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Rauisuchian archosaurs (Reptilia, Diapsida): An overview

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With 5 figures and 1 table

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Abstract: Current understanding of Rauisuchia is so poor that it is uncertain if taxa that are usually referred to the families Rauisuchidae, Prestosuchidae, Poposauridae, or Chatterjeeidae together represent a mono-, para-, or even polyphyletic assemblage. Rauisuchian distribution, osteology, taxonomy, phylogeny, and evolutionary patterns are reviewed. Problems in understanding seem to have been caused by the fragmentary nature of many of the fossils, their widespread distribution, confused alpha taxonomy, and insufficient 'primary' research. Recent work by several researchers on new and old specimens suggests that understanding of rauisuchian morphology, systematics, and evolution will improve, even in the short term.

Zusammenfassung: Rauisuchier (im Sinne dieser Studie) sind eine wichtige und diverse Gruppe triassischer basaler Archosaurier, die eine nahezu weltweite Verbreitung erreichte und möglicherweise einige der nächsten Verwandten der Crocodylomorpha enthält. Die gegenwärtige Kenntnis der Rauisuchier ist so gering, daß es als unsicher gelten muß, ob Taxa, die für gewöhnlich den Familien Rauisuchidae, Prestosuchidae, Poposauridae und Chatterjeeidae zugeordnet werden, eine mono-, para- oder polyphyletische Gruppe bilden. Eine historische Übersicht der Rauisuchier-Systematik wird gegeben und der momentane Kenntnisstand bezüglich Verbreitung, Osteologie, Alphataxonomie, Phylogenie und evolutionärer Zusammenhänge wird diskutiert. Es zeigt sich, daß die Probleme beim Verständnis der Rauisuchier ihre Gründe in der fragmentarischen Erhaltung vieler Exemplare, ihrer weiten geographischen Verbreitung, undurchsichtiger Alphataxionomie und ungenügender 'primärer' Bearbeitung des Fossilmaterials haben dürften. Die grundlegende Dokumentation der Morphologie der Rauisuchier, die Lösung alphataxonomischer Probleme und eine Fortführung und Erweiterung expliziter phylogenetischer Analysen, die detaillierte Diskussionen der zugrundegelegten Merkmale beinhalten, bieten sich als erfolgversprechende Felder zukünftiger Forschung an. Das bislang

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unausgeschöpfte Potential der bekannten Rauisuchierfunde, das Vorhandensein unbeschriebenen neuen Materials, die Entstehung eines phylogenetischen Rahmens für basale Archosaurier und das neugewonnene Interesse an der 'primären' Erforschung der Rauisuchier lassen hoffen, daß das Verständnis der Morphologie, Systematik und Evolution der Rauisuchier in absehbarer Zeit sehr vertieft werden kann.

Introduction

Viewing archosaur evolution with emphasis on the Recent members of the group highlights a major divergence of the archosaur crown group into two main lineages, one leading to crocodilians and the other to birds (Fig. 1). Over the last decade or so, consensus has emerged on the components of these two major lineages and, to some extent, on the interrelationships of the taxa that they encompass (GOWER & WILKINSON 1996). The crocodilian-line (= Crurotarsi SERENO & ARCUCCI 1990) is currently understood to be composed of several important clades (SERENO & ARCUCCI 1990, SERENO 1991, PARRISH 1993, JUUL 1994): Crocodylomorpha (Crocodyliformes and Sphenosuchia), Aetosauria, Parasuchia, Ornithosuchidae, and the (possibly non-monophyletic) group that is the focus of this overview, the Rauisuchia.

The aim of this article is to review historical research into rauisuchians and to summarise current knowledge of their distribution, morphology, and systematics. The last such review of rauisuchians (KREBS 1976) was carried out before the description of the majority of currently known taxa, before poposaurids were considered to be rauisuchians, and prior to the introduction of an explicit methodology in studies of archosaur phylogeny. Past developments in the understanding of this important, but far from well understood group, to some extent exemplify progress and resistance in the history of research into other extinct members of the Archosauria, and therefore should be of wider interest. In addition to a review, this article also aims to forward some potentially fruitful topics and approaches for future research on rauisuchians.

Terminology

Archosauria is here employed in terms of its traditional extent (see JUUL 1994) rather than the crown-group concept advocated by GAUTHIER (1986). Archosaurians *sensu* GAUTHIER are referred to as 'crown-group archosaurs'.

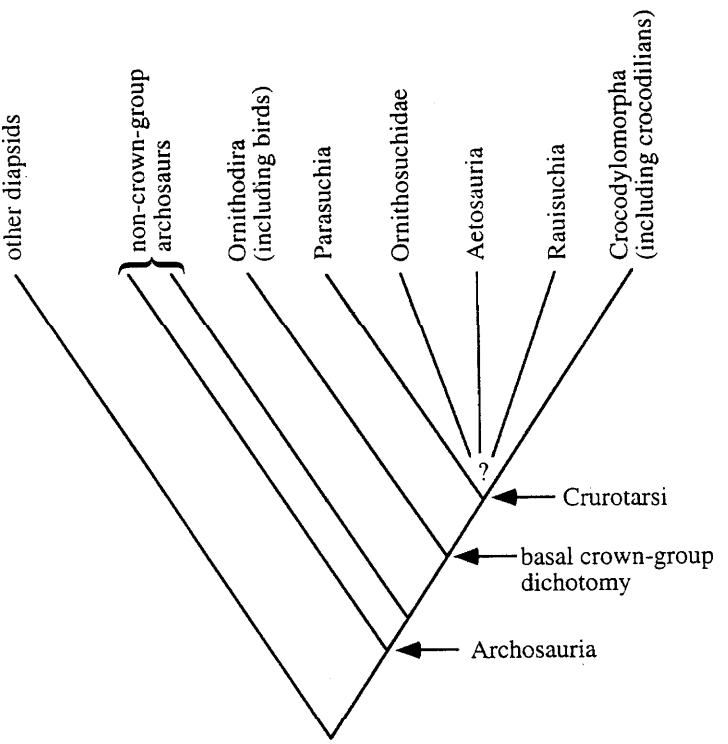

Fig. 1. Framework consensus phylogeny for basal archosaurs. Resolution is less than that shown in GOWER & WILKINSON (1996) because several lower-level taxa have been excluded, and because the possibly non-monophyletic Rauisuchia has not been divided into constituent taxa.

Rauisuchia BONAPARTE 1982 is used in a sense compatible with the studies by CHATTERJEE (1985), GALTON (1985), and LONG & MURRY (1995) - that is, a group composed of all of the taxa that might be referred to the families Rauisuchidae HUENE 1942, Prestosuchidae ROMER 1966, Poposauridae NOPCSA 1928, or Chatterjeeidae LONG & MURRY 1995. This meaning is employed irrespective of whether Rauisuchia or any of the families it includes are monophyletic or not. This is far from ideal, but lack of current consensus on the interrelationships of the genera commonly considered to be

rauisuchians is preventing a more phylogenetically-meaningful, stable, and useful definition of the taxon from being formulated. PARRISH (1993) used Rauisuchia in a different sense, referring to the clade hypothesized by him to incorporate Rauisuchidae (*sensu* PARRISH) + Paracrocodylomorpha (Crocodylomorpha + Poposauridae sensu PARRISH) + *Gracilisuchus stipanicicorum*. The validity, definition, and composition of Poposauridae, Rauisuchidae and Prestosuchidae is currently unclear, so that in this paper these terms will be avoided, or attempts will be made to clarify their employed meanings.

A brief history of rauisuchian research

Although MEYER (1861) and MEHL (1915) described specimens that have subsequently been referred to the Rauisuchia, the group can perhaps be considered to have been first recognized by HUENE (1942), when he described several new fossil reptiles (including *Rauisuchus tiradentes, Prestosuchus chiniquensis* and *P. loricatus*) from the Middle Triassic of Brazil. In earlier accounts, HUENE (1936a, 1936b, 1938a, 1938b) had mentioned the existence of this material and described a taxon (*Stagonosuchus nyassicus*) that has subsequently been identified as a rauisuchian. HUENE considered these forms to lie within a family composed chiefly of what are now recognized as aetosaurians, and it was not until after the discovery and description of *Saurosuchus galilei* REIG 1959 and *Ticinosuchus ferox* KREBS 1965, that REIG (1961) and KREBS (1965) proposed that rauisuchians were a widespread and distinct group of Triassic archosaurians whose affinities certainly lay more with "pseudosuchians" (an assemblage that includes the closest fossil relatives of crocodilians) than with earlier, non-crown-group archosaurs ("proterosuchians" as had been suggested by HUGHES (1963) and, in part, ROMER (1966). KREBS (1963, 1973) further described the structure of the tarsus in *Ticinosuchus ferox* and *Rauisuchus tiradentes* and demonstrated that a structurally complex, rotary ankle joint homologous with that of crocodilians was readily identifiable in these taxa and in some other groups of extinct archosaurs. This key observation helped

Tab. 1. Summary of taxa most commonly referred to Rauisuchia, listed by order of naming. This list is not comprehensive and inclusion is subjective. It excludes some taxa of questionable taxonomic validity and taxa only rarely referred to Rauisuchia, including *Arizonasaurus* WELLES 1947, *Dongusia* HUENE 1940, "*Mandasuchus*" CHARIG 1956, *Sinosaurus* YOUNG 1948, *Spondylosoma* HUENE 1942, *Wangisuchus*

YOUNG 1974, *Youngosuchus sinensis* (= *Vjushkovia sinensis* YOUNG 1973) SENNIKOV, in KALANDADZE & SENNIKOV 1985, *Zanclodon* PLIENINGER 1846. *Lotosaurus* is included even though only PARRISH (1993) has referred it to Rauisuchia.

