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New Aspects of Mesozoic Biodiversity

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Chapter 2
The Origin, Early History and Diversification of Lepidosauromorph Reptiles

Susan E. Evans and Marc E.H. Jones

2.1 Introduction

Lepidosauria was erected by Romer (1956) to encompass diapsids that lacked diagnostic archosaurian characters. The resulting assemblage was paraphyletic. In the intervening 50 years, new fossils and new phylogenetic approaches have transformed our concepts (e.g., Evans, 1980, 1984, 1988; Benton, 1985; Whiteside, 1986; Gauthier et al., 1988). Lepidosauria is now restricted to the last common ancestor of Squamata (lizards, snakes and amphisbaenians) and Rhynchocephalia (represented by *Sphenodon*), and all descendants of that ancestor (e.g., Gauthier et al., 1988). The clade is robustly diagnosed by hard and soft characters (e.g., Gauthier et al., 1988; de Braga and Rieppel, 1997; Evans, 2003; Hill, 2005) and is recognized by recent molecular phylogenies (e.g., Gorr et al., 1998; Rest et al., 2003; Townsend et al., 2004; Vidal and Hedges, 2005). Extant lepidosaurs are globally distributed with more than 7,000 species ranging from desert lizards to marine snakes. The fossil record provides evidence of their history and radiation but, despite advances, that record is patchy. It relies mainly on microvertebrate assemblages, supplemented by rare skeletons from lacustrine and other fine grained deposits. Inevitably, the record is geographically and geologically biased.

With reanalysis, many of Romer's "lepidosaurs" were transferred to the archosaurian stem within a new clade, Archosauromorpha (Gauthier et al., 1988). These included "Prolacertiformes" (probably paraphyletic, e.g., Dilkes, 1998), Trilophosauria, and Rhynchosauria (Benton, 1985; Gauthier et al., 1988). A sister group, Lepidosauromorpha, was erected for Lepidosauria and all taxa sharing a more recent common ancestor with it than with Archosauria (Gauthier et al., 1988). At first, the clade encompassed the Permo-Triassic Gondwanan Younginiformes

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(e.g., Benton, 1985; Evans, 1988), the Triassic Laurasian Kuehneosauridae (Robinson, 1962; Colbert, 1966), and several Permo-Triassic taxa from South Africa (Carroll, 1975), but younginiforms were subsequently removed (Laurin, 1991). Currently, Archosauromorpha + Lepidosauromorpha constitute the Sauria, and Sauria + Younginiformes constitute Neodiapsida (Laurin, 1991). In a reexamination of reptile relationships, de Braga and Rieppel (1997) obtained a clade encompassing turtles, sauropterygians and lepidosaurs. Under the stem-based definition of Gauthier et al. (1988), all three groups would fall within Lepidosauromorpha. This arrangement received mixed support from Hill (2005), who recovered a weakly supported lepidosaur-turtle clade, but sauropterygians fell outside Sauria. Alternative morphological (Müller, 2004) and molecular (e.g., Hedges and Poling, 1999; Rest et al., 2003) analyses suggest that if turtles are diapsids, they are closer to archosaurs than to lepidosaurs.

2.2 The Lepidosauromorph Record

2.2.1 Permo-Triassic Lepidosauromorphs

The earliest putative lepidosauromorphs are Late Permian in age: *Lanthanolania* (Russia, Modesto and Reisz, 2002) and *Saurosternon* (South Africa, Carroll, 1975). The first is a partial skull with an incomplete lower temporal bar but no other diagnostic features, and the second is a headless skeleton. They may be basal lepidosauromorphs, or lie lower on the saurian stem (e.g., Modesto and Reisz, 2002; Müller, 2004). Of other supposed Permo-Triassic lepidosauromorphs, *Santaisaurus* (China, Sun et al., 1992) and *Colubrifer* (South Africa, Carroll, 1982) are procolophonians (Evans, 2001); *Kadimakara* (Australia, Bartholomai, 1979) is a misinterpreted specimen of *Prolacerta* (SE pers. obs.); and *Kudnu* (Australia, Bartholomai, 1979) and *Blomosaurus* (Russia, Tatarinov, 1978) are too poorly preserved to interpret with confidence but are probably also procolophonian. *Paliguana* (Early Triassic, South Africa, Carroll, 1975) is represented by a single, damaged skull with a large, flared quadrate consistent with lepidosauromorph attribution. Roughly contemporaneous remains, referable to two distinct taxa, have recently been recovered from Early Triassic fissure infillings in Poland (Czatkowice, Borsuk-Białynicka et al., 1999). These taxa are described elsewhere (Evans and Borsuk-Białynicka, 2009; Evans, 2009) and include an early kuehneosaur (see below, Kuehneosauria) and a stem-lepidosaur. The Czatkowice deposits were formed in an arid environment with localized water bodies (Borsuk-Białynicka et al., 1999). The associated fauna includes fish; temnospondyl amphibians; the proanuran *Czatkobatrachus*; procolophonians; and several archosauromorphs. Less is known about the South African Donnybrook locality (*Paliguana*), but the general Early Triassic environment of the Karoo Basin has been described as a warm, arid floodplain with rivers, playas and lakes (e.g., Smith and Botha, 2005).

