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Notes

Rauisuchia

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Abstract: 'Rauisuchia' comprises Triassic pseudosuchians that ranged greatly in body size, locomotor styles and feeding ecologies. Our concept of what constitutes a rauisuchian is changing as a result of discoveries over the last 15 years. New evidence has shown that rauisuchians are probably not a natural (monophyletic) group, but instead are a number of smaller clades (e.g. Rauisuchidae, Ctenosauriscidae, Shuvosauridae) that may not be each other's closest relatives within Pseudosuchia. Here, we acknowledge that there are still large gaps in the basic understanding in the alpha-level taxonomy and relationships of these groups, but good progress is being made. As a result of renewed interest in rauisuchians, an expanding number of recent studies have focused on the growth, locomotor habits, and biomechanics of these animals, and we review these studies here. We are clearly in the midst of a renaissance in our understanding of rauisuchian evolution and the continuation of detailed descriptions, the development of explicit phylogenetic hypotheses, and explicit palaeobiological studies are essential in advancing our knowledge of these extinct animals.

During the Triassic Period, archosaurs radiated into a diverse array of body sizes, ecologies and morphologies (Benton & Clark 1988; Sereno 1991; Benton 1999, 2004; Nesbitt & Norell 2006; Brusatte *et al.* 2008, 2010; Nesbitt 2011). Basally, Archosauria split into two major lineages, the pseudosuchians (crocodylid line) and avemetatarsalians (bird line), early in the Triassic (Benton & Clark 1988; Sereno 1991; Benton 1999; Gower & Sennikov 2000; Brusatte *et al.* 2010, 2011; Nesbitt 2003, 2011; Nesbitt *et al.* 2011a). Pseudosuchians diversified into some easily recognized and clearly monophyletic groups during the Triassic, such as the heavily armoured aetosaurs and the more fleet-footed

crocodylomorphs. However, there are many other Triassic pseudosuchians that are not easily placed into discrete, well-diagnosed clades (e.g. *Ticinosuchus ferox*, *Gracilisuchus stipanicorum*).

Over the past century, large (2–7 m) hypercarnivorous archosaurs with recurved serrated teeth that are not clearly referable to other pseudosuchian or more inclusive archosauromorph clades (e.g. Aetosauria, Phytosauria, Ornithosuchidae or Crocodylomorpha) were often shoehorned into the poorly defined group 'Rauisuchia.' Many of these taxa were often also assigned to smaller subgroups (subdivisions of 'Rauisuchia'), such as Prestosuchidae, Popsauridae, Rauisuchidae or various ranks

associated with Rausuchidae (e.g. Rausuchiformes, Parrish 1993). Furthermore, many of these taxa, such as *Prestosuchus chiniquensis* and *Rausuchus tiradentes*, were represented only by incomplete fossils that provided information on only small portions of the skeleton. In addition, several Triassic pseudosuchians with divergent cranial and/or vertebral anatomies (e.g. *Lotosaurus adentus*, 'Chatterjeea elegans') were associated with more 'typical' rausuchians by virtue of their similar pelvic and hindlimb morphology. As a result, confusion about what diagnosed rausuchians and about their relationships to one another and to other pseudosuchians dominated the literature of the late 20th century, and little consensus had been reached. At the most basic level, it was not clear if rausuchians were a natural group, a paraphyletic group with respect to other pseudosuchian clades, or a polyphyletic assemblage spread among more easily recognized pseudosuchian groups (Gower 2000).

Given their generally poor fossil record and the absence of a clear taxonomy, rausuchians were largely bypassed in studies of Triassic vertebrate macroevolution until recently (although see Benton 1983; Bonaparte 1984). Nonetheless, rausuchians are now attracting an increased level of attention because of a series of recent discoveries of new taxa and also better material regarding previously known taxa (e.g. Gower 1999; Sen 2005; Sulej 2005; Li *et al.* 2006; Nesbitt & Norell 2006; Jalil & Peyer 2007; Desojo & Arcucci 2009; França *et al.* 2011; Gauthier *et al.* 2011; Trotteyn *et al.* 2011), advances in understanding character state distributions among pseudosuchians (Brusatte *et al.* 2010; Nesbitt 2011), redescrptions of important specimens (Nesbitt 2007; Weinbaum & Hungerbühler 2007; Brusatte *et al.* 2009; Butler *et al.* 2011; Lautenschlager & Desojo 2011; Weinbaum 2011), progress in pseudosuchian phylogenetics (Brusatte *et al.* 2010; Nesbitt 2011) and expansion of a general interest in these fascinating creatures. As a result of this influx of new research and fossil discoveries, the anatomy, systematics and evolutionary history of rausuchians are becoming increasingly clear, although many debates remain.

Whether a natural group or a collection of more distantly related groups, rausuchians are important for a number of reasons. They were an important component of Triassic faunas, especially during the Early–Middle Triassic when ecosystems were stabilizing after the Permo-Triassic extinction and 'modern ecosystems' were being established (Sues & Fraser 2010). Rausuchians were an integral part of the initial diversification of Archosauria in the Early Triassic, but went extinct by the end of the Triassic, seemingly quite suddenly and possibly due to the global end-Triassic mass extinction (Benton 2004). Some rausuchians, such as

the sail-backed ctenosauriscids, are some of the earliest archosaurs to appear in the fossil record and thus help to date the origin of Archosauria, which is an important calibration point in many molecular phylogenetic analyses (Nesbitt 2003, 2011; Butler *et al.* 2011; Nesbitt *et al.* 2011a; Parham *et al.* 2012). Furthermore, rausuchians were part of nearly all Triassic archosaur assemblages and have been found on nearly all portions of Pangaea with Lower to Upper Triassic deposits.

Rausuchians were both taxonomically and ecologically diverse. They include the first large-bodied carnivorous reptiles (up to 7 m in length) in the fossil record and were sometimes much larger than contemporary herbivores, which is unusual, because the opposite relationship between largest predator and herbivore size usually holds in modern terrestrial ecosystems (Sookias *et al.* 2012). Although most rausuchians were massive, quadrupedal predators (e.g. *Batrachotomus kuperferzellensis*, *Postosuchus kirkpatricki*, *Prestosuchus chiniquensis*, *Saurosuchus galilei*), some taxa departed from this body type. Some may have been partially aquatic (e.g. *Qianosuchus mixtus*) whereas others were more lightly built and probably bipedal (e.g. *Effigia okeeffeae*, *Poposaurus gracilis*, *Shuvosaurus inexpectatus*). Other taxa, such as ctenosauriscids and the beaked *Lotosaurus adentus*, sported elaborate sails on their backs. Intriguingly, several rausuchians were long misidentified as theropod dinosaurs because of some remarkable convergences between these groups (e.g. Colbert 1961; Chatterjee 1985, 1993; Benton 1986a; Nesbitt & Norell 2006; Nesbitt 2007; Brusatte *et al.* 2009; Bates & Schachner 2012). It seems likely, therefore, that rausuchians occupied many ecological niches that were subsequently filled by dinosaurs during the Jurassic and Cretaceous (Brusatte *et al.* 2008).

An understanding of the anatomy, ecology and systematics of rausuchians is clearly important for understanding the major patterns and processes in Triassic archosaur evolution. At this point in time, however, there are a number of problems that remain to be resolved. First and foremost, we cannot identify a rausuchian by unambiguous synapomorphies, which is key to identifying these animals in the field or in collections. This point also underscores a major phylogenetic problem: there are no clear apomorphies that unite all rausuchians together as a clade, and the relationships of several genera remain unclear. This naturally prevents a clear understanding of character evolution among these animals.

In general, taxa classically referred to as rausuchians share a large skull relative to their body, recurved teeth, and a few other character states highlighted by researchers over the past 75 years (Fig. 1). However, these long-assumed 'key characters' are

RAUISUCHIA

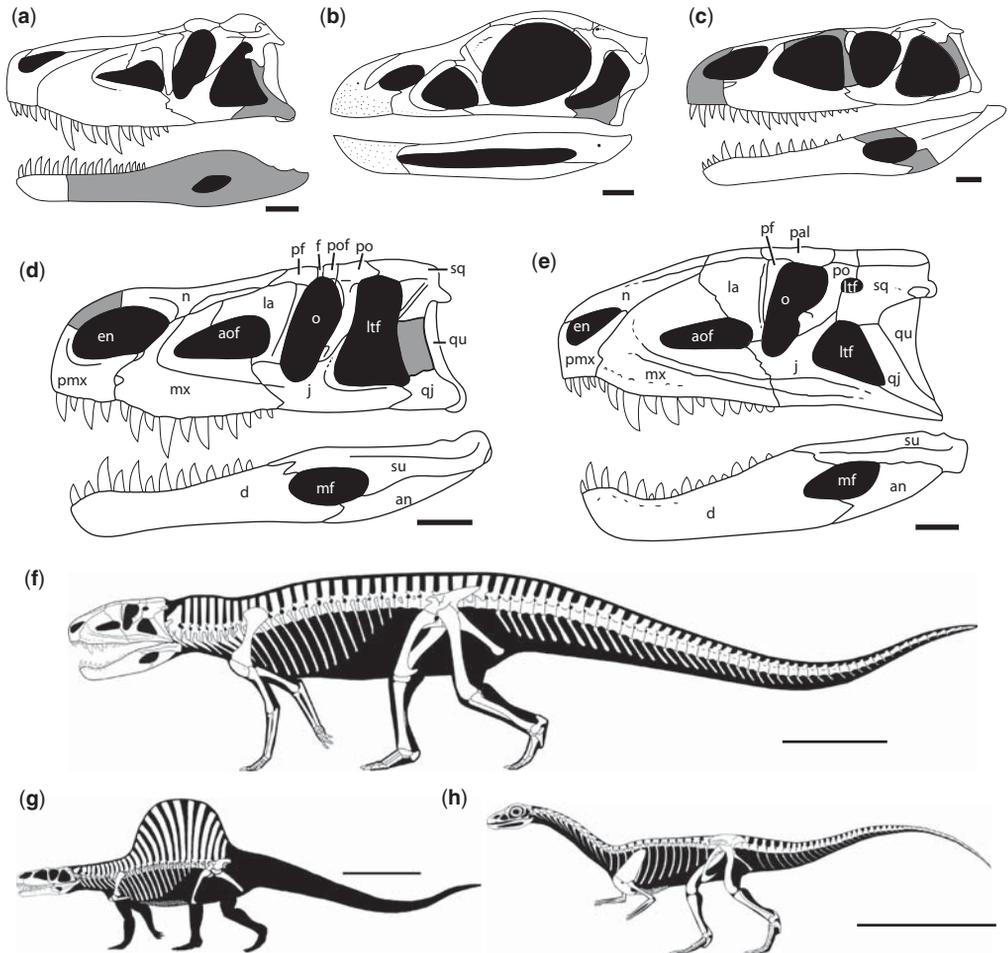


Fig. 1. Skulls and skeletons of rausuchians: (a) skull of *Saurosuchus galilei*; (b) skull of *Effigia okeeffeae*; (c) skull of *Arizonasaurus babbitti*; (d) skull of *Batrachotomus kupferzellensis* (from Gower 1999); (e) skull of *Postosuchus kirkpatricki*; (f) skeleton of *Postosuchus kirkpatricki*; (g) skeleton of *Arizonasaurus babbitti* (from Nesbitt 2005a); (h) skeleton of *Effigia okeeffeae* (from Nesbitt 2007). Grey areas indicate unknown portions of skulls. (a–c, e) from Nesbitt (2011). Scale bars: 1 cm (b, c); 5 cm (a, d, e); 50 cm (f–h). *Abbreviations:* an, angular; aof, antorbital fenestra; d, dentary; en, external naris; f, frontal; j, jugal; la, lacrimal; ltf, lower temporal fenestra; max, maxilla; mf, mandibular fenestra; n, nasal; o, orbit; pf, prefrontal; po, postorbital; pof, postfrontal; pmx, premaxilla; qj, quadratojugal; qu, quadrate; sq, squamosal; su, surangular.

not present in all rausuchians (e.g. the small and toothless shuvosaurids), and most of these features are widespread and/or plesiomorphic among early archosaurs. Although there may not be any clear character states supporting 'Rauisuchia' as monophyletic, a number of apomorphic character states do support the monophyly of various rausuchian subgroups, and a great deal of research over the past decade has succeeded in identifying and clarifying these features. For example, most members of Poposauroida (which includes the ctenosauriscids and shuvosaurids) share an increased number

of sacral vertebrae, a substantial boot on the distal end of the pubis, and a maxilla with a short ascending process (Nesbitt 2011). Members of another group of taxa often called Rauisuchidae, which includes quadrupedal predators such as *Polonosuchus silesiacus*, *Postosuchus kirkpatricki* and *Rauisuchus tiradentes*, share a bulbous ridge on the lateral side of the jugal and a distinct lateral ridge from the nasal to the squamosal (Brusatte *et al.* 2010; Nesbitt 2011; Weinbaum 2011). These examples illustrate some of the recent progress in understanding the anatomy of rausuchians and grouping

some of these taxa into discrete clades, although there is a long way to go.

Here, we briefly synthesize the current understanding of raiusuchians. We highlight current consensus in raiusuchian taxonomy and review the discrete clades (such as Pposauroida and Rausuchidae) that can be identified by derived characters and that have a similar taxonomic composition in recent phylogenetic analyses. We also review advances in studies of raiusuchian palaeobiology beyond systematics. Finally, we end with a road-map of what we consider to be important to future work on raiusuchians.

Terminology

Here, we use Archosauria to refer to the crown group defined by the common ancestor of birds and crocodylians, and all of its descendants (Gauthier & Padian 1985; Gauthier 1986; Sereno 1991). Pseudosuchia (Gauthier & Padian 1985) refers to archosaurs more closely related to crocodylians than to birds, whereas Avemetatarsalia (Benton 1999) refers to archosaurs more closely related to birds than to crocodylians. Note that several authors use the clade name Crurotarsi (node-based group originally) to refer to what we here call Pseudosuchia (e.g. Sereno & Arcucci 1990; Sereno 1991; Benton 1999, 2004; Brusatte *et al.* 2010).

In the late 20th century, Rausuchia Bonaparte 1975 came to encompass an assortment of Triassic genera that were sometimes (although not consistently and with varying definitions and content) partitioned into Linnean families such as Rausuchidae Huene 1942, Ctenosauriscidae Kuhn 1964, Prestosuchidae Romer 1966, Pposauridae (Nopcsa 1923) and Chatterjeeidae Long & Murry 1995 (see Gower 2000; Nesbitt 2011 for further discussion). In that 'Rausuchia', as understood here, includes genera generally referred to these higher taxa, it is highly likely to be non-monophyletic and is therefore used in inverted commas. Raiusuchians, in the sense used here, are best defined as almost all suchians that are not members of Aetosauria or Crocodylomorpha, with additional exceptions comprising a few non-raiusuchian, possible suchians such as *Gracilisuchus stipanicorum* and *Turfanosuchus dabanensis*. Other than Parrish (1993), who redefined Rausuchia to apply to a clade that also included Crocodylomorpha, most authors since the 1990s have understood 'Rausuchia' and raiusuchians in the sense used here.