TAXON	AUTHOR	HORIZON	AGE	LOCATION
Teratosaurus suevicus	V. MEYER 1861	Stubensandstein	Norian	S Germany
Poposaurus gracilis	MEHL 1915	Popo Agie Fm.+	mid-late Carnian to early Norian	SW USA
Stagonosuchus nyassicus	HUENE 1938b	Manda Fm.	Anisian	Tanzania
Rauisuchus tiradentes	HUENE 1942	Santa Maria Fm.	mid-late Carnian	S Brazil
Prestosuchus chiniquensis	HUENE 1942	Santa Maria Fm.	mid-late Carnian	S Brazil
Prestosuchus loricatus	HUENE 1942	Santa Maria Fm.	mid-late Carnian	S Brazil
Procerosuchus celer	HUENE 1942	Santa Maria Fm.	mid-late Carnian	S Brazil
Hoplitosuchus raui	HUENE 1942	Santa Maria Fm.	mid-late Carnian	S Brazil
Saurosuchus galilei	REIG 1959	Ischigualasto Fm.	Carnian	NW Argentina
Fenhosuchus cristatus	YOUNG 1964	Upper Ehrmaying Fm.	Middle Triassic	China
Ticinosuchus ferox	KREBS 1965	Grenzbitumenhorizont and equivalent	Anisian/Ladinian	Switzerland, N Italy
Luperosuchus fractus	ROMER 1971	Los Chañares Fm.	Ladinian	NW Argentina
Lotosaurus adentus	ZHANG 1975	Batung Fm.	Middle Triassic	China
Fasolasuchus tenax	BONAPARTE 1978	U. Los Colorados Fm.	late Norian	NW Argentina
Heptasuchus clarki	DAWLEY, ZAWISKIE & COSGRIFF 1979	Popo Agie Fm.	mid-late Carnian	Wyoming, USA
Unnamed taxon	DUTUIT 1979	Argana Fm.	mid-late Carnian	Morocco
Vjushkovisaurus berdjanensis	OCHEV 1982	Donguz Svita	Anisian - early Ladinian	European Russia
Bromsgroveia walkeri	GALTON 1985	Bromsgrove Sandst. Fm.	Anisian	England
Postosuchus kirkpatricki	CHATTERJEE 1985	Dockum Group +	mid Carnian - Norian	SW USA
Jushatyria vjushkovi	SENNIKOV, in KALANDADZE & SENNIKOV 1985	Bukobay Svita	mid-late Ladinian	European Russia
Energosuchus garjainovi	OCHEV 1986	Bukobay Svita	mid-late Ladinian	European Russia
Tikisuchus romeri	CHATTERJEE & MAJUMDAR 1987	Tiki Fm.	Carnian	Central India
Vytshegdosuchus zheshartensis	SENNIKOV 1988	U. Yarenga Gorizont	late Olenekian	European Russia
Dongusuchus efremovi	SENNIKOV 1988	Donguz Svita	Anisian - early Ladinian	European Russia
Tsylmosuchus jakovlevi	SENNIKOV 1990	U. Vetluga Super-Gorizont	Olenekian	European Russia
Tsylmosuchus samariensis	SENNIKOV 1990	U. Vetluga Super-Gorizont	Olenekian	European Russia
Tsylmosuchus donensis	SENNIKOV 1990	Yarenga Gorizont	Olenekian	European Russia
Jaikosuchus magnus	SENNIKOV 1990	Yarenga Gorizont	Olenekian	European Russia
Lythrosuchus langstoni	LONG & MURRY 1995	Dockum Group	? mid Carnian	Texas, USA
Chatterjeea elegans	LONG & MURRY 1995	Dockum Group	early/mid Carnian - early Norian	SW USA
Sillosuchus longicervix	ALCOBER & PARRISH 1997	Ischigualasto Fm.	Carnian	NW Argentina
Batrachotomus kupferzellensis (Kupferzell taxon)	GOWER 1999 (WILD 1980)	Lettenkeuper	late Ladinian	S Germany

to prompt later efforts (e.g. CRUICKSHANK 1979, THULBORN 1980, 1982, BRINKMAN 1981, CHATTERJEE 1982, CRUICKSHANK & BENTON 1985) to estimate archosaur phylogeny with evidence exclusively from tarsal structure and mechanics. More recently, explicit phylogenetic analyses based not only on tarsal characters or ankle types (SERENO & ARCUCCI 1990, SERENO 1991, PARRISH 1993, JUUL 1994) have provided further support for KREBS' hypothesis that a crocodilian-like ankle joint is the most distinctive synapomorphy of a major clade within the archosaur crown group.

Since the work of REIG (1961) and KREBS (1965), several new rauisuchian specimens and taxa have been described from North and South America, North Africa, Europe (including western Russia), and India (Tab. 1). In association with the creation of these new taxa and description of material, the understanding of rauisuchian systematics has continued to fluctuate markedly, with stability proving to be elusive. A list of previous classifications of rauisuchians is presented in the Appendix.

Classifications of archosaurs persisted with the understanding that rauisuchians comprised a single suprageneric group (Rauisuchidae) until CHATTERJEE (1985) described *Postosuchus kirkpatricki* from the Upper Triassic of Texas. CHATTERJEE recognized affinities between his new species and known "rauisuchids", but also argued that it was ancestral to carnosaurian theropod dinosaurs. He classified *Postosuchus kirkpatricki* in the Poposauridae with *Poposaurus gracilis* - a form previously often considered to be a dinosaur (see COLBERT 1961), but recognized by GALTON (1977) to represent a "pseudosuchian". In CHATTERJEE's scheme, Rauisuchia therefore comprised two families, Rauisuchidae and Poposauridae. In 1985, GALTON referred additional material to *Teratosaurus suevicus* and recognized it as a rauisuchian (as did BENTON 1986a), described *Bromsgroveia walkeri*, and supported CHATTERJEE's classification.

A further distinct phase in the history of rauisuchian systematics can be perceived to have been instigated by GAUTHIER's (1986) landmark depiction of the relationships of an assumed monophyletic Rauisuchia to other basal

Fig. 2. Hypotheses of the phylogeny of crurotarsans, including rauisuchians. **A,** redrawn from BENTON & CLARK (1988). **B,** redrawn from SERENO (1991), indicating the stated uncertain position of *Prestosuchus chiniquensis* in relation to Suchia, based on the skull described by BARBERENA (1978). **C,** redrawn from PARRISH (1993). **D,** redrawn from JUUL (1994). **E,** based on text in ALCOBER & PARRISH (1997). Pop = Poposauridae; Prest = Prestosuchidae; Rau = Rauisuchidae in the sense used in those studies represented here.

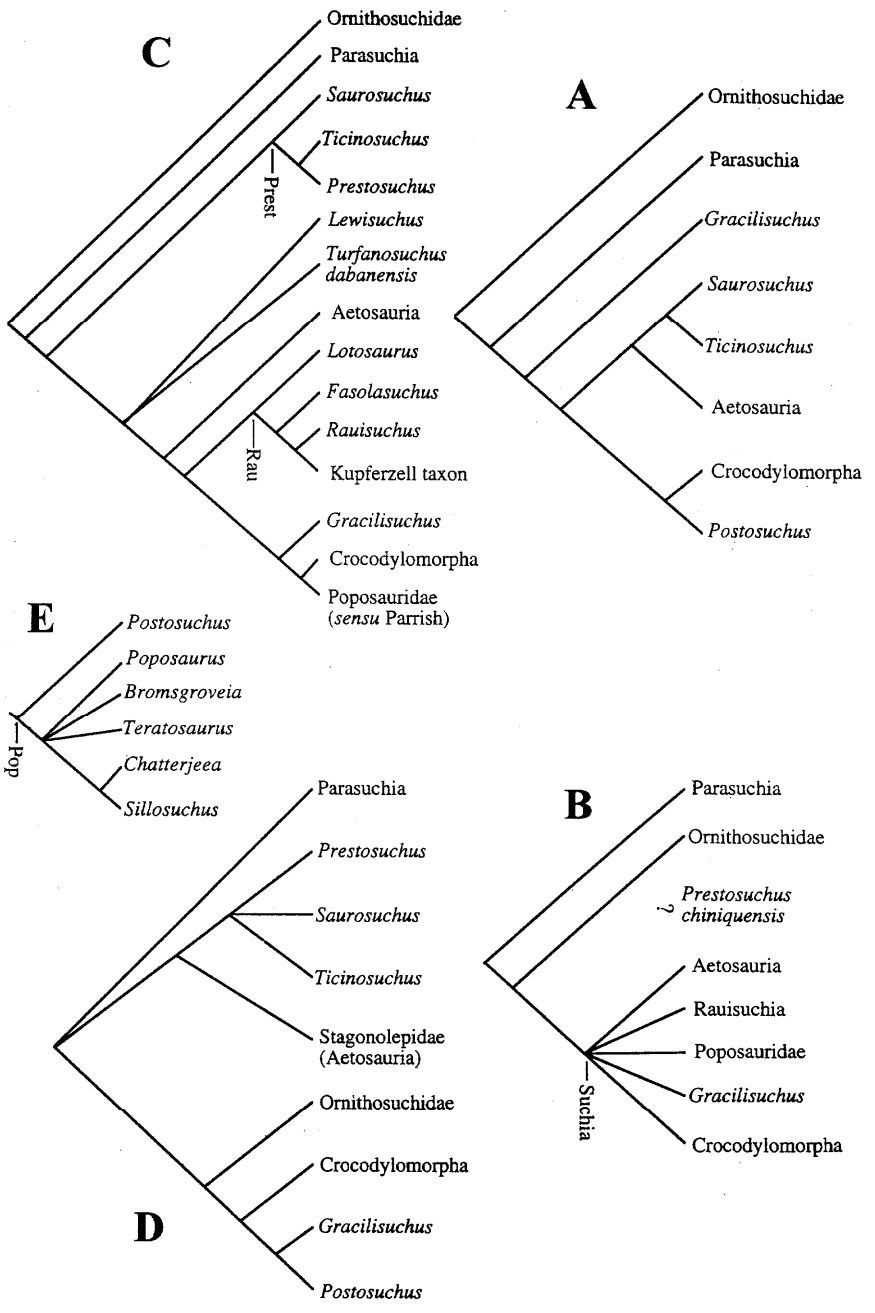

Fig. 2 (Legend see p. 452)

archosaurs in a cladogram, with nodes supported by lists of derived characters. Prior to GAUTHIER's study, there had been growing certainty expressed for the view that rauisuchians descended directly from non-crown-group archosaurs (e.g. REIG 1970), or more specifically the erythrosuchids (e.g. ROMER 1972, SILL 1974, BONAPARTE 1981). It had also been suggested that rauisuchians were ancestral to other groups of archosaurs e.g. sauropodomorph dinosaurs (CHARIG, in APPLEBY et al. 1967) or theropods (CHATTERJEE 1985). GAUTHIER, however, presented evidence indicating that erythrosuchids lie outside the archosaur crown group, while rauisuchians are within it, as part of the crocodilian rather than dinosaurian/bird lineage of the basal crown-group dichotomy. A further cladistic study followed GAUTHIER's analysis, in which BENTON & CLARK (1988) employed "rauisuchids" (represented by *Prestosuchus* and *Ticinosuchus*) and "poposaurids" (represented by *Postosuchus*) as distinct terminal taxa, and Rauisuchia was hypothesized to be polyphyletic, with "poposaurids" being more closely related to crocodylomorphs than to it rauisuchids". Since GAUTHIER's (1986) and BENTON & CLARK's (1988) studies, a more explicit approach has been taken to cladistic studies of archosaur phylogeny, with characters, data, and criteria for hypothesis choice being clearly presented (GOWER & WILKINSON 1996). The hypotheses forwarded by these studies are shown in Figure 2. The studies by PARRISH (1993) and JUUL (1994) have supported BENTON & CLARK's (1988) hypothesis that Rauisuchia is not monophyletic, and all cladistic studies to date have supported the hypothesis that rauisuchians group with the crocodilian lineage of the basal dichotomy of the archosaur crown group - therefore not having an especially close relationships with erythrosuchids or dinosaurs. Despite this agreement, some shortcomings in stability and robustness are present in the most recent analyses. For example, PARRISH (1993) has presented the only explicit analysis to include more than one sub-familial rauisuchian taxon, and he hypothesized that rauisuchians comprise a polyphyletic assemblage composed of three distinct families (his Rauisuchidae, Prestosuchidae, and Poposauridae), no two of which are sister taxa, but this study contains a number of problematical character definitions and codings, and discrepancies between text and data matrix (e.g. JUUL 1994, (LONG & MURRY 1995, GOWER 1996) that need to be reconsidered. Reconsideration is especially important in this case because several clades in PARRISH's hypothesis have low statistical support (GOWER & WILKINSON 1996). Additionally, the taxon used as an exemplar of the Poposauridae in all cladistic studies to date (*Postosuchus kirkpatricki* as conceived by CHATTERJEE 1985) has been claimed by LONG & MURRY (1995) to be based on a composite of three distinct rauisuchian taxa, with the single poposaurid component (*Lythrosuchus langstoni,* LONG & MURRY 1995) being represented by only a very small amount of the material originally described by CHATTERJEE (see

also MURRY & LONG 1989). LONG & MURRY (1995) also presented a new classification of rauisuchians, which recognizes the Rauisuchia as a group of similar composition and extent to the concept proposed by CHATTERJEE (1985) and GALTON (1985). This classification perhaps implies that Rauisuchia should be, contra BENTON & CLARK (1988), PARRISH (1987, 1993), and JUUL (1994), considered a monophylum, but LONG & MURRY (1995: 117) also suggested that it "is not inconceivable that the Rauisuchia are paraphyletic". LONG & MURRY made some phylogenetic statements in their study e.g. "the Chatterjeeidae were probably derived from the Poposauridae" (p. 153), but the relationship between their classification and any hypothesis of phylogeny remains ambiguous because of the absence of an explicit phylogenetic analysis (BENTON & GOWER 1997), or a fully detailed justification for their rejection of PARRISH's hypothesis (ALCOBER & PARRISH 1997). SENNIKOV (1995) has also presented a recent classification of basal archosaurs that incorporates the many Russian taxa that have been largely ignored by Western researchers, presumably because of their fragmentary and taxonomically problematic nature. SENNIKOV identifies two families within Rauisuchia, the "Rauisuchidae" and "Poposauridae", although, as with LONG & MURRY's scheme, this classification is not based on an explicit analysis of phylogeny.

