon their lack of derived neosuchian features. Pholidosaurs appear to be essentially longirostrine gonlopholids, but many of their similarities may not be derived.

Several features shared by thalattosuchians, dyrosaurs, and pholidosaurs, if considered to be independent, most parsimoniously demonstrate a close relationship (Fig. 8.10B), but they are here considered to be correlated with longirostry and not to affinity (see section on *Crocodyliformes* above). If these taxa form a clade then the

primitive characters of thalattosuchians would place the group as the sister-group of the other neosuchians, at a position more primitive than that of atoposaurs. Surprisingly, thalattosuchians, dyrosaurs, and pholidosaurs lack the intertympanic fenestra through the supraoccipital found in all other crocodyliforms (Edinger 1938; *pers. obs.*, *Sarcosuchus*), a feature not obviously related to longirostry. Pholidosaurs share most of the longirostrine features with dyrosaurs and the living gharial, and a close relationship between them is possible (Fig. 8.10C). However, the similarities between dyrosaurs on the one hand, and pholidosaurs and gharials on the other, are superficial, and most disappear when examined closely (e.g. the long rostrum is tubular in pholidosaurs and gharials, and is broad in dyrosaurs; and the supratemporal fenestrae are smaller and rounder in pholidosaurs and gharials). Although they are very similar, the features shared by gharials and pholidosaurs are, again, mostly related to longirostry, and this relationship is not accepted here. Curiously, if pholidosaurs and dyrosaurs are closely related to gharials, then they fall within the crown-group Crocodylia.

Bernissartia (Buffetaut 1975) and *Shamosuchus* (= *Paralligator*; Efimov 1983) both share several features of their osteoderms with eusuchians (list 16, Appendix 2), although those of *Shamosuchus* are poorly known. Furthermore, recent examination of *Bernissartia* (Norell and Clark, in preparation) revealed that it possesses a biconvex first caudal vertebra like that of eusuchians, although the distribution of this feature in other fossils is poorly known. An undescribed taxon from the Early Cretaceous of N. America (Langston 1973, 1974) appears to be the sister-taxon of eusuchians (list 17, Appendix 2). It is surprisingly similar to the living Dwarf Crocodile, *Osteolaemus*.

The Eusuchia

There are three taxa that are not clearly within the crown-group Crocodylia, and they may be the sister-taxa of the Crocodylia rather than members (list 18, Appendix 2). *Hylaeochampsia* Owen (1874; Andrews 1913) is known from only a single specimen, which includes the posterior part of a skull with the choana in the pterygoids. The type specimen of *Stomatosuchus* Stromer (1925), which was destroyed during the Second World War, had procoelous vertebrae and the choana within the pterygoid. *Leidyosuchus* (Erickson 1976) may be more closely related to crocodylians than the other two, but its synapomorphies with crocodylians are unknown for the latter.