2.2.2 Kuehneosauria

Kuehneosaurs are specialized, long-ribbed gliders/parachuters known from the Early Triassic of Poland and the Late Triassic (Carnian-Rhaetian) of England and North America. The English genera are *Kuehneosaurus latus* (Emborough Quarry, Robinson, 1962) and the longer-ribbed *Kuehneosuchus latissimus* (Batscombe Quarry, Robinson, 1967a). *Icarosaurus siefkeri* is based on a single skeleton from the Newark Basin, New Jersey, USA (Colbert, 1966, 1970), but partial jaws reported from the Triassic Chinle Formation (Arizona, New Mexico, Murry, 1987) are indeterminate. The new Czatkowice taxon (Evans, 2009) shows typical kuehneosaur skull morphology, but is less specialized postcranially than younger taxa. Nonetheless, the kuehneosaur *bauplan* had clearly evolved by the Early Triassic, extending the roots of the clade into the Permian (Fig. 2.1). This brings the kuehneosaurs temporally and geographically close to another group of specialized early gliders, the coelurosauravids of England, Germany and Madagascar (Evans, 1982; Evans and Haubold, 1987), but members of the two clades are morphologically distinct (SE pers. obs.).

Robinson (1962, 1967b) interpreted kuehneosaurs as primitive squamates, but this was challenged as early lepidosaurs became better known (e.g., Evans, 1980, 1984, 1988), and the first major cladistic analysis of lepidosauromorphs (Gauthier et al., 1988) placed kuehneosaurs on the lepidosaurian stem (Lepidosauria+Kuehneosauridae = Lepidosauriformes). Müller (2004) moved kuehneosaurs to the saurian stem, as the sister group of the peculiar Late Triassic Euramerican drepanosaurs. Reanalysis of Müller's matrix, with the data for *Kuehneosaurus* corrected and the Czatkowice taxon included, returned kuehneosaurs to Lepidosauromorpha.

Kuehneosaurus and *Kuehneosuchus* lived on small, relatively dry, offshore islands, in association with pterosaurs, archosauriforms, rhynchocephalians, and rare mammals (Robinson, 1962; Fraser, 1994). The Czatkowice environment was similar (Borsuk-Bialynicka et al., 1999), but *Icarosaurus* was preserved in a lacustrine assemblage of fish, temnospondyls, a drepanosaur, and several archosauromorphs including a phytosaur (Colbert and Olsen, 2001).

2.2.3 Other Mesozoic Non-lepidosaurian Lepidosauromorphs

Other designated Mesozoic lepidosauromorphs that lie outside Lepidosauria include the Middle Triassic *Coartaredens* (England, Spencer and Storrs, 2002) and *Megachirella* (Italy, Renesto and Posenato, 2003); the Early Jurassic *Tamaulipasaurus* (Mexico, Clark and Hernandez, 1994); and the Middle-Late Jurassic *Marmoretta* (UK, Portugal, Evans, 1991). *Coartaredens* (Spencer and Storrs, 2002) is represented by partial jaws that are almost certainly procolophonian (contra Spencer and Storrs, 2002). The affinities of *Megachirella* and *Tamaulipasaurus* remain unresolved.