In summary, while estimates of basal archosaur phylogeny have recently reached several points of consensus (GOWER & WILKINSON 1996), confusion and uncertainty in rauisuchian systematics is perhaps at its zenith. The validity of Rauisuchia, Rauisuchidae, Prestosuchidae, and Poposauridae as natural groups is unresolved.

What are rauisuchians?

In attempting to answer this question, some of the most significant gaps in current knowledge of the group become apparent. As outlined above, there is no current consensus on which taxa compose the Rauisuchia or how this taxon should be defined. It is difficult to define a group that might be para- or even polyphyletic, and uncertainty about the validity of the Rauisuchia as a natural group means that it is currently impractical to do much more than list a few characters that are present in members of the group - characters that might be synapomorphies of at least a subset of rauisuchians should the group form a clade. KREBS (1976) presented a diagnosis of the Rauisuchidae at a time before poposaurids were classified as rauisuchians. He listed several general characters including relatively long skull and hindlimbs, but features such as accessory processes on the caudal neural spines are more likely to be derived and might define at least a subset of rauisuchians. LONG & MURRY (1995: 117) listed "synapomorphies" in their diagnosis of their

Rauisuchia, but some of the features they list have either a wider distribution (e.g. "posteriorly-directed calcaneal tuber") or are not present in all the taxa they list as rauisuchians (e.g. "accessory slit-like antorbital fenestra").

While diagnoses are tricky, it is clear that rauisuchians are extinct, Triassic crurotarsan archosaurs with a well-defined rotary joint between astragalus and calcaneum very similar to that seen in crocodilians, and paired, paramedian dorsal osteoderms along the presacral vertebral column. Perhaps the most distinctive derived rauisuchian feature is the presence of a thickening, a ridge, or rugosity on the anterolateral surface of the ilium, immediately above the acetabulum (discussed in more detail below). Other clearly derived features that appear to be widespread, but possibly not universal, within the group are the presence of an opening in the dermatocranium between the naris and antorbital fenestra, more than two vertebrae in the sacrum, and strongly downturned sacral ribs and acetabula. Because Rauisuchia in the sense used here might not be a monophylum, some of these features might not be homologous across all members of the group, or might be present in other groups.

Why are rauisuchians of interest?

It is easier to provide a positive answer to this question. Rauisuchians represent a significant component of the Archosauria, and they are therefore clearly of interest if a comprehensive understanding is to be achieved of the vast radiation that archosaurs underwent in the early Mesozoic. GOWER & WILKINSON (1996) have highlighted disagreement among hypotheses of the relationships of rauisuchians to other crocodilian-line archosaurs as one of the most conspicuous areas of the archosaur evolutionary tree for which there is not a current consensus. Resolving this situation is one of the most pressing requirements for completing a framework of basal archosaur relationships. Disagreement on the phylogenetic relationships of various rauisuchian taxa within Crurotarsi is part of the reason that there is no current consensus on which taxon is most closely related to Crocodylomorpha - some/all rauisuchians, isolated species such as *Gracilisuchus stipanicicorum*, or perhaps other major clades such as the aetosaurians. Further understanding of the origin of the distinctive morphology of crocodylomorphs (including crocodilians, which have modern representatives), therefore depends upon resolution of this part of the archosaur tree and an improved understanding of rauisuchian morphology.

It has long been recognized that important faunal changes occurred during the Triassic and early Jurassic, when most of the Recent major groups of terrestrial vertebrates and the dinosaurs and pterosaurs first appeared (e.g.

PADIAN 1986, FRASER & SUES 1994a). In particular, BENTON (1983, 1986b, 1986c, 1991, 1993a) has suggested that a major ecosystem collapse occurred in the Late Carnian, when the dominant herbivores, dicynodonts, chiniquodontids, and rhynchosaurs, died out. Over the following 10 My, dinosaurs radiated dramatically and took over herbivore niches. Through this time of upheaval, rauisuchians continued as top carnivores worldwide, probably preying first on the therapsids and rhynchosaurs, and then on the early herbivorous dinosaurs of the Norian. Rauisuchians apparently disappeared at the end of the Triassic, and the first large theropods evolved to replace them in the earliest Jurassic. Improved understanding of rauisuchians will enhance understanding of the timing of these key events in vertebrate history and will allow hypotheses about their causes to be tested.

Finally, PARRISH (1993) has hypothesized that the morphologically divergent crufotarsan archosaur, *Lotosaurus adentus*, from the Middle Triassic Batung Formation of China is a member of a monophyletic subset of rauisuchians (= PARRISH's Rauisuchidae). *L. adentus* is edentulous and possibly herbivorous, and therefore might represent one of the earliest instances of herbivory within Archosauria, a group in which a great diversity of herbivorous forms eventually evolved. If the interpretation forwarded by PARRISH is correct, then the morphological diversity of the Rauisuchia was perhaps greater than that of other major taxa of basal crurotarsan archosaurs of the early Mesozoic.

Distribution

Knowledge of rauisuchian distribution depends on the delimitation of Rauisuchia, for which there is no current agreement. It is possible, however, to review the geographical and stratigraphical occurrences of those taxa currently considered to be rauisuchians. Rauisuchians are restricted to the Triassic, and have been recorded from every continent except Australia and Antarctica, including North (USA) and South America (Argentina and Brazil), Africa (Tanzania), Europe (including Russia), and Asia (China and India). A summary of the temporal and spatial occurrence of the most important taxa is given in Table 1.

Osteology

Some of the aspects of rauisuchian morphology that are of immediate interest and that highlight currently important issues in rauisuchian research are discussed below. These are the presence of additional openings in the anterior of the dermatocranium, and derived features of the sacrum, the ilium, and the rest of the pelvis.

Additional openings in the dermatocranium

In general, the osteology of the skull and mandible of rauisuchians is poorly known and cranial material has not even been discovered or documented for some groups, e.g. "Poposauridae" and "Chatterjeeidae" (sensu LONG & MURRY 1995). LONG & MURRY (1995: 162) speculated that the skull of *Shuvosaurus inexpectatus*, described by CHATTERJEE (1993) as an ornithomimosaur dinosaur, might belong with the postcranial material recognized by them as *Chatterjeea elegans*, but while this is an intriguing possibility, published evidence for this is currently no more than circumstantial. Issues concerning aspects of the detailed osteology of the rauisuchian skull can be illustrated with a brief discussion of the variably present additional opening in the dermatocranium between the naris and antorbital fenestra. Such an opening in rauisuchians (Fig. 3) has been referred to as a subnarial fenestra/foramen (e.g. CHATTERJEE 1985, GALTON 1985, PARRISH 1993) or extra/accessory antorbital fenestra (e.g. SILL 1974; DAWLEY et al. 1979, BENTON 1986A, LONG & MURRY 1995).

The presence of an extra opening has at various times been interpreted as phylogenetically significant for certain subsets of rauisuchians. For example, CHATTERJEE (1985: 444) listed it as a diagnostic character of his Rauisuchia, and this was followed by BENTON (1986a) and LONG & MURRY (1995). Additionally, it has been stated (e.g. BENTON 1986a, LONG & MURRY 1995) that the presence of an extra opening is associated with a movable joint between the premaxilla and maxilla, itself representing a further diagnostic character of rauisuchians. However, several recent research developments have introduced problems for any systematic interpretations. Firstly, phylogenetic hypotheses forwarded by some recent studies (BENTON & CLARK 1988, PARRISH 1993, JUUL 1994) imply that the presence of this additional opening is homoplastic because of the hypothesized non-monophyly of Rauisuchia. It has also been pointed out that, while these additional openings might be absent in certain rauisuchians, such as in the skull referred to *Prestosuchus chiniquensis* by BARBERENA (1978), they are present in a number of other non-crown-group and crown-group archosaurs. For example, the openings in rauisuchians have been compared with those in the erythrosuchid *Shansisuchus shansisuchus* (Fig. 3D; see PARRISH 1993) and a number of dinosaurs (see JUUL 1994). WELMAN (1998) has suggested that a second opening is present in even the-non-crown-group archosaur *Proterosuchus*. SERENO & NOVAS (1993) have described in *Herrerasaurus ischigualastensis* both a "subnarial foramen" and a "premaxilla-maxilla fenestra" (Fig. 3E), with the former opening below the naris and, internally, below the premaxillary palate, and the latter opening behind the naris and, internally, above the premaxillary palate. The same authors interpreted the premaxilla-

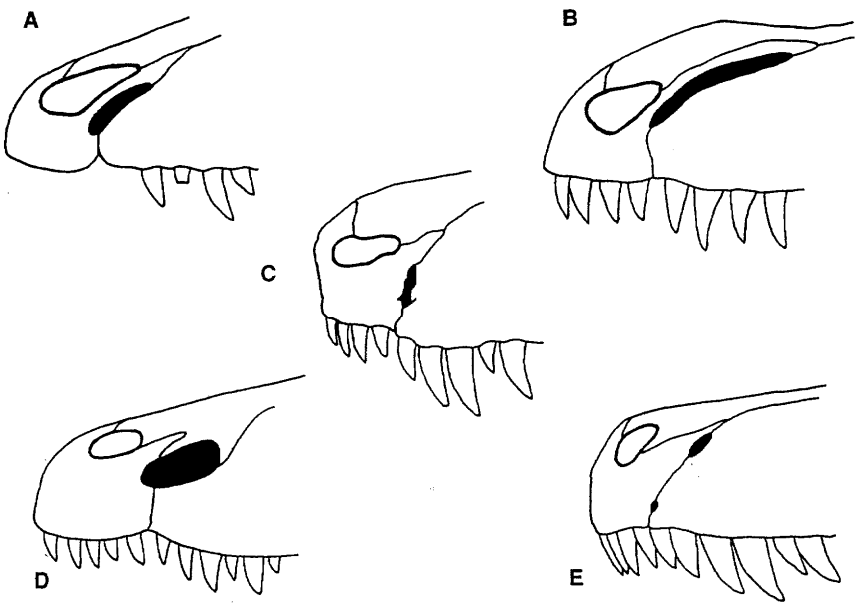

Fig. 3. Comparison of left lateral views of the skulls of various archosaurs, with additional cranial openings behind the naris shown in black. **A,** *Saurosuchus galilei* redrawn from PARRISH (1993: fig. 6D). **B,** *Luperosuchus fractus* redrawn from (ROMER 1971: fig. 3). **C,** *Postosuchus kirkpatricki* redrawn from LONG & MURRY (1995: fig. 123A). **D,** *Shansisuchus shansisuchus* after YOUNG (1964) and pers. obs.. **E,** *Herrerasaurus ischigualastensis* redrawn from SERENO & NOVAS (1993: fig. 8). SERENO & NOVAS (1993) identifed both a lower subnarial foramen and an upper premaxilla-maxilla fenestra posterior to the naris in *H. ischigualastensis*.

maxilla fenestra as an autapomorphy of *H. ischigualastensis*, and the subnarial foramen as a synapomorphy of *H. ischigualastensis* + saurischian dinosaurs that apparently evolved convergently in e.g. *Saurosuchus galilei*. Openings in this region of the skull of archosaurs are clearly in need of reassessment.