Phylogenetic definitions

Shifting ideas (most not strongly supported) about the relationships among raiusuchians and other

pseudosuchians has led to a number of challenges when presenting a natural classification based on explicit phylogenetic definitions (*sensu de Queiroz & Gauthier 1990, 1992*). Most workers who have applied numerical phylogenetic methods agree that 'Rausuchia' is not monophyletic, and most have converted pre-cladistic names to clade names (e.g. Rausuchidae: Parrish 1993). Some authors have tied explicit definitions to these latter two types of clade names (e.g. Sereno *et al.* 2005; Weinbaum & Hungerbühler 2007; Brusatte *et al.* 2010), but others have not (e.g. Parrish 1993).

To add to the confusion, different authors even in the cladistic age have used various names to refer to clades with a similar composition and/or the same names for different groups (compare, for example, the use of Rausuchia by Gauthier (1986) and Parrish (1993) and the use of Rausuchidae by Parrish (1993) and Brusatte *et al.* (2010) and Nesbitt (2011)). Although the higher-level relationships of raiusuchians in the most recent large-scale analyses (Brusatte *et al.* 2010; Butler *et al.* 2011; Nesbitt 2011) are far from full agreement, several smaller clades of raiusuchians are compatible (Fig. 2). Therefore, the following list of clade definitions is split into two sections. The first set of clade names refers to groups that have been found in recent analyses using different data sets, and thus appear to be relatively stable. The second set refers to monophyletic groups that have been found in some analyses, but denote a set of either paraphyletic or polyphyletic groups in other analyses. The clade names in the second set should be re-evaluated if subsequent phylogenetic analyses find that the clades, as defined by the phylogenetic definitions, turn out to include other pseudosuchians (e.g. Aetosauria) not intentionally included in the definition.

First set

Rausuchidae Huene 1942. Stem-based definition – the most inclusive clade containing *Rausuchus tiradentes* Huene 1938b but not *Aetosaurus ferratus* Fraas 1877, *Prestosuchus chiniquensis* Huene 1938b, *Poposaurus gracilis* Mehl 1915 or *Crocodylus niloticus* (Laurenti 1768). (*Sensu* Sereno *et al.* 2005.)

Poposauroida Nopcsa 1923. Stem-based definition – the most inclusive clade containing *Poposaurus gracilis* Mehl 1915 but not *Rausuchus tiradentes* Huene 1938b, *Crocodylus niloticus* (Laurenti 1768), *Ornithosuchus longidens* (Huxley 1877) or *Aetosaurus ferratus* Fraas 1877. (*Sensu* Weinbaum & Hungerbühler 2007.)

Shuvosauridae. Node-based definition – the least inclusive clade containing *Shuvosaurus inexpectatus* Chatterjee 1993 and *Sillosuchus*

RAUISUCHIA

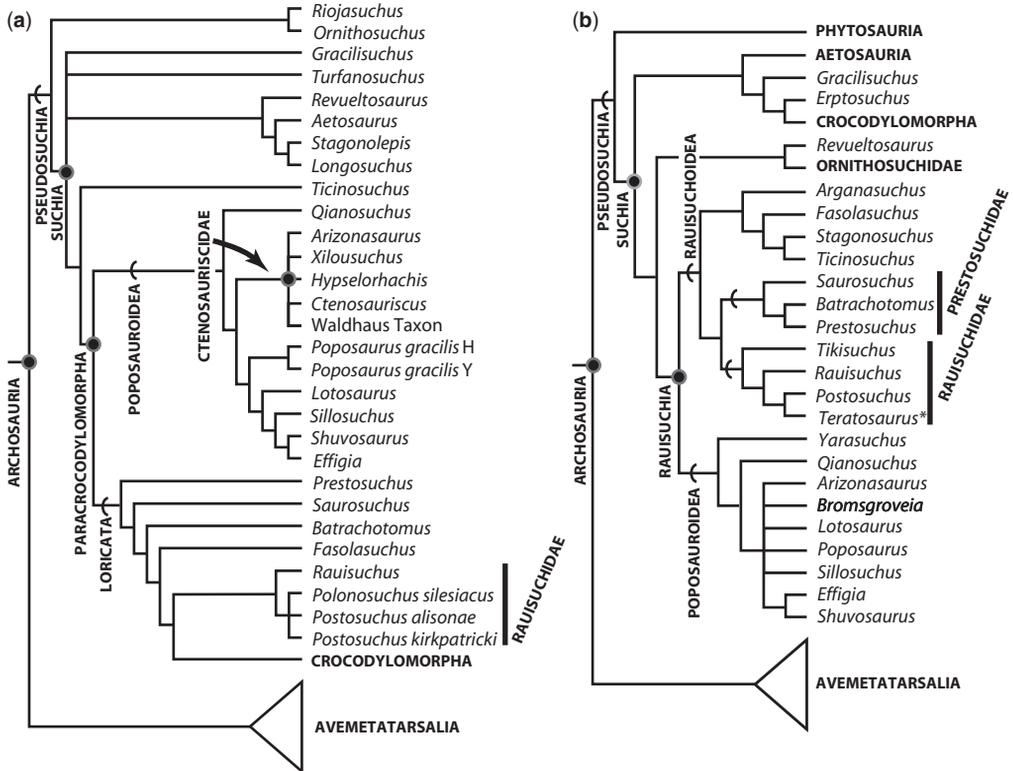


Fig. 2. Recent hypotheses of the relationships of rausuchians within Archosauria of (a) Nesbitt (2011) and (b) Brusatte *et al.* (2010) presented with additional ctenosauriscids in Butler *et al.* (2011). Some larger clades have been simplified (e.g. Avemetatarsalia, Crocodylomorpha) from the original analyses. * refers to *Polonosuchus* after the work of Brusatte *et al.* (2009).

longicervix Alcober & Parrish 1997. (*Sensu* Nesbitt 2011.)

Ctenosauriscidae Kuhn 1964. Stem-based definition – the most inclusive clade containing *Ctenosauriscus koeneni* (Huene 1902) but not *Poposaurus gracilis* Mehl 1915, *Effigia okeeffeae* Nesbitt & Norell 2006, *Postosuchus kirkpatricki* Chatterjee 1985, *Crocodylus niloticus* Laurenti 1768, *Ornithosuchus longidens* (Huxley 1877) or *Aetosaurus ferratus* Fraas 1877. (*Sensu* Butler *et al.* 2011.)

Second set

Rausuchia Bonaparte 1975. Node-based definition – the least inclusive clade containing *Poposaurus gracilis* Mehl 1915, *Batrachotomus kupferzellensis* Gower 1999, *Prestosuchus chiniquensis* Huene 1938b and *Rausuchus tiradentes* Huene 1938b, but not *Crocodylus niloticus* Laurenti 1768, *Ornithosuchus longidens* (Huxley 1877) or *Aetosaurus ferratus* Fraas 1877. (New explicit definition.) This clade name applies only if there is a clade that contains most of the taxa classically

considered rausuchians (i.e. *Postosuchus*-like taxa and *Poposaurus*-like taxa).

Rausuchoidea. Stem-based definition – the most inclusive clade containing *Rausuchus tiradentes* Huene 1938b, but not *Crocodylus niloticus* Laurenti 1768, *Ornithosuchus longidens* (Huxley 1877), *Aetosaurus ferratus* Fraas 1877 or *Poposaurus gracilis* Mehl 1915. (New explicit definition.) This clade name applies only if Rausuchia is monophyletic; in this case, it would refer to a major clade of rausuchians as the sister taxon of Poposauroidae (see Brusatte *et al.* (2010) for an example of this on one phylogenetic topology).

Prestosuchidae Romer 1966. Stem-based definition – the most inclusive clade containing *Prestosuchus chiniquensis* Huene 1938b but not *Rausuchus tiradentes* Huene 1938b, *Aetosaurus ferratus* Fraas 1877, *Poposaurus gracilis* Mehl 1915 or *Crocodylus niloticus* Laurenti 1768. (*Sensu* Sereno *et al.* 2005.)

Paracrocodylomorpha Parrish 1993. Node-based definition – the least inclusive clade

containing *Poposaurus gracilis* Mehl 1915 and *Crocodylus niloticus* Laurenti 1768. (*Sensu* Weinbaum & Hungerbühler 2007.)

Loricata Merrem 1820. Stem-based definition – the most inclusive clade containing *Crocodylus niloticus* Laurenti 1768 but not *Poposaurus gracilis* Mehl 1915, *Ornithosuchus longidens* (Huxley 1877) or *Aetosaurus ferratus* Fraas 1877. (*Sensu* Nesbitt 2011.) This clade name applies only if Paracrocodylomorpha is monophyletic.

Fossil record

Distribution and biogeography

Rauisuchians have been found in sedimentary deposits dating from the Early Triassic to the end of the Late Triassic (Table 1) and have a nearly cosmopolitan distribution (Fig. 3). With one possible exception (see below), rauisuchians are restricted to the Triassic. Most rauisuchians are found in continental terrestrial deposits laid down in floodplains and/or river channels from fluvial environments such as the Chinle Formation of North America (Stewart *et al.* 1972), the Ischigualasto Formation in Argentina (Alcober 2000; Currie *et al.* 2008) and the Santa Maria Formation of Brazil (Schultz *et al.* 2000). Some are clearly from strongly seasonal environments, including taxa from the major known clades, such as *Ticinosuchus ferox*, *Effigia okeeffeae* and *Rauisuchus tiradentes* (Golonka & Ford 2000; Pires *et al.* 2005; Nützel *et al.* 2010). A few terrestrial rauisuchians, however, were fossilized after apparently being washed into a brackish lagoon/lake (e.g. *Batrachotomus kupferzellensis*; Schoch 2002; Hagdorn & Mutter 2011) or marine intraplatform basin (e.g. *Ticinosuchus ferox*, found in one of the most diverse Triassic Lagerstätten) environments (Krebs 1965; Lautenschlager & Desojo 2011), and at least one taxon (*Qianosuchus mixtus*) was possibly semi-aquatic and is preserved in coastal limestones (Li *et al.* 2006; Nesbitt 2011).

Rauisuchians are commonly present in most vertebrate-producing Triassic formations. With that being said, we urge caution in interpreting some published records of rauisuchian distribution. Many reports of Triassic vertebrate faunas/assemblages from around the world include rauisuchians in faunal lists (e.g. Renesto *et al.* 2003; Heckert 2004; Heckert *et al.* 2012), but many of these occurrences are based exclusively on teeth, which we consider non-diagnostic to any subgroup of rauisuchians at this point in time (because rauisuchian-like recurved teeth are present in many groups of amniotes). Therefore, we have not included those occurrences in our review and have focused on named and diagnostic material.

North America boasts one of the most diverse fossil records of rauisuchians and has yielded members of the clades Ctenosauriscidae, Shuvosauridae and Rauisuchidae, as well as a few other forms. Furthermore, the fossil record of North American rauisuchians extends from the early part of the Middle Triassic to nearly the end of the Triassic (Fig. 3). The earliest forms are from the top (early Anisian portion) of the Moenkopi Formation in Arizona and New Mexico (Nesbitt 2003, 2005a, b; Schoch *et al.* 2010). *Heptasuchus clarki* from central Wyoming was always considered to be Upper Triassic in age (Dawley *et al.* 1979), but recent work suggests that it may be Middle Triassic (Zawiskie *et al.* 2011). The majority of North American rauisuchian taxa are from the Upper Triassic Chinle Formation of Utah (Gauthier *et al.* 2011), Arizona (Long & Murry 1995; Parker & Irmis 2005), Colorado (Small 2001) and New Mexico (Long & Murry 1995), and also the Dockum Group of New Mexico (Hunt 1994) and Texas (Chatterjee 1985; Long & Murry 1995). These rauisuchians have been found throughout the aforementioned formations and are commonly found in major bonebeds, including the *Placerias* Quarry (Long & Murry 1995), the Post Quarry (Chatterjee 1985), the Otis Chalk Quarries (Elder 1978), Hayden Quarry (Irmis *et al.* 2007) and the *Coelophys* Quarry (Nesbitt & Norell 2006; Nesbitt 2007). Only one specimen, of *Postosuchus alisonae*, has been found in the Newark Super Group of the eastern portion of North America (Peyer *et al.* 2008).

Rauisuchians are also widespread across Eurasia, with specimens ranging from the Early to the Late Triassic. Well-preserved material has been found at various stratigraphic levels throughout the Germanic Basin, including the upper Lower Triassic Solling Formation (= Middle Buntsandstein) of Germany (Butler *et al.* 2011), the Middle Triassic Erfurt Formation of southern Germany (Gower 1999; Gower & Schoch 2009), the Upper Triassic Löwenstein Formation (= Stubensandstein) of Germany (Galton 1985; Benton 1986a) and the Upper Triassic strata of southern Poland (Sulej 2005; Brusatte *et al.* 2009). Additional remains of named forms in western Europe are from the Middle Triassic of the United Kingdom (Benton & Gower 1997) and *Ticinosuchus ferox* from near the Anisian–Ladinian boundary in Switzerland (Krebs 1965) and possibly from Besano, Northern Italy (Lautenschlager & Desojo 2011). A number of reptiles referred to different subgroups of rauisuchians have been reported from the Triassic formations along the flanks of the Ural Mountains in Russia. However, with a single exception, these forms cannot be confidently assigned to any rauisuchian subgroups (Gower 2000; Gower & Sennikov

Table 1. Summary of rauisuchian taxa.