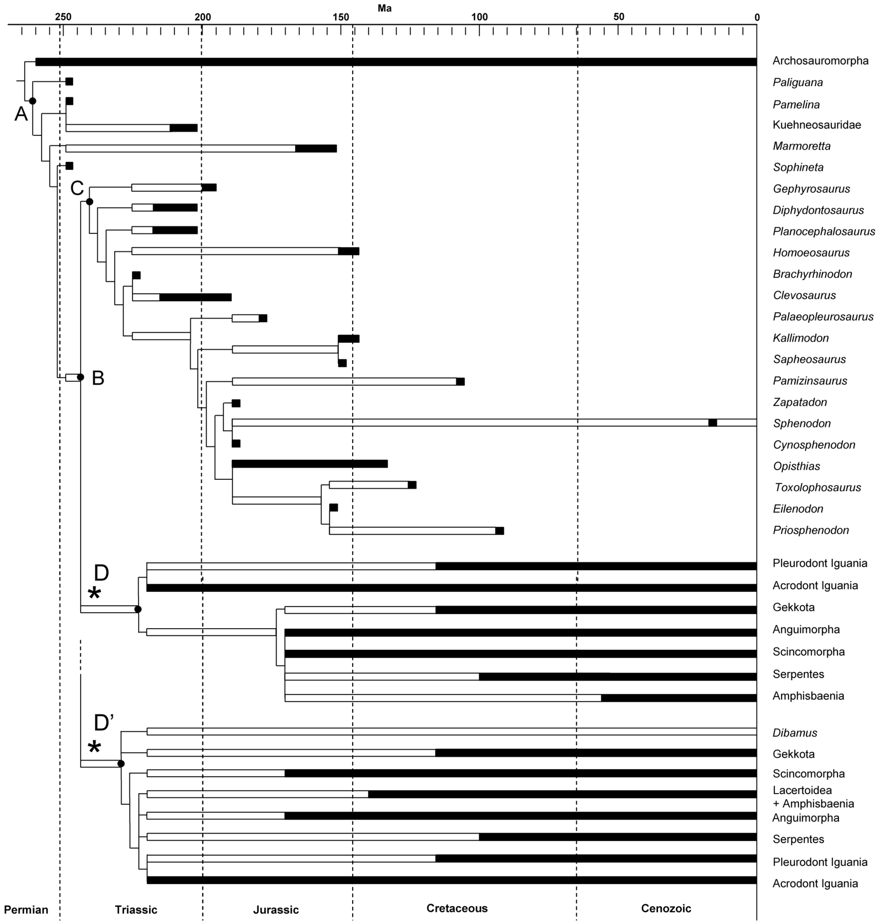

Fig. 2.1 Stratophylogenetic tree of Lepidosauromorpha using the timescale of Gradstein and Ogg (2004) with the latest possible branching points for lineages, based mainly on Evans (2003) and Jones (2006a) with additional data from Datta and Ray (2006, *Tikiguana*), Benton and Donoghue (2007, Archosauromorpha, *Protorosaurus*), Conrad and Norell (2006, Autarchoglossa [Scincomorpha+Anguimorpha], *Parviraptor*), Evans and Borsuk-Białynicka (2009, Czatkowice 1) and Evans (2009, Czatkowice 2). *A*, Lepidosauromorpha; *B*, Lepidosauria; *C*, Rhynchocephalia (phylogeny of Apesteguía and Novas, 2003); *D*, Squamata (morphological tree of Estes et al., 1988); *D’*, Squamata (modified molecular phylogeny of Townsend et al., 2004)

2.2.4 Rhynchocephalia

Rhynchocephalia (Günther, 1867) was erected for *Sphenodon* and its fossil relatives, but the later addition of unrelated acrodont taxa (e.g., rhynchosaurs, claraziids, Romer, 1956) rendered the group polyphyletic (Benton, 1985). Subsequent redefinition of a monophyletic Rhynchocephalia (Gauthier et al., 1988), based around

Sphenodon as originally intended, has now been widely accepted (e.g., Sues and Baird, 1993; Reynoso, 1996, 2000, 2005; Reynoso and Clark, 1998; Gorr et al., 1998; Lee, 1998; Ferigolo, 1999; Schwenk, 2000; Evans, 2003; Wu, 2003; Jones, 2004, 2006a, b, c). Some authors use Sphenodontida in place of Rhynchocephalia (e.g., Vidal and Hedges, 2005), but we strongly advocate usage of the original terminology.

The Early Jurassic *Gephyrosaurus* (Evans, 1980) is the sister taxon of all other rhynchocephalians, with the Late Triassic *Diphydontosaurus* (Whiteside, 1986) and the fully acrodont *Planocephalosaurus* (Fraser, 1982) crownward of it (Fraser and Benton, 1989; Wilkinson and Benton, 1996). Of remaining taxa, the Jurassic *Eilenodon* (Russmusen and Callison, 1981) and Early Cretaceous *Toxolophosaurus* (Throckmorton et al., 1981) appear related to *Sphenodon*, and a clevosaur clade is generally recognized (e.g., Reynoso and Clark, 1998), but there consensus ends (e.g., Wilkinson and Benton, 1996; Reynoso and Clark, 1998; Reynoso, 2005).

