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At the feet of the dinosaurs: the early history and radiation of lizards

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ABSTRACT

Lizards, snakes and amphisbaenians together constitute the Squamata, the largest and most diverse group of living reptiles. Despite their current success, the early squamate fossil record is extremely patchy. The last major survey of squamate palaeontology and evolution was published 20 years ago. Since then, there have been major changes in systematic theory and methodology, as well as a steady trickle of new fossil finds. This review examines our current understanding of the first 150 million years of squamate evolution in the light of the new data and changing ideas. Contrary to previous reports, no squamate fossils are currently documented before the Jurassic. Nonetheless, indirect evidence predicts that squamates had evolved by at least the middle Triassic, and had diversified into existing major lineages before the end of this period. There is thus a major gap in the squamate record at a time when key morphological features were evolving. With the exception of fragmentary remains from Africa and India, Jurassic squamates are known only from localities in northern continents (Laurasia). The situation improves in the Early Cretaceous, but the southern (Gondwanan) record remains extremely poor. This constrains palaeobiogeographic discussion and makes it difficult to predict centres of origin for major squamate clades on the basis of fossil evidence alone. Preliminary mapping of morphological characters onto a consensus tree demonstrates stages in the sequence of acquisition for some characters of the skull and postcranial skeleton, but many crucial stages – most notably those relating to the acquisition of squamate skull kinesis – remain unclear.

Key words: lizard, Lepidosauria, Squamata, evolution, phylogeny, biogeography, skull morphology, fossils, Mesozoic.

CONTENTS

I. INTRODUCTION

(1) General comments

Under current definitions, living reptiles (*sensu stricto*) fall into three groups: Chelonia (turtles, tortoises), Archosauria (crocodiles and birds), and Lepidosauria (lizards, snakes and their relatives). Lepidosauria, in turn, incorporates two subgroups, Rhynchocephalia and Squamata. Rhynchocephalia is represented today only by the two species of tuatara (genus *Sphenodon*), confined to small islands off the coast of New Zealand. By contrast, living squamates include more than 7000 species of lizards, snakes, and amphisbaenians ('worm-lizards'), distributed across all but the coldest parts of the world. Members of the group range in length from a few millimetres [e.g. species of the Leaf Chamaeleon, *Brookesia* (18 mm mean snout-vent, s-v, length) and of the gekkotan *Sphaerodactylus* (16 mm mean s-v length – the smallest known amniotes; Hedges & Thomas, 2001)] to several metres (e.g. the Anaconda, *Eunectes murinus*, and the Komodo Dragon, *Varanus komodoensis*). They include specialist climbers (chamaeleons, geckos), gliders (the agamid genus *Draco*, 'Flying Dragons'), parachuters (e.g. the gekkotan genus *Ptychozoon*), swimmers (e.g. the Marine Iguana *Amblyrhynchus cristatus* and the extinct mosasaurs), burrowers and sand-swimmers (e.g. amphisbaenians, typhlopid snakes, and some scincid lizards), and facultative bipedal runners (e.g. the iguanian genera *Basiliscus* and *Chlamydosaurus*), as well as many ground dwellers. Limblessness has arisen repeatedly (e.g. snakes, amphisbaenians and many lizard groups: Gans, 1962, 1975; Greer, 1991; Coates & Ruta, 2000). Most lizards are insectivores, but a few are herbivores (e.g. members of the genus *Iguana*), omnivores (e.g. some lacertids and xantusiids), or durophages (e.g. the teiid *Dracaena guianensis*), and some are active predators (especially Monitor Lizards of the genus *Varanus*, and many snakes). Uniquely amongst living tetrapods, some advanced squamate predators use venom to subdue prey (e.g. the Gila Monster, *Heloderma suspectum*, and many higher snakes), while reproductive strategies include both egg laying and live birth. At least eight groups (agamids, chamaeleons, gekkotans, lacertids, xantusiids, teiids, gymnophthalmids, and the typhlopid snakes) include one or more all-female (parthenogenetic) species (Zug, 1993). Overall, this diversity sets squamates apart.

The great 'Age of Reptiles', the Mesozoic, extended from the beginning of the Triassic approximately 250 million years ago (Ma) until the end of the Cretaceous (65 Ma), culminating in the K-T extinction. Late Cretaceous lizard assemblages incorporate representatives of most modern lineages, and are comparatively well-known from northern continents (the ancient Laurasia): China (Gao & Hou, 1995, 1996), Mongolia (Gilmore, 1943; Borsuk-Białynicka, 1984, 1988, 1991, 1996; Alifanov, 1989*a*, *b*, 1993*a–c*, 1996, 2000; Gao & Norell, 1998, 2000), the USA (Gilmore, 1928; Estes, 1964, 1970), Canada (Gao & Fox, 1991, 1996), and Spain (Astibia *et al.*, 1991; Rage, 1999). By far the most spectacular assemblages known are those of the Campanian (approximately 83–71 Ma) of Mongolia, with more than 40 genera representing a majority of major lizard clades (but no snakes) and a diversity of ecological niches (including insectivores, carnivores and rare herbivores; surface dwellers and specialist burrowers; Gao & Norell, 2000). The southern (Gondwanan) lizard record is much poorer and is limited to Brazil (Estes & Price, 1973), India (Rage & Prasad, 1992), and, most recently, Madagascar (Krause, Evans & Gao, 2002). For reasons not yet understood, the snake record shows a reverse pattern, with a relatively diverse Gondwanan history in the Late Cretaceous (e.g. Albino, 1996; Rage & Werner, 1999), but fewer records from Laurasia. Squamates survived the K-T extinction relatively unscathed, except for some groups of teiids and the marine varanoids (e.g. Sullivan, 1987; Macleod *et al.*, 1997). Modern genera are first recorded from the Eocene (e.g. the agamid *Uromastyx* and anguid *Ophisaurus* in Europe, Rage & Auge, 1993; Barbadillo, García & Sanchíz, 1997), with most appearing from the Miocene onwards (e.g. Estes, 1983*a*; Roĉek, 1984; Rage & Auge, 1993; Sullivan & Holman, 1996; Barbadillo *et al.*, 1997; Venzcel, 1999).

By contrast, the first half of squamate history has a much more limited record. In the last major review, Estes (1983*a*) listed only 25 lizard genera for the approximately 150 Ma period encompassing the Triassic to the end of the Early Cretaceous (Albian), and of these, nine were subsequently reclassified outside Squamata (see below, and Appendix). Since Estes' review, our understanding of squamate relationships has changed considerably, as have our ideas of what constitutes a lepidosaur, a rhynchocephalian, and a squamate. The fossil record has also improved, with a doubling of named taxa, and more in the process of being described from localities around the world. The geographical range now includes Europe, North and South Africa, North and South America, Central Asia, Siberia, India, China, and Japan. This review discusses our current knowledge of early squamate history based on these new perspectives.

(2) Old and new concepts of Lepidosauria

Amongst tetrapods, Synapsida (mammals and lineages ancestral to mammals) and Reptilia (by modern definition including birds, e.g. Gauthier, 1986, 1994) together constitute the Amniota, a group characterized by the common possession of an egg with extra-embryonic membranes. Amniota dates from at least the Late Carboniferous (approximately 310 Ma, e.g. Berman, Sumida & Lombard, 1997). Traditionally (e.g. Osborn, 1903; Williston, 1917; Romer, 1956), amniotes were classified according to the configuration and fenestration of the postorbital (temporal) region of the skull: Anapsida (solid, no fenestrae); Parapsida (one upper fenestra); Synapsida (one lower fenestra); and Diapsida (upper and lower fenestrae).

The American palaeontologist A. S. Romer (1956) subdivided known diapsids into Archosauria (crocodiles, dinosaurs, pterosaurs and related taxa) and Lepidosauria (all non-archosaurian diapsids). Romer's arrangement was consistent with the systematic practices of the time (which involved sorting taxa into discrete circumscribed sets rather than the branching trees of today), and his classification remained standard well into the 1980s. However, definitions and diagnoses frequently relied on the common possession of primitive (plesiomorphic) character states or (and it amounts to the same thing) the absence of derived 'key' characters. Thus Romer's Lepidosauria was essentially a 'hold-all' for all diapsids that lacked archosaurian traits. Modern phylogenetic systematics requires that groups (clades) are monophyletic (containing all, and only, the descendents of a single common ancestor), with diagnoses based on a suite of derived (apomorphic) character states. Most of Romer's 'lepidosaurs' are now classified in other parts of the reptilian cladogram (e.g. Evans, 1980, 1984, 1988; Gauthier, 1984, 1994; Benton, 1985; Gauthier, Estes & De Queiroz, 1988*a*), and Lepidosauria *sensu stricto* has a tightly constrained node-based definition: it encompasses the last common ancestor of Rhynchocephalia and Squamata, and all descendants of that ancestor (e.g. Evans, 1984, 1988; Gauthier, 1984; Gauthier *et al.*, 1988*a*).

Although Rhynchocephalia and Squamata each show distinctive features (see below), they share at least 55 derived character states (e.g. Evans, 1988; Gauthier *et al.*, 1988*a*; Gauthier, 1994). These include:

(1) A derived skin structure with a specialized shedding mechanism involving distinct epidermal generations that are periodically lost and replaced, linked to a cyclic alternation between α and β keratogenesis (Lange, 1931; Maderson, 1972 and P. F. A. Maderson, personal communication, November 2001; Maderson *et al.*, 1998; Maderson & Alibardi, 2000). The possession of a crest of projecting scales along the dorsal midline of the body and tail (Gauthier, 1994) may also be unique to members of this group.

(2) Paired male hemipenes housed in eversible pouches at the posterior corners of a transverse cloacal slit. These hemipenes are well developed in squamates and rudimentary in *Sphenodon* (e.g. Gauthier *et al.*, 1988*a*; Gauthier, 1994).

(3) Notching of the tongue tip, possibly in relation to the development of the vomero-nasal system (Schwenk, 1988).

(4) Separate centres of ossification in the epiphyses of the limb bones (a condition acquired independently in mammals and some birds) (e.g. Haines, 1969; Evans, 1988; Gauthier *et al.*, 1988*a*; Carter, Mikić & Padian, 1998).

(5) Specialized mid-vertebral fracture planes in tail vertebrae to permit caudal autotomy (e.g. Arnold, 1984; Bellairs & Bryant, 1985; Evans, 1988; Gauthier *et al.*, 1988*a*), facilitated by the organisation of associated soft tissue.

(6) A unique knee joint in which the fibula meets a lateral recess on the femur (not end to end as in many tetrapods) (Gauthier *et al.*, 1988*a*).

(7) Specialized foot and ankle characters including a hooked fifth metatarsal, a specialized mesotarsal joint with a fused astragalocalcaneum and an enlarged fourth distal tarsal (Robinson, 1975; Brinkman, 1980).

(8) Other soft tissue features include a sexual segment on the kidney; reduction or absence of the ciliary process in the eye; presence of a tenon (cartilaginous disc) in the nictitating membrane and its attachment to the orbital wall (Gauthier *et al.*, 1988*a*; Zug, 1993).