Taxa	Occurrence	Age	Material
Poposauroidae Nopsca 1923 <i>Qianosuchus mixtus</i> Li <i>et al.</i> 2006	Guanling Fm./Guizhou, China	Middle Triassic: Anisian	Nearly complete skull and postcranial skeleton (based on three articulated specimens) (3)
Ctenosauriscidae Kuhn 1964 <i>Arizonasaurus babbitti</i> Welles 1947	Moenkopi Fm./Arizona and New Mexico, SW USA	Middle Triassic: Anisian	Partial skull, cervical, dorsal and sacral vertebrae, and nearly complete pectoral and pelvic girdles (2+)
<i>Xilousuchus sapingensis</i> Wu 1981	Heshangou Fm./Shaanxi, China	Lower–Middle Triassic: late Olenekian–?early Anisian	Partial skull, anterior region of axial skeleton and appendicular fragments (1)
<i>Ctenosauriscus koeneni</i> Huene (1902) <i>sensu</i> Kuhn 1964 (=‘ <i>Ctenosaurus koeneni</i>)	Upper Middle Buntsandstein, Solling Fm./Lower Saxony, north Germany	Lower Triassic: Olenekian	Partial axial skeleton, including some cervical, dorsal, sacral and caudal vertebra and ribs; unidentified fragments (? pectoral girdle) (1)
<i>Hypselorhachis mirabilis</i> Butler <i>et al.</i> 2009	Lifua Mb., Manda beds./SW Tanzania	Middle Triassic: late Anisian	Anterior dorsal vertebra (1)
<i>Bromsgroveia walkeri</i> Galton 1985	Bromsgrove Sandstone Fm./Warwickshire, England	Middle Triassic: Anisian	Dorsal, sacral and caudal fragmentary vertebra, and partial pelvic girdle (~1)
‘Waldhaus taxon’ Butler <i>et al.</i> 2011	Röt Fm./Baden-Württemberg, Germany	Middle Triassic: earliest Anisian	Ilium, vertebrae (~5)
<i>Poposaurus gracilis</i> Mehl 1915 <i>sensu</i> Weinbaum & Hungerbühler 2007	Popo Agie Fm., Chinle Fm., and Dockum Gr./SW USA	Late Triassic: early–mid Norian	Cranial fragments and nearly complete postcranial skeleton (based on several specimens) (10+)
<i>Poposaurus langstoni</i> Long & Murry (1995) <i>sensu</i> Weinbaum & Hungerbühler 2007 (=‘ <i>Lythrosuchus langstoni</i>)	Colorado City Fm. Dockum Gr./Texas, SW USA	Late Triassic: early Norian	Cervical and dorsal fragmentary vertebra, and partial pelvic girdle (1)
<i>Lotosaurus adentus</i> Zhang 1975	Butang Fm./Hunan, China	Middle Triassic: Anisian	Articulated and disarticulated individuals, including cranial and postcranial remains (10+)
‘Moenkopi Shuvosaurid’	Moenkopi Fm./Arizona and New Mexico, SW USA	Middle Triassic: Anisian	Partial pelvic girdle, femora (5)
Shuvosauridae Chatterjee 1993 <i>Sillosuchus longicervix</i> Alcober & Parrish 1997	Ischigualasto Fm./San Juan, Argentina	Late Triassic: late Carnian	Partial postcranial skeleton, referred material (3)

(Continued)

Table 1. *Continued*

Taxa	Occurrence	Age	Material
<i>Shuvosaurus inexpectatus</i> Long & Murry 1995 <i>sensu</i> Nesbitt 2007	Cooper Canyon Fm., Dockum Grp./ Texas, SW USA	Late Triassic: early–mid Norian	Nearly complete skull and partial postcranial (based on several specimens, including ' <i>Chatterjeea elegans</i> ') (10+)
<i>Effigia okeeffeae</i> Nesbitt & Norell 2006	Chinle Fm. (<i>Coelophysis</i> Quarry)/New Mexico, SW USA	Late Triassic: late Norian	Nearly complete skull and postcranial skeleton (based on four articulated specimens) (4+)
Rauisuchidae Huene 1942			
<i>Rauisuchus tiradentes</i> Huene 1938b	Santa Maria Fm. (<i>Hyperodapedon</i> AZ)/Santa Maria Area (Rio Grande do Sul), S Brazil	Late Triassic: Carnian	Partial cranial and postcranial skeleton (based on four original specimens from two distinct localities) (1)
<i>Polonosuchus silesiacus</i> Sulej (2005) <i>sensu</i> Brusatte <i>et al.</i> 2009 (= ' <i>Teratosaurus</i> ' <i>silesiacus</i>)	Drawno Beds, Krasiejów/Opole Silesia, S Poland	Late Triassic: Norian	Nearly complete skull and partial anterior region of axial skeleton, partial mid-caudal series (1)
<i>Postosuchus kirkpatricki</i> Chatterjee 1985	Cooper Canyon Fm., Dockum Grp. and Chinle Fm. SW USA	Late Triassic: Norian	Nearly complete cranial and postcranial skeleton (based on several specimens) (2)
<i>Postosuchus alisonae</i> Peyer <i>et al.</i> 2008	Deep River Basin, Newark Supergroup./North Carolina	Late Triassic: mid Norian	Fragmentary cranial bones and partial postcranial skeleton (1)
<i>Tikisuchus romeri</i> Chatterjee & Majumdar 1987	Tiki Fm./ Madhya Pradesh, Indian	Late Triassic: Carnian	Partial cranial and postcranial remains (1+)
? <i>Teratosaurus suevicus</i> Meyer 1861	Löwenstein Formation (=middle Stubensandstein/Baden- Württemberg, Germany	Late Triassic: ?mid Norian	Isolated right maxilla (1)
Rauisuchians			
<i>Ticinosuchus ferox</i> Krebs 1965	Middle Grenzbitumenzone (<i>polymorphus</i> -Z)/Switzerland and north Italy	Middle Triassic: late Anisian	Partial cranial and nearly complete postcranial skeleton (3)
<i>Prestosuchus chiniquensis</i> Huene 1938b	Santa Maria Fm. (<i>Dinodontosaurus</i> AZ)/Rio Grande do Sul, south Brazil	Middle Triassic: Ladinian	Nearly complete cranial and postcranial elements (based on two original specimens from two distinct localities and at least three other specimens from other localities) (5)
<i>Prestosuchus loricatus</i> Huene 1938b	Santa Maria Fm. (<i>Dinodontosaurus</i> AZ)/Chiniquá Area (Rio Grande do Sul), south Brazil	Middle Triassic: Ladinian	Teeth fragments, osteoderms, cervical and caudal vertebrae and appendicular fragments (e.g. scapula, calcaneum, ischium and metatarsal) (2)
<i>Saurosuchus galilei</i> Reig 1959	Ischigualasto Fm./San Juan and La Rioja, NW Argentina	Late Triassic: late Carnian	Nearly complete cranial and postcranial skeleton (based on several specimens) (5+)
<i>Batrachotomus kupferzellensis</i> Gower 1999	Lower Keuper, Erfurt Fm. (Upper Lettenkeuper sequence)/ Baden-Württemberg, south Germany	Middle Triassic: Ladinian	Nearly complete skull and postcranial skeleton, except manus (5+)

<i>Fasolasuchus tenax</i> Bonaparte 1981 'Otis Chalk taxon'	Upper Los Colorados Fm./La Rioja, NW Argentina Colorado City Fm. Dockum Grp./ Texas, USA	Late Triassic: late Norian Late Triassic	Partial skull elements, including partial mandible, and postcranial skeleton (2) Complete maxilla and partial skull (2)
<i>Heptasuchus clarki</i> Dawley <i>et al.</i> 1979	Popo Agie Fm./Wyoming, SW USA	Late Triassic: early Norian	Partial cranial and postcranial skeleton (based on at least four specimens) (3+)
<i>Arganasuchus dutuiti</i> Jalil & Peyer 2007	Irohalene Mb., Timezgadiouine Fm. (Lower part of unit T5)/Argana, Morocco	Late Triassic: Carnian	Maxilla, partial mandibles, partial vertebrae, ribs, pubis and hindlimb (4+)
<i>Stagonosuchus nyassicus</i> Huene 1938a	Lifua Mb., Manda Beds/SW Tanzania	Middle Triassic: late Anisian	Cranial fragments and partial postcranial skeleton (2)
<i>Luperosuchus fractus</i> Romer 1971	Chañares Fm./La Rioja, SW Argentina	Middle Triassic: Ladinian	Partial skull roof and palate (2)
' <i>Mandasuchus tanyauchen</i> ' Charig 1956	Lifua Mb., Manda Beds/SW Tanzania	Middle Triassic: late Anisian	Partial mandible and postcranial skeletons (3)
' <i>Pallisteria angustimentum</i> ' Charig 1967	Lifua Mb., Manda Beds/SW Tanzania	Middle Triassic: late Anisian	Partial skull and postcranial fragments (1)
<i>Vytshegdosuchus zheshartensis</i> Sennikov 1988	Upper Yarenskian Horizon/Komi, Russian	Lower Triassic: late Olenekian	Cranial fragments, ilium, fragmentary femur and other postcranial bones (~1)
<i>Decuriasuchus quartacolonina</i> França <i>et al.</i> 2011	Santa Maria Fm. (<i>Dinodontosaurus</i> AZ)/Quarta Colonia Area, Rio Grande do Sul, south Brazil	Middle Triassic: Ladinian	Nearly complete skull and postcranial skeleton (10+)
SAM 383 Problematica	upper Elliot Fm./South Africa	?Early Jurassic	Partial maxilla with teeth (1)
<i>Dongusuchus efremovi</i> Sennikov 1988	Donguz Horizon/Orenburg, Russia	Middle Triassic: Anisian	Cervical vertebra and femur (~1)
<i>Energosuchus garjainovi</i> Ochev 1986	Bukobay Horizon/Orenburg, Russian	Middle Triassic: Ladinian	Cervical vertebra, humerus, radius, incomplete coracoid (~1)
<i>Fenhosuchus cristatus</i> Young 1964	Upper Ehrmayng Fm./Shanxi, China	Middle Triassic	Cranial and postcranial fragments (?)
<i>Jaikosuchus magnus</i> Sennikov 1990	Yarenga Horizon/Orenburg, Russia	Lower Triassic: late Olenekian	Two cervical vertebrae (1)
<i>Jushatyria vjushkovi</i> Kalandadze & Sennikov 1985	Bukobay Horizon/Bashkortostan, Russian	Middle Triassic: Ladinian	Incomplete maxilla (1)
<i>Procerosuchus celer</i> Huene 1938b	Santa Maria Fm. (<i>Dinodontosaurus</i> AZ)/Chiniquá Area (Rio Grande do Sul), south Brazil	Middle Triassic: Ladinian	Cranial fragments, pectoral girdle and appendicular fragments (2)

(Continued)

Table 1. *Continued*

Taxa	Occurrence	Age	Material
<i>Scythosuchus basileus</i> Sennikov 1999	Lipovskaya Fm./Sirovinskaya, Ilovinskiy District, Russia	Lower Triassic: late Olenekian	Skull fragments (squamosal, postfrontal, maxillae, teeth and articular region of lower jaw ramus), fragmentary axial elements axial, partial humerus, ilium and femur, complete tibia and calcaneum with some distal tarsals (?)
<i>Tsylmosuchus donensis</i> Sennikov 1990	Yarenga Horizon/Volgograd, Russia	Lower Triassic: late Olenekian	Cervical vertebra (1)
<i>Tsylmosuchus jakovlevi</i> Sennikov 1990	Ustmylian Horizon/Komi, Russia	Lower Triassic: Olenekian	Cervical vertebra and incomplete ilium (~1)
<i>Tsylmosuchus samariensis</i> Sennikov 1990	Rybinkian Horizon/Obshchii Syrt Area, Russia	Lower Triassic: Induan	Incomplete vertebra (1)
' <i>Youngosuchus</i> ' <i>sinensis</i> (Young, 1973) <i>sensu</i> Kalandadze & Sennikov 1985	Kelamauy Fm./Sinkiang, China	Middle Triassic	Partial skull, cervical vertebra, ribs, pectoral girdle and forelimb (1)
<i>Vjushkovisaurus berdjansensis</i> Ochev 1982	Donguz Horizon/Orenburg, Russian	Middle Triassic: Anisian	Cervical and dorsal vertebra, and humerus (~1)
<i>Wangisuchus tzeyii</i> Young 1964	Ermaying Fm./Shanxi, China	Middle Triassic: Anisian	Maxilla and other postcranial remains (~1)
<i>Yarasuchus deccanensis</i> Sen 2005	Yerrapalli Fm./Andhra Pradesh, India	Middle Triassic: Anisian	Skull fragments and partial postcranial skeleton (2+)

Numbers in parentheses refer to number of unique specimens.

RAUISUCHIA

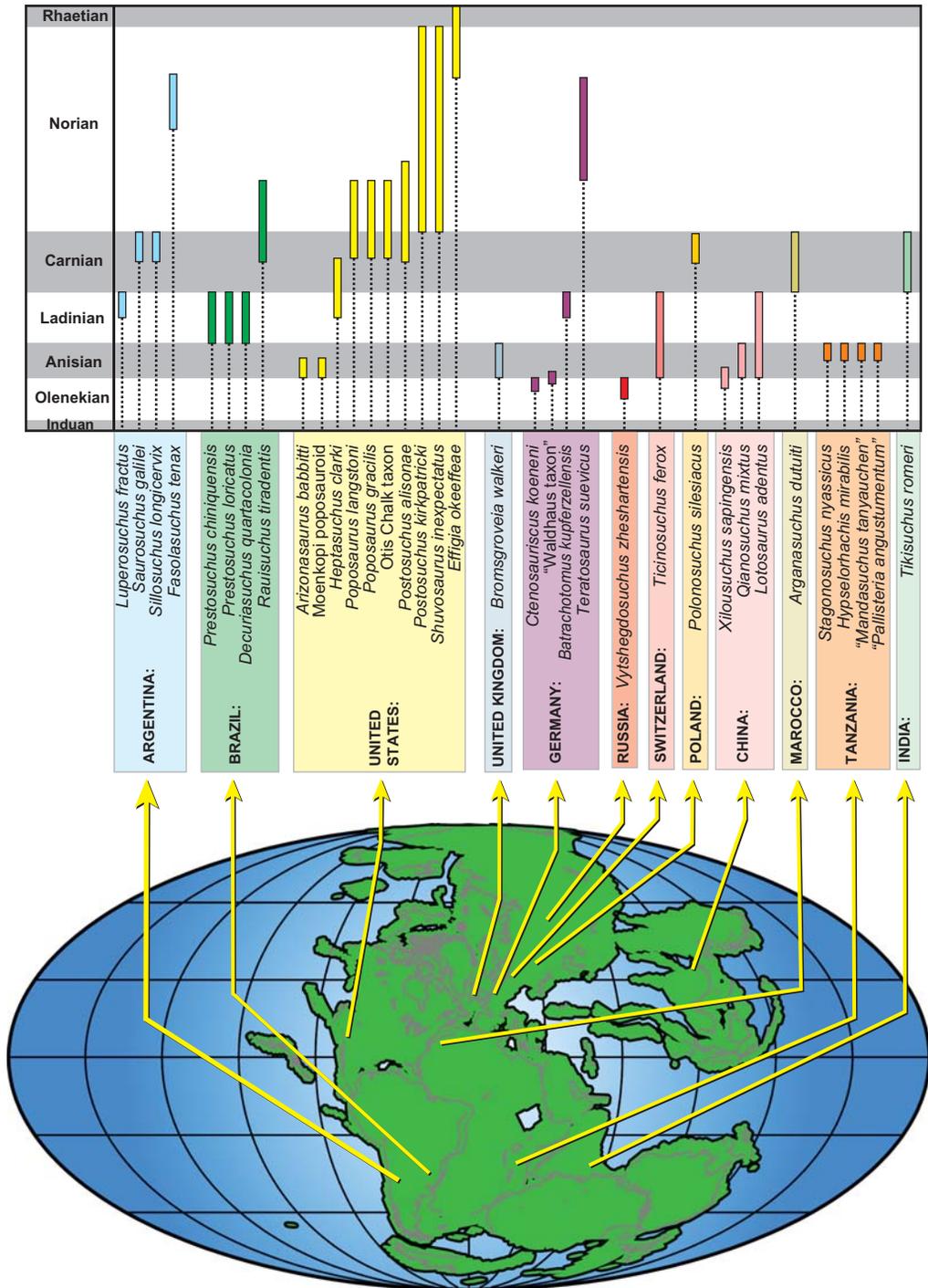


Fig. 3. Distribution of rausuchians in time and space. The ranges of the individual taxa represent age error and do not represent stratigraphic range. Modified from França 2011.