One of the first issues that needs to be addressed is a clarification of the detailed morphology of this region in various taxa. The mere presence of an

opening in this region across taxa has been mentioned as a phylogenetic character in a manner that suggests that similarity criteria have been satisfied to the extent that the primary homology of these openings can be accepted. Even within rauisuchians, however, there is a diversity of morphologies, as demonstrated by the long and narrow opening in *Saurosuchus galilei* (SILL 1974; Fig. 3A) and *Luperosuchusfractus* (ROMER 1971; Fig. 3B), the hourglass or keyhole-shaped opening in *Postosuchus kirkpatricki* (CHATTERJEE 1985, LONG & MURRY 1995; Fig. 3C), and the relatively much smaller foramen in the Kupferzell rauisuchian (PARRISH 1993: fig. 8, GOWER 1999). Superficially similar (and therefore potentially equivalent) openings in other archosaurian taxa can differ quite markedly again from these 'types', e.g. the large, rounded opening in *Shansisuchus shansisuchus* (YOUNG 1964) which incorporates the nasal into its border, and the entirely maxillary-bound maxillary and promaxillary fenestrae (WITMER 1997a) of some dinosaurs. Alternative character formulations (= hypotheses of homology) that make use of more detailed aspects of the relevant morphologies might provide better information on the taxonomic distribution, homology, phylogenetic informativeness, and evolution of additional openings in the dermatocrania of rauisuchians, and they should be investigated to that end. There has been little effort made to interpret the possible function of additional openings in this region of the archosaur skull, but specific hypotheses that it is associated with the craniofacial air sinus system (as is the main antorbital fenestra - see WITMER 1987, 1995, 1997a, 1997b), or blood vessel/nerve transmission, need to be formulated and tested. Future study of the detailed morphology of this region of the rauisuchian skull should also incorporate a reassessment of the possibility that a movable joint exists between the maxilla and premaxilla of certain taxa. A loose contact between premaxilla and maxilla does not necessarily mean that kinesis was actually realised in life, but if movement did occur between these elements then it might have been accommodated by some mobility elsewhere in the cranium.

Derived features of the sacrum

Some of the most distinctive aspects of what is currently known about rauisuchian osteology are represented by derived features of the sacrum. Chiefly, these are the incorporation of additional vertebrae into the sacrum and the strong ventral deflection of the articular faces of the sacral ribs for attachment to the ilia. Importantly, these features show variation within Rauisuchia and seem not to be universally present across the group. The plesiomorphic condition for crurotarsan archosaurs (e.g. as seen in parasuchians), is for two sacral vertebrae, and this is retained in at least some

rauisuchians, including *Stagonosuchus nyassicus* (HUENE 1938b; pers. obs.) and, apparently, *Ticinosuchus ferox* (KREBS 1963). A third sacral is present in e.g. *Teratosaurus suevicus* (GALTON 1985) and the Kupferzell taxon (GOWER 1997, 1999), while four or more have been reported for e.g. *Poposaurus gracilis* (LONG & MURRY 1995) and *Sillosuchus longicervix* (ALCOBER & PARRISH 1997). The homology of the incorporation of additional sacral vertebrae into the sacrum is uncertain within Rauisuchia because there are no robust phylogenies upon which to map character distributions. Homoplastic evolution of additional sacral vertebrae has undoubtedly occurred within Archosauria, with examples including birds, pterosaurs, ornithosuchids (e.g. *Ornithosuchus longidens;* WALKER 1964), several times within theropod dinosaurs (HOLTZ 1994), and a reversal to the plesiomorphic condition of two sacrals in *Herrerasaurus ischigualastensis* (NOVAS 1993) if that taxon is interpreted as a theropod dinosaur.

Although the homology of extra sacral vertebrae in rauisuchians is in doubt, a brief consideration of sacral and pelvic morphology within the group suggests that the presence of additional sacrals might covary to some extent with certain other derived features of the sacrum/pelvis. For example, all those taxa (e.g. *Poposaurus gracilis, Chatterjeea elegans, Sillosuchus longicervix*) that possess a well-defined, anterodorsally extending, rugose ridge on the ilium above the acetabulum apparently also have at least one extra sacral vertebra and short, horizontally-directed sacral ribs.

Ventrally-directed distal articular surfaces of the sacral ribs for attachment to the ilia, which are thus held subhorizontally rather than vertically, occur in rauisuchians such as *Stagonosuchus nyassicus* and *Saurosuchus galilei*. BONAPARTE (1984) was the first to describe this in detail and he argued that, as a consequence, the acetabular socket was ventrally-deflected and that the femur was probably held more-or-less vertically and moved largely parasagittally - in a manner convergent with that of dinosaurs. BONAPARTE (1984) considered this adaptation to be universally present in the "Rauisuchidae" - a group including e.g. *Poposaurus* and therefore approximately equivalent to Rauisuchia in the sense used here. Subsequent authors (e.g. BENTON 1986a) also listed this feature as present in a group that included *Poposaurus*, while BENTON & CLARK (1988) underlined the distinction between the "pillar-erect" hindlimbs of rauisuchians and the clearly convergent "buttress-erect" condition of dinosaurs. However, LONG & MURRY (1995) showed that in *Poposaurus gracilis* the distal articular surfaces of the sacral ribs are not ventrally-deflected to any great degree (= the plesiomorphic condition for archosaurs), but that the femur may still have been held vertically because the supraacetabular crest of the ilium is strongly developed and harbours a partially ventrally-facing acetabular socket. Further study is necessary to determine whether the probably vertical inclination of the femur in various

rauisuchians is homologous and whether the laterally directed sacral ribs of e.g. *Poposaurus gracilis* represent a retention of a plesiomorphic archosaurian feature or a condition derived over that seen in rauisuchians with ventrally deflected sacral ribs.

LONG & MURRY's (1995) subdivision of Rauisuchia into "rauisuchids" and "poposaurids" was partly supported by the ventral or lateral extension of the sacral ribs and associated subhorizontal or subvertical inclination of the ilium respectively. The possibility that a certain subset of rauisuchians might be diagnosed by the presence of ventrally-downturned sacral ribs is uncertain, however, because of the reported presence of this feature in other basal archosaurs. For example, BONAPARTE (1984: 213) remarked that it also occurs in some aetosaurians, and BENTON (1986a) and BENTON & CLARK (1988) considered a subhorizontal rather than vertical blade to the ilium and a ventrally-directed acetabular socket to be a synapomorphy of a clade (their Pseudosuchia) composed of *Saurosuchus, Ticinosuchus*, and Stagonolepididae (aetosaurians). The other potential problem in using this as a diagnostic feature is that even in e.g. parasuchians and non-crown-group archosaurs the distal articular surfaces of the sacral ribs are ventrally-deflected to some extent (e.g. HUGHES 1963: fig. 4), potentially creating difficulties in the identification of discrete states.

BONAPARTE's (1981, 1984) work on rauisuchian locomotion was influenced by CHARIG's (1972) understanding that the evolution of locomotor systems in archosaurs followed a trend of improvement from a primitive, "sprawling" type to a derived "erect" type of gait, via an intermediate "semi-erect" type. More recently, SERENO (1991) and PARRISH (1993) have highlighted problems with identifying locomotor grade types and have argued that there has been a more complex pattern of convergence and reversal in the evolution of gait in archosaurs than was previously recognized. Understanding the evolution of morphological features associated with locomotion in rauisuchians will be an important part of forming a more complete and accurate picture of the evolution of hindlimb and pelvis form and function for archosaurs as a whole.

Derived features of the ilium

One of the most distinctive morphological features that can be attributed to perhaps most rauisuchians is the presence of a "buttress", "swelling", or a possibly rugose "ridge" on the lateral surface of the ilium, above the upper (superior or supraacetabular) rim of the acetabulum (Fig. 4). At its most mild expression (e.g. *Stagonosuchus nyassicus*, pers. obs., Fig. 4A), this is expressed as no more than a fairly indistinct subvertical thickening or weakly-defined ridge, extending from the midpoint of the dorsal rim of the

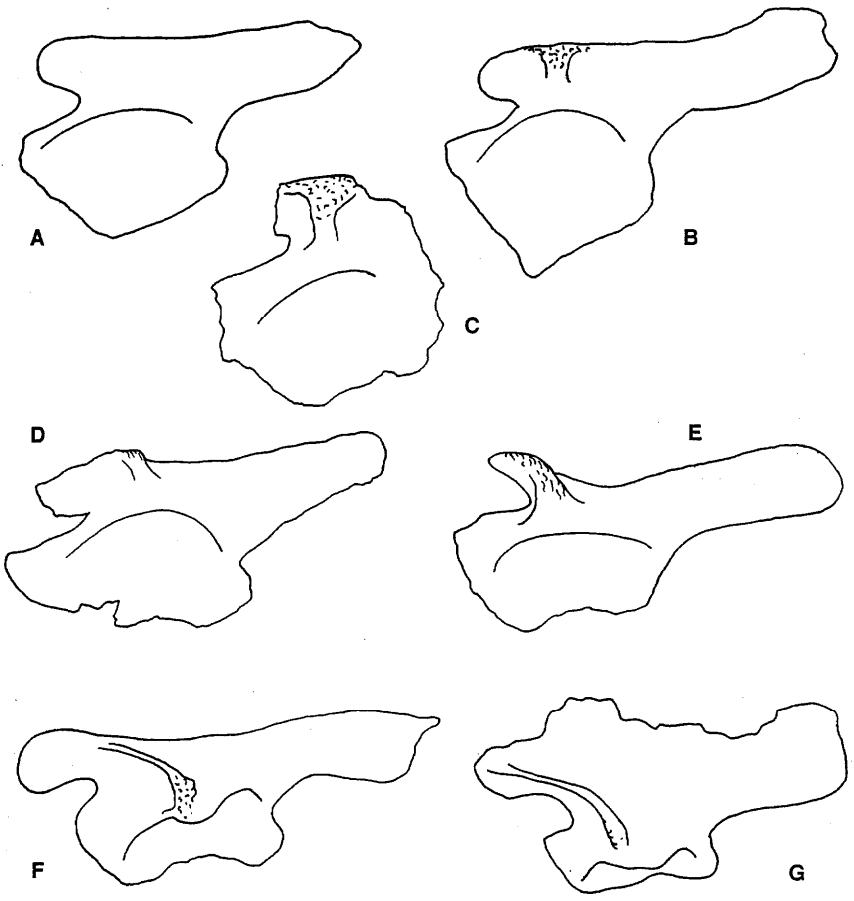

Fig. 4. Comparison of rauisuchian ilia in left lateral view. **A,** *Stagonosuchus nyassicus* after HUENE (1938b: fig. 27). **B,** Kupferzell taxon after GALTON (1985: fig. 1A) and pers. obs.. **C,** *Postosuchus kirkpatricki* after LONG & MURRY (1995: fig. 137B). **D,** *Teratosaurus suevicus* after GALTON (1985: fig. 2C). **E,** *Bromsgroveia walkeri* after BENTON & GOWER (1997: fig. 10A). **F,** *Poposaurus gracilis* after LONG & MURRY (1995: fig. 152). **G,** *Chatterjeea elegans* after LONG & MURRY (1995: fig. 165A).