In addition to these characters, all lepidosaurs show one of two kinds of tooth implantation, pleurodonty and acrodonty. In pleurodonty, the teeth have a substantial attachment to the lingual surface of the jaw in addition to the subdental shelf. In acrodonty, the teeth are fused to the crest of the jaw and are not replaced. There is an intermediate condition (or range of conditions), pleuroacrodonty, where the teeth are fused, or held by ankylosing bone, to the lingual surface of the jaw.

The monophyly of Lepidosauria as currently defined is widely accepted amongst morphologists and palaeontologists (e.g. Evans, 1984, 1988; Gauthier, 1984, 1994; Estes, De Queiroz & Gauthier, 1988; Gauthier *et al.*, 1988*a*; Gauthier, Kluge & Rowe, 1988*b*; Rieppel & De Braga, 1996; Maderson *et al.*, 1998), but has been questioned by some molecular biologists. Hedges & Poling (1999), for example, argued that *Sphenodon* was more closely related to archosaurs than to squamates. This would require independent acquisition of a wide range of specialized features and takes no account of the fossil histories of the groups in question.

Following revision of Romer's 'Lepidosauria' (e.g. Evans, 1980, 1984, 1988; Benton, 1983, 1985; Gauthier, 1984; Gauthier *et al.*, 1988*a*), there remained a small subset of taxa sharing a limited suite of derived character states with Lepidosauria *sensu stricto* (e.g. Gauthier, 1984; Evans, 1988, 1991; Gauthier *et al.*, 1988*a*). To encompass these, Jacques Gauthier (Camp Memorial Symposium, Louisville, Kentucky, December 1982; Gauthier, 1984; Gauthier *et al.*, 1988*a*) introduced the term Lepidosauromorpha (Lepidosauria + stem taxa). The concept of Lepidosauromorpha as the sister taxon of Archosauromorpha (Archosauria + stem taxa) is now well established, although relatively few basal lepidosauromorphs have been described (the Late Triassic kuehneosaurs, Robinson, 1962, 1967*a*, *b*; Colbert, 1966, 1970; the Middle Jurassic *Marmoretta*, Evans, 1991; an unnamed Lower Triassic genus from Poland, Borsuk-Białynicka *et al.*, 1999; and, less certainly, the Permo-Triassic *Paliguana*, Carroll, 1975, 1977). The position of the burrowing *Tamaulipasaurus* from the Early-Middle Jurassic of Mexico (Clark & Hernandez, 1994) is problematic. Arguments for the inclusion of sauropterygians (e.g. nothosaurs, plesiosaurs) and turtles (e.g. Rieppel, 1993; De Braga & Rieppel, 1997) remain equivocal, and are beyond the scope of this article.

(3) Protolizards and the definition of Squamata

In 1867, Günther reported that the lizard-like New Zealand tuatara, *Sphenodon*, had a fully diapsid skull in contrast to the open 'cheek' region and streptostyly (independent mobility of the quadrate) of squamates. This initiated a protracted debate on lizard evolution and relationships, focusing on the origin of the distinctive squamate skull morphology. Watson (1914) and Williston (1914, 1917) favoured ventral emargination of the unfenestrated lower temporal region in a parapsid skull, and Williston's (1914) *Araeoscelis* (Lower Permian, USA) provided a model ancestor (Fig. 1) (although this genus has now been interpreted as a basal diapsid; Reisz, Berman & Scott, 1984). Under this hypothesis, *Sphenodon*, as a diapsid, was not related to squamates. The rival camp (e.g. Osborn, 1903; Broom, 1925) argued that the embayed squamate temporal region evolved by reduction, and then loss, of the lower temporal bar in a diapsid ancestor (Fig. 1). This second hypothesis found support in a series of small gracile diapsids from the Permo-Triassic of South Africa, most notably the Lower Triassic *Prolacerta* (Parrington, 1935). *Prolacerta* retained a posterior process on the jugal as evidence of its diapsid ancestry, but the corresponding anterior process of the quadratojugal was reduced, leaving the lower temporal bar incomplete (Fig. 2).

Prolacerta was heralded as the archetypal protolizard (e.g. von Huene, 1956; Robinson, 1967*a*; Wild, 1973),

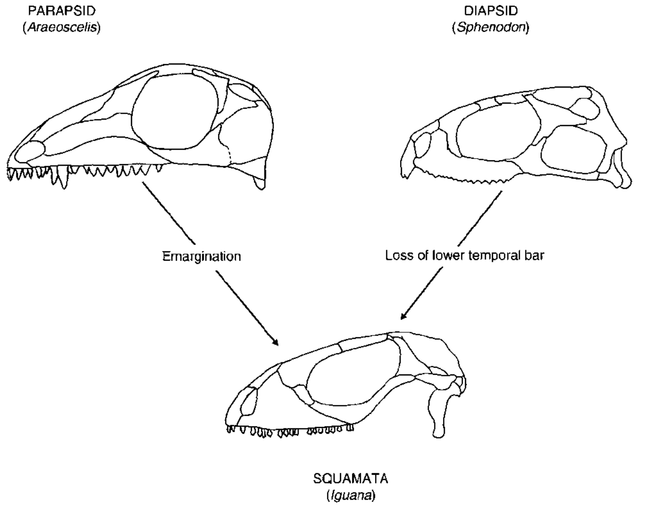

Fig. 1. The early controversy over the origin of the squamate skull condition, parapsid versus diapsid ancestry. Skull of *Araeoscelis* redrawn from Reisz *et al.* (1984); others original.

and reduction of the lower temporal bar came to be regarded as a uniquely presquamate condition (a 'key' character linked to the acquisition of squamate streptostyly, e.g. Parrington, 1935; Romer, 1956; Robinson, 1967*a*). From this perspective, focusing on the temporal region almost to the exclusion of the rest of the skull and skeleton, the next step required only loss of the quadratojugal and a further reduction of the jugal and squamosal. The Upper Triassic gliders *Kuehneosaurus* (U.K., Robinson, 1962, 1967*a*; Fig. 2) and *Icarosaurus* (Colbert, 1966) therefore seemed perfect intermediates (but see Hoffstetter, 1962; Kluge, 1967), and their classification as basal squamates ('eolacertilians') paved the way for other taxa (e.g. *Tanystropheus*, Wild, 1973; *Cteniogenys*, Seiffert, 1973; *Fulengia*, Carroll & Galton, 1977). The inclusion of the 'paliguanids' took squamates into the Late Permian (Carroll, 1975, 1977).

Around the same time, however, a combination of new fossil discoveries and new systematic ideas began to question the existing consensus, since it gradually became clear that loss of the lower temporal bar was not restricted to stem squamates (Robinson, 1973; Gow, 1975; Evans, 1980; Whiteside, 1986), and that other characters were important to the discussion. One problem was raised, unexpectedly, by *Prolacerta* itself, when the discovery of associated skull and postcranial material (Gow, 1975) demonstrated that it was actually related to archosaurs rather than squamates. Further clarification came with the description of basal rhynchocephalians showing an unexpected combination of skull and postcranial characters (Evans, 1980; Whiteside, 1986). The Early Jurassic *Gephyrosaurus* (Evans, 1980) and Late Triassic *Diphydontosaurus* (Whiteside, 1986) had reduced the lower temporal bar, but retained a large squamosal, a small quadratojugal, and an immobile quadrate, placing them below kuehneosaurs in the existing scheme (Fig. 2). However, in all other features of the skull and skeleton, they showed a much greater resemblance to squamates (as, in fact, did *Sphenodon*). Moreover, these early rhynchocephalians demonstrated that the complete lower temporal bar of *Sphenodon* was not primitive, but had been reacquired (Whiteside, 1986). Many of the shared similarities of *Gephyrosaurus*, *Diphydontosaurus*, *Sphenodon*, and squamates are now recognized as diagnosing Lepidosauria, to the exclusion of taxa like *Kuehneosaurus* and *Icarosaurus* (Evans 1980, 1984, 1988; Gauthier, 1984; Gauthier *et al.*, 1988*a*) in which the temporal structure is convergent.

Under current node-based definitions, Squamata accommodates the last common ancestor of the living Iguania and Scleroglossa and all of its descendants, and is diagnosed by a robust suite of derived character states (e.g. Evans, 1984, 1988; Estes *et al.*, 1988; Gauthier *et al.*, 1988*a*; Rieppel, 1988*b*) including:

(1) a specialized quadrate articulation with a dorsal joint typically supplied by the deeply placed supratemporal, reduced squamosal, and distally expanded paroccipital process of the braincase; reduction/loss of pterygoid/quadrate overlap; loss of quadratojugal;

(2) loss of attachment between the quadrate and epipterygoid, with the development of a specialized ventral synovial joint between the epipterygoid and pterygoid;

(3) subdivision of the primitive metotic fissure of the braincase to give separate openings for the vagus nerve (dorsally) and the perilymphatic duct and glossopharyngeal nerve (via the lateral opening of the recessus scalae tympani ventrally). This leads to the development of a secondary tympanic window for compensatory movements and is associated with expansion of the perilymphatic system (Baird, 1970) and closure of the medial wall of the otic capsule;

(4) loss of ventral belly ribs (gastralia);

(5) emargination of the anterior border of the scapulocoracoid;

(6) hooked fifth metatarsal with double angulation (Robinson, 1975) and more complex mesotarsal joint (Brinkman, 1980);

(7) a suite of soft tissue characters including greater elaboration of the vomeronasal apparatus; a single rather than paired meniscus at the knee; the presence of femoral and preanal organs; fully evertible hemipenes; and pallets on the ventral surface of the tongue tip (Gauthier *et al.*, 1988*a*; Schwenk, 1988).

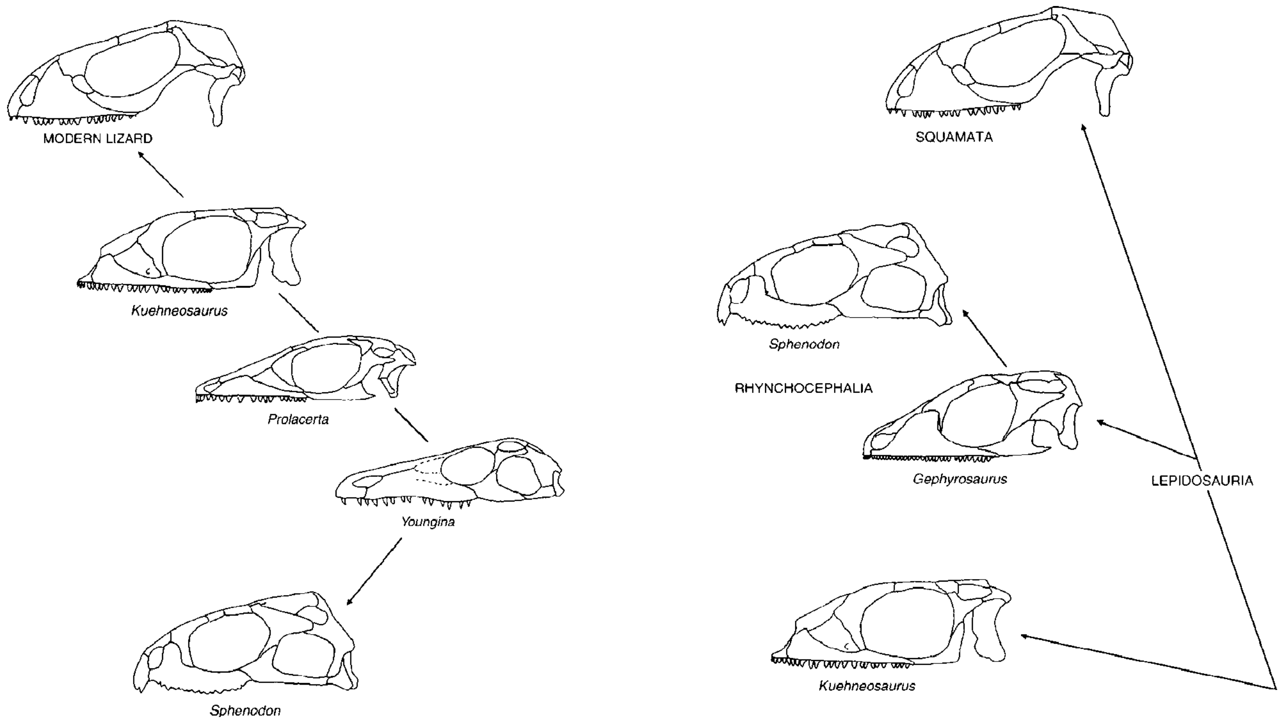

Fig. 2. Left, scheme of squamate skull evolution reformatted from Robinson (1973). Right, modified scheme of lepidosaurian skull evolution. Individual skull views from Robinson (1973), Evans (1980) and original.