2000; Butler *et al.* 2011; Nesbitt 2011). Some well-preserved raiisuchian skeletons have been found throughout the Triassic formations in China, including one of the oldest forms from the Early–Middle Triassic Heshanggou Formation (Nesbitt *et al.* 2011a) as well as others from the Middle Triassic Batung Formation (Zhang 1975; Nesbitt 2011) and the marine deposits of the Anisian Guanlang Formation (Li *et al.* 2006). Only one clear raiisuchian (*Tikisuchus romeri*, which is probably a member of Raiisuchidae) has been found so far in the Late Triassic formations of India (Chatterjee & Majumdar 1987), but other possible raiisuchian material (*Yarasuchus deccanensis*; see below) is from the underlying Middle Triassic Yerrapalli Formation (Sen 2005).

Raiisuchians were first recognized from the extensive Triassic deposits in South America, and remains have been recovered from several Middle-to-Late Triassic formations in both Argentina and Brazil. The oldest forms are *Luperosuchus fractus* from the Middle Triassic Chañares Formation of Argentina (Romer 1971) and Huene's raiisuchids (*Prestosuchus chiniquensis*, '*Prestosuchus*' *loricatus*, *Procerosuchus celer*) from the Middle Triassic portion of the Santa Maria sequence (Santa Maria 1 Sequence, *Dinodontosaurus* Assemblage Zone) in Brazil (Zerfass *et al.* 2003; Langer 2005; Desojo & Rauhut 2009; França *et al.* 2011). *Sillosuchus longicervix* and *Saurosuchus galilei* co-occur in the end-Carnian portion of the Ischigualasto Formation in Argentina (Nesbitt 2011), whereas *Fasolasuchus tenax* is from the Late Triassic Los Colorados Formation of Argentina (Bonaparte 1981), and *Raiisuchus tiradentes* is from the Late Triassic portion of the Santa Maria sequence (Santa Maria 2 Sequence, *Hyperodapedon* Assemblage Zone) in Brazil.

A reasonable amount of African raiisuchian material is known, although much of this has only been studied recently. A number of diverse forms occur in the Anisian Manda beds of Tanzania, including the large taxon *Stagonosuchus nyassicus* (Huene 1938a; Gebauer 2004; Lautenschlager & Desojo 2011) and the sail-backed form *Hypselorhachis mirabilis* (Charig 1967; Butler *et al.* 2009). These two taxa co-occur with specimens that have yet to be formally described but have been referred to in the literature as '*Mandasuchus tanyauchen*', '*Pallisteria angustimentum*' and '*Teleocrater rhadinus*', as well as with a new form that may pertain to a raiisuchian (Nesbitt *et al.* 2011b; see also Charig 1956). This is the most diverse concurrent assemblage of raiisuchians yet known. Another African taxon, *Arganasuchus dutuiti*, is known from well-preserved but fragmentary remains from the Late Triassic Timezgadiouine Formation of Morocco (Jalil & Peyr 2007).

The absence of a robust, well-resolved comprehensive raiisuchian phylogeny has prevented the establishment of well-supported biogeographical hypotheses to explain the distribution of these taxa. However, it is possible to comment on the distribution of certain subgroups whose relationships are better defined. Members of the sail-backed *Ctenosauriscidae* ranged from the end of the Early Triassic to the end of the Anisian (Butler *et al.* 2011), and during this short duration the group was established across Pangaea, reaching a cosmopolitan distribution before any other archosaur subgroup (Butler *et al.* 2011; Nesbitt 2011). Members of the large-skulled Raiisuchidae had a wide range during the Late Triassic, including South America, North America and Europe, but this clade may have been present only from the end Carnian through the mid-Norian. One of the longest-lived clades was the Shuvosauridae and their immediate sister taxa (unnamed node within *Poposauroida*) (Fig. 2). Anisian members of this clade have been reported (Nesbitt 2005b; Schoch *et al.* 2010), but better-known members of Shuvosauridae represented by nearly complete skeletons (e.g. *Effigia okeeffeae*: Nesbitt & Norell 2006) nearly reach the end of the Triassic. Shuvosauridae also has a fossil record spanning North and South America (Alcober & Parrish 1997; Nesbitt 2011).

Oldest record

A handful of species from the Early Triassic of Russia have been named and classified as raiisuchians by Ochev (1979, 1982, 1986), Kalandadze & Sennikov (1985) and Sennikov (1988, 1990, 1999). These are based on fragmentary fossils with no clear association; their ages are poorly constrained and they (mostly) preserve no clear synapomorphies linking them to raiisuchian clades (Table 2; Gower & Sennikov 2000). That being said, at least some of the holotype material (an ilium) of *Vytshegdosuchus zheshartensis* shares character states with other raiisuchians (Gower & Sennikov 2000; Nesbitt 2011), and we suggest that this specimen probably pertains to a raiisuchian.

The oldest confirmed raiisuchians are ctenosauriscid poposauroids, which appear in at least two locations in northern Pangaea during the late Olenekian to the early Anisian (Fig. 3). The oldest record is *Ctenosauriscus koeneni* Kuhn 1964 from the upper Middle Buntsandstein, Solling Formation, latest Olenekian (Butler *et al.* 2011). Similar in age but possibly slightly younger is *Xilosuchus sapingensis* Wu 1981, known from good head and neck material of a single specimen from China from the late Olenekian/early Anisian (Nesbitt *et al.* 2011a; see Butler *et al.* 2011 for a detailed discussion on the ages of *Ctenosauriscus koeneni* and

Table 2. *Taxa once considered to be raulisuchians*

Taxon	Occurrence	Age	Material	Current classification	Raulisuchian classification
<i>Zanclodon</i> sp. Plieninger 1846	Various localities from Europa	Triassic	Fragmentary bones	Archosauriformes Schoch (2011)	Raulisuchia Sennikov (1995)
<i>Typothorax</i> sp. Cope 1875	Chinle Fm., Bull Canyon Fm./Arizona, New Mexico, Texas, SW USA	Late Triassic	Several specimens	Aetosauria	Raulisuchidae Huene (1956)
<i>Ornithosuchus</i> <i>woodwardi</i> Huxley 1877 <i>sensu</i> Walker 1964	Lossiemouth Sandstone Fm./Elgin Area, Scotland	Late Triassic: ?late Carnian	Partial cranial and postcranial (based on several specimens)	Early Pseudosuchia: Ornithosuchidae Nesbitt (2011)	Raulisuchia: Ornithosuchidae França <i>et al.</i> (2011)
' <i>Episcoposaurus</i> ' <i>horridus</i> Cope 1887	Petrified Forest Mb., Chinle Fm./New Mexico, SW USA	Late Triassic: mid Norian	Skull fragment, two caudal vertebra and appendicular skeleton fragments	<i>Typothorax horridus</i> Huene (1915)/junior subjective synonym of <i>Typothorax</i> <i>coccinarum</i> Lucas <i>et al.</i> (2007)/Aetosauria	Raulisuchidae Huene (1956)
' <i>Episcoposaurus</i> ' <i>haplocerus</i> Cope 1887	Dockum Grp./Texas SW USA	Late Triassic: Norian	Several vertebrae, scapula, osteoderms	<i>Desmotosuchus haplocerus</i> Gregory (1953)/ Aetosauria	Raulisuchidae Huene (1956)
<i>Hoplitosuchus rauli</i> Huene 1938b	Santa Maria Fm. (<i>Hyperodapedon</i> AZ)/ Santa Maria Area (Rio Grande do Sul), south Brazil	Late Triassic: Carnian	Femur, tibia, osteoderms and possibly calcaneum	?Archosauria/ <i>nomem</i> <i>dubium</i>	Prestosuchidae (Raulisuchidae) Romer (1972)
<i>Dongusia colorata</i> Huene 1940	Donguz Fm./Orenburg, Russian	Middle Triassic: Anisian	Isolated dorsal vertebra	Erythrosuchidae Gower & Sennikov (2000)	Raulisuchia Sennikov (1995)
<i>Spondylosoma</i> <i>absconditum</i> Huene 1942	Santa Maria Fm. (<i>Dinodontosaurus</i> AZ)/ Chiniquá Area, Rio Grande do Sul, south Brazil	Middle Triassic: Ladinian	Partial axial skeleton	Dinosauria indet. Langer (2004)	Raulisuchian Galton (2000)

(Continued)

Table 2. *Continued*

Taxon	Occurrence	Age	Material	Current classification	Rauisuchian classification
<i>Cerritosaurus binsfeldi</i> Price 1946	Santa Maria Fm./Santa Maria Area, Rio Grande do Sul, south Brazil	Middle–Late Triassic (unspecified site)	Partial cranial and postcranial skeleton	Proterochampsidae	Rauisuchidae Huene (1956)
<i>Sinosaurus triassicus</i> Young 1948	Lufeng Fm./Yunnan, China	?Late Triassic–?Lower Jurassic	Maxilla, partial mandible and tooth	Saurischia (Dinosauria) Young (1948)/basal Theropoda (Dinosauria) Rauhut (2003)	Rauisuchian Carroll (1988); Sennikov (1995)
<i>Cuyosuchus huenei</i> Reig 1961	Cachueta Fm./Mendoza, Argentina	Late Triassic	Partial postcranial skeleton	Archosauriformes indet.	Rauisuchidae Huene (1956)
<i>Shansisuchus shansisuchus</i> Young 1964	Ermaying Fm./Wuhsiang, China	Middle Triassic: Anisian	Partial cranial and postcranial skeleton	Erythrosuchidae Charig & Reig (1970)	Rauisuchidae Huene (1956)
<i>Riojasuchus tenuisiceps</i> Bonaparte 1967	Los Colorados Fm./El Salto, Argentina	Late Triassic: Norian–?Rhaetian	Complete skull and nearly complete postcranial skeleton (based in four specimens)	Early Pseudosuchia: Ornithosuchidae Nesbitt (2011)	Rauisuchia: Ornithosuchidae França <i>et al.</i> (2011)
<i>Gracilisuchus stipaniceorum</i> Romer 1972	Chañares Fm./La Rioja, Argentina	Middle Triassic: Ladinian	Nearly complete skull and postcranial skeleton	Early Suchia Nesbitt (2011)	Rauisuchia Parrish (1993)

RAUISUCHIA

Xilosuchus sapingensis). These well-constrained ages for these ctenosauriscids also double as the oldest confirmed dates for both Pseudosuchia and Archosauria as a whole (Nesbitt 2011; Nesbitt *et al.* 2011a; Butler *et al.* 2011; Brusatte *et al.* 2011).

A variety of other raiusuchians are known from the Middle Triassic, including the Anisian ‘*Mandasuchus tanyauchen*’ (Charig 1967), *Stagonosuchus nyassicus* (Huene 1938a) and possibly ‘*Pallisteria angustimentum*’ from the Manda beds, and *Prestosuchus chiniquensis* (Huene 1938b) and *Decuriasuchus quartacolonina* (França *et al.* 2011) from the Ladinian (*Dinodontosaurus* Assemblage Zone) part of the Santa Maria Formation. However, the exact ages of these rocks are not clear.

Youngest record

Analyses of the end-Triassic extinction (e.g. Benton 1986b, 1994; Olsen & Sues 1986) have depicted raiusuchians extending to the end of the Triassic. However, the previously presented data have three notable limitations: (i) the raiusuchians used in these studies are not monophyletic; (ii) revisions in the Triassic timescale (Muttoni *et al.* 2004; Furin *et al.* 2006; Mundil *et al.* 2010) have changed stratigraphic ranges; and (iii) the vertebrate fossil record in the latest Triassic is poor globally (Sues & Fraser 2010). *Fasolasuchus tenax* from the top of the Los Colorados Formation was previously thought to be one of the youngest occurrences from the latest Triassic (Lucas 1998; Arcucci *et al.* 2004), but new magnetostratigraphic data (Santi Malnis *et al.* 2011) suggest a mid-Norian date approximately equivalent to the age of *Postosuchus kirkpatricki*, c. 217–215 million years ago (mya) (Irmis *et al.* 2010). The youngest known poposauroid is clearly *Effigia okeeffeae* from the late Norian or Rhaetian *Coelophysis* Quarry (Nesbitt 2007; Zeigler & Geissman 2011). A specimen referred to *Postosuchus sp.* (CM 73372) was recorded from the same quarry (Long & Murry 1995; Weinbaum 2002; Novak 2004; Peyer *et al.* 2008), and if it belongs to *Postosuchus kirkpatricki* it would represent the youngest known occurrence of Raiusuchidae. Recently, however, Nesbitt (2011) hypothesized a crocodylomorph relationship for this specimen. Clearly, the discovery and study of latest Triassic raiusuchians is a pressing area of future research.