acetabulum to the dorsal edge of the ilium. In certain other taxa, such as "*Postosuchus kirkpatricki*" (LONG & MURRY 1995: figs. 135, 137B, Fig. 4C) and the Kupferzell rauisuchian (GALTON 1985: fig. 1 A, Fig. 4B), a similar ridge occurs, but it is more clearly defined relative to the surrounding bone and it has a rugose dorsolateral surface. Another derived condition is seen in e.g. *Bromsgroveia walkeri* (GALTON 1985, GALTON & WALKER 1996, BENTON & GOWER 1997, Fig. 4B) and *Poposaurus gracilis* (e.g. COLBERT 1961, LONG & MURRY 1995, Fig. 4F). These forms also possess a rugose ridge, but it extends anterodorsally from the dorsal rim of the acetabulum and along the anterior process of the crest of the ilium, and forms the posterior border to a deep anterolateral fossa. In *Sillosuchus longicervix* (ALCOBER & PARRISH 1997) and *Chatterjeea elegans* (LONG & MURRY 1995, Fig. 4G), the apparently equivalent ridge is thin, very well-defined, and similar to that of e.g. *Poposaurus gracilis* in curving anterodorsally, and in partially bounding a deep fossa. COLBERT (1961) believed that the rugosity in Poposaurus gracilis represented the site of origin of the iliofemoralis muscle, while CHATTERJEE (1985) suggested that the rugose ridge in the material he referred to *Postosuchus kirkpatricki* was for the iliotibialis 2: neither author provided reasoning for these proposals.

The morphology of rauisuchian ilia prompts several questions: (1) what is meant precisely by the terms 'buttress', 'rugosity', 'ridge', and 'swelling' in this context (the distinctions have not always been made clear)? - (2) what is the exact distribution of these features throughout Rauisuchia? (3) What is the homology of these features? (4) What is their function? The third of these questions is particularly pertinent because there appears to be a largely implicit understanding that the rounded, subvertical ridge of e.g. *Saurosuchus galilei* might be homologous with the rugose ridge of e.g. *Postosuchus kirkpatricki* and perhaps the more strongly defined, anterodorsally-extending ridge of e.g. *Poposaurus gracilis*, but this is less plausible if PARRISH's (1993) phylogenetic hypothesis is correct. While PARRISH's phylogenetic hypothesis does not support the homology of the ridges in all rauisuchians (unless the ridge was lost independently in Crocodylomorpha and *Gracilisuchus stipanicicorum*) it was suggested by PARRISH (1993: 301) that the rounded ridge seen in e.g. *Rauisuchus tiradentes* "appears to be homologous with the supraacetabular buttress characteristic of poposaurids". PARRISH's (1993) text implies that a swelling, ridge, or rugosity is absent from the ilia of the Prestosuchidae (sensu PARRISH), but extraction of further information is hampered by discrepancies between the text and data matrix caused by an error during the publication of the matrix (J. M. PARRISH, pers. comm.) - character 32 ("rounded swelling of the ilium") is listed as a synapomorphy of PARRISH's Rauisuchidae (p. 301) while the matrix records missing data for this character in these taxa.

Other features of the pelvis

There are a number of other interesting derived features of the pelvis that exhibit marked variation within the Rauisuchia, including a possibly perforate acetabulum (e.g. *Poposaurus gracilis* - but see ALCOBER & PARRISH 1997: 555); the length and form of the pre- and postacetabular processes of the iliac blade; extent of acetabular overhang; length, form, and extent of symphisis of pubes and ischia; development and form of a distal foot on the pubis. A number of these features appear to covary in their occurrence within Rauisuchia, but further work is required if robust patterns are to be demonstrated and explained.

Alpha taxonomy

Problems associated with the alpha taxonomy of rauisuchians are manifestly abundant and they adversely affect the understanding of the group by preventing accurate delineations of taxa - essential for all further investigations. The difference between the concept of *Postosuchus kirkpatricki* adopted by CHATTERJEE (1985) and LONG & MURRY (1995) has been cited above, and further examples are available. CHARIG (1956), in an unpublished Ph.D. thesis described several archosaur taxa from Africa and referred to the names he had given to these new taxa in a later, full publication (CHARIG, in APPLEBY et al. 1967), but the lack of properly published, formal descriptions means that e.g. *Mandasuchus tanyauchen* CHARIG, in APPLEBY et al. 1967 has been treated as a nomen nudum (e.g. SILL 1974, KREBS 1976), while PARRISH (1993: 297) has additionally suggested that "*Mandasuchus*" might be congeneric with *Ticinosuchus*. A further example of taxonomic confusion is provided by the genus *Prestosuchus* from the Santa Maria Formation of Brazil. HUENE (1942) originally described two species, *Prestosuchus chiniquensis* (type species) and *P. loricatus* on the basis of fragmentary and largely postcranial material. BARBERENA (1978) briefly described a complete skull from the Santa Maria Formation and referred it to *Prestosuchus chiniquensis*. PARRISH (1993) coded HUENE's and BARBERENA's material separately in his phylogenetic analysis, but believed these specimens to represent a single species (PARRISH 1993: 296). SERENO (1991: 12) suggested that the skull referred to *P. chiniquensis* by BARBERENA (1978) might not be a suchian, on the basis of the morphology of its lateral temporal fenestrae. HUENE (1942) did not assign type specimens when he described his new Brazilian genera and species, but he was explicit about how he conceived each taxon by stating which discrete specimens (retrieved from a series of numbered excavations) were grouped together. KREBS (1976) sub-

sequently designated lectotype and paralectotype specimens for each of HUENE's taxa and suggested that at least *Prestosuchus chiniquensis* and *P. loricatus* might be synonymous, but that a reexamination of the original material was required. Most recently, KISCHLAT & BARBERENA (1999) have examined new and old material and reconsidered the problem. They have argued that the skull described by BARBERENA is demonstrably similar to the paralectotype of *P. chiniquensis*, but that they both differ from the lectotype of *P. chiniquensis*. They conclude that HUENE's type material is composite, and KISCHLAT (in press) has designated the skull described by BARBERENA as the holotype of a new taxon.

LONG & MURRY's (1995) revision of the rauisuchians of the southwestern United States of America is to be welcomed, but several aspects of their work deserve further comment. I believe that LONG & MURRY are correct in their proposal that the material originally described and referred to *Postosuchus kirkpatricki* is heterogenous enough to be considered taxonomically distinct. Particularly telling (pers. obs.) is the disparate morphology of the ischia, ilia, astragali, and calcanea that they refer to *P. kirkpatricki* and *Chatterjeea elegans*. The ilium referred to *Lythrosuchus langstoni* is also morphologically distinct from the only ilium among CHATTERJEE's material that LONG & MURRY accept as representing *P. kirkpatricki*. The basis for some of LONG & MURRY's assignations of referred specimens is less clear. For example, among the material that LONG & MURRY figure, referrals to *P. kirkpatricki* that will probably require further investigation are some cranial and mandibular fragments (their fig. 125) and a sacrum (their fig. 136). It has not yet been satisfactorily demonstrated that these elements exhibit diagnostic features that can be linked to the holotype of *P. kirkpatricki*. It might also be borne in mind that current knowledge of rauisuchian ontogenetic variation is minimal. Until at least the small specimen considered by LONG & MURRY (1995: figs. 145, 146) to be a juvenile *P. kirkpatricki* is formally described, the large size difference between the type material of *Chatterjeea elegans* and *P. kirkpatricki* remains a potential (though admittedly unlikely) complication. LONG & MURRY's (1995) study will probably not be the last word on the taxonomy of these specimens.

Fenhosuchus cristatus YOUNG 1964 is a further example of problematic taxonomy, but in this instance the problems are also associated with uncertainty that this taxon is even a rauisuchian. YOUNG described the monospecific *Fenhosuchus* from selected, largely isolated elements that were recovered from several localities in the Upper Ehrmaying Formation of Shanxi province, China. These are the same localities that yielded the type material of the erythrosuchids *Shansisuchus shansisuchus* and *S. heiyuekouensis*, and the small "thecodontian" *Wangisuchus tzeyii* (considered a rauisuchian by e.g. BENTON 1993c, 1994), also described by YOUNG (1964).

YOUNG referred *Fenhosuchus cristatus* to the "Rauisuchidae" on the basis of comparisons with taxa including *Stagonosuchus*. CHARIG & REIG (1970: 136) considered *F. cristatus* as *incertae Sedis*, but not a member of Proterosuchia - a group of non-crown-group archosaurs. KREBS (1976: 72, 92) believed that the type vertebrae were undiagnostic, and proposed that the composite material should not be considered a rauisuchian, while BONAPARTE (1984: 210) stated that at least some of the material that YOUNG referred to *F. cristatus* is rauisuchian. LONG & MURRY (1995: 117) considered "*Fenhosuchus* (emend.)" to be a member of their Rauisuchidae, but provided no further discussion. Despite this uncertainty, *Fenhosuchus* has been listed as questionably one of the oldest known rauisuchians by e.g. BENTON (1993c, 1994).

I have recently reexamined the material described by YOUNG during a study of the osteology of the erythrosuchid *Shansisuchus* (partly published by GOWER 1996, GOWER & SENNIKOV 1996), and this allowed a reassessment of the taxonomic validity of *F. cristatus* and the possibility that at least some of YOUNG's material might be rauisuchian. The material referred to *F. cristatus* by YOUNG can be loosely divided into four categories: (1) elements indistinguishable from those of *Shansisuchus*; (2) indeterminate elements; (3) incorrectly identified elements; (4) elements possibly belonging to a rauisuchian.