The Crocodylia

The diagnosis of the crocodylian crown-group is difficult to determine

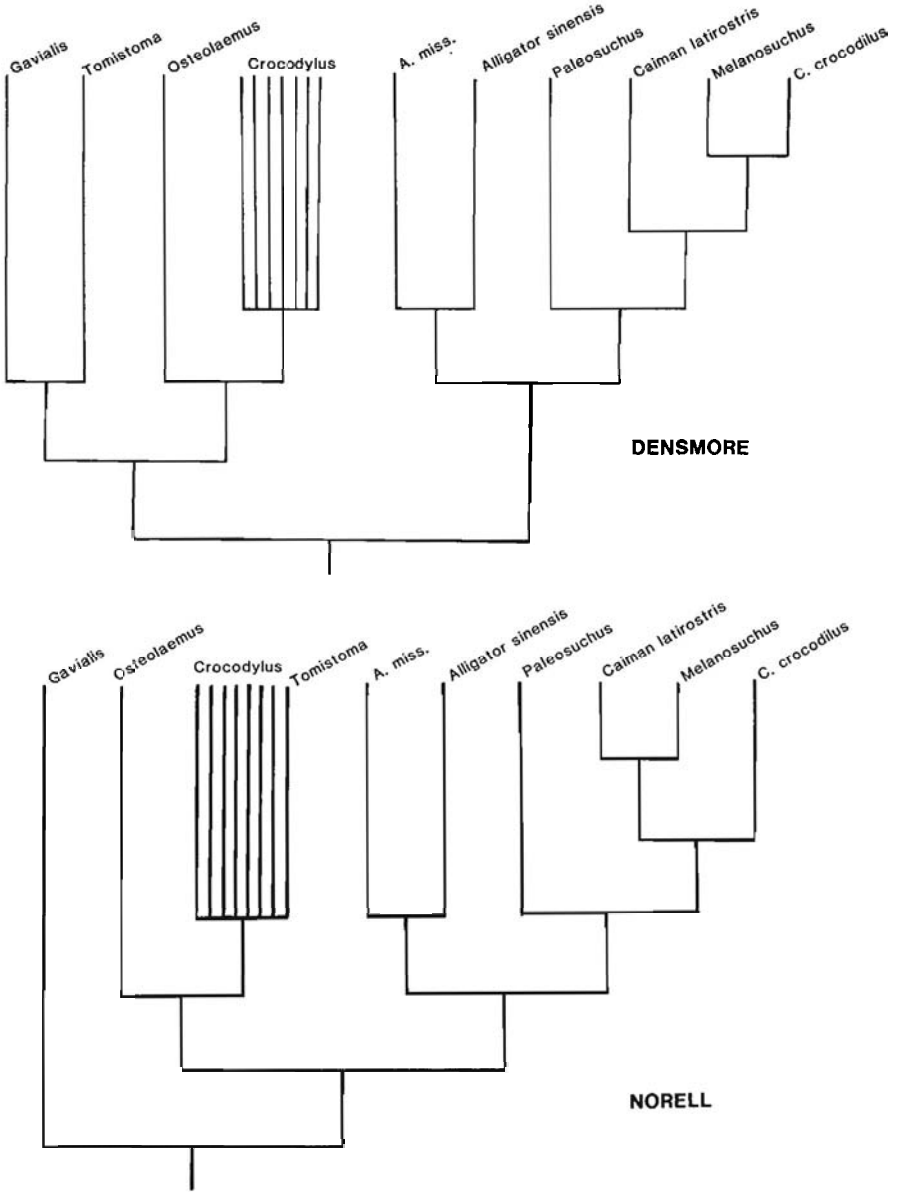


Fig. 8.11. Two hypotheses of relationships for living crocodylians. A, The hypothesis of Densmore, based upon a phenetic analysis of biochemical characters; B, the hypothesis of Norell (*pers. comm.*) based upon osteological characters.

because the outgroups, except *Leidyosuchus*, are not well known. All have scapulae that do not broaden dorsally as greatly as in more primitive crocodyliforms, but this is variably developed in some forms (e.g. some alligatorids).

The morphology of the living crocodylians has not yet been cladistically analysed, but this approach is currently being pursued by Mark Norell, who has found a plethora of characters. Lewellyn Densmore has examined blood proteins using phenetic analyses, and his results (Fig. 10A) reinforce the traditional division into alligatorid, crocodylid, and gavialid lineages with the interesting exception that the false gharial, *Tomistoma*, appears to be more closely related to the true gharial than to crocodylids. Mark Norell is analysing some of this data cladistically and is using restriction enzymes on proteins in the DNA of alligatorids. His preliminary results analysing morphology (Fig. 10B) indicate that there is little or no support for the *Tomistoma-Gavialis* grouping.

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Appendix 1

Synapomorphies used in the analysis of early archosaur phylogeny.