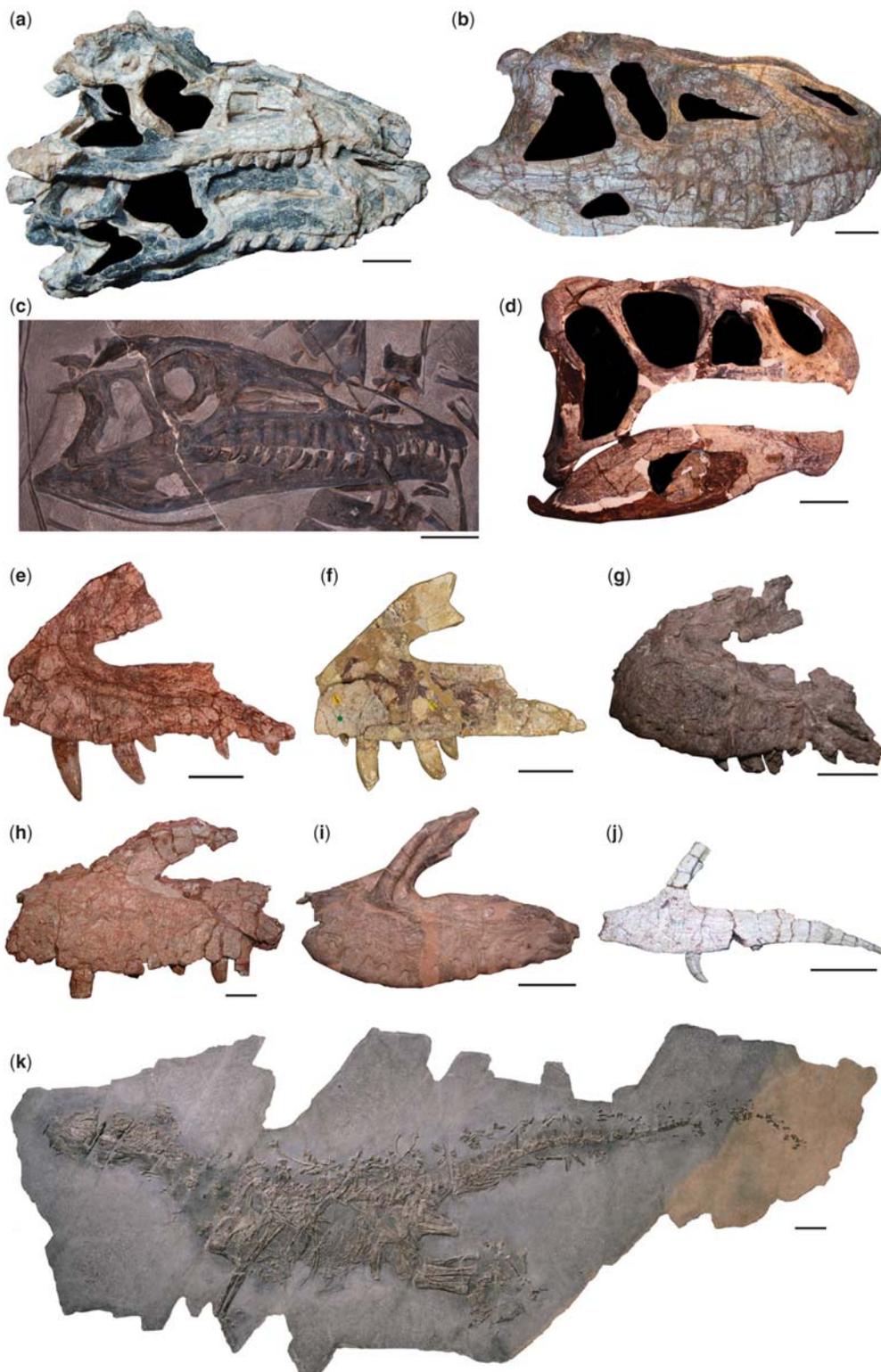
The only possible early Jurassic record of a raiusuchian belongs to a single specimen from the upper Elliot Formation of South Africa (Nesbitt and R. Smith unpublished data). The specimen (SAM 383) consists of the posterior portion of a maxilla with portions of five teeth from an animal with a skull length estimated to be c.1 m. It is unclear if some features of the maxilla that it shares with raiusuchians (e.g. *Fasolasuchus tenax*) are apomorphic

(rectangular posterior portion of the maxilla in lateral view, fused interdental plates, shallow antorbital fossa, large posteriorly opening foramen on posterior portion maxilla in medial view). Alternatively, it is possible that the maxilla could belong to an early crocodylomorph. Additional material and a better understanding of character evolution in raiusuchians and early crocodylomorphs are needed to more confidently identify this intriguing specimen.

Relationships and evolution

Raiusuchian taxonomy and evolution have been poorly understood because of a number of factors, including poor preservation of specimens, a fragmentary fossil record, incomplete descriptions, confusion in sorting alpha-level taxonomy and an incomplete understanding of Triassic pseudosuchian relationships. Details of the tortured taxonomic history of raiusuchian classification are provided elsewhere (see Gower 2000; Brusatte *et al.* 2010; Nesbitt 2011) and will not be repeated here. However, the combination of an increasingly more complete fossil record with advances in phylogenetic methodologies (e.g. character construction, Sereno 2007; taxon inclusion, Brusatte 2010) in studying early archosaurs has led to a number of breakthroughs in understanding raiusuchian systematics. For example, early archosaur phylogenies (e.g. Juul 1994) including raiusuchians often used composite scoring for suprageneric taxa that assumed the monophyly of groups such as Prestosuchidae. Lately, better-sampled archosaur phylogenies (Brusatte *et al.* 2010; Butler *et al.* 2011; Nesbitt 2011) including raiusuchians have used species- or genus-level terminal taxa that do not assume the monophyly of Raiusuchia or major subgroups of raiusuchians. Even with those methodologies in place, however, there is still no consensus about raiusuchian relationships as a whole, although the framework of one does seem to be emerging. This will, of course, only become clear with further analyses.

The following descriptions of the relationships and evolution of raiusuchians follow the recent works of Brusatte *et al.* (2010) and Nesbitt (2011) and revised iterations of those matrices in Butler *et al.* (2011). These two large analyses disagree on the fundamental relationships of raiusuchians; Brusatte *et al.* (2010) found a monophyletic Raiusuchia (albeit with minimal support, and overturned by the revised analysis in Butler *et al.* 2011), whereas Nesbitt (2011) found a paraphyletic ‘Raiusuchia’ with respect to Crocodylomorpha (Fig. 2). However, although these two analyses differ fundamentally, both works recovered similar relationships



RAUISUCHIA

among raiusuchids and poposauroids, and the relationships of these two clades will be expanded on below. The relationships of the remaining raiusuchians included in Brusatte *et al.* (2010) and Butler *et al.* (2011) and some included in Nesbitt (2011) – *Arganasuchus dutuiti*, *Fasolasuchus tenax*, *Stagonosuchus nyassicus*, *Ticinosuchus ferox*, *Saurosuchus galilei*, *Batrachotomus kuperferzellensis* and *Prestosuchus chiniquensis* – will not be discussed further as the relationships of these taxa are far from understood at this point in time.

Poposauroidae

The phylogenetic analyses of Nesbitt (2003), Nesbitt & Norell (2006), Weinbaum & Hungerbühler (2007), Brusatte *et al.* (2010) and Nesbitt (2011) have examined the relationships of a diverse array of raiusuchians (Figs 3 & 4) and have found a group of raiusuchians with affinities to *Poposaurus gracilis*. This clade, Poposauroidae (see definition above), is one of the best-supported subgroups of raiusuchians. Poposauroidae (equivalent to ‘group X’ of Nesbitt 2007) includes an eclectic array of archosaurs ranging in body size, locomotor strategies and seemingly dietary ecologies, with a stratigraphic range from the end of the Early Triassic (*Ctenosauriscus koeneni*) to the end of the Triassic (*Effigia okeeffeae*). Taxonomically, Poposauroidae comprises *Qianosuchus mixtus*, *Lotosaurus adentus*, *Poposaurus gracilis*, *Poposaurus langstoni*, Ctenosauriscidae and Shuvosauridae.

Both Brusatte *et al.* (2010) and Nesbitt (2011) recovered a similar set of taxa within Poposauroidae, but there are a few important differences between the studies. Brusatte *et al.* (2010) found *Yarasuchus deccanensis* as the sister to all other members of their Poposauroidae, whereas Nesbitt (2011) did not include the taxon in his phylogenetic analysis. A recent examination by one of us (JBD) suggests that the type series and referred specimens of *Yarasuchus deccanensis* described by Sen (2005) may include a minimum of two different archosauromorph taxa, and it is unclear whether any of this material even pertains to a pseudosuchian. Nevertheless, the position of *Yarasuchus deccanensis* is only weakly resolved in Brusatte *et al.*'s (2010) analysis. The sister taxon to all

other (non-*Yarasuchus*) poposauroids in Brusatte *et al.*'s (2010) analysis, and the sister taxon to all other poposauroids in Nesbitt's (2011) analysis, is *Qianosuchus mixtus*. The monophyly of *Qianosuchus mixtus* + other poposauroids is supported by a number of features rare among pseudosuchians including, but not limited to, a maxilla that borders the external naris, the entrance of the cerebral branches of the internal carotid artery positioned on the ventral surface of the braincase, and at least three sacral vertebrae (only two are present in *Qianosuchus mixtus*) (Fig. 1). *Qianosuchus mixtus* is the only poposauroid to bear osteoderms, a character state that is apomorphically absent in all other poposauroids.

The recently phylogenetically defined Ctenosauriscidae (Butler *et al.* 2011) comprises a clade of sail-backed poposauroids (Fig. 1) globally widespread from the end of the Early Triassic to the end of the Anisian (Nesbitt 2003; Butler *et al.* 2009, 2011; Nesbitt 2011). Presacral, sacral and anterior caudal vertebrae with extremely elongated neural spines (which would have supported a sail) have been known for more than a century from the Early–Middle Triassic deposits of Germany, Africa and China, but the affinities of these animals were poorly understood. After the discovery of a well-preserved specimen of *Arizonasaurus babbitti*, Nesbitt (2003, 2005a) hypothesized that sail-backed archosaurs formed a clade among *Poposaurus*-like taxa. Later work corroborated this hypothesis (Butler *et al.* 2011; Nesbitt 2011), but hypothesized also that the sail-backed form *Lotosaurus adentus* was not part of Ctenosauriscidae but instead was more closely related to Shuvosauridae, and thus may have evolved its sail convergently. Butler *et al.* (2011) presented revised analyses of the Brusatte *et al.* (2010) and Nesbitt (2011) data sets that included greater taxon sampling, and found that *Ctenosauriscus*, *Hypselorhachis mirabilis*, a German Anisian group of specimen referred to a single taxon (= ‘Waldhaus taxon’), *Xilousuchus sapingensis*, *Arizonasaurus babbitti* and *Bromsgroveia walkeri* comprise the Ctenosauriscidae. This clade is diagnosed by several character states relating to the neural spines, including dorsal neural spines that are more than seven times taller than centrum height and strongly curved dorsal neural spines.

Fig. 4. Raiusuchian skull morphology: (a) two skulls of the newly named *Decuriasuchus quartacolonina* (MCN PV10105c, d) from França *et al.* (2011); (b) likely skull of *Prestosuchus chiniquensis* (UFRGS 0156-T) (reversed); (c) holotype skull of *Qianosuchus mixtus* (IVPP V14300); (d) skull of the poposauroid *Lotosaurus adentus* (IVPP V 48013); (e) holotype maxilla of *Postosuchus kirkpatricki* (TTUP 9000); (f) holotype maxilla of *Teratosaurus suevicus* (NHMUK 38646) (reversed); (g) holotype maxilla of *Polonosuchus silesiacus* (ZPAL Ab III/563); (h) referred maxilla of *Fasolasuchus tenax* (PVL 3851); (i) holotype maxilla of *Batrachotomus kuperferzellensis* (SMNS 52970); (j) holotype maxilla of *Xilousuchus sapingensis* (IVPP V6024); (k) holotype skeleton of *Ticinosuchus ferox* (PIZ T2817). Scale bars: 5 cm (a–j); 10 cm (k). See appendix for institutional abbreviations.

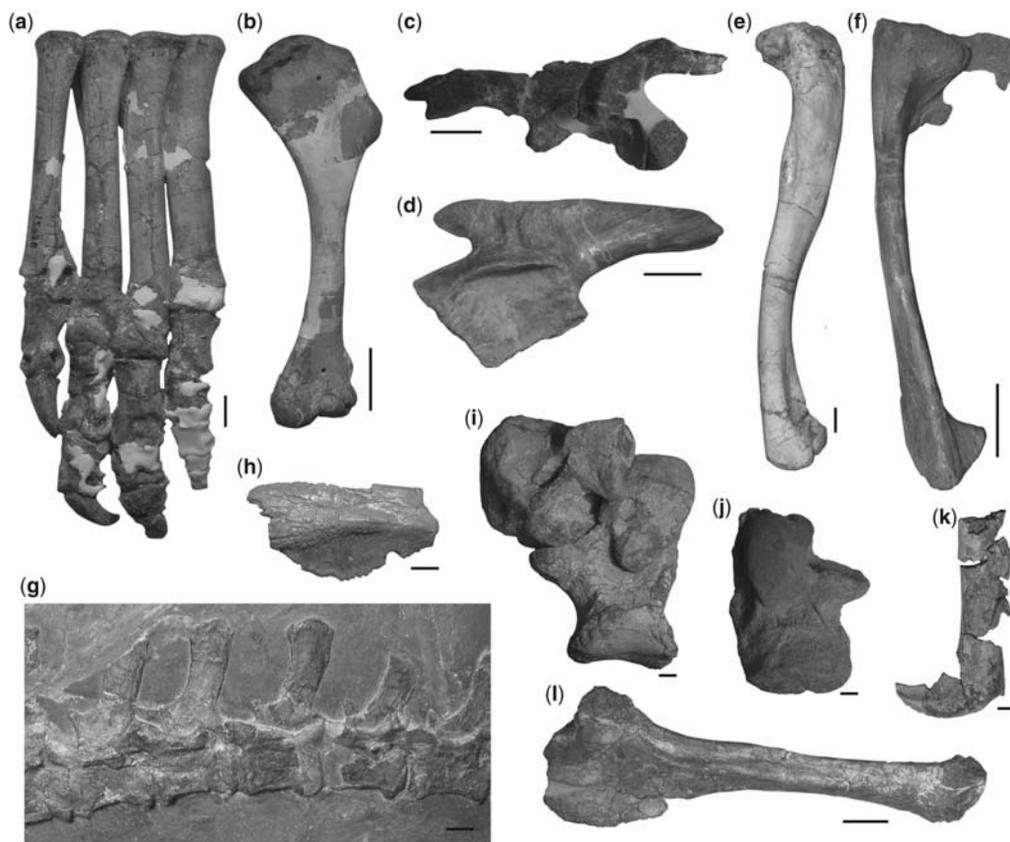


Fig. 5. Selected postcranial elements of rauisuchians: (a) right foot of *Postosuchus alisonae* (UNC 15575) in dorsal view; (b) left humerus of *Postosuchus alisonae* (UNC 15575) in anterior view; (c) right ilium of *Poposaurus gracilis* (TTU-P 10419) in lateral view; (d) left ilium of *Batrachotomus kuperferzellensis* (SMNS unnumbered) in lateral view; (e) right femur of Shuvosauridae (TTU-P 3870) in posteromedial view; (f) left pubis of *Batrachotomus kuperferzellensis* (SMNS 80279) in lateral view; (g) articulated caudal vertebrae of *Ticinosuchus ferox* (PIZ T2817) in lateral view; (h) dorsal osteoderm of *Batrachotomus kuperferzellensis* (SMNS unnumbered) in dorsal view; (i) right articulated ankle of *Fasalasuchus tenax* (PVL 3850) in proximal view; (j) left calcaneum of *Batrachotomus kuperferzellensis* (SMNS 90018) in proximal view; (k) distal end of the right pubis of *Poposaurus gracilis* (TMM 43683-1) in lateral view; (l) left ischium of *Postosuchus kirkpatricki* (TTU-P 9000) in lateral view. Scale bars: 1 cm (a, e, g–k); 5 cm (b, d, f, l). See appendix for institutional abbreviations.