(4) Rhynchocephalia: definitions, diagnosis and relationships

The Tuataras of New Zealand (*Sphenodon guentheri* and *S. punctatus*, Daugherty *et al.*, 1990) are the only surviving rhynchocephalians, but these rare animals have a heritage that extends back into the Triassic. At one time, Rhynchocephalia had a worldwide distribution, and close to 30 Mesozoic fossil genera have been described to date (for recent reviews, see Reynoso, 1997, 2000; Evans, Prasad & Manhas, 2001). Known taxa show considerable diversity (in tooth morphology, habits), but share a unique combination of character states that makes them easily identifiable as fossils (e.g. Evans, 1988; Gauthier *et al.*, 1988*a*), including:

(1) an acrodont dentition (with some early exceptions, Evans, 1980; Whiteside, 1986);

(2) an enlarged lateral palatine tooth row running parallel, or sub-parallel, to the maxillary row and permitting either propalinal or orthal shear;

(3) a posterior extension of the dentary which braces the accessory jaw bones;

(4) loss or fusion of the supratemporal bone.

The Early Jurassic *Gephyrosaurus* (Evans, 1980) is the sister taxon of all other rhynchocephalians (which together comprise the Sphenodontia, Whiteside, 1986; Gauthier *et al.*, 1988*a*; Fig. 3). Within Sphenodontia, the pleuroacrodont Upper Triassic *Diphydontosaurus* (Whiteside, 1986) is basal, with the fully acrodont *Planocephalosaurus* (Fraser, 1982) lying one node crownward (Fraser & Benton, 1989; Wilkinson & Benton, 1996). All higher taxa show a further reduction in the number of palatine tooth rows, a reduction in the total number of teeth, and evidence of either orthal or propalinal shear (e.g. the Triassic *Clevosaurus*, Robinson, 1973; Fraser, 1988; the Jurassic *Homoeosaurus*, Cocude-Michel, 1963, and *Eilenodon*, Rasmussen & Callison, 1981; and the Cretaceous *Toxolophosaurus*, Throckmorton, Hopson & Parks, 1981).

A full review of rhynchocephalian evolution and systematics is beyond the scope of this paper, but some aspects of their palaeontology contribute to our understanding of lepidosaurian evolution as a whole, and thus, ultimately, also to our understanding of squamate history. Unlike squamates, rhynchocephalians have a relatively good Triassic and Early Jurassic record, providing information on the timing and pattern of early lepidosaurian diversification (see below). Similarly, the analysis of basal rhynchocephalians like *Gephyrosaurus* provided a clearer picture of early lepidosaurian morphology (e.g. Evans, 1980, 1984), and thus had a role in the development of more robust definitions and diagnoses of both Lepidosauria and Squamata (Evans, 1984; Gauthier *et al.*, 1988*a*).

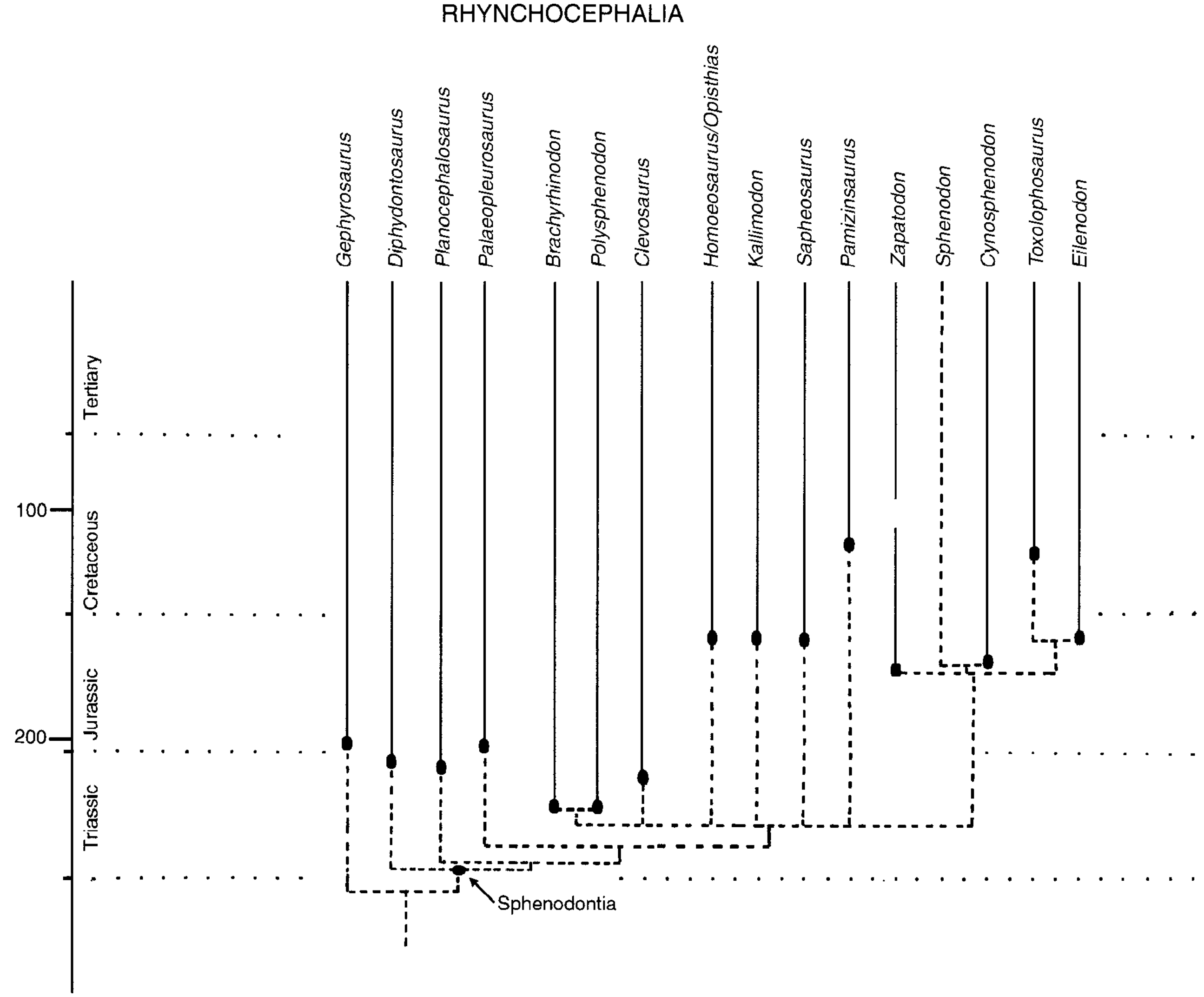

Fig. 3. Phylogenetic diagram showing hypothesis of relationships for Rhynchocephalia (taken mostly from Reynoso, 1996, 1997; Wilkinson & Benton, 1996) plotted against time (after Gradstein *et al.*, 1995). Dots show known early records and dotted lines minimum estimates of lineage extension (data mostly from Evans *et al.*, 2001, and references therein).

(5) Phylogenetic relationships within Squamata – an overview

There is, as yet, no detailed consensus on the relationships of crown-group squamates and a comprehensive systematic reanalysis is beyond the scope of the present review. Nonetheless, since evolutionary discussion requires a phylogenetic framework, some of the main areas of both consensus and debate are outlined below.

(*a*) '*Eolacertilia*'

Eolacertilia (Robinson, 1967*a*) was erected to accommodate the Late Triassic gliding reptile *Kuehneosaurus* (see Section 1.3) and other taxa regarded as basal squamates (e.g. Colbert, 1970; Carroll, 1975, 1977). In his review of fossil lizards, Estes (1983*a*) listed nine 'eolacertilian' genera. Of these, the 'paliguanids' (*Paliguana*, *Palaeagama*, *Saurosternon*), *Kuehneosaurus*, *Icarosaurus*, and *Fulengia* are discussed in more detail below (Section II.3), but none are squamates. Of the remaining three, *Kuehneosuchus* Robinson 1967*b* is a close relative of *Kuehneosaurus* (perhaps congeneric), while the Jurassic–Early Cretaceous *Cteniogenys* Gilmore 1928 (Seiffert, 1973) is an early choristodere (a group of aquatic reptiles characterized by the Cretaceous/Tertiary *Champsosaurus*: Evans, 1990). The last of Estes' (1983*a*) 'eolacertilians', the Late Cretaceous *Litakis* Estes 1964, is based on a single, isolated, dentary. In fact, it is a true squamate (S. E. Evans, unpublished data), possibly allied to teiids (relatively shallow tooth implantation, weak subdental ridge).