1. Archosauria: (a) possession of antorbital fenestra; (b) postfrontal reduced; (c) postparietals are fused or absent; (d) posterior border of lower temporal fenestra is bowed; (e) marginal teeth are laterally compressed; (f) presence of an ossified laterosphenoid; (g) no ectepicondylar foramen on humerus; (h) possession of a fourth trochanter on femur.

2. Unnamed Group A: (a) loss of the supratemporal; (b) possession of a lateral mandibular fenestra; (c) coronoid reduced or absent (enlarged in some crocodylomorphs); (d) presacral intercentra are absent behind the axis; (e) ossified portion of the scapula is very tall and narrow (at least twice as tall as width of base); (f) coracoid is small, and glenoid faces largely backwards (enlarged in crocodylians); (g) deltopectoral crest extends at least one-quarter of the way down the shaft of the humerus; (h) distal end of the humerus is narrower than the proximal; (i) pelvis is markedly three-rayed, with a long downturned pubis and ischium; (j) iliac blade has a small anterior process; (k) pubis has a strongly downturned anterior tuber when seen in side-view; (l) ischium has a large posteroventral process (the ischium is longer than the iliac blade); (m) tarsus contains only four elements; (n) metatarsals II, III, and IV subequal in length, with III the longest; (o) loss of anterior proximal 'hook' on metatarsal V.

3. Unnamed Group B: (a) parietal foramen absent; (b) otic notch well developed; (c) possession of thecodont dentition; (d) ribs all one- or two-headed; (e) hindlimbs are under the body (semi-erect or erect gait); (f) possession of 'crocodyloid' tarsus (foramen is lost, and rotation between astragalus and calcaneum possible); (g) possession of dermal armour with one pair of osteoderms per vertebra.

4. Unnamed Group C: (a) loss of postfrontal (parallelism with *Crocodylomorpha*); (b) pelvis massive, and not three-rayed (reversal of character (i) in list 2).

5. Unnamed Group D: (a) antorbital fenestra is large and it lies in a depression; (b) nasals run forwards between the nares; (c) diapophysis is placed fairly high on the neural arch of cervical vertebrae; (d) parapophysis transfers to the neural arch in anterior dorsal vertebrae; (e) diapophysis and parapophysis fuse in the posterior dorsal vertebrae and the ribs become single-headed.

6. Unnamed Group E (=Archosauria s.s. of Gauthier 1986): (a) parietals send posterior processes into the occiput which meet the supraoccipital; (b) discrete postparietal and exoccipitals absent beyond juvenile stages of development; (c) pterygoids meet medially in the palate; (d) palatal teeth are absent.

7. *Crocodylotarsi*: (a) crocodile-normal tarsus; (b) large posterior calcaneal tuber; (c) cervical ribs short and stout; (d) deltopectoral crest

extends less than one-quarter of the way down the humerus shaft (reversal of character (g) in list 2).

8. Suchia: (a) septomaxilla is absent (parallelism in Ornithosuchia); (b) lower temporal fenestra is reduced in size and triangular in shape, with a dorsal point; (c) axial diapophysis is reduced or absent; (d) no pubo-ischiadic plate, and much reduced contact between pubis and ischium (parallelism in Ornithosuchia); (e) pubis is long and narrow and subvertically oriented (parallelism in Ornithosuchia); (f) pubis is longer than the ischium (parallelism in Ornithosuchia); (g) proximal head of femur is turned inwards at about 45° (not in Stagonolepis); (h) advanced crocodile-normal tarsus; (i) digit V of the foot is reduced (shorter than I) (parallelism in Ornithosuchia).

9. Unnamed Group F: (a) postparietals are absent in posthatching stages (Gauthier 1986); (b) pit between basioccipital and basisphenoid (=foramen intertympanicum of living crocodylians; Clark 1986); (c) atlas centrum and axis intercentrum are fused from the juvenile stage (Gauthier 1986); (d) accessory neural spine on caudal vertebrae (not in Stagonolepis); osteoderms on the ventral surface of the tail.