Lotosaurus adentus also has a dorsal sail, but the sail is much less tall and other features in the skull and postcrania indicate that *Lotosaurus adentus* is more closely related to Shuvosauridae than to any other ctenosauriscid (Butler *et al.* 2011; Nesbitt 2011).

The two named species of *Poposaurus* – *P. gracilis* and *P. langstoni* – represent ‘mid-grade’ poposauroids more closely related to shuvosaurids than to other poposauroids (ctenosauriscids and possibly *Lotosaurus adentus*). Although few specimens of *Poposaurus* preserve more than a few vertebrae and portions of the pelvis (Colbert 1961; Weinbaum & Hungerbühler 2007), a recently discovered, nearly complete and articulated specimen sheds

new light on the relationships and locomotor habits of *P. gracilis* (Gauthier *et al.* 2011; Schachner *et al.* 2011; Bates & Schachner 2012). Demonstrably bipedal, *P. gracilis* had long, slim legs that were held underneath the body, a three-toed foot, and short and gracile arms, all of which are character states found in early theropod dinosaurs. *Poposaurus* shares a number of pelvic modifications with shuvosaurids, including a supra-acetabular crest (= supra-acetabular rim) of the ilium that projects ventrally (Fig. 5), an anterodorsally inclined crest dorsal to the supra-acetabular crest/rim of the ilium, and an anterior (= preacetabular, = cranial) process of the ilium that is long. Furthermore,

RAUISUCHIA

Poposaurus and shuvosaurids share flattened, hoof-like unguals (Nesbitt 2011).

Shuvosaurids and their possible sister taxon, *Lotosaurus adentus*, deviate the most among raiusuchians from the typical pseudosuchian body plan. Shuvosaurid fossils are relatively common (although generally not especially complete) in the Chinle Formation and the Dockum Group of the western USA (Long & Murry 1995; Nesbitt 2007). Nesbitt (2005b) hypothesized that a close relative of shuvosaurids ('Moenkopi chatterjeid' of Nesbitt 2005b) was present in the Anisian portion of the Moenkopi Formation of Arizona, but this has never been tested with an explicit phylogenetic analysis. Shuvosaurids and *Lotosaurus adentus* possess a number of unusual, apomorphic cranial characters including the modification of the jaws into a beak that probably supported a rhamphotheca in life (Fig. 4), an enormous orbit, and a mandibular fenestra that is larger than half the length of the entire mandible (Nesbitt 2011). *Lotosaurus adentus*, which Nesbitt (2011) found to be the sister taxon of shuvosaurids (but see Butler *et al.* (2011) for an alternative view), is even more unusual in that it has a sail like that of ctenosauriscids but was quadrupedal and more heavily built than any other well-known poposauroid. In contrast, shuvosaurids were lightly built, had very tiny hands, huge pubic boots and large ilia, and were probably bipedal like *Poposaurus* (Nesbitt 2011). As with *Poposaurus*, fossils of shuvosaurids have long been confused with those of early dinosaurs due to the striking convergences of nearly all portions of the skeleton (Nesbitt & Norell 2006; Nesbitt 2007). Indeed, the first skull of *Shuvosaurus inexpectatus* was originally hypothesized to be an early member of the ornithomimid dinosaurs, a group that lived 100 million years later during the Cretaceous (Chatterjee 1993).

Raiusuchidae

A discrete clade of raiusuchians with strong affinities to *Raiusuchus tiradentes* (Fig. 4) was recovered by the recent phylogenetic analyses of Brusatte *et al.* (2010) and Nesbitt (2011), and both studies recover strong character support for Raiusuchidae centred on *Raiusuchus tiradentes* (Fig. 2). This is one of the major points of agreement between the two analyses. For these reasons, we consider this clade, which is termed Raiusuchidae by reference to the phylogenetic definition above (also see Sereno *et al.* 2005), to be robustly supported.

At a minimum, Raiusuchidae contains three genera: the monotypic *Raiusuchus tiradentes* (Huene 1938b; Lautenschlager 2008) and *Polonosuchus silesiacus* (Sulej 2005; Brusatte *et al.* 2009) and *Postosuchus* (Fig. 4), which contains two species, *P. kirkpatricki* Chatterjee 1985 (see

Weinbaum 2011) and *P. alisonae* Peyer *et al.* 2008. Note that Brusatte *et al.* (2010) used the genus name *Teratosaurus* to refer to *Polonosuchus silesiacus*, following from Sulej's (2005) original referral of the type species of *Polonosuchus* (*P. silesiacus*) to *Teratosaurus*. Subsequent to Sulej's (2005) original description of this species, Brusatte *et al.* (2009) showed that '*Teratosaurus*' *silesiacus* did not share any unique characters with the type species of *Teratosaurus* (*T. suevicus* Meyer 1861, represented by a fragmentary maxilla; Galton 1985; Benton 1986a). Therefore, Brusatte *et al.* (2009) removed '*T.*' *silesiacus* from *Teratosaurus* and assigned it to its own genus, *Polonosuchus*.

It is possible that *Teratosaurus suevicus* is also a member of Raiusuchidae, but the fragmentary nature of the holotype makes it difficult to test this proposition using cladistic analysis (Brusatte *et al.* 2009). In the same vein, Brusatte *et al.* (2010) recovered the Indian *Tikisuchus romeri* to be a member of Raiusuchidae, as the outgroup to *Raiusuchus tiradentes* + (*Postosuchus kirkpatricki* + *Polonosuchus silesiacus*). Nesbitt (2011) did not include *Tikisuchus romeri* in his analysis, because he was unable to score the material from personal observations, but he did acknowledge it as a 'potential member' of Raiusuchidae based on previous studies that reported derived characters of (and suggested close relationships) between *Tikisuchus* and other raiusuchids (Gower 2002; Sulej 2005).

All known members of Raiusuchidae share the same general body plan: they were mid- to large-sized quadrupedal predators, with relatively large, robust skulls and recurved teeth. Based on the known fossil material of the genera, *Postosuchus* (including both species) is probably the largest raiusuchid, with a skull estimated at *c.* 60 cm in length based on the holotype (Weinbaum 2011). The holotypes of *Polonosuchus silesiacus* and *Tikisuchus romeri* were approximately two-thirds (Sulej 2005) and half this size, respectively. A size estimate for *Raiusuchus tiradentes* is difficult based on the fragmentary condition of the holotype skull, but it was smaller than the holotype of *Postosuchus kirkpatricki*. The type maxilla of *Teratosaurus suevicus* is approximately the same size as that of *Postosuchus kirkpatricki* (Sulej 2005; Brusatte *et al.* 2009). The temporal range of Raiusuchidae extended from the late Carnian (*Polonosuchus silesiacus*: Sulej 2005, Dzik & Sulej 2007) to the Norian (*Postosuchus*: Peyer *et al.* 2008; Nesbitt 2011).

All raiusuchids share several derived characters that have been optimized as synapomorphies of the group (or less inclusive subgroups) in recent phylogenetic analyses. The variable optimization of these characters results largely from missing data, because some raiusuchids are missing large portions of the skeleton (e.g. only fragments of the

skull are known for *Rauisuchus tiradentes*). Nesbitt (2011) reported four unequivocal synapomorphies of Rauisuchidae, including a rugose lateral ridge on the nasal, a lateral temporal fenestra that is bisected by squamosal–postorbital contact, a longitudinal ridge on the lateral surface of the jugal, and an axis with two paramedian keels on its ventral surface (Fig. 1). Several other characters were found to represent either rausuchid synapomorphies that cannot be scored in *Rauisuchus tiradentes* because of missing data, or characters supporting a *Polonosuchus silesiacus* + *Postosuchus* clade. These include fused interdental plates on the maxilla, a longitudinal ridge on the lateral surface of the maxilla (continuous with the ridge on the jugal), a maxillary ascending process that remains wide across its entire length, a dorsoventrally oriented crest on the posterior surface of the quadrate, a large exit for cranial nerve VII on the braincase, and triangular palpebrals over the orbits that share a suture with the frontals. Brusatte *et al.* (2010) also reported several synapomorphies for Rauisuchidae and ingroup clades. Some of these were found to be more widely distributed by Nesbitt (2011), but most importantly, Brusatte *et al.* (2010) also found a lateral ridge on the jugal, triangular palpebrals, a divided lateral temporal fenestra, and a lateral ridge on the nasal to diagnose Rauisuchidae or ingroup clades (Fig. 1).

Palaeobiology

Rauisuchians lie at a critical junction between the earliest archosaurs and the single subgroup of pseudosuchians to survive the end-Triassic extinction, the crocodylomorphs (including living crocodylians) (Nesbitt 2011). To understand the evolution of crocodylomorph biology and life history (diet, ecology, locomotion and growth strategies), we have to turn to their closest relatives, rausuchians and other pseudosuchian groups, just as researchers have turned to non-avian theropods to study the origin of birds and avian biology (Gauthier 1986). In the following paragraphs, we summarize recent breakthroughs in the study of rausuchian palaeobiology. Rauisuchians are also key to understanding the evolution of vertebrate faunas, and vertebrate biology and ecology, through the Triassic and beyond.

Diet and ecology

Most rausuchians were probably carnivorous, based on their large, generally labio-lingually compressed, pointed, recurved and serrated (ziphodont) teeth and relatively tall, narrow skulls (which are often similar in overall shape and proportions to

the skulls of carnivorous theropod dinosaurs such as *Tyrannosaurus*: Chatterjee 1985). Rocks yielding rausuchian fossils tend to have a high abundance and high diversity of potential prey in the form of medium to large herbivorous tetrapods (e.g. *Hyperodapeton sanjuanensis*, *Ischigualastia jenseni*, *Stahleckeria potens*). For example, the South American *Saurosuchus galilei* and *Prestosuchus chiniquensis* were at least broadly sympatric with dicynodonts, rynchosaurs and herbivorous therapsids and dinosauromorphs (e.g. Zerfass *et al.* 2004; Langer *et al.* 2007). These two rausuchians grew to considerably larger sizes than other carnivorous tetrapods in their environment (e.g. *Herrerasaurus ischigualastensis*, *Zupaysaurus rougieri*, *Coelophysis bauri*, *Liliensternus liliensterni*, *Staurikosaurus pricei*) and consequently were probably primary predators in these Triassic faunas. The largest known rausuchians are *Fasolasuchus tenax*, which may have reached a total body length of 8–10 m, and the shuvosaurid *Sillosuchus longicervex*, which also may have reached 8–10 m in length (Nesbitt 2011). Fossil remains are generally not complete enough to allow confident estimates of average or maximum sizes of most taxa, but it is probable that some adult rausuchians were not the largest predators in their ecosystems. For example, all known fossils of *Rauisuchus tiradentes* are smaller than those of the saurischian dinosaur *Staurikosaurus pricei* from the Late Triassic of Brazil.

Despite the fact that many rausuchians were probably large, terrestrial hypercarnivores, rausuchian dentition and skull morphology are widely variable, which indicates a potential diversity of diets and food-processing abilities (Figs 1 & 4). The possibly semi-aquatic *Qianosuchus mixtus* has an elongated and low premaxilla with nine needle-sharp teeth, generally similar to those of living crocodylians and other tetrapods that primarily eat fish (Fig. 4). Therefore, *Qianosuchus* may have possibly fed on aquatic vertebrates such as the sauropterygians, protorosaurs, ichthyosaurs and fish that have been found in the same deposits (Li *et al.* 2006). The edentulous jaws (and possible rhamphothecae) of *Lotosaurus adentus*, *Effigia okeeffeae* and *Shuvosaurus inexpectatus* do not suggest a specific diet, but it is clear that these animals must have been feeding differently than the ziphodont-toothed and large-skulled hypercarnivorous rausuchians. The diets of these edentulous poposauroids may have included plants, invertebrates and/or vertebrate eggs, in addition to meat, based on similar hypotheses proposed for edentulous theropod dinosaurs (e.g. Gower 2000, p. 457; Nesbitt 2007; Lautenschlager & Desojo 2011, p. 379; see Barrett 2005 for a discussion of diet in toothless theropod dinosaurs).

RAUISUCHIA

Fossilized gastrointestinal contents of raiusuchians are rare, but are preserved in the nearly complete and articulated holotype of *Ticinosuchus ferox* and the well-preserved, partially articulated holotype of *Postosuchus alisonae*. The preserved gastrointestinal contents of *Ticinosuchus ferox* (Nesbitt 2011, p. 26) include fish scales, although the rather unspecialized skull and mandible of this species bear no indications that it was a specialized piscivore. The diverse gastrointestinal contents of the *Postosuchus alisonae* specimen include part of an aetosaur, a traversodontid cynodont, phalanges of a dicynodont and possibly an amphibian (Peyer *et al.* 2008).

The discovery of multiple (ten) associated individuals of *Decuriasuchus quartacolonina* (França *et al.* 2011) is rare for pseudosuchians. França *et al.* (2011) interpreted this associated assemblage as a possible indication of social grouping, a behaviour well known in various ornithomirans, including Triassic dinosaurs (e.g. Sander 1992). This hypothesis is consistent with the discovery of other raiusuchians, such as *Batrachotomus kupferzellensis*, *Heptasuchus clarki*, *Postosuchus kirkpatricki*, *Effigia okeeffeae* and *Shuvosaurus inexpectatus*, in fossil assemblages that include specimens of various ontogenetic stages. Furthermore, some raiusuchian assemblages include multiple individuals of different raiusuchian taxa. For example, other raiusuchians (e.g. *Prestosuchus chiniquensis* UFRGS-PV-0629-T) were found in the same quarry that yielded the *D. quartacolonina* specimens (Langer *et al.* 2007; Mastrantonio 2010; França 2011). Other multi-taxon raiusuchian assemblages are also known, for example from the Manda beds (Nesbitt *et al.* 2010) of East Africa and the Dockum Group and Chinle Formation of the western USA (e.g. Long & Murry 1995; Nesbitt 2011). More than one species of raiusuchian are sometimes found together in bone beds. For example, the holotypes of *Postosuchus kirkpatricki* and *Shuvosaurus inexpectatus* were found associated in the Post Quarry in the Upper Triassic Dockum Group of North America. It is clear, therefore, that many raiusuchian faunas in the Triassic were diverse.