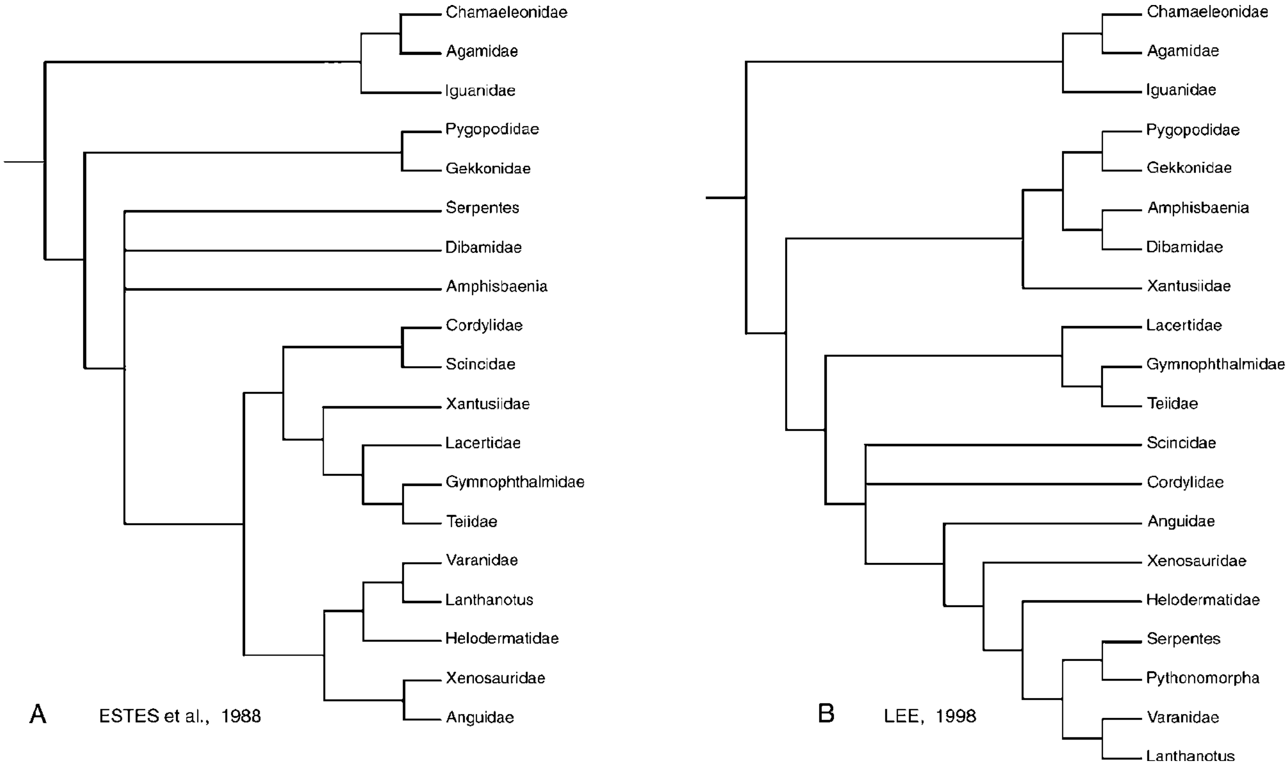

Fig. 4. Comparison of hypothesis of relationships for Squamata taken from (A) Estes *et al.* (1988) and (B) Lee (1998).

(*b*) *The divisions of crown-group Squamata*

Traditional classifications (e.g. Romer, 1956) divided Squamata between Lacertilia (lizards, amphisbaenians) and Ophidia (=Serpentes, snakes). Amphisbaenians were subsequently placed in a clade of their own (Gans, 1978). However, cladistic analysis (e.g. Estes *et al.*, 1988) demonstrates that 'lizards' do not form a monophyletic group: they cannot be diagnosed to the exclusion of either snakes or amphisbaenians. Formal names like 'Lacertilia' or 'Sauria' should therefore be avoided since they imply monophyly. In the context of this review, the term lizard is used as shorthand to mean a squamate that is neither a snake nor an amphisbaenian. In fact, the primary dichotomy within Squamata is between Iguania (e.g. iguanas, chamaeleons) and Scleroglossa (all other squamates including amphisbaenians and snakes).

Many squamate trees have been published since 1900 (see Rieppel, 1988*b* for a review). Fig. 4 compares the results of two studies. Estes *et al.* (1988) performed the first comprehensive cladistic analysis for Squamata, while that of Lee (1998) is one of the more recent. There is a broad level of agreement between these phylogenies (and those of other authors e.g. Evans & Barbadillo, 1997; Donellan, Hutchinson & Saint, 1999; Reynoso & Callison, 2000), in terms of the monophyly of Iguania, Gekkota and Anguimorpha, and the position of snakes. Differences mainly concern the relationships between the three major scleroglossan groups, the relationships between the various scincomorph lineages, and the relationships of amphisbaenians and dibamids.

(*c*) *Iguania*

Iguania is a large, diverse clade. Traditionally (e.g. Romer, 1956), its members were classified on the basis of tooth morphology. Those with a typically pleurodont dentition formed the Iguanidae, in contrast to the two acrodont families, Agamidae and Chamaeleonidae. Living pleurodont iguanians are mainly distributed through the Americas, with outliers in Fiji and Tonga (*Brachylophus*), and in Madagascar (*Chalarodon*, *Oplurus*). The agamids and chamaeleons are their 'Old World' counterparts. Early cladistic analyses (e.g. Estes *et al.*, 1988; Frost & Etheridge, 1989) challenged the monophyly of the traditional Iguanidae and Agamidae with respect to chamaeleons, while recognising that of Acrodonta as a whole (a conclusion also supported by molecular studies, e.g. Joger, 1991; Macey *et al.*, 1997). Frost & Etheridge (1989) proposed eight monophyletic subunits within pleurodont iguanians (used subsequently at either subfamily or family level), but resolution of their interrelationships has proved intractable. Moreover, molecular analyses (e.g. Joger, 1991;

Macey *et al.*, 1997, 2000) continued to recover a monophyletic 'Iguanidae' in the traditional sense, and this conclusion has recently received support from a study combining morphological and molecular data (Frost *et al.*, 2001).

(*d*) *Scleroglossa*

The three remaining squamate clades, Gekkota, Scincomorpha and Anguimorpha, comprise the Scleroglossa (*sensu* Estes *et al.*, 1988). Gekkota consists primarily of specialist nocturnal climbers, although it also embraces the limbless Australian pygopodids. Scincomorpha is more complex but includes many 'typical' lizards (e.g. scincids, cordylids, lacertids, teiids), while Anguimorpha encompasses anguids (e.g. *Anguis*, the European Slow Worm), xenosaurs, the Gila Monster and Beaded Lizard (genus *Heloderma*), and the successful varanids (Monitor Lizards). Under current hypotheses of relationship, Anguimorpha also includes snakes (Rieppel, 1988*b*; Caldwell & Lee, 1997; Lee, 1998; Coates & Ruta, 2000; Lee & Caldwell, 2000; Tchernov *et al.*, 2000), but the highly specialized, burrowing dibamids and amphisbaenians are more problematic, with recent analyses linking them alternatively to snakes (e.g. Rieppel & Zaher, 2000*a*, *b*), to gekkotans (Lee, 1998; Caldwell, 1999; Lee & Caldwell, 2000), or to teiids (Wu *et al.*, 1993; Wu, Brinkman & Russell, 1996; Kearney, 1999).

Estes *et al.* (1988) placed Gekkota as the sister taxon of Autarchoglossa (Scincomorpha + Anguimorpha, Fig. 4A). Subsequent analyses either supported this (e.g. Hallerman, 1998) or suggested alternatives, namely Scincomorpha + Gekkota (e.g. Presch, 1988; Reynoso & Callison, 2000) or Anguimorpha + Gekkota (e.g. Evans & Chure, 1998*b*; Gao & Norell, 1998; Reynoso, 1998). Lee (1998) united Gekkota with dibamids, amphisbaenians and the enigmatic xantusiids in a new clade, Nyctisauria, that is the sister group of other scleroglossans (Fig. 4B). The difficulties are exacerbated by uncertainty over the monophyly of Scincomorpha (see below), by gekkotan paedomorphy, and by the paucity of the gekkotan and xantusiid fossil record (Estes, 1983*a*; Alifanov, 1989*b*).

As commonly defined (Estes *et al.*, 1988), Scincomorpha (Camp, 1923) contains Scincidae, Cordyliformes (cordylids and gerrhosaurs), Lacertidae, Teioidea (teiids and gymnophthalmids), and, less certainly, xantusiids (e.g. Camp, 1923; Estes *et al.*, 1988; Hallerman, 1998; Reynoso, 1998; Rieppel, 1988*a*). Most authors support a relationship between teioids and lacertids (e.g. Camp, 1923; Estes *et al.*, 1988; Rieppel, 1988*b*; Hallerman, 1998), and between scincids and cordyliforms (Estes, 1983*a*; Estes *et al.*, 1988; Rieppel, 1988*b*; Evans & Chure, 1998*b*; Hallerman, 1998; Reynoso & Callison, 2000). In older classifications, cordyliforms were sometimes classified with anguimorphs (e.g. Camp, 1923), a hypothesis resurrected by Lee (1998) who united scincids and cordyliforms with anguimorphs in a new clade Diploglossa (Fig. 4B). However, the inclusion of Mesozoic paramacellodids (see below) in phylogenetic analyses (e.g. Evans & Chure, 1998*b*; Reynoso & Callison, 2000) consolidates the relationship between scincids and cordyliforms (with paramacellodids as their sister group) and tends to bring scincomorphs together into a single clade.

By contrast with scincomorphs, the monophyly of Anguimorpha has widespread support (e.g. Borsuk-Białynicka, 1984; Estes *et al.*, 1988; Rieppel, 1988*b*; Evans & Barbadillo, 1997; Lee, 1997, 1998). Traditionally, living anguimorph lizards were divided into two groups – the varanoids (*Varanus*, *Heloderma* and *Lanthanotus*) and the 'anguioids' – anguids and xenosaurs (Camp, 1923; Romer, 1956; Hallerman, 1998). Alternative hypotheses place either xenosaurs (e.g. Lee, 1998) or anguids (e.g. Evans & Barbadillo, 1998; Gao & Norell, 1998) as closer to varanoids. Amongst fossil anguimorphs, the mosasauroids (marine mosasaurs, aigialosaurs, adriosaurs, coniasaurs, and dolichosaurs, Bell, 1997*a*) form the largest group. Most authors consider these aquatic taxa to be varanoid derivatives (Camp, 1923; Nopsca, 1923; McDowell & Bogert, 1954; Borsuk-Białynicka, 1984; Lee, 1997; Gao & Norell, 1998; Lee & Caldwell, 2000). Similarly, a majority of recent analyses have placed snakes within Anguimorpha, although their precise relationships continue to be fiercely debated (e.g. Rieppel, 1988*a*,*b*; Caldwell & Lee 1997; Lee, 1997, 1998; Lee & Caldwell, 1998, 2000; Caldwell, 1999; Lee, Bell & Caldwell, 1999; Zaher & Rieppel, 1999; Cundall & Greene, 2000; Rage & Escuillié, 2000; Rieppel & Zaher, 2000*a*, *b*; Tchernov *et al.*, 2000; Rieppel & Kearney, 2001; see Coates & Ruta, 2000 for a comprehensive and impartial review).

Amphisbaenians and dibamids are specialized burrowers. Most are limbless, although one – the Central American amphisbaenian *Bipes* – has well-developed forelimbs (an unusual condition amongst limbless reptiles where limb reduction generally proceeds from front to rear). The rare and secretive dibamids (*Anelytropsis*, *Dibamus*) remain enigmatic (e.g. Estes *et al.*, 1988), although recent work relates them to amphisbaenians (e.g. Rieppel, 1984, 1988*b*; Greer, 1985; Hallerman, 1998; Lee, 1998; Reynoso, 1998; Rieppel & Zaher, 2000*a*, *b*). Camp (1923), and later Wu *et al.*

(1993, 1996), derived amphisbaenians from teiids, while Underwood (1957) documented resemblances between the gekkotan and dibamid adrenal glands. His arrangement (inclusive of amphisbaenians) has been recovered by several recent analyses (e.g. Evans & Barbadillo, 1997; Evans & Chure, 1998*b*; Lee, 1998; Reynoso, 1998). By contrast, Hallerman (1998) and Rieppel & Zaher (2000*a*, *b*) concluded that dibamids and amphisbaenians are the sister group of snakes.