10. Pseudosuchia: (a) dorsal centra are very constricted in ventral view; (b) acetabulum is subhorizontal and it faces downwards, giving a 'pillar-like' erect posture of the hindlimb; (c) iliac blade is oriented subhorizontally; (d) iliac blade is low and long; (e) pubis attaches to an anteroventral face on the ilium.

11. Rauisuchidae: (a) extra slit-like fenestra between the maxilla and premaxilla; (b) movable joint between the maxilla and premaxilla; (c) main antorbital fenestra is low in front; (d) tall orbit with a 'stepped' postorbital/jugal bar behind; (e) lacrimal forms a heavy ridge over the orbit; (f) proximal distance between the ischia is less than that between the pubes; (g) pubis is shorter than the ischium (reversal of character (f) in list 8).

12. Unnamed Group G: (a) posterior border of lower temporal fenestra is not bowed (reversal or character (d) of list 1); (b) short descending process of squamosal and tall quadratojugal that contact the postorbital (this may be a convergence: *Postosuchus* has a second lower temporal fenestra above this contact which is absent in crocodylomorphs, and the latter generally lack a descending process of the squamosal); (c) maxillary-vomer secondary palate (also in *Chanaresuchus*); (d) enlarged pneumatic basiptyergoid processes (Gauthier 1986; in *Poposaurus*, but not in *Postosuchus*); (e) reduction or loss of clavicle (parallelism in Dinosauria); (f) forelimb:hindlimb ratio is about 0.5 (parallelism in Ornithosuchia); (g) acetabulum is perforated (parallelism in Ornithosuchia); (h) supra-acetabular crest on ilium (parallelism in Ornithodira; ?also in *Saurosuchus*); (i) pubis is more than three times the length of the width of the acetabulum (parallelism in Ornithodira; ?also in *Saurosuchus*); (j) pedal digit V has

no phalanges (but not in *Terrestriusuchus*); (k) stance is digitigrade (parallelism in *Ornithodira*).

13. *Crocodylomorpha*: (a) loss of postfrontal (parallelism in *Chanaresuchus* and *Doswellia*); (b-j) see Appendix 2.

14. *Ornithosuchia* (Gauthier 1986): (a) septomaxilla is absent (parallelism in *Suchia*); (b) squamosal is reduced and descending ramus is gracile (also in *Euparkeria*); (c) manus digit I is short and equipped with a diverging claw; (d) no pubo-ischiadic plate, and much reduced contact between pubis and ischium (parallelism in *Suchia*); (e) pubis is long and narrow and subvertically oriented (parallelism in *Suchia*); (f) pubis is longer than the ischium (parallelism in *Suchia*); (g) possession of a lesser trochanter; (h) fourth trochanter is a sharp flange; (i) shaft of femur is bowed dorsally; (j) prominent cnemial crest on tibia (also in *Gracilisuchus*); (k) ventral flange of astragalus is absent (also in *Euparkeria*); (l) digit V of the foot is reduced (shorter than I) (parallelism in *Suchia*).

15. *Ornithodira* (Gauthier 1986): (a) presacral vertebral column is divided into three regions (cervical, cervical-thoracic, lumbar); (b) centra are steeply inclined in at least cervicals 3-6; (c) zygapophyses of the middle and posterior caudals are inclined posteroventrally; (d) loss of the interclavicle (?also in *Postosuchus*); (e) acetabulum is perforated (parallelism in *Postosuchus* and *Crocodylomorpha*); (f) supra-acetabular crest on ilium (parallelism in *Saurosuchus*, *Postosuchus*, *Crocodylomorpha*); (g) pubis length is more than three times the width of the acetabulum (parallelism in *Saurosuchus*, *Postosuchus*, *Crocodylomorpha*); (h) fourth trochanter is a wing-like process; (i) fourth trochanter runs down one-third to one-half of the length of the femur shaft (parallelism in *Erythrosuchus* and *Chanaresuchus*); (j) distal end of femur forms two subterminal condyles; (k) knee articulates at 90°; (l) stance is digitigrade (parallelism in *Gracilisuchus*, *Postosuchus*, *Crocodylomorpha*); (m) mesotarsal ankle joint with astragalus and calcaneum fused to the tibia; (n) calcaneum with no tuber at all; (o) ascending process of astragalus fits between the tibia and fibula; (p) metatarsals II-IV are closely bunched as a unit; (q) metatarsals II-IV are elongated and the foot is functionally tridactyl.