The recognition that *Sphenodon* was not a lizard (Günther, 1867) prompted a long debate as to its relationships. Its fully diapsid skull was interpreted as primitive (e.g., Watson, 1914; Parrington, 1935) and *Sphenodon* came to be regarded as a "living fossil", a surviving representative of a conservative ancient diapsid lineage. Now, the fossil record lists more than 40 rhynchocephalian taxa, with a temporal range from Late Triassic (Carnian: Scotland, Fraser and Benton, 1989; Texas, Heckert, 2004; Poland, Dzik and Sulej, 2007) to Recent, and a geographical distribution including Europe, North and South America, China, India, Morocco, South Africa, and New Zealand (Jones, 2006a, b; Jones et al., 2009). Flynn et al.'s (2006, Fig. 10) purported Middle Jurassic rhynchocephalian from Madagascar appears to be a partial theropod tooth.

Mesozoic rhynchocephalians were diverse. They ranged in size over more than an order of magnitude (Fig. 2.2) and included long-bodied marine swimmers (pleurosaurs, sapheosaurs, e.g., Carroll and Wild, 1994), gracile runners (*Homoeosaurus*, e.g., Cocude-Michel, 1963), the armoured *Pamizinsaurus* (Reynoso, 1997) and large bodied genera with hoof-like unguals (*Priosphenodon*, Apesteguia and Novas, 2003). Trophically (Jones, 2006a, c), they included insectivores (e.g., *Gephryosaurus*; *Diphydontosaurus*), opportunistic "carnivores" (*Sphenodon*, e.g., Dawbin, 1962; Cree et al., 1999), supposedly venomous predators (*Sphenovipera*, Reynoso, 2005), and specialized herbivores (e.g., *Toxolophosaurus*, Throckmorton et al., 1981; *Priosphenodon*, Apesteguía and Novas, 2003). Although in some characters they are less derived than lizards (e.g., the fifth metatarsal, the inner ear), the rhynchocephalian feeding apparatus is sophisticated (Jones, 2006a, c; Jones, 2008) and some apparently primitive traits are secondary (e.g., lack of an eardrum and quadrate conch, complete lower temporal bar). *Sphenodon* can remain active at temperatures well below those at which lizards function (5.2°C, Thompson and Daugherty, 1998). This characteristic, in concert with the long reproductive cycle and long life span (Crook, 1975), could be primitive or, more plausibly, an adaptation to life in a cool, relatively high latitude environment (Gans, 1983). The fact that New Zealand lizards show similar, though less extreme, adaptations (Gans, 1983; Cree, 1994; Bannock et al., 1999) supports the latter interpretation.