II. THE FOSSIL RECORD

(1) The limitations of the fossil record

With some obvious exceptions (e.g. mosasaurs), lepidosaurs are relatively small animals (typically < 300 mm total length; < 100 g in mass, Zug, 1993). Their gracile skeletons require a suitable depositional environment for preservation (low energy, fine sediments) and a search strategy appropriate for small fossils. In consequence, many Mesozoic lizard remains are a by-product of the hunt for either birds or mammals, with their state of preservation and depositional context varying accordingly.

A majority of Mesozoic feathered dinosaurs (avian and non-avian) come from fine-grained 'lithographic' limestones like those of Solnhofen (Upper Jurassic, Germany), Las Hoyas (Lower Cretaceous, Spain), and Liaoning (Lower Cretaceous, China). All of these localities also yield rare lizards, and some (e.g. Solnhofen) produce rhynchocephalians (Cocude-Michel, 1961, 1963; Hoffstetter, 1962, 1964; Evans & Barbadillo, 1997, 1998, 1999). The specimens are usually complete and fully articulated, and they provide valuable data for the understanding of morphological evolution and phylogeny. Nonetheless, in order to develop a comprehensive understanding of temporal and geographical radiation, these comparatively rare specimens must be supplemented by material from other sources.

Additional data are derived from microvertebrate deposits, for example cave/fissure fillings or pond/lagoonal horizons, where small animal bones accumulate. Matrix collected in bulk is then macerated to produce a concentrate of isolated elements. Microvertebrate sites came to prominence in the hunt for early mammals. They have the advantage of producing large numbers of specimens and a more comprehensive picture of the assemblage as a whole (i.e. fish, amphibians, reptiles, mammals and sometimes birds). Their disadvantage is that the bones are disarticulated and, frequently, broken. Analysis is time-consuming and requires expertise, but the resulting data are useful in plotting distributions. Microvertebrate material can also play a role in phylogenetic and morphological discussion, provided skeletal elements are sufficiently representative and accurately reconstructed. The three-dimensional preservation of individual elements is often exquisite (e.g. Evans, 1980, 1991; Fraser, 1982; Whiteside, 1986).

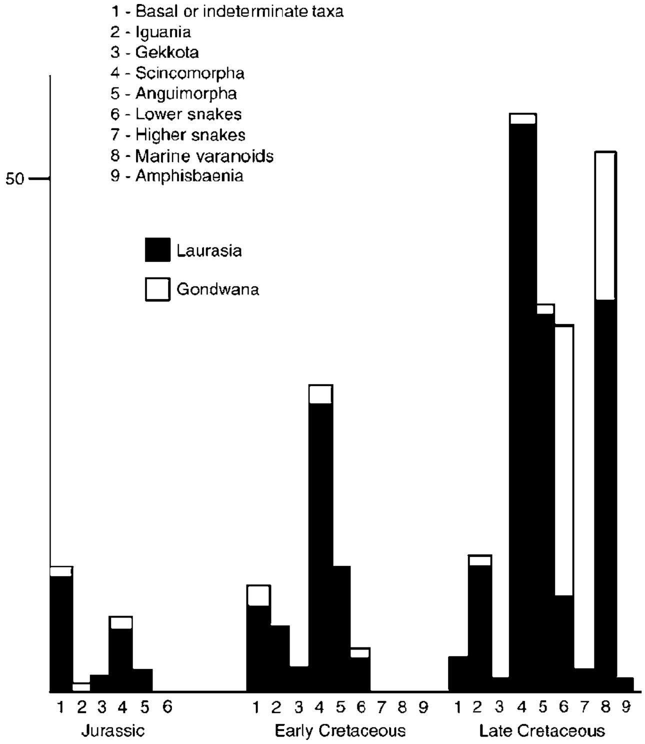

Fig. 5. Histograms comparing data on known taxa of fossil squamates recovered from Jurassic and Cretaceous localities in Laurasia (solid bars) and Gondwana (open bars). Data taken from sources listed in the references section but mainly: Gilmore (1928, 1943); Seiffert (1973); Estes (1983*a*); Rage (1984, 1999); Nessov (1985, 1988); Winkler *et al.* (1990); Astibia *et al.* (1991); Borsuk-Białynicka (1991); Rowe *et al.* (1992); Alifanov (1993*b*, 2000); Evans (1993, 1998*a*, *b*); Werner & Rage (1994); Reynoso (1996); Sullivan & Holman (1996); Bell (1997*a*, *b*); Cifelli *et al.* (1997, 1999); Nydam *et al.* (1997); Broschinski (2000); Gao & Norell (2000); Evans & Searle (2002).

Two fundamental gaps currently exist in the squamate fossil record – one temporal and one geographic. There is little information on basal lepidosauromorphs, no Early or Middle Triassic history for lepidosaurs in general, and no recorded history of squamates prior to the Early-Middle Jurassic. The Jurassic and Early Cretaceous are poorly sampled by comparison with the Late Cretaceous (Fig. 5). Within squamates, the Mesozoic record for gekkotans, amphisbaenians, dibamids, and xantusiids, is dismal, contributing to the

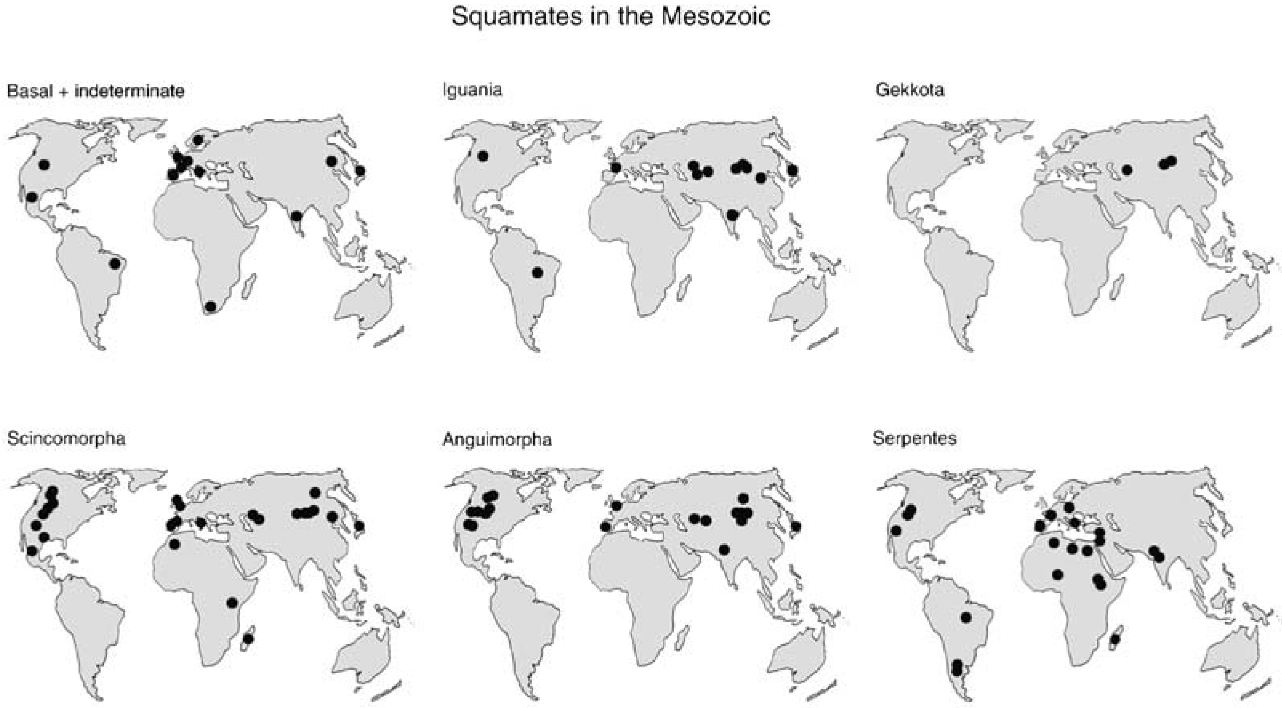

Fig. 6. Known localities yielding Mesozoic fossil squamates plotted onto modern world maps to illustrate the bias towards modern continents, with the exception of Serpentes (snakes). The marine varanoids (mosasaurs and their relatives) are excluded. Data from references listed, but particularly those listed in the legend to Fig. 5.

problems of phylogeny reconstruction. There is also a strong geographical bias (Figs 5 and 6). For terrestrial lizards, the entirety of the Gondwanan Mesozoic is represented by a handful of specimens (Appendix 1): fragmentary jaws from the Early-Middle Jurassic of India (Evans, Prasad & Manhas, 2000, 2002) and rare Late Cretaceous remains (including possible anguids and, reportedly, gekkotan eggshell) from the Intertrappean beds of the same continent (Prasad & Rage, 1995; Bajpai & Prasad, 2000); rare and fragmentary paramacellodid scincomorphs from Tanzania (Upper Jurassic, Broschinski, 1999) and Morocco (Lower Cretaceous, Richter, 1994*b*); an enigmatic burrower, *Tarratosaurus*, from Morocco (Broschinski & Sigogneau-Russell, 1996); an indeterminate braincase from the Lower Cretaceous of South Africa (Ross, Sues & De Klerk, 1999); important but largely undescribed material from the mid-Cretaceous of Brazil (Bonfim-Júnior & Marques, 1997; Evans & Yabumoto, 1998; Bonfim-Júnior, 1999; Hussam Zaher, personal communication, October 2002); the single problematic skull of *Prisciguana*, from the Late Cretaceous of Brazil (Estes & Price, 1973); and a partial skeleton of a small scincomorph from the Late Cretaceous of Madagascar (Krause *et al.*, 2002). These establish the presence of squamates in Gondwana during the Jurassic and Cretaceous, but provide little information on assemblage structure and distribution.

Two groups provide conspicuous exceptions to this pattern, the marine mosasaurs and snakes. The relative abundance of mosasaurs in both northern and southern deposits reflects both their large size and the quantity of suitable marine deposits. For snakes, the explanation is less obvious. Some, certainly, are aquatic but there are several terrestrial localities (e.g. those of the Sudan: Werner & Rage, 1994; Rage & Werner, 1999; and of South America: Albino, 1996; Caldwell & Albino, 2001), where snakes have been recovered but lizards have not, despite careful scrutiny.