I believe that the first of these categories includes the vertebrae (including the type material designated by YOUNG), both premaxillae, the quadrates, dentary, sacral ribs, scapula, humeri, left radius and ulna, femora, tibiae, fibulae, pubes, and ankle and foot elements. The slight differences noted by YOUNG between this material and the corresponding elements of *Shansisuchus* (the form that dominates the fauna) can be readily accounted for by intraspecific variation and preservational imperfections. Indeterminate elements include YOUNG's "lacrimal", the probably pathological "right ulna", and the assortment of bone fragments interpreted as "dermal scutes". Elements incorrectly identified by YOUNG are the "coracoids", which are more probably proximal fragments of pubes that can perhaps be referred to *Shansisuchus*, and the calcaneum in YOUNG's figure 35F, which is a basioccipital also possibly referrable to *Shansisuchus* (GOWER 1996: 363). The element interpreted by YOUNG (his figure 46D) as an ilium is not readily identifiable as any basal archosaur element. The only elements referred to *F. cristatus* that are not indeterminate or referrable to *Shansisuchus*, and might represent a rauisuchian are the articulated distal ends of a pair of ischia, shown in YOUNG's figure 46G. In being apparently rod-like, they probably belong to a taxon with a much more strongly triradiate pelvis than possessed by *Shansisuchus*. Although little information is available, comparisons can be made between these ischia and those of e.g. "*Postosuchus kirkpatricki*"

(LONG & MURRY 1995: fig. 138), including the shallow depression on the ?dorsal surface. In isolation, they do not represent compelling evidence for the presence of rauisuchians in the Upper Ehrmaying Formation, but some of the material from the same localities referred to *Wangisuchus tzeyii* by YOUNG includes elements such as a crocodilian-like calcaneum (PARRISH 1992: 191, 1993: 294; pers. obs.) that provide support for the possibility that rauisuchians did exist in rocks of this age (earliest Middle Triassic?).

In summary, most of the material referred to *Fenhosuchus cristatus* is not diagnostic, or can be referred to the erythrosuchid *Shansisuchus shansisuchus*. This includes the type vertebrae, so that *Fenhosuchus cristatus* can be considered a subjective junior synonym of *Shansisuchus shansisuchus*, or *Fenhosuchus* and *F. cristatus* are nomina dubia if the vertebrae are considered to be indeterminate. Of the material that YOUNG referred to *F. cristatus*, only the distal ends of a pair of ischia might be considered to belong to a rauisuchian, and it remains unproven that rauisuchians were present in the Upper Ehrmaying Formation.

SENNIKOV (in KALANDADZE & SENNIKOV 1985) argued that the erythrosuchid genus *Vjushkovia* HUENE 1960 is synonomous with *Garjainia* OCHEV 1958. SENNIKOV therefore erected the new genus *Youngosuchus* for the only other species of *Vjushkovia*, the demonstrably distinct Chinese taxon *V. sinensis* YOUNG 1973. SENNIKOV also suggested that the Chinese taxon represented a rauisuchian rather than an erythrosuchid. PARRISH (1992) rejected the synonomy of *Vjushkovia* and *Garjainia*, and the possibility that *Vjushkovia* (*Youngosuchus*) *sinensis* is a rauisuchian. A subsequent assessment (GOWER & SENNIKOV in press) noted some errors in PARRISH's morphological observations, and concluded that the type species of *Vjushkovia, V. triplicostata* HUENE 1960, is a synonym of the only known species of *Garjainia, G. prima* OCHEV 1958. In light of this, and the apparently more widespread than previously appreciated distribution of three-headed pectoral ribs among early archosaurs (e.g. GOWER & SENNIKOV 1997, in press; pers. obs.), the genus *Youngosuchus* is here supported, and it is proposed that SENNIKOV's (in KALANDADZE & SENNIKOV 1985) suggestion that *Y. sinensis* might not be an erythrosuchid is reconsidered.

Fragmentary and isolated archosaur remains from the Lower and Middle Triassic of European Russia have formed the basis for the description of several taxa that have been referred to the Rauisuchia (OCHEV 1982, 1986, KALANDADZE & SENNIKOV 1985, SENNIKOV 1988, 1990, 1995). Whether or not these are truly rauisuchians, it is clear that many taxonomic problems exist because of the incomplete and disarticulated nature of these remains (see review by GOWER & SENNIKOV in press). Problematic taxa described as rauisuchians from European Russia and from China should not be ignored, however, because they are potentially important in providing data on the

earliest occurrence of rauisuchians, and therefore on the origin and early evolution of the group.

In commenting briefly on some of the problems in taxonomy facing students of rauisuchians, it is perhaps worthwhile establishing which taxa can be considered currently devoid of such problems - taxa that could be used as points of stability in the development of future research. Likely candidates might be sought among those taxa most commonly employed as exemplars of various rauisuchian groups in phylogenetic analyses. Problems associated with *Postosuchus* and *Prestosuchus* have already been discussed. PARRISH (1993: 297) and ALCOBER & PARRISH (1997: 555) have recently suggested that the material previously referred to *Saurosuchus galilei*, one of the better known taxa, might be composite to some extent. BENTON & CLARK (1988: 312) stated, without discussion, that *Heptasuchus* (DAWLEY et al. 1979) is equivalent to *Poposaurus*, while PARRISH (1993: 301) and LONG & MURRY (1995) considered these two taxa to be distinct. LONG & MURRY (1995: 152) have raised the possibility that *Heptasuchus clarki* ("*clarkei*") is at least congeneric with their newly described *Lythrosuchus langstoni*, and WROBLEWSKI (1997) has reported that most of the holotype of *H. clarki* is missing and claims that it and other material referred to this species is composed of more than one taxon. The holotype of *Ticinosuchus ferox* is an essentially complete individual (KREBS 1963) and therefore exempt from any suspicion that it represents more than a single taxon, but problems might be encountered in the future when good cranial material of comparable rauisuchians is discovered - because of the relatively uninformative preservation of the skull of *T. ferox*. *Tikisuchus romeri* CHATTERJEE & MAJUMDAR, 1987 is another species free from taxonomic problems, but it remains to be seen if this reflects a real situation or simply the currently incomplete knowledge of its morphology and that of other Indian basal archosaurs.

Suprageneric systematics within Rauisuchia

Some earlier studies proposed various ancestor-descendant sequences between various rauisuchian genera (Fig. 5A, 5B), or trees incorporating spatial and temporal data (Fig. 5C), but PARRISH's (1993) study remains the only explicit analysis to date of interrelationships among rauisuchians below the familial level, where data and criteria used in hypothesis choice were made explicit. While PARRISH (1993: 304) reported that support for rauisuchian (in the sense used here) polyphyly is relatively strong, GOWER & WILKINSON (1996) showed that decay indices are generally low across the tree as a whole. Furthermore, it is possible that *Postosuchus kirkpatricki* as

described by CHATTERJEE (1985) should not have been assumed by PARRISH to be a valid "poposaurid" exemplar (LONG & MURRY 1995). These problems aside, it appears to be generally accepted (based on PARRISH's and various recent non-cladistic studies) that there is a clear, presumably phylogenetically based, difference between those taxa that have a morphology re-

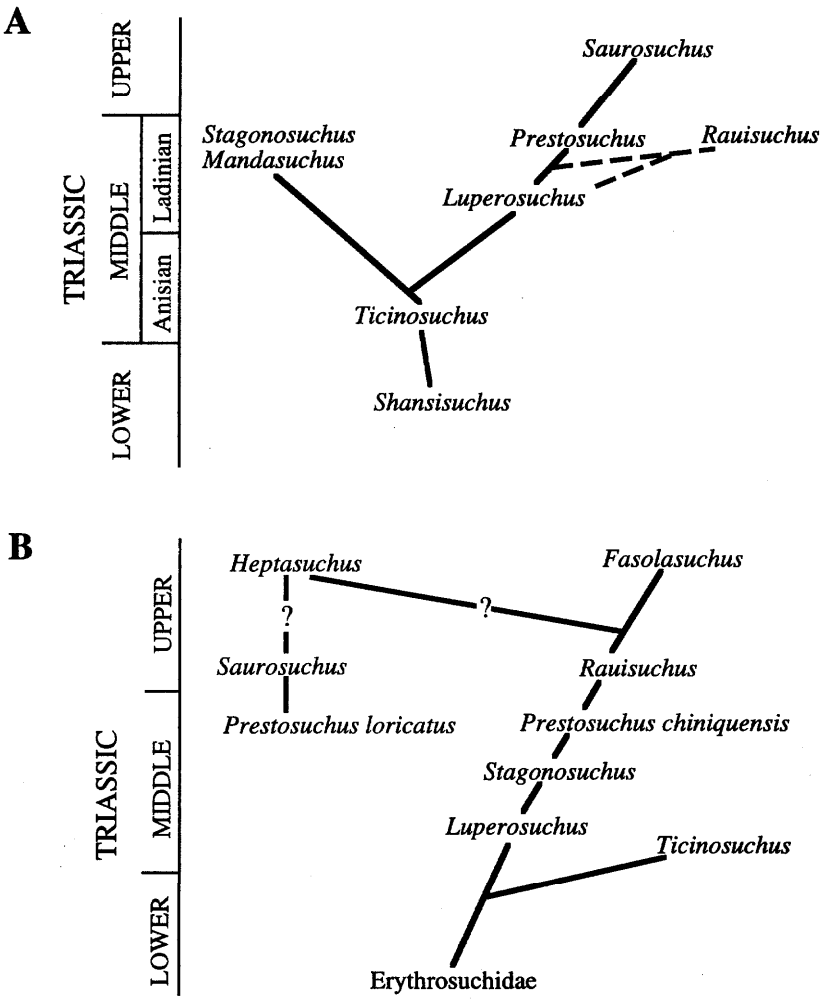

Fig. 5 A, B (Legend see p. 471)

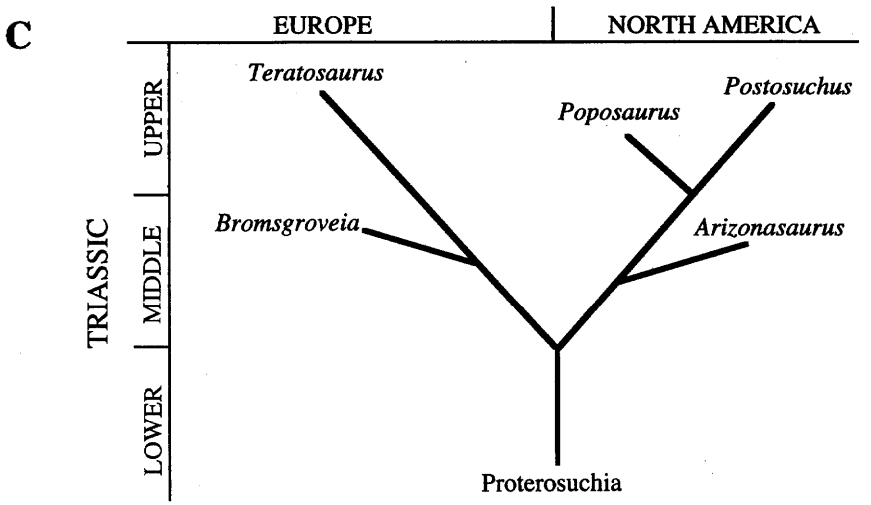

Fig. 5. Evolutionary trees depicting relationships of Triassic rauisuchians. **A,** ancestor-descendent tree redrawn from SILL (1974). **B,** ancestor-descendent tree redrawn from BONAPARTE (1981). **C,** tree incorporating data from geography, as well as stratigraphy and morphology, redrawn from CHATTERJEE (1985).

sembling *Poposaurus gracilis* and the better known rauisuchians such as *Ticinosuchus ferox*. This point has been made by LONG & MURRY (1995), who have proposed that what might be termed "rauisuchid" or "prestosuchid" rauisuchians have e.g. two or three strongly downturned sacral vertebrae and a rugose supraacetabular ridge that is perpendicular to the dorsal margin of the ilium, while "poposaurids" have three or four sacral vertebrae with shorter ribs that are not downturned, and the rugose supra acetabular ridge that continues up onto the anterodorsal margin of the ilium. Further comparisons are extremely limited, because, if LONG & MURRY (1995) are correct in interpreting most of CHATTERJEE's original *Postosuchus kirkpatricki* material as non-"poposaurid", then cranial material of unequivocal "poposaurids" remains undocumented to date. ALCOBER & PARRISH

(1997) have accepted LONG & MURRY's (1995) referral of part of the original *Postosuehus kirkpatricki* (sensu CHATTERJEE 1985) material to the new species *Chatterjeea elegans*, but they do not accept LONG & MURRY's suggestion that *C. elegans* belongs to a family distinct from the "Poposauridae", or that "prestosuchids" (sensu PARRISH 1993) are more closely related to all other rauisuchians than are crocodylomorphs and aetosaurians. Additionally, ALCOBER & PARRISH (1997) elected to consider *Postosuchus kirkpatricki* to be the most basal "poposaurid" rather than a "rauisuchid" (sensu PARRISH 1993 or LONG & MURRY 1995).