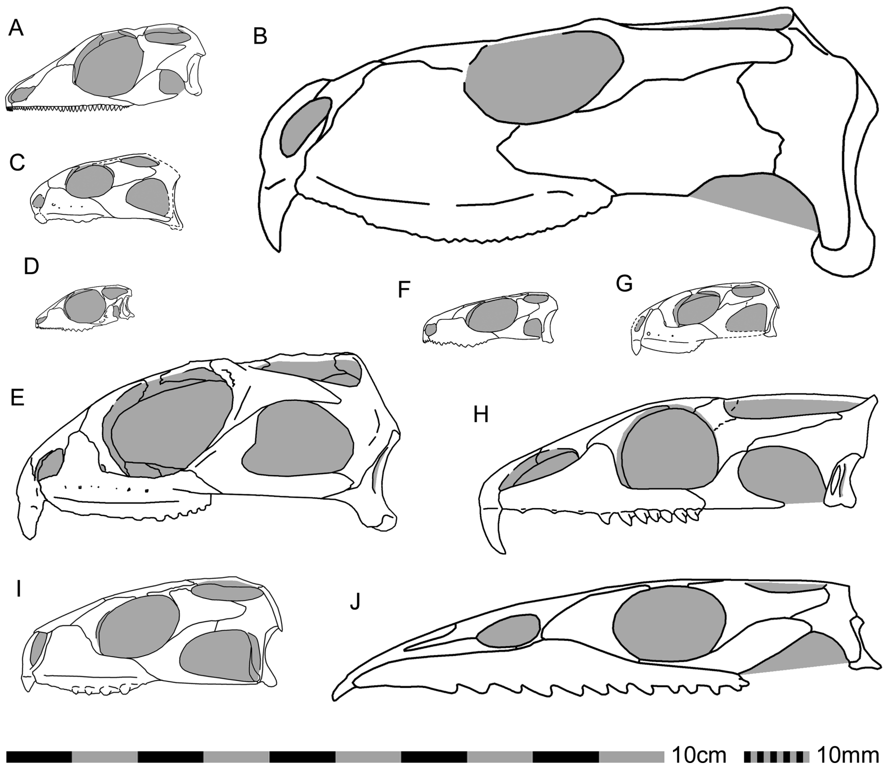

Fig. 2.2 Lateral views of selected rhynchocephalian skulls to illustrate morphological and size diversity. (**a**) *Gephyrosaurus* (Early Jurassic, Wales, Evans, 1980); (**b**) *Priosphenodon* (Late Cretaceous, Argentina, Apesteguía and Novas, 2003); (**c**) *Brachyrhinodon* (Late Triassic, Scotland, Fraser and Benton, 1989); (**d**), *Diphydontosaurus* (Late Triassic, UK, Whiteside, 1986); (**e**) *Sphenodon* (?Miocene-Recent, New Zealand); (**f**) *Planocephalosaurus* (Late Triassic, UK, Fraser, 1982); (**g**) *Clevosaurus* (Late Triassic, Canada, Sues et al., 1994); (**h**) *Palaeopleurosaurus* (Early Jurassic, Germany, Carroll and Wild, 1994); (**i**) *Clevosaurus* (Late Triassic, UK, Fraser, 1988); (**j**) *Pleurosaurus* (Jurassic, Europe, Carroll and Wild, 1994)

2.2.5 Squamata

Squamata includes over 7,000 extant species (e.g., Zug et al., 2001), ranging from tiny geckos to Komodo Dragons and Anacondas, and from fully limbed to limbless morphotypes (Evans, 2003), with specialized gliders, burrowers, climbers, runners and swimmers. Historically (Romer, 1956), squamates were divided into two groups, "Lacertilia" (lizards, Amphisbaenia) and Ophidia (now Serpentes, snakes), but phylogenetic analyses (e.g., Estes et al., 1988; Lee, 1998; Townsend et al., 2004; Vidal and Hedges, 2005) have shown that "Lacertilia" in this sense is not monophyletic. Use of the informal "lizard" is acceptable for a definitive squamate that is neither a snake nor an amphisbaenian, but Lacertilia should not be used.

The first cladistic analysis using morphological characters (Estes et al., 1988) divided Squamata into Iguania (pleurodont and acrodont lineages) and Scleroglossa (all non-iguanian squamates), and most morphological trees show a similar topology (e.g., Lee, 1998; Conrad and Norell, 2006; Sánchez-Martinez et al., 2007; Conrad, 2008). However, molecular trees (e.g., Townsend et al., 2004; Vidal and Hedges, 2005) nest Iguania within Scleroglossa (rendering the latter paraphyletic). Given the uncertainty in the relationships of "lizard" clades, Squamata is best defined as all lepidosaurs that are more closely related to snakes than to *Sphenodon*.

Timing the origins of major squamate groups (e.g., Iguania, Anguimorpha) depends on the tree used (morphological or molecular, Fig. 2.1) and the attribution of early taxa, notably *Tikiguana* (Carnian, India, Datta and Ray, 2006), *Bharatagama* and its pleurodont contemporary (Early Jurassic, India, Evans et al., 2002), and lizards from the Middle Jurassic of the UK (Evans, 1994, 1998), Central Asia (Nessov, 1988, Fedorov and Nessov, 1992; Martin et al., 2006), and China (Clark et al., 2006). Nonetheless, the first radiation must have occurred between the Late Triassic and Middle Jurassic. Many Jurassic-Early Cretaceous taxa are either stem-squamates or basal members of major clades, but mid-Cretaceous fossil squamates demonstrate increased morphological diversity (e.g., Evans et al., 2006; Li et al., 2007) and provide the first records of modern families (Evans, 2003). Whether this represents a real Cretaceous trend, or is simply a reflection of the more complete Cretaceous record remains to be determined.