(2) Triassic squamate history

Although Rhynchocephalia have been recovered from Upper Triassic deposits in most continents (see Evans *et al.*, 2001, for a review), there are no confirmed records of Triassic lizards. Of previously cited examples, *Tanystropheus* (Wild, 1973) is a prolacertiform (Gow, 1975; Evans, 1980); *Fulengia* (Carroll & Galton, 1977) is a hatchling prosauropod dinosaur (Evans & Milner, 1989); *Colubrifer* (Carroll, 1982), *Santaisaurus* (Sun *et al.*, 1992) and probably *Blomosaurus* (Tatarinov, 1978) are non-diapsid procolophonians (Evans, 2001); *Lacertulus*

(Carroll & Thompson, 1982) is indeterminate, but not a squamate (Estes, 1983*a*); and *Kudnu* (Bartholomai, 1979) may be a juvenile prolacertiform (S. E. Evans, personal observations, 2001). The Permian *Palaegama* (Carroll, 1975, 1977) is a primitive diapsid, but the preservation is poor and there is no evidence for lepidosauromorph affinity (Evans, 1988; Gauthier *et al.*, 1988*a*). The headless *Saurosternon* (Carroll, 1975, 1977) is also problematic. Although *Paliguana* (a single, poorly preserved skull, Carroll, 1975, 1977) and the kuehneosaurs are currently included within Lepidosauromorpha, kuehneosaurs lack the diagnostic character states of crown-group lepidosaurs, while *Paliguana* is too fragmentary for detailed assessment. "*Perparvus*" (Carroll, 1988, see Appendix) was an informal working name that the late Dr Pamela L. Robinson (UCL) used for a Late Triassic 'lizard' subsequently described by Whiteside (1986) as the rhynchocephalian *Diphydontosaurus* (Frances Mussett, personal communication, 1993). This, presumably, was also the more 'typical lizard' material from the British Triassic noted by Estes (1983*b*), as a personal communication from Pamela Robinson.

(3) The first squamate assemblages

At present, the earliest recorded true squamates are from the Early-Middle Jurassic of India (Prasad, 1986; Evans *et al.*, 2001), Britain (Evans, 1993, 1994*a*, 1998*a*; Waldman & Evans, 1994), and Central Asia (e.g. Nessov, 1988; Fedorov & Nessov, 1992).

Material recently recovered from the Kota Formation of India includes at least two lizard taxa (Evans *et al.*, 2000, 2002). One is pleurodont, but with only two fragmentary specimens, further identification is impossible. The second lizard, *Bharatagama*, is also fragmentary but represented by more than 100 specimens. From comparisons with living and fossil genera, it was interpreted as an early acrodont iguanian, the earliest record of this group to date. Middle Jurassic (Bathonian) lizard assemblages from Britain are more diverse (Evans, 1994*a*, 1998*a*), with at least 5–7 discrete taxa. The fauna appears to be exclusively scleroglossan (scincomorphs, anguimorphs and, less certainly, gekkotans), but includes representatives of relatively derived lineages. One of these is the anguimorph *Parviraptor*, currently regarded as a basal varanoid (Evans, 1994*a*; Nydam, 2000). Lizard remains have also been recovered from the Callovian of Kirghizia, Central Asia (Nessov, 1988; Fedorov & Nessov, 1992). The named genus, *Changetisaurus* (Fedorov & Nessov, 1992) was interpreted as an anguimorph, related to *Dorsetisaurus* from the Upper Jurassic of Portugal (Broschinski, 2000) and North America (Prothero & Estes, 1980; Evans & Chure, 1998*a*, *b*, 1999), and the Lower Cretaceous of Britain (Hoffstetter, 1967; Milner & Evans, 1998).

(4) The Late Jurassic and Early Cretaceous record: radiation and transition

(*a*) *Introduction*

The squamate fossil record improves substantially in the Late Jurassic and Early Cretaceous, although there remains a strong disparity between Laurasia and Gondwana. In general, the assemblages from this time interval are closely similar (e.g. Evans, 1998*b*; Nydam & Cifelli, 2002*b*), with many Jurassic genera surviving into the Cretaceous. However, many of these taxa cannot easily be accommodated within the major squamate clades (e.g. Reynoso, 1996, 1998; Evans & Barbadillo, 1998, 1999; Reynoso & Callison, 2000; *contra* e.g. Hoffstetter, 1962; Estes, 1983*a*, *b*). The list includes: *Bavarisaurus*, *Eichstaettisaurus*, and *Ardeosaurus* from the Upper Jurassic Solnhofen limestones of Germany (Hoffstetter, 1953, 1962, 1967; Mateer, 1982; Estes, 1983*a*; Evans, 1994*c*); *Hoyalacerta* and *Scandensia* from the Lower Cretaceous (Barremian) Las Hoyas locality of Spain (Evans & Barbadillo, 1998, 1999); and *Huehuecuetzpalli* from the Lower Cretaceous (Aptian-Albian) Tlayua Formation of Mexico (Reynoso, 1998). Four other genera: *Yabeinosaurus* (Lower Cretaceous, Liaoning, China; Endo & Shikama, 1942); *Palaeolacerta* (Upper Jurassic, Solnhofen, Germany; Cocude-Michel, 1961); and *Costasaurus* and *Chometokadmon* (Lower Cretaceous, Pietraroja, Italy; Barbera & Macuglia, 1988, 1991), have yet to be reanalysed (much of the original material of *Yabeinosaurus* is either missing or very poor), while *Euposaurus* (Upper Jurassic, Cerin, France; Jourdan, 1862) is a poorly ossified juvenile skeleton and is indeterminate (Evans, 1994*b*).

Of these enigmatic taxa, *Bavarisaurus* genuinely seems primitive (see Section III. 2), and this is reflected in recent phylogenies (e.g. Reynoso, 1996, 1998; Evans & Barbadillo, 1998, 1999; Reynoso & Callison, 2000). These cladistic analyses also place *Hoyalacerta*, *Scandensia*, *Eichstaettisaurus* and *Ardeosaurus* outside a node-based Squamata, although the latter two genera share some similarities with basal scleroglossans. The Mexican *Huehuecuetzpalli* (Reynoso, 1998) is also problematic, since it combines primitive features (amphicoelous vertebrae) with some derived characteristics apparently unique to Iguania (e.g. the reduced postfrontal). Further resolution must await new material (many of these taxa are represented by single specimens) and new, more detailed analyses.

Interestingly, many of these apparently basal (and thus relict) lizard taxa are found either in Europe or in the Mexican locality of Tepexi de Rodriguez (Reynoso, 1996, 1998; Reynoso & Callison, 2000). For much of the Mesozoic, Western Europe was essentially an archipelago of small islands, and this may also have been true for the area around Tepexi de Rodriguez (Reynoso, 1996). It may help to explain the retention of an essentially relictual lepidosaurian assemblage throughout the Early Cretaceous (Pietraroja and Tepexi de Rodriguez, for example, contain the last known Laurasian records of rhynchocephalians).

(*b*) *Iguania*

Upper Cretaceous localities in Mongolia, China, North America, France, and, perhaps, Brazil, contain a diversity of both pleurodont and acrodont iguanians (e.g. Estes & Price, 1973; Estes, 1983*a*; Borsuk-Białynicka & Moody, 1984; Borsuk-Białynicka & Alifanov, 1991; Gao & Fox, 1991; Gao & Hou, 1995, 1996; Rage, 1999). Until recently, however, nothing was known of their earlier history, and even now the record is very fragmentary. The new Kota material (see above) suggests that acrodont iguanians were in India (then part of Gondwana) in the Early to Middle Jurassic (Evans *et al.*, 2000, 2002), and this accords with predictions based on molecular studies (e.g. Macey *et al.*, 2000). The Late Jurassic *Euposaurus* (Kimmeridgian, France; Hoffstetter, 1964) is not an acrodont iguanian as once thought (e.g. Estes, 1983*a*, *b*); the generic holotype is an indeterminate pleurodont lizard, while attributed acrodont specimens are juvenile sphenodontians (Evans, 1994*b*), hence the confusion over the dentition. The earliest described Laurasian material is therefore from the Aptian-Albian of Mongolia (acrodonts, Alifanov, 1993*b*) and Central Asia (indeterminate taxa; Gao & Nessov, 1998).

(*c*) *Gekkota*

Living gekkotans are paedomorphic and lightly built. Their skeletons are rarely preserved, even in modern and subfossil accumulations (e.g. owl pellets). For example, of thousands of Late Cretaceous lizard skulls recovered from the sites around Ukhaa Tolgod in Mongolia, only one has been referred to the Gekkota (Gao & Norell, 2000), and that is an extremely odd and robustly built form of questionable affinity. The earliest certain record of a gekkotan is that of *Hoburogecko* from the Aptian-Albian of Hööbör (Khobur), Mongolia (Alifanov, 1989*b*), although possible gekkotan vertebrae were described from the Middle Jurassic of Britain (Evans, 1998*a*). Hoffstetter (1962) referred the Solnhofen genera *Bavarisaurus*, *Eichstaettisaurus*, *Ardeosaurus* and *Palaeolacerta* to the Gekkota, an attribution accepted by Estes (1983*a*), but not supported by recent phylogenetic analyses (see above). The skull of *Eichstaettisaurus* shows some characters reminiscent of gekkotans (e.g. fused frontal with deep ventrolateral flanges, straight, simple fronto-parietal suture; unsculptured skull bones; wide interpterygoid vacuity and simple palatine/pterygoid sutures; short, rounded antorbital skull), but none are unique to geckos and the retention of both upper temporal and post-orbital bars is in marked contrast to the condition in living taxa (but see Gao & Norell, 2000). Recently, eichstaettisaur-like specimens have also been recovered from the basal Cretaceous of Spain (Montsech; Evans, Lacasa-Ruis & Erill Rey, 1999) and the mid-Cretaceous of Italy (Pietraroja, S. E. Evans, P. Raia & C. Barbera, in preparation).

(*d*) *Scincomorpha*

Scincomorphs dominate most Laurasian lizard assemblages in the Mesozoic (e.g. Hoffstetter, 1967; Estes, 1983*a*, Evans & Chure, 1998*b*; Reynoso & Callison, 2000; see Appendix, Fig. 6), but there are too few data to determine the pattern in Gondwana. Most early taxa are based on fragmentary remains (typically jaws) and cannot be classified with precision. These include *Bellairsia* (Middle Jurassic, England; Evans, 1998*a*), the robust jawed *Saurillodon* (Late Jurassic, Guimarota, Portugal: Seiffert, 1973; Broschinski; 2000; Late Jurassic, USA: Evans, 1996), a limb-reduced form possibly related to *Saurillodon* (Middle Jurassic, England; Evans, 1998*a*), *Schilleria* (Late Jurassic, Morrison Formation, USA; Evans & Chure, 1998*a*), *Sakurasaurus* (Early Cretaceous, Japan; Evans and Manabe, 1999), the basal Cretaceous English Purbeck genera *Pseudosaurillus*, *Saurillus* and *Durotrigia* (Hoffstetter, 1967; Evans & Searle, 2002), *Pachygenys* (Early Cretaceous, China; Gao & Cheng, 1999), and *Tarratosaurus* (Early Cretaceous, Morocco; Broschinski & Sigogneau-Russell, 1996). By far the most widespread Laurasian group was the Paramacellodidae (Fig. 7). Paramacellodids were small to medium-sized scincomorphs with a covering of rectangular bony plates (osteoderms), not unlike those of some living cordyliforms. They have been recorded from the the Middle Jurassic (Late Bathonian) of Britain (Evans, 1993, 1998*a*; Evans & Milner, 1994; Waldman & Evans, 1994); the Upper Jurassic (Kimmeridgian) of North America (Morrison Formation; Prothero & Estes, 1980; Evans & Chure, 1998*a*, *b*, 1999), Kazakhstan (Hecht & Hecht,