Cranial and mandibular mechanics

Studying the feeding habits, skull strength, bite forces and possible cranial kinesis of raiusuchians is an interesting area of research that is only beginning to be explored with explicit, quantitative methodologies. One subject that has been the focus of considerable research is cranial mechanics in extant reptiles (e.g. Erickson *et al.* 2003; Metzger *et al.* 2005), although this is difficult to study in fossil taxa. Even in extant taxa it can be difficult to demonstrate functional and active cranial kinesis,

even with access to living animals and knowledge of soft, as well as hard, tissue anatomy (Smith & Hylander 1985). For extinct vertebrates, inferences are made by studying the shape of and contacts between skull bones (Rayfield 2005; Liparini 2008), although care must be taken because apparently movable bony joints in fossil material might not be involved in kinesis in life (e.g. Bühler *et al.* 1988; Gower 1999).

With respect to raiusuchians, Chatterjee (1985), Gower (1999) and Liparini (2008) suggested potential, but probably greatly restricted and passive cranial kinesis for adult *Postosuchus kirkpatricki*, *Batrachotomus kupferzellensis* and *Prestosuchus chiniquensis*, respectively (Fig. 6d). Gower (1999) argued that the poor preservation of the edges of incompletely preserved cranial elements in *B. kupferzellensis* prevented firm conclusions regarding cranial mechanics, but he was able to rule out notable kinesis due to the rigid skull roof. However, it is important to acknowledge that restricted passive intracranial mobility of local parts might have occurred even if other fused regions of the skull prevented more extensive intracranial movements. The mandibular symphysis, where known, appears to be relatively simple in raiusuchians, but potential inter- or intra-mandibular joints are difficult to assess because of lack of detailed information about the middle part of the mandibular ramus (e.g. the joints between dentary, surangular and angular) in the vast majority of raiusuchian fossils. Some workers have highlighted a supposedly moveable premaxilla–maxilla joint in some raiusuchians (e.g. Benton & Clark 1988; Long & Murry 1995), but detailed biomechanical investigations of this portion of the skull have not been undertaken and no firm evidence has been forwarded in support of anything other than small amounts of passive movement in this region.

Much additional work on cranial mechanics in raiusuchians is clearly needed. Liparini (2008) suggested that the main areas to look for possibly kinetic joints in raiusuchian skulls include the contact between the maxilla and premaxilla, jugal and lacrimal, and between the pterygoid and the basisphenoid process of the basisphenoid, quadrate and ectopterygoid (Fig. 6). However, detailed descriptions of the histology and bone texture of these regions of the skull, and comparisons among many raiusuchian taxa, have yet to be undertaken. Detailed craniofacial and mandibular muscular reconstructions would assist in investigations of kinesis, but these have also not yet been undertaken. Another approach that is likely to yield useful information in future is integrated biomechanical modelling. For example, finite element analysis (FEA) has been used to examine differences in cranial mechanics during biting with or without intracranial

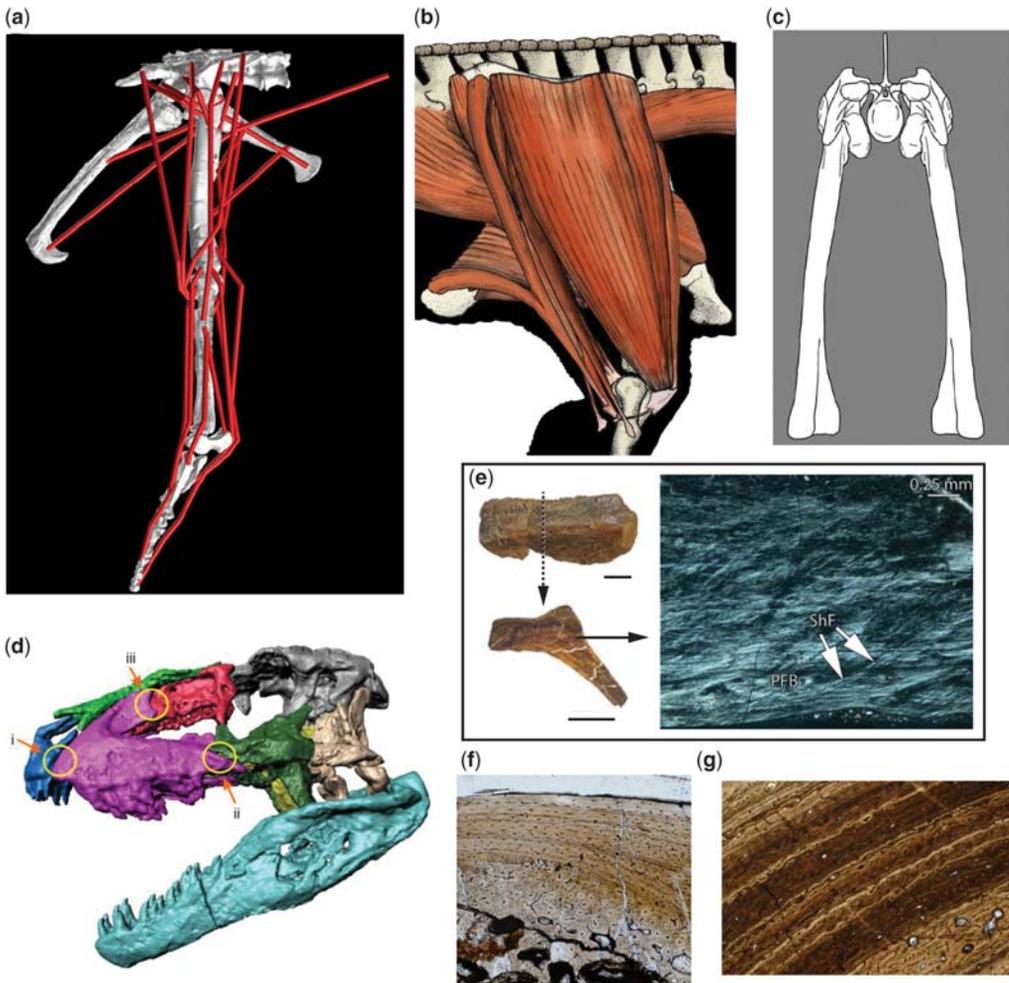


Fig. 6. Examples of palaeobiological studies on rauisuchians: (a) three-dimensional reconstruction of the musculoskeletal system of the hindlimb of the poposaurid *Poposaurus gracilis* (from Bates & Schachner 2012); (b) muscle reconstructions of the hindlimb of *Prestosuchus chiniquensis* (from Liparini 2011); (c) example of the 'pillar-erect' hindlimb posture of *Poposaurus gracilis*, in posterior view (from Schachner *et al.* 2011); (d) three-dimensional model of skull and mandible of *Prestosuchus chiniquensis* illustrating movable joints (labelled i–iii) between the skull bones (modified from Liparini 2008); (e) histological sections through a dorsal osteoderm of *Batrachotomus kupferzellensis* showing Sharpey's fibres (ShF) and parallel-fibred bone tissues (PFB) (scale bars: 1 cm) (from Scheyer & Desojo 2011); (f) histological section through the femur of *Effigia okeeffeae* (AMNH FR 30589); (g) histological section through the femur of *Postosuchus* (UCMP 28353). See appendix for institutional abbreviations.

mobility in, for example, extinct theropod dinosaurs (e.g. Rayfield 2004), and might usefully be extended to rauisuchians.

There is also an ontogenetic dimension to cranial mechanics and diet, and this also requires future research with respect to rauisuchians. Some smaller, presumably younger, rauisuchian individuals are known from disarticulated skull

elements, in contrast to the completely articulated skulls of larger, presumably older, conspecific specimens. This phenomenon is observed, for example, in *Luperosuchus fractus* (Desojo & Arcucci 2009) and *Prestosuchus chiniquensis* (see Mastrantonio (2010) and Barberena (1978) for comparison). This might be related to differences in the relative degree of mobility of cranial joints

RAUISUCHIA

between juveniles and adults (as well as size, and therefore amounts of associated connecting soft tissue), which might thus indicate a reduction of kinesis with age. Walker (1990) suggested a similar ontogenetic trajectory for the crocodylomorph *Sphenosuchus acutus*, and thought this might explain the presence of potentially moveable joints in a seemingly rigid adult skull (smaller/younger specimens were not available to test this hypothesis).

Sexual dimorphism, ontogeny and growth

There is no compelling evidence for sexual dimorphism in any raiusuchian and little information on growth rates or ontogenetic trends, but this is unsurprising given the fragmentary nature of much of the fossil material and the general lack of palaeobiological analyses for raiusuchians. Very recently, however, some raiusuchians have been studied using histological analyses, which offer potential to provide insights into these questions about growth and ontogeny, as well as other areas of raiusuchian palaeobiology (Nesbitt 2007; Cerda *et al.* 2011; Scheyer & Desojo 2011; Scheyer *et al.* 2011). Histology can provide data on growth rates, the origin and development of bony structures, the osteogenic mechanisms linked to the development of these structures (e.g. osteoderm ornamentation), and the relation of bones to soft tissues. Few histological studies of the long bones of raiusuchians have been conducted, but the handful of published studies has generated some important data. Ricqlès *et al.* (2003, 2008) examined long bones referred to *Postosuchus kirkpatricki* (Fig. 6g), '*Mandasuchus tanyuchen*' and *Luperosuchus fractus* (for which no limb material was reported to be found with the holotype skull), and found their histology to be similar to that of phytosaurs, aetosaurs and extant crocodylians. Based on these comparisons, they suggested that raiusuchians had high growth rates early in ontogeny and achieved large adult sizes through protracted cyclical growth. Nesbitt (2007) reported a similar histological structure in the femur of *Effigia okeeffeae* (Fig. 6f), although indicative of perhaps higher growth rates than in other pseudosuchians except non-crown-group crocodylomorphs. The most general result of these studies is that raiusuchian growth rates do not seem to have approached the rapid rates of dinosaurs or pterosaurs (Padian *et al.* 2001; Erickson 2005).

In many pseudosuchians, osteoderms constitute the most consistently well-preserved fossil elements, and thus justify detailed analysis. Recent studies of archosaur osteoderm histology have generated important data for systematic and functional studies (e.g. Scheyer & Sander 2004; Main *et al.*

2005; Hill 2005; Hayashi *et al.* 2010; Cerda & Desojo 2011). Raiusuchian osteoderms (Fig. 6e) were rather compact bones, usually lacking substantial bone remodelling or large areas of cancellous bone, and thus presenting good growth records. Of the raiusuchians examined thus far, only *Tikisuchus romeri* and the possible raiusuchian *Yarasuchus deccanensis* deviate from this trend and have osteoderms with a slightly larger central area of cancellous bone, forming a diploë structure. Preliminary studies of osteoderms of *Prestosuchus chiniquensis* and indeterminate raiusuchians indicate, however, that there is some intraspecific variation in terms of bone compactness and degree of remodelling (Cerda *et al.* 2011). Comparison with extant crocodylians suggests that this variation might be related to the relative age, sex and reproductive status of the individual animal (Scheyer *et al.* 2011). However, age estimation based on the count of growth marks in raiusuchian osteoderms will be accurate only in those specimens that lack internal remodelling (i.e. only for individuals that died at a young age). Interestingly, nearly all poposauroids (with the exception of *Qianosuchus*) lack osteoderms.

Growth-associated changes have been documented by comparing the cranial and postcranial skeletons of presumably younger (smaller and less firmly sutured) and older (larger and more firmly sutured) individuals of *Prestosuchus chiniquensis* (Huene 1938b, 1942; Barberena 1978; Mastrantonio *et al.* 2008). These ontogenetic changes may also be characteristic for raiusuchians more widely, because they also seem to occur in taxa with less complete representation of younger (smaller) individuals, such as both species of *Postosuchus* (Weinbaum 2002, 2011; Peyer *et al.* 2008), *Batrachotomus kupferzellensis* (Gower 1999) and *Decuriasuchus quartacolonina* (França *et al.* 2011). In all these taxa, presumed younger individuals differ from older ones in lacking fusion between some bones (e.g. neural arches and centra; scapula and coracoid) and having less tightly connected cranial and mandibular elements. In *Saurosuchus galilei*, for example, one of the most complete skeletons known (PVSJ 32) is skeletally immature (based on the work of Brochu 1996 and Irmis 2007) because it has unfused cervical neural arch–centrum articulations. Furthermore, its skull bones are relatively poorly ossified (e.g. articular end of the quadrate, poor ossification between exoccipital and basioccipital), and several skull bones (e.g. braincase) were preserved disarticulated (Alcober 2000; Trotteyn *et al.* 2011) (Fig. 4). Gower & Schoch (2009, p. 118) reported less robust limb and pelvic girdle bones and less strongly pronounced muscle attachment sites in smaller individuals of *Batrachotomus kupferzellensis*.

Locomotion

Schaeffer (1941) pointed out that a terminal proximal femoral head, contrasting with one offset from the long axis of the femur, is capable only of horizontal or slightly oblique movements and is associated with a generally sprawling locomotion with little vertical component, as observed in extant crocodylians. This femoral configuration is plesiomorphic for Archosauria, characteristic of all raiusuchians, and is also observed in extant crocodylians. This led some authors, notably Charig (1972), to interpret such groups as functionally and evolutionarily intermediate forms between ancestral 'sprawlers', such as non-archosaurian archosauriforms, and derived 'fully improved' (upright) locomotors, such as dinosaurs and birds. Beyond the limits of his typological approach, Charig's interpretations are incompatible with current understanding of archosaur phylogeny. In addition, Bonaparte (1984) identified an alternative mode of locomotion and posture in raiusuchians, characterized by a largely unmodified femur but upright hindlimbs and a parasagittal gait (Fig. 6c). Bonaparte (1984) drew attention to changes in the pelvic girdle that permitted such a posture without substantial changes in femur morphology, including more ventrally directed distal ends of sacral ribs, an almost horizontally held ilium with a low dorsal blade, a deep acetabulum bordered by a prominent supra-acetabular crest, and an elongated pubis and ischium (Fig. 5). Since Bonaparte's (1984) work, it has become apparent that raiusuchians have notable variations on this theme. For example, *Prestosuchus chiniquensis* (Fig. 6b) has a combination of the plesiomorphic and derived pelvic/hindlimb characters and has been considered to have a less upright and parasagittal gait than *Postosuchus kirkpatricki* and *Effigia okeeffeae* (Liparini 2011).