16. *Dinosauria*: (a) three or more sacral vertebrae (parallelism in *Postosuchus* and *Ornithosuchidae*); (b) scapula is long and strap-like, without an expanded tip; (c) glenoid faces fully backwards; (d) deltopectoral crest is low and runs one-third or one-half of the way down the shaft; (e) acetabulum is fully open (not just a slit); (f) proximal head of femur is fully offset, with a distinct neck and ball; (g) femur is shorter than the tibia (parallelism in *Crocodylomorpha*); (h) fibula is greatly reduced; (i) ascending process of astragalus is well developed.

Appendix 2

Synapomorphies used in the analysis of crocodylomorph phylogeny.

1. Crocodylomorpha: (a) squamosal broadly overhangs quadrate laterally; (b) postfrontal absent; (c) post-temporal fenestra small or absent (poorly known in *Saltoposuchus*), (d) prootic does not broadly contact anterior surface of paroccipital process (unknown for *Pseudhesperosuchus*); (e) proximal carpals elongated (unknown for *Sphenosuchus*); (f) primary contact of quadrate head with prootic (Walker 1972); (g) pneumatic space in body of basisphenoid (unknown for *Pseudhesperosuchus*, *Saltoposuchus*); (h) mastoid antrum enters into prootic (unknown for *Pseudhesperosuchus*, *Saltoposuchus*); (i) pedal digit IV with four phalanges (unknown for *Pseudhesperosuchus*, *Sphenosuchus*, *Dibothrosuchus*); synapomorphies found also in poposaurids—(aa) quadratojugal reaches dorsally to postorbital, descending process of squamosal concomitantly reduced; (bb) parietal relatively narrow on occiput, squamosal relatively wide; (cc) maxillae form secondary palate (with vomer). Other possible synapomorphies (vary with optimization procedure)—(1) jugal does not form posterior border of antorbital fenestra (forms border in *Gracilisuchus* but not in other suchians); (2) quadrate foramen absent between quadrate and quadratojugal (poorly preserved in 'sphenosuchians', absent in crocodyliforms). A subcapsular process on the otoccipital may also be a crocodylomorph synapomorphy (Walker 1972), but the conditions in *Postosuchus* and *Pseudhesperosuchus* are not known. A posteroventral process is found in the coracoid of all crocodylomorphs, but the 'sphenosuchian' condition differs from that of other crocodylomorphs and is not unquestionably homologous (Crush 1984).

2. Unnamed Group A: (a) antorbital fenestra relatively small, about as tall as long; (b) parietals fused. Another possible synapomorphy—maxillary secondary palate without vomer contribution (unknown for *Pseudhesperosuchus*, and uncertain for *Saltoposuchus*).

3. Unnamed Group B: (a) lateral edge of squamosal with groove; (b) dorsal osteoderms rectangular in shape; another possible synapomorphy—great anterior extent of quadrate beneath squamosal.