2.3 The Lower Temporal Bar in Lepidosaurian Evolution

The fully diapsid skull and fixed quadrate of *Sphenodon* was long considered primitive by comparison with the open temporal region and streptostyly of squamates (e.g., Robinson, 1967b). However, a combination of new material (e.g., Evans, 1980; Whiteside, 1986) and new phylogenies (e.g., Gauthier et al., 1988; Müller, 2004) showed that the lower temporal bar was already absent in the last common ancestor

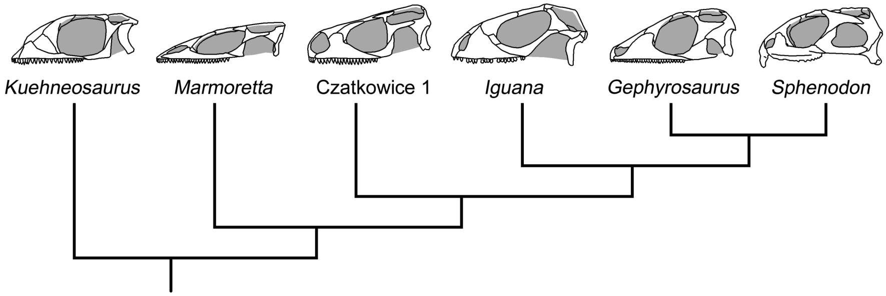

Fig. 2.3 Phylogenetic series of lepidosauromorph skulls in lateral view showing characters relating to the quadrate and lower temporal bar. Redrawn from Evans (2003), with the addition of the stem-lepidosaur (Czatkowice 1) from Poland (Evans and Borsuk-Białynicka, 2009)

of archosauromorphs and lepidosauromorphs (e.g., Müller, 2004), and more basal lineages, like the coelurosauravids (Evans, 1982; Evans and Haubold, 1987), also lack a bar (*Youngina* may have regained it). Thus the first lepidosauromorphs inherited a skull in which the ventral margin of the lower temporal fenestra was open, the quadratojugal was small, and the jugal lacked a posterior process (Fig. 2.3).

Enlargement of the quadrate conch occurred subsequently (as in *Paliguana*, kuehneosaurids, and the new Czatkowice genera). Squamates further modified the temporal region by reducing the bony links within the palatoquadrate (quadrate/epipterygoid), between the palatoquadrate and the rest of the skull (especially epipterygoid/pterygoid; quadrate/pterygoid joints), and between the braincase and the dermal skull roof – variously developing squamate metakinesis, streptostyly and mesokinesis, presumably as an aid to improved prey handling (e.g., Schwenk, 2000; Metzger, 2002). Rhynchocephalians followed a different trajectory, developing a more powerful, shearing bite (Robinson, 1976) and complex dentitions, and reacquiring a lower temporal bar as an adaptation to stabilize the quadrate (Whiteside, 1986; Fraser, 1988; Jones, 2006a, 2008; Moazen et al., 2009). Neither skull type is more primitive than the other, as demonstrated by the recent discovery of Late Cretaceous lizards from China with a complete lower temporal bar (Lü et al., 2008; Mo et al., 2009).

2.4 Discussion

2.4.1 Rhynchocephalians and Squamates

The contrast between the Triassic records of squamates and rhynchocephalians raises questions about taphonomy, habitat preferences, and palaeobiogeography (Evans, 1995, 2003). Rhynchocephalians occurred in both seasonally dry (e.g., the UK Triassic fissure assemblages, Fraser, 1985, 1994; Fraser and Walkden, 1983) and mesic habitats (e.g., Chinle Group, USA, Murry, 1987; Kaye and Padian, 1994; Heckert, 2004; Irmis, 2005), but typically in association with procolophonids, archosauriforms, trilophosaurs, rhynchosaurs, synapsids, and sometimes temnospondyls and phytosaurs. Post-Triassic, however, the association changed dramatically, as many lineages became extinct (Kaye and Padian, 1994). In Early Jurassic fluviolacustrine deposits (e.g., Lufeng, China, Luo and Wu, 1994; Kayenta, Arizona, Sues et al., 1994; McCoy Brook Formation, Nova Scotia, Shubin et al., 1994; La Boca, Mexico, Clark and Hernandez; Fastovsky et al., 1998; Kota Formation, India, Yadagiri, 1986), rhynchocephalians occur with a different assemblage of Triassic survivors, including tritylodont synapsids, mammals, crocodylomorphs, dinosaurs, and turtles. These taxa are joined in the Glen Canyon Formation (Kayenta, Arizona) by the first known crown-group frog and the first recorded gymnophionan (Sues et al., 1994), but no squamates, salamanders, or choristoderes, and in the Kota Formation, India, by very rare frogs and lizards (Yadagiri, 1986; Evans et al., 2002).