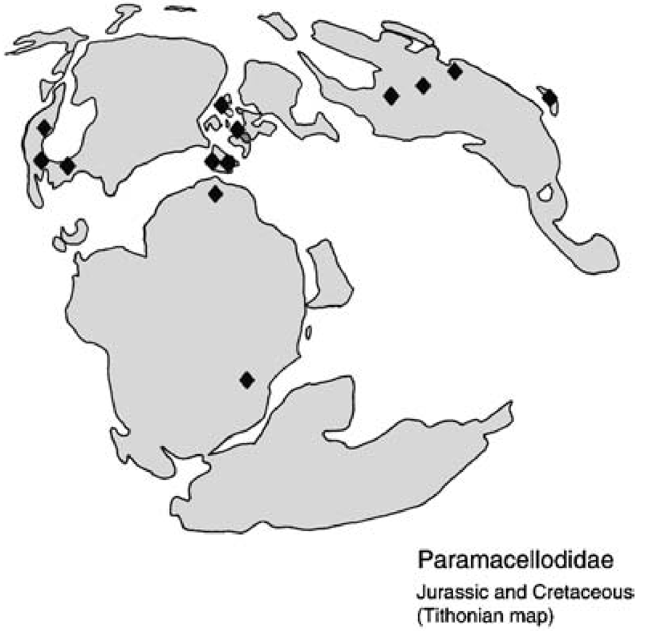

Fig. 7. Palaeobiogeographical map for the Jurassic and Early Cretaceous (based on a Tithonian map, Smith *et al.*, 1994) for the Paramacellodidae. Data taken mainly from Evans (1993), Evans & Chure (1998*b*), Evans *et al.* (1998), Averianov & Skutchas (1999), Leshchinskiy *et al.* (2001), and references therein.

1984), Portugal (Guimarota; Seiffert, 1973; Broschinski, 2000), Tanzania (Zils *et al.*, 1995; Broschinski, 1999), and China (Li, 1985); and from the Lower Cretaceous of Britain (Hoffstetter, 1967; Estes, 1983*a*; Milner & Evans, 1998; Evans & Searle, 2002), Spain (Richter, 1994*b*), Russia (Averianov & Skutchas, 1999; Leshchinskiy *et al.*, 2001), Mongolia (Alifanov, 1993*b*), Morocco (Broschinski & Sigogneau-Russell, 1996), North America (Texas, Utah, Oklahoma: Winkler, Murry & Jacobs, 1990; Cifelli *et al.*, 1997, 1999; Nydam & Cifelli, 2002*a*, *b*), and Japan (Evans *et al.*, 1998). Although earlier authors classified paramacellodids with cordylids (e.g. Estes, 1983*a*), phylogenetic analysis based on more complete material (e.g. Evans and Chure, 1998*b*; Reynoso & Callison, 2000) places these lizards as the sister group of scincids + cordyliforms. Most of the records are Laurasian, but the occasional Gondwanan occurrence (particularly that in Tanzania), if correct, suggests an origin prior to the break-up of Pangaea.

Extant scincomorph lineages are not recorded with any confidence until later in the Cretaceous. Barbera & Macuglia (1988) referred the Albian *Chometokadmon* (Pietraroja, Italy) to the Scincidae, but this is not supported by parietal morphology (S. E. Evans, personal observations). Similarly, attribution of the extremely fragmentary jaw of the Barremian *Cuencasaurus* Richter 1994*b* (Uña, Spain) to the Scincidae is tentative, at best, although its contemporary, *Meyasaurus* (Uña, Montsech, Las Hoyas, Galve, Spain: Richter, 1994*a*; Evans & Barbadillo, 1997), consistently emerges as the sister group to teioids (Evans & Barbadillo, 1997; Evans & Chure, 1998*b*; Reynoso & Callison, 2000). Other early teioids (belonging to the Late Cretaceous Asian-American family Polyglyphanodontidae) have been described from the Albian-Cenomanian boundary (approximately 98 Ma) of the USA (Nydam, 1999; Nydam & Cifelli, 2002*a*), and from the Lower Cretaceous (Aptian-Albian) of Brazil (Bonfim-Júnior, 1999).

(*e*) *Anguimorpha*

As documented above, the earliest recorded anguimorphs are also from the Middle Jurassic of Britain (*Parviraptor*; Evans, 1994*a*, 1998*a*) and Kirghizia (*Changetisaurus*; Fedorov & Nessov, 1992). Dorsetisaurs, the group to which *Changetisaurus* was tentatively referred, are anguimorphs of uncertain position originally described from the basal Cretaceous Purbeck Limestone Formation of Britain (*Dorsetisaurus*; Hoffstetter, 1967), but known also from the Late Jurassic of Portugal (Seiffert, 1973; Broschinski, 2000) and North America (Prothero & Estes, 1980; Evans, 1996; Evans & Chure, 1998*a*, *b*), and from several Early Cretaceous localities (e.g. Alifanov, 1993*b*; Milner & Evans, 1998; S. E. Evans & P. M. Barrett, in preparation). Further, as yet undescribed, anguimorphs have been recovered from the Early Cretaceous (probably Valanginian-Hauterivian) of Japan (Evans & Manabe, 1999, 2000) and the mid-Cretaceous (Albian-Cenomanian) of North America (Utah; Cifelli *et al.*, 1999) and Siberia (Leshchinskiy *et al.*, 2001). The first record of an extant anguimorph family is that of a helodermatid (*Primaderma*) from the mid-Cretaceous (Albian-Cenomanian) of North America (Utah; Nydam, 2000).

The earliest putative snake record was a vertebra from the Barremian of Spain (Uña; Rage & Richter, 1995), but this attribution has subsequently been questioned (Rage & Werner, 1999). The first uncontested snakes are from the Albian-Cenomanian of the USA (Gardner & Cifelli, 1999) and Algeria (Cuny *et al.*, 1990), and further specimens are documented from the Cenomanian of France, Portugal, Egypt and the Sudan (Rage & Werner, 1999). The Sudanese material is the most diverse, with representatives of at least seven families, including the first colubroids.

More controversial are a series of specimens from the Cenomanian of Bosnia-Herzegovina and Palestine (e.g. Caldwell & Lee, 1997; Lee & Caldwell, 1998; Rage & Escuillé, 2000; Tchernov *et al.*, 2000; Caldwell & Albino, 2001) that appear to document a major radiation of limbed (hind) aquatic snakes in the shallow coastal regions of the Western Tethys sea during the mid-Cretaceous (along with aquatic varanoid lizards such as the dolichosaurs, coniasaurs, adriosaurs, and aigialosaurs, e.g. Dal Sasso & Pinna, 1997; Lee & Caldwell, 2000; Caldwell & Albino, 2001). The phylogenetic position of this early snake material (basal or crown group) is still uncertain (Coates & Ruta, 2000).

(*f*) *Amphisbaenia and Dibamidae*

The Mesozoic record of these specialized burrowers is currently (but controversially, see below) limited to *Sineoamphisbaena* (Wu *et al.*, 1993, 1996) from the Upper Cretaceous (Campanian) of China, and, even more tentatively, to fragmentary jaws from the Aptian-Albian of Uzbekistan and Mongolia (*Hodzhakulia* Nessov, 1985; Gao & Nessov, 1998; Alifanov, 1993*b*, 2000). Wu *et al.* (1993, 1996) classified *Sineoamphisbaena* within Amphisbaenia, but subsequent analyses have placed it as the sister group of either Amphisbaenia + Dibamidae (Lee, 1998) or of Serpentes + Amphisbaenia + Dibamidae (Rieppel & Zaher, 2000*a*, *b*).

III. DISCUSSION

(1) Early squamate history and the Iguania-Scleroglossa dichotomy

The re-interpretation of the Triassic 'eolacertilians' removed all trace of a Triassic record for Squamata. This resulting disparity between the fossil records of rhynchocephalians and squamates has led some authors to speculate that squamates might have been derived directly from rhynchocephalians in the Late Triassic or Early Jurassic. Witten (1994) and Witten & Moody (1997) proposed a scenario whereby acrodont iguanian lizards evolved directly from acrodont rhynchocephalians, with iguanian (and then scleroglossan) pleurodonty evolving from acrodonty. However, all available evidence supports the contrary view that pleurodonty is primitive for Lepidosauria, for Rhynchocephalia, and for Squamata (e.g. Auge, 1997). The lepidosauromorph taxa most closely related to the crown (e.g. *Marmoretta*; Evans, 1991) are pleurodont, albeit weakly so. All phylogenetic analyses of Rhynchocephalia, using a wide compendium of skeletal characters (e.g. Evans, 1988; Gauthier *et al.*, 1988*a*; Reynoso, 1997, 2000; Wilkinson and Benton, 1996: Fig. 3), have placed the pleurodont *Gephyrosaurus* in a basal position. Furthermore, all recent analyses (using a very large and diverse data set) have also put primitive pleurodont squamates (e.g. the Solnhofen *Bavarisaurus*) at the base of Squamata (e.g. Reynoso, 1996, 1998; Evans & Barbadillo, 1997, 1998, 1999; Evans & Chure, 1998*b*; Reynoso & Callison, 2000).

Derivation of Squamata from within pleurodont rhynchocephalians is equally unparsimonious. Despite its pleurodonty, *Gephyrosaurus* already shows diagnostic rhynchocephalian characters, including a slowed replacement of the posterior teeth; an enlargement of the lateral palatine tooth row; the development of a propalinal shearing mechanism on the jaw; and an elongation of the dentary to brace the accessory jaw bones. Crownward of *Gephyrosaurus*, further rhynchocephalian characters are added and refined in a stepwise sequence. To derive squamates from basal rhynchocephalians without a secondary loss of rhynchocephalian character states, it would be necessary to begin from a pre-*Gephyrosaurus* stage, but this hypothetical taxon would no longer be diagnostically rhynchocephalian. It would be the undifferentiated Early-Middle Triassic stem lepidosaur predicted by the more traditional view.