In summary, certain morphological features (largely of the sacrum and pelvis) underlie a general understanding that distinct and possibly monophyletic suprageneric taxonomic units are identifiable within (a possibly non-monophyletic) Rauisuchia. To date, this has been tackled in an explicit analysis only by PARRISH (1993). The approach of even the most recent studies has been to some extent typological, but this is understandable given the generally low level of knowledge of rauisuchian morphology and taxonomy. It is suggested here that the validity, definition, composition, and interrelationships of Prestosuchidae, Rauisuchidae, Poposauridae, and Chatterjeeidae are all currently poorly supported and remain in question.

Phylogenetic relationships to other archosaurs

The absence of consensus on the mono-, para-, or polyphyly of Rauisuchia, makes it unsurprising that the relationships of rauisuchians to other basal archosaurs is uncertain. The only agreement that seems to exist is that rauisuchians are members of the crocodilian-line, rather than bird-line, of the basal dichotomy in the archosaurian crown group, and are probably more closely related to aetosaurians and crocodylomorphs than to parasuchians. This hypothesis is based partly on, and supported by, the close similarity between the tarsus of aetosaurians, crocodylomorphs, and rauisuchians. Robust non-tarsal characters that might resolve relationships at this level seem to be more elusive, or at least much less well understood. For example, details of braincase morphology in basal crurotarsans remain virtually undocumented and have yet to be exploited for phylogenetic data. Resolution of the relationships among these taxa is further complicated by the possibilities that Rauisuchia is non-monophyletic, and that *Postosuchus kirkpatricki* (*sensu* CHATTERJEE 1985) is a chimaera - because this taxon has been used as an exemplar in the recently reached consensus (GOWER & WILKINSON 1996) that poposaurids are more closely related to Crocodylomorpha than to other rauisuchians (e.g. BENTON & CLARK 1988, PARRISH 1993).

Evolutionary patterns

The discovery of robust temporal or spatial patterns in the evolution of any major taxon is obviously influenced by the understanding of that group's systematics. In terms of the Rauisuchia, it is not therefore possible to outline fine details of robust morphological, temporal, and spatial patterns among various higher taxa within Rauisuchia. However, it is worth mentioning examples of the work that has been carried out in this direction to date.

Some studies have considered the role of rauisuchians in faunal changes that occurred late in the Triassic. SENNIKOV (1996) included rauisuchians in his interpretation of changes in food webs and faunal composition during the Triassic in European Russia, but this clearly depends on the interpretation of fragmentary and taxonomically problematic fossils (GOWER & SENNIKOV in press). In other studies, several issues concerning the terrestrial vertebrate record have been the focus of much recent debate, particularly whether there were two extinctions or a single major event at the end of the Triassic, the cause of faunal turnovers, the correlation of fossil faunas, and the meaning of gaps in the fossil record (e.g. BENTON 1986b, 1986c, 1993a, 1993b, 1994, OLSEN & SUES 1986, FRASER & SUES 1994b, PADIAN 1994). BENTON (1986b, 1991, 1993a, 1994) has argued for a Late Carnian extinction event as well as an end-Triassic one, although this is not apparent in the rauisuchian data alone, with both the "Rauisuchidae" and "Poposauridae" extending in distribution from before the Ladinian through the Carnian-Norian boundary and to the end of the Triassic. OLSEN & SUES (1986) and HUNT & LUCAS (1992), among others, have argued against the reality of a Late Carnian mass extinction (see thorough overview by HALLAM & WIGNALL 1997). Different causes invoked for extinction(s) in the late Triassic include triggering by a catastrophic extraterrestrial impact (see BENTON 1993b), competition (CHARIG 1984), and noncompetitive ecological processes (BENTON 1983, 1991, 1994). FRASER & SUES (1994b) and PADIAN (1994) have discussed problems affecting the interpretation of data in attempting to achieve a more accurate understanding of what happened in the Late Triassic, including poor stratigraphic controls on many of the fossil occurrences, a relatively poor knowledge of Norian tetrapods, and difficulties in correlating the relevant fossiliferous strata. BENTON (1994) has argued that sampling the fossil record for indications of major faunal changes at the family level is valid because "for a long time, most tetrapod families have been defined by sharply indicated unique characters". Interpretation of data for rauisuchians is therefore rendered even more problematic because of serious doubts about the validity and/or composition of family-level taxa (see above). It will be of interest to see how varying interpretations of the

suprageneric systematics of rauisuchians fit alternative hypotheses of the number and timing of late Triassic extinctions.

LONG & MURRY (1995) have studied the distribution of various tetrapod groups throughout the Late Triassic of the southwestern USA, but clear patterns do not emerge from the data - their figure 199 indicates that representatives of their Rauisuchidae, Poposauridae, and Chatterjeeidae are present throughout each of the Mid Carnian, Late Carnian, and Early Norian.

The taxonomic validity and affinities of the Early Triassic Russian 'rauisuchians' is in doubt (e.g. LONG & MURRY 1995, GOWER & SENNIKOV in press), so that the timing and place of origin of the group remains uncertain. The oldest taxa that can more confidently be referred to the Rauisuchia are from Anisian/Ladinian rocks and include taxa that already exhibit what are understood to be derived features for the group e.g. the Anisian *Bromsgroveia walkeri* (see GLATON & WALKER 1996, BENTON & GOWER 1997). The earliest records of rauisuchians used in studies of faunal change and extinction (e.g. BENTON 1993c, 1994) are based on many of the more problematic taxa, including *Fenhosuchus cristatus* and *Vjushkovisaurus berdjanensis*. Current data provide no evidence that rauisuchians survived into the Jurassic.

ALCOBER & PARRISH's (1997) recent description of *Sillosuchus longicervix* as the first clear record of "Poposauridae" from Gondwana illustrates two pertinent points about the present possibility of detecting patterns in the evolution of the Rauisuchia: firstly the big impact that each new discovery can have at this early stage of improving the knowledge of the group, and, secondly, how pervasive the fragility of competing taxonomic schemes currently is - other workers might alternatively consider *S. longicervix* as the first clear record of Chatterjeeidae (LONG & MURRY 1995) from Gondwana.

Why are there problems in understanding rauisuchians?

Most rauisuchians are known from a single, or few, incomplete and often poorly-preserved specimens, a not uncommon situation for those Mesozoic organisms that occupied the top terrestrial carnivore niche. This is exacerbated for e.g. Middle Triassic European archosaurs because the rocks deposited during Anisian time are mostly represented by marine deposits of the Muschelkalk, while continental formations of the same age have produced only sparse remains (BENTON & GOWER 1997). The small number and often incomplete or poorly-preserved nature of early crown-group archosaurs was cited by PARRISH (1993: 304) as one of the main problems hampering the determination of the group's phylogeny.

The worldwide distribution achieved by rauisuchians is echoed by the important museum collections being spread across Europe, North and South America, Russia, India, and China. Most students of rauisuchians have been able to examine only a very small sample of the group's known diversity. An example of the difficulties that this can create is provided by the confused alpha taxonomy of *Prestosuchus* outlined above. PARRISH (1993) noted that comparisons between the material described by HUENE (1942) and BARBERENA (1978) were problematic because the former consists mostly of postcranial elements with part of a lower jaw, while the latter is a complete skull with a partial vertebral column. Difficulties in making comparisons are compounded by the fact that the original material is stored in Germany (München), while the complete skull is in Brazil (Porto Alegre). A second example is provided by fragmentary and isolated remains from e.g. European Russia and India, where workers have largely lacked the benefit of access to decent and relevant comparative material.

While there have been many recent studies of basal archosaur phylogeny and even of the interrelationships of various rauisuchians, there has been relatively little recent work on details of basic morphology and taxonomy, even though these areas will provide data for the improvement of estimates of phylogeny. Over the last decade, research on basal archosaurs has been dominated by attempts to establish a framework phylogeny for the group, so that new morphological information has largely been presented in character-taxon matrices without any detailed documentation or discussion. As PATTERSON (1998: 1108) put it, "good morphology lasts forever, whereas today's matrix and the cladograms it yields will [or might] soon be superseded". Only very recently (LONG & MURRY 1995, ALCOBER & PARRISH 1997, GOWER 1997, 1999, SEDLMAYR & SMALL 1997, WROBLEWSKI 1997) has new primary research once again been carried out, and this has highlighted the lack of a satisfactory taxonomic and morphological literature for rauisuchians.

PARRISH (1993: 304) suggested that the major problem hampering the determination of the phylogeny of early crown-group archosaurs, apart from deficiencies in the fossil record, is that "the group as a whole is characterized by extremely high levels of parallelism and convergence, involving several structural/functional complexes". This is possible, but a precise hypothesis has yet to be formulated and tested. If high levels of homoplasy are found in phylogenetic analyses of basal archosaurs, they might be the result of unsatisfactory homology statements (= character formulations), resulting from insufficient morphological research, rather than a reflection of high levels of convergence.

Prospectus

The detailed documentation of osteology is essential for the long-term success of all further evolutionary studies of fossil vertebrates. To this effect, the recent papers by LONG & MURRY (1995) and ALCOBER & PARRISH (1997) are to be welcomed, and will hopefully encourage a series of studies reassessing the osteology of existing and new material. Recently published reports (GOWER 1997, 1999, SEDLMAYR & SMALL 1997, WROBLEWSKI 1997) and ongoing work on new material (e.g. personal communications from E.-E. KISCHLAT, Porto Alegre, and K. SEN, Calcutta) indicate that work is being carried out to this effect, and it is hoped that this represents a new impetus to tackle basic problems in the Rauisuchia. WITMER's (1997a) study of the craniofacial air sinus system has demonstrated the high level of detail and accuracy that can be achieved in modern comparative studies of the morphology of fossil archosaurs. WITMER's study also demonstrated how a detailed consideration of soft tissues can focus assessments of homology, as well as improving the understanding of the biology of extinct organisms. Understanding of the ilial ridges, pubic feet, and additional cranial openings seen in some rauisuchians might benefit from a similar approach. Rauisuchians were not discussed in detail in WITMER's (1997a) paper, probably because of the lack of accurate morphological and systematic data for the group, but this might be taken as further incentive to improve the situation. A consideration of soft tissues and function might also assist the understanding and phylogenetic utility of rauisuchian osteoderm morphology. In living crocodilians, osteoderms are intimately integrated with the vertebrae, ribs and associated soft tissues into a carrying system (FREY 1988). A consideration of rauisuchian osteoderm morphology within the framework of this background knowledge would probably inform the formulation of better phylogenetic characters from the observed variation.