In the Carnian Tiki Formation of India, the only recorded Triassic lizard, *Tikiguana* (a single acrodont jaw), occurs in a typical Triassic assemblage like that described above (a phytosaur, a rauisuchid archosauriform, a rhynchosaur, and a non-mammalian cynodont); the only more derived taxon is an early mammal (Datta and Ray, 2006). However, apart from *Tikiguana*, *Bharatagama*, and fragmentary pleurodont remains from the Kota Formation, the earliest recorded lizards come from the Middle Jurassic of Laurasia (the UK, Kyrgyzstan, China, Evans, 1994, 1998; Fedorov and Nessov, 1992; Clark et al., 2006). From this time onwards, many squamates are found in mesic deposits with fish, amphibians (salamanders, albanerpetontids, frogs, rare caecilians), crocodiles, turtles, and frequently choristoderes. This stable assemblage persisted in Laurasia until the Miocene and typically represents lowland, freshwater lagoonal or wetland deposits (e.g., Middle Jurassic Forest Marble, UK, Evans and Milner, 1994; Late Jurassic, Guimarota, Portugal, Martin and Krebs, 2000; Early Cretaceous, Las Hoyas, Spain, Buscalioni and Fregenal-Martinez, 2006; Early Cretaceous Jehol Biota, China, Chang et al., 2003). No Triassic/Early Jurassic deposit has yielded an equivalent assemblage and thus the pre Middle Jurassic record of all component groups is poor. One key difference between the mesic Triassic/Early Jurassic Laurasian deposits that yield rhynchocephalians (e.g., Chinle Group, Glenn Canyon Formation), and those of the Middle Jurassic onward that produce squamates, is the presence in the latter but not the former of salamanders and choristoderes. These clades must have been present in the Triassic but are unrecorded (the choristoderan status of *Pachystropheus* [Storrs and Gower, 1993] is questionable). Rhynchocephalians and squamates are found together in some Jurassic/Cretaceous deposits, but rarely in equal proportions (Evans, 1995). Typically, where squamates are common, rhynchocephalians are rare (e.g., Kirtlington; Purbeck Limestone Group, UK) or absent (e.g., Guimarota), and vice versa (e.g., Solnhofen, Germany; Cerin, France). It is difficult to see how this distinction could be purely taphonomic and it may indicate a subtle difference between early squamate and rhynchocephalian ecology. Perhaps Triassic rhynchocephalians could tolerate a wider range of environmental conditions than early squamates, with this tolerance facilitating the post-Triassic survival of rhynchocephalians in more marginal habitats.

2.4.2 Evolution, Diversification and Extinction

Reisz and Müller (2004) proposed a molecular calibration date of 257–252 million years (Ma) for the archosauromorph-lepidosauromorph dichotomy, but this Late Permian date is difficult to reconcile with levels of Permo-Triassic archosauromorph diversity, or with the, admittedly poorer, lepidosauromorph record. More recent estimates placed the split ~299.8–259.7 Ma (Benton and Donoghue, 2007) or 303.9–263.0 Ma (Sanders and Lee, 2007), during the Lower-Middle Permian, and this is more congruent with the fossil evidence. Early lepidosauromorphs survived the end-Permian crisis, aided perhaps by small size and lower energy needs, and then radiated within the degraded Early Triassic ecosystems (Benton et al., 2004; Roopnarine et al., 2007). The well-nested phylogenetic position of the earliest known Carnian rhynchocephalians argues strongly for an unrecorded Middle Triassic history (Fig. 2.1) and a squamate – rhynchocephalian split in the Early to Middle Triassic (roughly consistent with hemoglobin analysis, Gorr et al., 1998). Rhynchocephalians apparently radiated first, achieving a global Late Triassic distribution (Jones et al., 2009). Both groups survived the end Triassic (or Carnian-Norian) extinctions and continued to diversify, but with differing fates. The Laurasian squamate record steadily improves throughout the Mesozoic. In contrast, rhynchocephalians are not recorded in Asia after the Early Jurassic, despite many apparently suitable small vertebrate localities (e.g., Nessov, 1988; Alifanov, 1993; Gao and Hou, 1996; Gao and Norell, 2000; Chang et al., 2003; Martin et al., 2006; Jones, 2006b). In Euramerica, they survived into the Early Cretaceous, but are unrecorded post-Albian. In the south, however, rhynchocephalians are known from the Late Cretaceous of South America (Apesteguía and Novas, 2003; Apesteguía, 2005a, b; Apesteguía and Rougier, 2007) and possibly the Palaeocene of Morocco (Augé and Rage, 2006). *Sphenodon* is recorded with certainty on New Zealand from the Pleistocene onwards (e.g., Crook, 1975; Holdaway and Worthy, 1997; Worthy, 1998; Worthy and Grant-Mackie, 2003), but rhynchocephalian jaw material is known from the Miocene (Jones et al., 2009). How long rhynchocephalians survived on other southern continents remains unknown (Apesteguía, 2005a).