4. Crocodyliformes: (a) otoccipital contacts ventromedial part of quadrate to enclose carotid artery and form passage for cranial nerves IX-XI; (b) basisphenoid rostrum (cultriform process) dorsoventrally expanded (primitive condition known only for *Sphenosuchus* among outgroups); (c) basiptyergoid processes reduced, basiptyergoid joint closed suturally; (d) pterygoid extends dorsally to form ventrolateral edge of trigeminal foramen; (e) otoccipitals broadly meet dorsal to foramen magnum (paralleled in some ornithischians); (f) eustachian tubes enclosed between basioccipital and basisphenoid (paralleled in

birds); (g) antorbital fenestra much smaller than orbit (paralleled in several archosaurs); (h) premaxilla and maxilla sutured together along butt joint (paralleled in several archosaurs); (i) parietal lacks broad occipital portion (reversal of suchian character); (j) ventromedial end of coracoid anteroposteriorly expanded, anterior edge concave; (k) quadrate hollow, with several fenestrae in dorsal surface (absent in longirostrine crocodyliforms); (l) mastoid antrum extends through supraoccipital (absent in most longirostrine crocodyliforms); (m) two large palpebrals are present (modified in most later forms); (n) dorsal head of quadrate contacts laterosphenoid (absent in thalattosuchians); (o) 'skull table' in temporal region with nearly flat dorsal surface (absent in thalattosuchians); (p) postorbital lies medial to jugal on postorbital bar (opposite relations in thalattosuchians); (q) scapula broadens dramatically dorsal (modified within thalattosuchians and in eusuchians); other possible synapomorphies — (1) quadratojugal very broad (present in poposaurs but poorly known in 'sphenosuchians'); (2) maxilla shorter than jugal (polarity of character depends upon position of *Eopneumatosuchus*, with presumably elongated rostrum); (3) fifth pedal digit lacks phalanges (unknown for outgroups except *Saltoposuchus*); (4) pubis at least partially excluded from acetabulum by a distinct anterior process of ischium (unknown for outgroups except *Saltoposuchus*); (5) tail surrounded by osteoderms (unknown for outgroups except *Saltoposuchus*).

5. Unnamed Group C: (a) ventrolateral contact of otoccipital with quadrate relatively broad (Busbey and Gow 1984); (b) squamosal relatively thick; another possible synapomorphy — vomer transversely broad, not rod-like (not known for *Gobiosuchus*).

6. Unnamed Group D: (a) rostrum relatively broad, broadens gradually posteriorly; (b) palatal part of premaxillae meet posteriorly (reversed in *Fruita* form); (c) notch between premaxilla and maxilla closed (reversed in *Fruita* form).

7. *Mesoeucrocodylia*: (a) secondary palate composed of maxillary and palatine; (b) pterygoids fused posterior to choana (varies in some living crocodylians); (c) canal for cranial nerves IX–XI situated well within otoccipital; (d) cranio-quadrateg canal (for tempero-orbital vein, seventh cranial nerve) enclosed by quadrate, otoccipital, and squamosal; (e) anterior process of ilium small; other possible synapomorphies — (1) pubis completely excluded from acetabulum (not known for *Gobiosuchus*); (2) pterygoid completely surrounds bottom of trigeminal foramen (unknown for *Gobiosuchus*, *Orthosuchus*); (3) complete fusion of exoccipital and opisthotic (unknown for *Gobiosuchus*, *Orthosuchus*); (4) reduction in size of subcapsular process (unknown for *Gobiosuchus*, *Orthosuchus*).

8. *Metasuchia*: (a) exposure of basisphenoid on ventral surface of braincase shorter than basioccipital; (b) frontals fused (paralleled

within Thalattosuchia); (c) anterior process of ilium nearly absent; (d) ventrolateral part of otoccipital greatly reduced in size; (e) cranioquadrate canal bordered by very broad contact of squamosal, quadrate, and otoccipital; (f) pterygoid strongly sutured to quadrate; (g) surangular arched dorsally (paralleled in protosuchids, reversed in Group H); (h) maxilla with single wave of enlarged teeth (absent in *Notosuchus*, which has specialized dentition); (i) palatines meet along midline total length without diverging posteriorly (paralleled within Thalattosuchia).