Taxonomic issues need to be addressed in concert with osteological revisions. Lessons might be learned from the problematic status of most of the rauisuchian taxa that have been based on fragmentary remains. Workers should perhaps be cautious in the formal naming of newly discovered fragmentary material, but the documentation of this material should not be discouraged and such documentations should not be ignored, because they might provide important evidence on the range of taxa, or on the variation and diagnostic value of particular morphological features.

A reassessment and revision of rauisuchian interrelationships (and their relationships to other major archosaur taxa) is an obvious necessity if the improved documentation of morphological, spatial, and temporal patterns within the group are to be further investigated and ultimately understood in a proper evolutionary context. JUUL (1994) argued that too many characters

that were employed in the earliest 'cladistic' studies of archosaur phylogeny have been ignored by recent studies without any explicit justification. Examples mentioned by JUUL that are relevant to the Rauisuchia include a "stepped" postorbital bar and the orientation of the ilium/acetabulum - characters used by e.g. BENTON & CLARK (1988), but neglected without discussion by e.g. PARRISH (1993). The possibility of employing these characters in future analyses needs to be addressed.

The approach used by PARRISH (1993), where rauisuchian families were not assumed a priori to be monophyla should, I believe, be followed for the foreseeable future. Similarly, an open mind on rauisuchian monophyly needs to be maintained at present. If suprageneric groups need to be discussed or employed in analyses, the definition being used needs to be stated explicitly. As advocated by CHARIG (1993) and GOWER & WILKINSON (1996), higher taxa hypothesized from the outcome of single phylogenetic analyses should preferrably not be given new names, and suprageneric names within Rauisuchia should not be altered significantly in their meaning, until it is deemed that the hypothesized relationships are robust. Modern phylogenetic techniques enable a wide range of methods to be employed that not only produce trees, but also assess the robustness of resulting phylogenetic hypotheses. At a minimum, workers forwarding new phylogenetic hypotheses based on numerical analyses should attempt to present measures of the support for those relationships, so that weaknesses can be highlighted as areas for future research rather than hidden away as inconveniences. As with detailed morphological interpretation and documentation, detailed character discussions and formulations, data exploration, and support analysis, are time consuming endeavours that often produce long (and perhaps currently unfashionable) manuscripts, but it is difficult to argue against their value as both lasting contributions and immediate stimuli to the field.

Concluding remarks

Rauisuchian research has been dogged by poorly preserved, unsatisfactorily documented fossil specimens, and systematic disarray. Much of the known rauisuchian material is undeniably fragmentary and taxonomically problematic, but until its full potential has been realized in terms of extraction of morphological data, there is no basis for genuine pessimism. Indeed, there are several reasons to be positive about the future. Levels of research interest are high, areas of consensus exist for a framework phylogeny for basal archosaurs based on explicit analyses, areas for research that should offer immediate success have been identified, and recent work suggests that there is something of a renaissance in documenting rauisuchian morphology and

resolving problems in alpha taxonomy. This should enable more accurate and robust phylogenetic hypotheses to be established which, in turn, will stimulate all areas of research into rauisuchians.

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Appendix: Rauisuchian Classifications

This appendix lists previously proposed classifications of rausuchians in chronological order. It is not comprehensive, either in terms of including all published comments on rauisuchian classification, or in listing all taxa covered in these publications. For example, it was not practical to track all of the most labile taxa throughout various taxa within Archosauria. This appendix aims to facilitate understanding of the various configurations of suprageneric rauisuchian taxa, and also to communicate changes in rauisuchian classification over the last 60+ years. In all those classifications where an ordinal rank was specified, rauisuchians were included in the Thecodontia. Annotations that I have added are in square parentheses.

HUENE (1936a, 1936b, 1942)

Suborder Pseudosuchia
- Family Stagonolepidae
  - Subfamily Desmatosuchinae
    - *Hoplitosuchus*?/*Hoplitosaurus*
  - Subfamily Rauisuchinae
    - *Rauisuchus, Prestosuchus*
  - ?Subfamily
    - *Procerosuchus*

HUENE (1956)

Suborder Pseudosuchia
- Familienkreis Chirotheroidea
  - Family Rauisuchidae
    - *Episcoposaurus, Typothorax, Cerritosaurus, Rauisuchus, Prestosuchus, Hoplitosuchus, Dolichobrachium, Procerosuchus, Stagonosuchus, Chirotherium*
  - Family Ornithosuchidae
    - "*Mandasuchus*"

ROMER (1956)

Suborder Pseudosuchia
- Family Ornithosuchidae
  - *Prestosuchus?, Procerosuchus?, Rauisuchus?, Stagonosuchus?*
- Family Stagonolepidae
  - *Hoplitosaurus*

HUGHES (1963)

Suborder Proterosuchia
- Family Erythrosuchidae
  - *Hoplitosaurus, Rauisuchus?, Saurosuchus?*

KREBS (1965)

Suborder Pseudosuchia
- Family Rauisuchidae
  - *Rauisuchus, Prestosuchus, Procerosuchus, Stagonosuchus, Ticinosuchus*

ROMER (1966)

Suborder Proterosuchia
- Family Erythrosuchidae
  - *Hoplitosuchus* (*Hoplitosaurus*)?, *Rauisuchus*?, *Saurosuchus*?

Suborder Pseudosuchia
- Family Prestosuchidae
  - *Mandasuchus?, Prestosuchus?, Procerosuchus?, Stagonosuchus?*

Charig, in Appleby et al. (1967)

Suborder Pseudosuchia
Family Prestosuchidae
"Mandasuchus", Stagonosuchus, Ticinosuchus, Saurosuchus [*Rauisuchus* excluded]

Romer (1972)

Suborder Proterosuchia
Family Prestosuchidae (Rauisuchidae)
Prestosuchus, Rauisuchus, Saurosuchus, Luperosuchus, Ticinosuchus, "Mandasuchus", Cuyosuchus, Shansisuchus, Hoplitosaurus (*Hoplitosuchus*), *Fenhosuchus, Stagonosuchus, "Pallisteria", Spondylosoma*?
Family Proterochampsidae
Procerosuchus?

Krebs (1976)

Suborder Pseudosuchia
Family Rauisuchidae
Rauisuchus, Ticinosuchus, Mandasuchus, Stagonosuchus, Prestosuchus, Procerosuchus, Saurosuchus, Luperosuchus

Bonaparte (1981)

Suborder Proterosuchia
Family Rauisuchidae
Fasolasuchus, Poposaurus, Saurosuchus, Rauisuchus, Prestosuchus, Luperosuchus, Ticinosuchus, Stagonosuchus, Fenhosuchus, Heptasuchus?, *Teratosaurus*?, Morocco Form, Warwick Form [*Bromsgroveia*], Kupferzell Form

Bonaparte (1984)

Suborder Erythrosuchia
Infraorder Rauisuchia
Family Rauisuchidae
Fenhosuchus, Ticinosuchus, Stagonosuchus, Luperosuchus, Prestosuchus, Rauisuchus, Saurosuchus, Heptasuchus, Fasolasuchus, Poposaurus, "Mandasuchus", Teratosaurus?.

Chatterjee (1985)

Suborder Pseudosuchia
Infraorder Rauisuchia
Family Rauisuchidae
Rauisuchus, Prestosuchus, Procerosuchus, Mandasuchus, Stagonosuchus, Luperosuchus, Saurosuchus, Fasolasuchus, Heptasuchus, Ticinosuchus.
Family Poposauridae
Poposaurus, Postosuchus, Teratosaurus, Arizonasaurus, Warwick Form [*Bromsgroveia*].

GALTON (1985)

Suborder Pseudosuchia
Infraorder Rauisuchia
Family Rauisuchidae
Bromsgroveia
Family Poposauridae
Poposaurus, Postosuchus, Teratosaurus.

BENTON & CLARK (1988)

Pseudosuchia
Rauisuchidae
Luperosuchus, Saurosuchus, Ticinosuchus
"Unnamed Group G"
Poposauridae
Postosuchus, Poposaurus (including *Heptasuchus*)

CARROLL (1988)

Suborder Rauisuchia
Family Rauisuchidae
Fasolasuchus, Heptasuchus?, *Hoplitosaurus*?, *Procerosuchus*?, *Luperosuchus*, "*Mandasuchus*", *Stagonosuchus, Prestosuchus, Rauisuchus, Saurosuchus, Ticinosuchus, Vjushkovisaurus*?
Family Poposauridae
Poposaurus, Postosaurus, Teratosaurus?, *Sinosaurus*?

PARRISH (1993)

Prestosuchidae
Prestosuchus, Ticinosuchus [stated as perhaps including "*Mandasuchus*"], *Saurosuchus.*
Rauisuchiformes
Rauisuchia
Rauisuchidae
Rauisuchus, Fasolasuchus, Lotosaurus, Kupferzell taxon [stated as perhaps equivalent to *Rauisuchus*).
Paracrocodylomorpha
Poposauridae
Poposaurus, Postosuchus, Bromsgroveia.

LONG & MURRY (1995)

Rauisuchia
Rauisuchidae
Rauisuchus, Postosuchus, Prestosuchus, Saurosuchus, Fasolasuchus, Stagonosuchus, Teratosaurus, Fenhosuchus (emend.), Holbrook Quarry Form.
Poposauridae
Poposaurus, Lythrosuchus, Bromsgroveia, Heptasuchus?
Chatterjeeidae
Chatterjeea.

SENNIKOV (1995)

Suborder Pseudosuchia
- Infraorder Rauisuchia
  - Family Rauisuchidae
    - Subfamily Ticinosuchinae SENNIKOV 1995
      Ticinosuchus, Tsylmosuchus, Vytshegdosuchus, Dongusuchus, Energosuchus, Dongusia.
    - Subfamily Rauisuchinae
      - Tribe Vjushkovisaurini SENNIKOV 1995
        Jaikosuchus, Vjushkovisaurus, Jushatyria, Fenhosuchus, Youngosuchus [= *Vjushkovia sinensis* YOUNG 1973].
      - Tribe Rauisuchini HUENE 1942
        Stagonosuchus, Zanclodon, Bromsgroveia, Tikisuchus, Luperosuchus, Rauisuchus, Prestosuchus, Spondylosoma, Hoplitosuchus, Procerosuchus, Saurosuchus, Fasolasuchus, Heptasuchus.
  - Family Poposauridae
    Poposaurus, Postosuchus, Teratosaurus, Sinosaurus.

ALCOBER & PARRISH (1997)

Paracrocodylomorpha
- Poposauridae
  Poposaurus, Postosuchus, Teratosaurus, Bromsgroveia, Chatterjeea, Sillosuchus.