Although muscular reconstructions for extinct dinosaurs have been attempted since Dollo (1888), only in the 1990s did researchers begin to reconstruct the soft tissues of extinct archosaurs using the extant phylogenetic bracketing methodology, which depends on an explicit phylogenetic context (Bryant & Russell 1992; Witmer 1995). The only comprehensive soft tissue reconstruction for a raiusuchian that has been published thus far is for the pelvic and hindlimb myology of *Poposaurus gracilis* (Fig. 6a) presented by Schachner *et al.* (2011), although the unpublished theses of Kischlat (2003) and Liparini (2011) also discuss muscular reconstructions for *Prestosuchus chiniquensis* (Fig. 6b) and other south Brazilian raiusuchians. Notable features of Schachner *et al.*'s (2011) reconstruction include elongation and expansion of muscle-attachment areas in the bone for the muscles that flex

and extend the hip and knee articulations. For *Prestosuchus chiniquensis*, similar, but less accentuated modifications have been reconstructed by Liparini (2011). The distinctive raiusuchian ridge above the supra-acetabular crest is inferred to be for the origin of the *M. iliofemoralis*, the expanded pre-acetabular process of the ilium for part of the *M. puboischiofemoralis internus*, and the external surfaces of the extended distal parts of the pubes and ischia largely for parts of the *M. puboischiofemoralis externus* group. The architecture of the hip joint probably restricted femoral extension, flexure and abduction relative to that found in parasagittal ornithomirans. Despite the derived nature of raiusuchian pelvic osteology, these reconstructions have not had to argue for any novel myological elements. This suggests that the complement of inferred muscles in extinct and extant archosaurs was probably fairly conservative, even though muscular arrangements and locomotor function were diverse (Liparini 2011; Schachner *et al.* 2011).

Biomechanical and functional analyses of the raiusuchian crurotarsal ankle joint and the metatarsus indicate a predominantly plantigrade posture, where the whole plantar region of the foot participates in at least part of the stride phase (Bonaparte 1984; Parrish 1986; Carrano 1997). The caudally/posteriorly orientated calcaneal tuber of raiusuchians (in contrast to a more obliquely or almost lateral one, as observed, for example, in crocodylians and phytosaurs) suggests a narrower, more parasagittal gait (Brinkman 1980). A longer calcaneal tuber is better suited to support greater body weights and to impress greater (more powerful) foot strokes rather than high speed and amplitude movements of the feet (Carrano 1997) (Fig. 5). The footprint fossil record (e.g. of *Chirotherium storetonense*) provides some evidence in support of the interpretation that the hindlimbs of even quadrupedal raiusuchians were held in a relatively upright and narrow gait (Kubo & Benton 2009).

Raiusuchians studied thus far seem to lack notable adaptations for supporting extreme body mass or facilitating extreme cursoriality. Medium-sized (4.5 m) individuals of *Prestosuchus chiniquensis* are estimated to have weighed up to 400 kg (Liparini 2011), much less than the tons of kilograms of members of several dinosaur lineages (e.g. Christiansen & Fariña 2004; Erickson *et al.* 2004; Sereno *et al.* 2009; Sander *et al.* 2011). Traits of *Prestosuchus chiniquensis* such as relatively short limbs, a digit III that is not elongated, marginal digits that are not notably reduced, similar proportions of both hindlimb epipodials, and a metatarsal III that is approximately half the length of the tibia indicate a subcursorial habit for this species, without obvious adaptations for running (Liparini 2011). Accordingly, it seems that this and similar

RAUISUCHIA

rauisuchians were possibly better ambush hunters than pursuit hunters.

Possible bipedality has been addressed for some raiusuchians that have derived features sometimes considered characteristic of both obligatorily parasagittal hindlimbs and a bipedal gait (Figs 1 & 6c). The shuvosaurid *Effigia okeeffeae*, for example, has a well-developed preacetabular process of the ilium, an elongated and slender pubis and ischium with expansion of their distal extremities (pubic and ischiadic 'boots'), additional sacral vertebrae (four or more), and reduced forelimb proportions relative to hindlimbs (Nesbitt 2007). There have been disagreements about the degree to which these features indicate bipedality. For example, *Postosuchus kirkpatricki* has been reconstructed as a biped (Chatterjee 1985; Weinbaum 2007; Gauthier *et al.* 2011) or quadruped (Long & Murry 1995; Peyer *et al.* 2008), although this case is complicated by differing views as to what material can be referred to this genus. Where the entire presacral vertebral column is preserved, it is possible to estimate where the main stresses would occur, and use this to infer the extent to which forelimbs were used in support and locomotion (Christian & Preuschoft 1996). Applying this method, Weinbaum (2007) presented evidence for obligate bipedality in *Postosuchus kirkpatricki*, and Liparini (2011) for facultative bipedality in *Prestosuchus chiniquensis*. Weinbaum (2007) also used evidence from the endocast to argue for bipedality in *Postosuchus kirkpatricki*. Endocasts of *Postosuchus* (TTU-P 9002 and UMMP-7473) indicate the presence of an enlarged flocculus, and the general posterior brain morphology is strikingly similar to that of large bipedal theropod dinosaurs (Weinbaum 2007). Schachner *et al.* (2011) interpreted their pelvic and hindlimb muscle reconstruction for *Poposaurus gracilis* as indicating a derived increase in the muscle moment arms that could have facilitated bipedal locomotion in this taxon. Bipedality was probably associated with an increased potential for cursoriality. Gower (2000, p. 476) pointed out that dorsal axial osteoderms have an important biomechanical function in extant crocodylians (Frey 1988) and that a consideration of this might help to understand and exploit osteoderms as sources of phylogenetic characters among raiusuchians. The fact that raiusuchian taxa variably have (all non-poposauroids) or lack (almost all poposauroids) osteoderms suggests further that they should be considered in models established to help infer raiusuchian locomotion and its evolution.

Cervical and dorsal vertebral morphology seems to be somewhat bimodal in raiusuchians (e.g. Trotteyn *et al.* 2011), in that vertebrae are usually either short, high and robust with hyposphenes and hypantra (e.g. *Saurosuchus galilei*, *Prestosuchus*

chiniquensis, *Fasolasuchus tenax* and *Batrachotomus kupferzellensis*) or longer, lower and more gracile and lacking accessory articular structures (e.g. *Arizonasaurus babbitti* and *Sillosuchus longicervix*). Cervical differences in these forms are correlated to some degree at least with maximum body size and sacral and pelvic anatomy. Even if these coincident occurrences prove to be explained by phylogeny, they are likely to have locomotor consequences, and this might be addressed in detail in future studies to better understand the diversity of raiusuchian palaeobiology.

Several poposauroids have vertebrae with elongated neural spines that form a substantial sail-like structure (*Arizonasaurus babbitti*: Nesbitt 2005a, b, 2007; *Ctenosauriscus koeneni*: Butler *et al.* 2011; *Lotosaurus adentus*: Zhang 1975). Some other poposauroids known from much less complete fossils had greatly elongated neural spines and so also probably had a similar 'sail' (*Hypselorhachis mirabilis*: Butler *et al.* 2009; *Xilousuchus sapingenensis*: Nesbitt *et al.* 2010; possibly *Bromsgroveia walkeri*: Benton & Gower 1997). Ebel *et al.* (1998) argued that the sail of *C. koeneni* had an important biomechanical function in bipedality, but their arguments were refuted by Butler *et al.* (2011), who interpreted this taxon as quadrupedal, as did Nesbitt (2005a, b) for *A. babbitti*. To the best of our knowledge, other potential functions of the 'sail', such as thermoregulation or display, have not been specifically proposed for poposauroids, and certainly have never been tested explicitly.

Pneumaticity

Gower (2001) argued that osteological features typically used to infer the presence of postcranial skeletal pneumaticity (PSP) – the invasion of the postcranial skeleton by diverticula of the lungs – were not restricted to ornithomirans among archosauriforms, but were also present in at least some raiusuchians (e.g. *Batrachotomus kupferzellensis*, *Postosuchus kirkpatricki*, '*Mandasuchus tanyauchen*'). O'Connor (2006) rejected Gower's (2001) arguments and suggested instead that these features (vertebral fossae) were superficial, possibly associated with other soft tissues (e.g. fat deposits), and could not be deemed unambiguous evidence of PSP. Alcober & Parrish (1997) reported 'distinct pleurocoels' in *Shuvosaurus inexpectatus* and *Sillosuchus longicervix*. Nesbitt & Norell (2006; see also Nesbitt 2007) reported 'true pleurocoels' on cervical vertebrae of *Effigia okeeffeae*, which was then cited as evidence of PSP by Farmer (2006) and Sereno *et al.* (2008). Gower & Schoch (2009) described 'possibly pneumatic' fossae on the vertebrae of *Batrachotomus kupferzellensis*. Butler *et al.* (2009, 2012) examined specimens of, and micro-computed

tomography (micro-CT) data for, cervical vertebrae of *Bromsgroveia walkeri*, *Effigia okeeffeae*, *Hypselorhachis mirabilis* and *Batrachotomus kupferzellensis* and reconsidered archosaur PSP more broadly, concluding that no rauisuchians display unambiguous evidence of PSP. However, rauisuchians do have features (well-developed vertebral laminae and fossae) that are absent in extant diapsids that lack PSP, and which do accompany instances of unambiguous evidence for PSP in extinct archosaurs. Thus, rauisuchians (and some other non-ornithomirans) may have had a non-invasive system of pulmonary air sacs. Extant birds and crocodylians have unidirectional lung ventilation (Farmer & Sanders 2010; Sanders & Farmer 2012), and phylogenetic character optimization suggests that this may have evolved in their common ancestor (i.e. at the base of Archosauria) and therefore may also have been present in rauisuchians (Perry *et al.* 2011; Butler *et al.* 2012). The relationship between various inferred extinct lung morphologies and metabolism has yet to be worked out.

Future directions

Interest in Triassic vertebrates has skyrocketed over the past 15 years and there is little to suggest that it will slow down soon. Rauisuchians or some of their more probably monophyletic subgroups (e.g. Shuvosauridae) lie at the heart of this Triassic renaissance, not least because some of them have been confused with many other groups of Triassic archosaurs, and knowledge of them clearly impacts what we know of pseudosuchians and of early archosaurs more broadly. This current volume attests to the recent and ongoing research on rauisuchians because more than half of the volume is devoted to these organisms. Even though there is renewed interest and a number of important finds, there are, however, a number of challenges that lie ahead.

Rauisuchian palaeontology has changed enormously since Gower's (2000) overview of the group. To a large degree, the optimism expressed by Gower (2000, pp. 476–478) has proven well founded. Since 2000, the levels of interest and research effort focused on these organisms have grown dramatically, and the number and geographical distribution of rauisuchian researchers has expanded healthily (especially as many early-career researchers have begun to work on the group). Technological advances have played their part, from the use of digital photography to greatly enhance the speed and accuracy of recording information on specimens that are too numerous and large to be loaned between collections, to the application of computed tomography to examine internal structures of bones non-destructively. Gower (2000)

wrote only in vague terms about advances in rauisuchian palaeobiology (beyond systematics) that could come from focused, careful research, and he did not clearly foresee the speed and scope of discovery that, since then, has included many spectacular new fossils, detailed descriptions, new phylogenetic hypotheses, muscle reconstructions, histological studies and considerations of possible pneumaticity.

Gower (2000) highlighted a number of points of caution that lay at the heart of establishing a foundation for rauisuchian studies, emphasizing detailed osteological documentation of both newly discovered and previously described material as vital to all other vertebrate palaeontological contributions, including studies of function, ecology and evolution built on such morphological data. Improvement in this basic documentation has undoubtedly contributed to the great increase in knowledge of rauisuchians since 2000, and the field would do well to continue to pay attention to this aspect. Other potential pitfalls noted by Gower (2000) also seem to have been largely avoided, including restricting the use of suprageneric taxa as terminals in phylogenetic analyses, assessing the support of phylogenetic hypotheses, and restraint in naming new suprageneric taxa on the basis of each new phylogenetic hypothesis. We now additionally recommend that continued effort is expended to avoid chimeric holotypes (a problem in previous taxonomic studies of rauisuchians), and that morphological studies bear in mind the ongoing need to resolve and find additional homologies for use in systematic analyses.

Very few researchers currently argue for the monophyly of rauisuchians based on explicit phylogenetic analyses, so does the term 'Rauisuchia' for this unnatural 'group' still have any use? The most recent, large-scale archosaur phylogenies (e.g. Brusatte *et al.* 2010; Butler *et al.* 2011; Nesbitt 2011) suggest that we are closer to being able to apply some suprageneric names to particular groups of rauisuchians (Poposauroidea, Shuvosauridae) with more confidence that these are monophyletic. However, several taxa are still far from completely known; many have not been included in all of the largest recent phylogenetic analyses (e.g. '*Mandasuchus*', *Heptasuchus*, *Luperosuchus*), and many rauisuchian nodes in published trees have not been compellingly resolved. Thus, an umbrella term (rauisuchians) for most of the non-ornithosuchid, non-aetosaurian and non-crocodylomorph (and possibly non-phytosaurian) pseudosuchians probably still has some use – if only to serve as an ongoing reminder that a robust, comprehensive phylogeny has yet to be achieved, and to prevent misunderstanding when trying to find ways to precisely and accurately refer to particular groups without

RAUISUCHIA

resorting to inappropriate (e.g. Krell & Cranston 2004) language for describing any group (basal, early/late-branching, primitive, and so on). As more clades within Pseudosuchia become robustly resolved, we anticipate that the need for the term 'Rauisuchia' will dissipate naturally.

One thing has not changed in the 12 years since 2000. Interpreting the evolution of rausuchians and their palaeobiology ultimately requires a sound understanding of phylogenetic relationships, and advancing both the systematic and wider palaeobiological knowledge of this group demands high-quality documentation and analysis of the available fossils. We believe that many of the limitations of older studies of rausuchians have been surmounted. Recent discoveries combined with the breadth and depth of current expertise and interest in Triassic archosaurs make us very optimistic about the next 12 years.

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Appendix

Institutional abbreviations

AMNH, American Museum of Natural History, New York, NY, USA; BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MCN PV, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Brazil; NHMUK, Natural History Museum, London, UK; PIZ, Paläontologisches Institut und Museum der Universität, Zurich, Switzerland; PVL, Instituto Miguel Lillo, Tucuman, Argentina; SAM, Iziko South African Museum, Cape Town, South Africa; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; TTU, Texas Tech University Museum, Lubbock, TX, USA; UCMP, University of California Museum of Paleontology, Berkeley, CA,

USA; UFRGS, Institute of Geosciences, Federal University of Rio Grande do Sul, Porto Alegre, Brazil; UMMP, University of Michigan Museum of Paleontology, Ann Arbor, MI, USA; UNC, University of North Carolina, Chapel Hill, NC, USA; ZPAL, Institute of Palaeobiology, Polish Academy of Sciences, Warsaw, Poland.

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