9. Unnamed Group E: (a) anterior part of jugal relatively broad; (b) postorbital bar relatively robust, unsculpted; (c) prefrontal pillar meets palate (paralleled in *Pseudhesperosuchus*, *Dibothrosuchus*, and *Gobiosuchus*); another possible synapomorphy — foramina for nerve IX and nerves X–XI separate in otoccipital (paralleled within Thalattosuchia, unknown for *Fruita* form).

10. Unnamed Group F: (a) fenestrae in quadrate reduced in number; (b) posterior edge of quadrate strongly concave dorsal to otoccipital contact (Hecht and Tarsitano 1983); (c) reduction of antorbital fenestra to tiny hole (reversed in *Araripesuchus*; fenestra completely absent in *Baurusuchus* and *Sebecus*, possibly absent in *Libycosuchus*).

11. *Sebecosuchia*: (a) teeth laterally compressed and serrated; (b) rostrum high and narrow; (c) extremely large choana.

12. Unnamed Group G: (a) premaxillae subvertical; (b) postorbital bar inset and columnar; other possible synapomorphies — (1) loss of broad transverse flange at top of prefrontal (unknown for 'notosuchians'); (2) prefrontal pillar contact with palatine robust (unknown for *Sebecus*).

13. Unnamed Group H: (a) quadratojugal narrows dorsally; (b) single palpebral ossification (presence of two in *Goniopholis* (*Nanosuchus gracilidens* uncertain)); (c) postorbital without broad anterolateral edge; (d) premaxillary teeth homodont (paralleled in thalattosuchians).

14. *Neosuchia*: (a) maxilla and dentary with two sinusoidal waves of enlarged teeth; (b) maxilla subvertical; (c) retroarticular process narrow, posteriorly directed; other possible synapomorphies — (1) vascular foramen within postorbital (unknown for *Sebecus*); (2) neural spines of posterior cervical vertebrae anteroposteriorly narrow (unknown for *Sebecus*, *Araripesuchus*).

15. Unnamed Group I: (a) basisphenoid virtually unexposed on ventral surface of skull (paralleled in *Libycosuchus*); (b) nasals do not contact narial border (paralleled in thalattosuchians, reversed in some eusuchians); (c) nares confluent (paralleled in thalattosuchians, reversed in some crocodylians); (d) premaxillae expanded anterior to nares (reversed in primitive alligatorines).

16. Unnamed Group J: (a) osteoderms in more than two longitudinal

rows; (b) osteoderms do not overlap; another possible synapomorphy — biconvex first caudal vertebra (unknown for outgroups down to *Fruita* form).

17. Unnamed Group K: (a) choana nearly within pterygoid (paralleled in at least some dyrosaurs); (b) procoelous vertebrae (paralleled in *Fruita* form, some vertebrae of *Theriosuchus*).

18. Eusuchia: (a) choana entirely within pterygoid; other possible synapomorphies — (1) posterior cervical vertebrae with well-developed hypapophyses (unknown for *Hylaeochampsia*, *Shamosuchus*); (2) condyles on first caudal vertebra well developed (unknown for Glen Rose form, *Stomatosuchus*, *Shamosuchus*); (3) atlas intercentrum elongated (unknown for Glen Rose form, *Stomatosuchus*, *Hylaeochampsia*; reversed in crocodylids).

19. Crocodylia: (a) scapula with nearly horizontal anterior and posterior edges (paralleled within *Thalattosuchia*; variable in some crocodylians).

20. Features considered to be correlated with longirostry: (a) nasals do not reach nares; (b) nares confluent; (c) nasals do not reach premaxillae; (d) supratemporal fenestrae larger than orbits; (e) basioccipital tubera large; (f) jugal reduced to a rod beneath lateral temporal fenestra; (g) mandibular symphysis elongated; (h) teeth homodont; (i) teeth conical; (j) lateral edge of maxilla straight; (k) premaxilla/maxilla contact without indentation.