Currently, the earliest known terrestrial snakes are from the Albian-Cenomanian of North America (Gardner and Cifelli, 1999); putative records from the Late Jurassic (Callison, 1987) are misidentified (SE, pers. obs.). However, in sharp contrast to lizards (e.g., Gao and Hou, 1996; Gao and Fox, 1996; Gao and Nessov, 1998; Gao and Norell, 2000), snakes are rare in the Mesozoic deposits of Euramerica and are unrecorded in Asia until well into the Cenozoic. By contrast, snakes are relatively common in southern continents from the Late Cretaceous onwards (e.g., Albino, 1996; Werner and Rage, 1994; Krause et al., 2003), and lizards are rare (e.g., Krause et al., 2003; Apesteguía et al., 2005; Apesteguía and Zaher, 2006). This has fuelled speculation that there were important differences between the Mesozoic lepidosaurian faunas of northern and southern continents (Apesteguía and Novas, 2003; Krause et al., 2003; Apesteguía, 2005a; Apesteguía and Zaher, 2006; Apesteguía and Rougier, 2007). The typical mesic lizard/salamander/choristodere assemblage that characterizes Laurasian microvertebrate horizons has not been recovered from Gondwana. That of Anoual (Early Cretaceous, Morocco, Sigogneau-Russell et al., 1998) is close, in that it contains fish, amphibians (frogs, caecilians, albanerpetontids), lizards, rhynchocephalians, turtles, crocodiles, dinosaurs, pterosaurs, and mammals, but it lacks both salamanders and choristoderes. Choristoderes have never been found in southern continents and, recent plethodontid range expansions excepted, the salamander record is limited to rare sirenid-like taxa from the Late Cretaceous of Sudan, Niger and South America (Evans et al., 1996). These differences between northern and southern small vertebrate assemblages are tantalizing, and warrant more detailed work.

Terrestrial squamates were little affected by the end-Cretaceous crisis, with the exception of a clade of large herbivorous Asian-American lizards (Evans, 2003), the boreoteiioids (*sensu* Nydam et al., 2007). The fate of the surviving Cretaceous Gondwanan rhynchocephalians is not yet known. *Sphenodon* eats a wide range of invertebrates and small vertebrates (e.g., Dawbin, 1962; Walls, 1981; Markwell, 1998; Cree et al., 1999; Moore and Godfrey, 2006), but known Late Cretaceous South American taxa (e.g., *Priosphenodon*, Apesteguia and Novas, 2003) were large herbivores. It is possible that the latter declined, like the herbivorous boreoteiioids, because of global cooling; digestion of plant material in reptiles being dependent on external ambient temperatures (Harlow et al., 1976; Troyer, 1987; van Marken Lichtenbelt, 1992; Tracy et al., 2005). The more generalist sphenodontines may have been better able to survive at the southern periphery.

2.5 Conclusions

Lepidosauromorphs probably diverged from archosauromorphs in the mid-Permian. They survived the end-Permian crisis and joined a depauperate Early Triassic fauna characterized by small, versatile tetrapods (the ancestors of lissamphibians, mammals, dinosaurs, etc.). Ancestral lepidosauromorphs had a skull without a lower temporal bar. Lepidosauria probably originated in the Early-Middle Triassic. Rhynchocephalians may have been the first lineage to achieve a global distribution, as part of a Late Triassic assemblage including procolophonians, phytosaurs, temnospondyls, synapsids, archosauromorphs and basal archosaurs. Unlike most of these groups, however, rhynchocephalians survived the end-Triassic (and/or Carnian/Norian) extinctions, but declined first in Asia (Early Jurassic) and then Euramerica (mid-Cretaceous) as limbed squamates diversified (although the two events are not necessarily causally linked, Jones, 2006b). In southern continents, rhynchocephalians survived into the Late Cretaceous (South America) and beyond, in association with a terrestrial assemblage that included abundant snakes but rarer lizards. Herbivorous rhynchocephalians (like herbivorous lizards) may have been more vulnerable to environmental changes (e.g., cold) at the Cretaceous-Palaeogene boundary than their opportunistic relatives, some of which survived and reached New Zealand (although it is not known when). Future discoveries in Mesozoic and Palaeogene deposits around the world will test these hypotheses but as Pamela Robinson recognized more than 50 years ago, India could be pivotal, having a unique palaeobiogeography (long isolation); important Mesozoic horizons, and tantalizing fossils (e.g., *Tikiguana*, *Bharatagama*).

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