The apparent absence of squamates from Triassic deposits is more likely to be an artefact of preservation and sampling. The richest lizard localities of the Jurassic and Early Cretaceous (e.g. Kirtlington, Purbeck, Guimarota, parts of the Morrison Formation, S. E. Evans, personal observations) are those characterized by a freshwater assemblage including frogs, salamanders and other freshwater reptiles like turtles, crocodiles, and choristoderes (Evans & Milner, 1994). These assemblages were generally deposited under mesic conditions (lacustrine or lagoonal). The majority of Triassic localities sampled to date for small terrestrial tetrapods represent dry upland environments, sometimes on small islands (e.g. the rhynchocephalian-rich fissure assemblages of South West Britain and Wales; Fraser 1982, 1986, 1988), or regions with little standing fresh water. Very few seem to match the mesic localities of the later Mesozoic, and none shows a similar faunal composition. Consequently, it is not only squamates that lack a Triassic record. The same is true for salamanders, caecilians, albanerpetontid amphibians, choristoderes, and, with the exception of rare Lower Triassic stem taxa, frogs. Nonetheless, there is compelling evidence of a Late Permian/Early Triassic origin for Lissamphibia (e.g. Evans & Borsuk-Białynicka, 1998) and Choristodera (e.g. Evans, 1990), and there

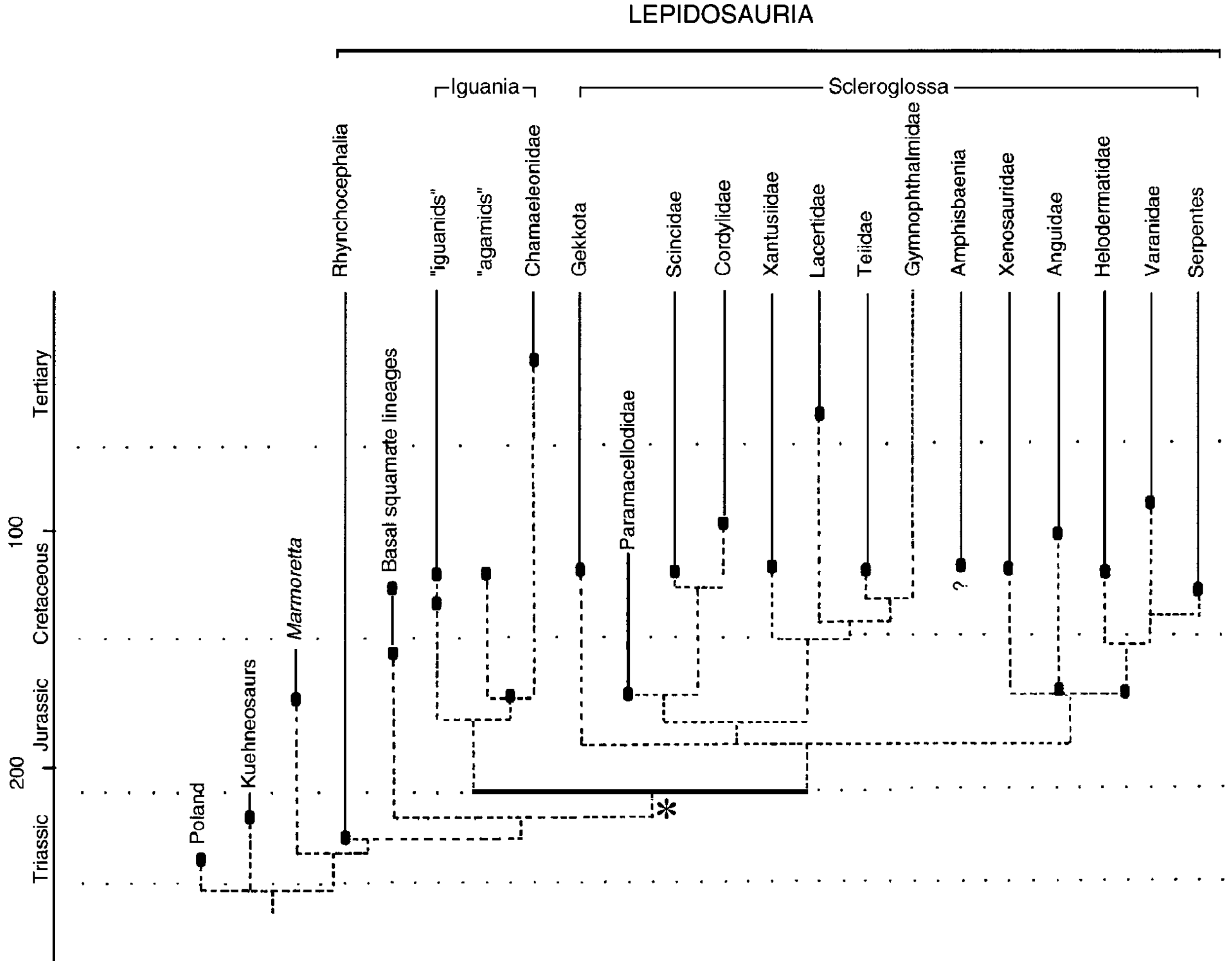

Fig. 8. Phylogenetic diagram showing hypothesis of relationship for major lineages of Lepidosauromorpha, taken mostly from Estes *et al.* (1988), Lee (1997, 1998), and the author's own work (e.g. Evans 1980, 1984, 1988, 1991). The tree is plotted against time (after Gradstein *et al.*, 1995) with dots showing known early records and dotted lines minimum estimates of lineage extension (data mostly from Evans, 1993, 1998*a*, *b*; Gao & Nessov, 1998; Borsuk-Białynicka *et al.*, 1999; Evans *et al.*, 2000; references therein, and references given in Figs 6 and 7). The solid line and asterisk mark the estimated divergence time for iguanians and scleroglossans.

is equally persuasive indirect evidence for the Triassic origin and radiation of squamates.

The earliest known rhynchocephalians are *Brachyrhinodon* and *Polysphenodon* from the early Late Triassic (Carnian, approximately 225 Ma) of Britain and Germany respectively (Fraser & Benton, 1989). However, despite their age, these taxa are not basal but are nested within the crown-group (Wilkinson & Benton, 1996: Fig. 3), suggesting that Rhynchocephalia had already undergone an extended period of evolution and diversification before the beginning of the Late Triassic. Morphologically, the Early Jurassic *Gephyrosaurus* was a surviving Middle Triassic relict. This is significant, because if Rhynchocephalia was already established by the Early-Middle Triassic then, by inference, so too was its sister group, Squamata.

Further evidence for an early squamate origin comes from the first extensive lizard assemblages known. Bathonian lizards include anguimorphs, scincomorphs, and possible gekkotans. The presence of the basal varanoid *Parviraptor* (Evans, 1994*a*, 1998*a*) shows that the principal anguimorph lineages had already separated by this time (approximately 165 Ma) (Fig. 8). This in turn implies a still earlier diversification of Scleroglossa, and of Squamata as a whole. Similarly, the presence of an acrodont iguanian in deposits of Early-Middle Jurassic age in India (Evans *et al.*, 2000, 2002) provides support for an early radiation of Iguania (as predicted by the molecular evidence, e.g. Macey *et al.*, 2000) and thus for the separation of Iguania and Scleroglossa at or before the end of the Triassic. Janke *et al.* (2001) recently placed the origin of

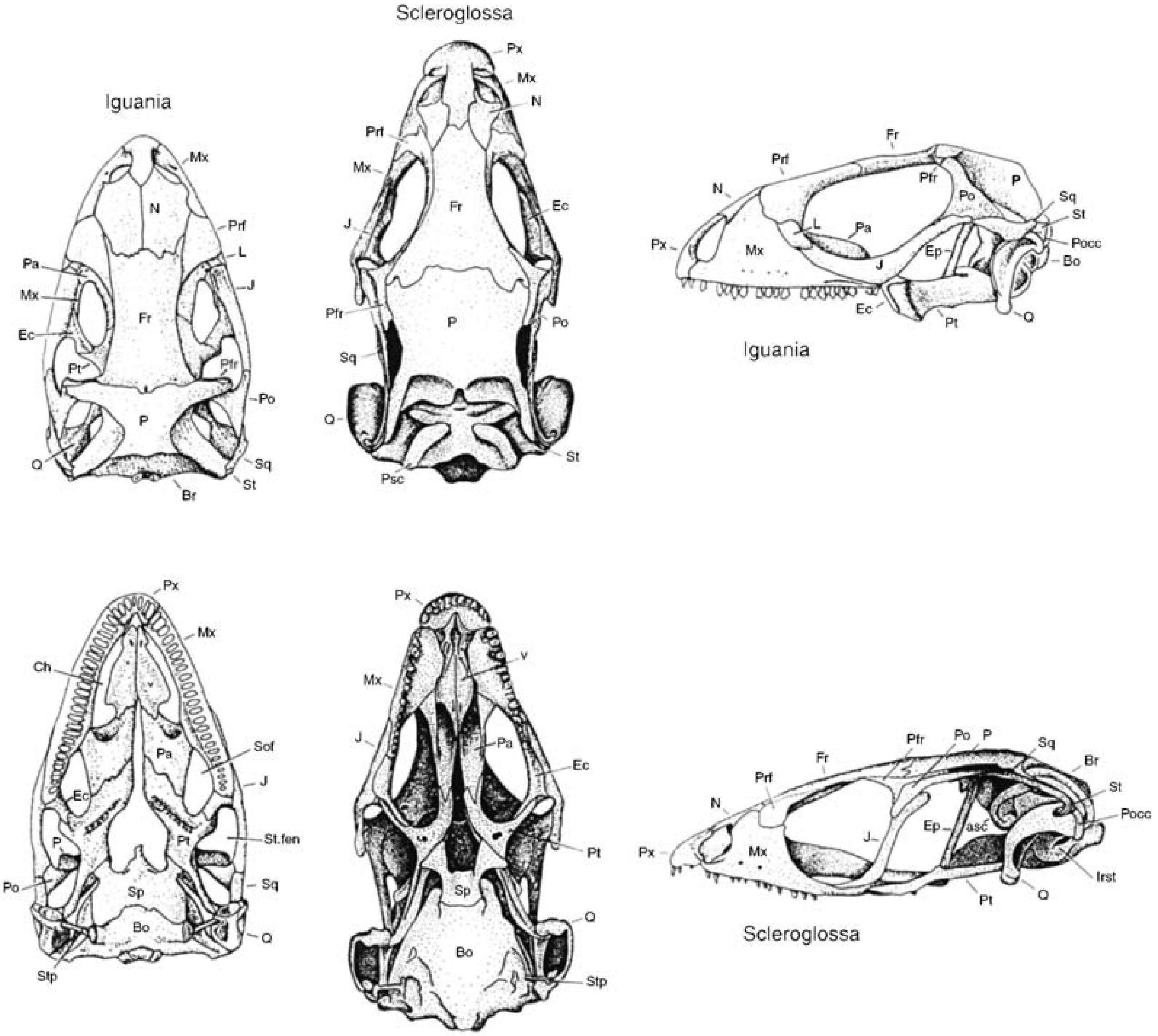

Fig. 9. The skulls of modern iguanian (*Iguana*) and scleroglossan (*Gymnophthalmus*) lizards in dorsal, palatal, and left lateral views to show the nomenclature and arrangement of the bones, as well as differences between the two groups, for example in the structure of the postorbital bar, upper temporal fenestra and palate. asc, anterior semicircular canal; Bo, basioccipital; Br, braincase; Ch, choana; Ec, ectopterygoid; Ep, epipterygoid; Fr, frontal; J, jugal; L, lacrimal; lrst, lateral opening of recessus scalae tympani; Mx, maxilla; N, nasal; P, parietal; Pa, palatine; Pfr, postfrontal; Po, postorbital; Pocc, paroccipital process; Prf, prefrontal; Psc, posterior semicircular canal; Pt, pterygoid; Px, premaxilla; Q, quadrate; Sof, suborbital fenestra; Sp, sphenoid; Sq, squamosal; St, supratemporal; St.fen, subtemporal fenestra; Stp, stapes; v, vomer. (*Iguana*, original; *Gymnophthalmus*, redrawn from Fig. 2 in Maclean, 1974). Not to scale.

squamates at around 294 Ma (Late Carboniferous) on the basis of mitochondrial DNA; 240–230 Ma would accord better with existing fossil data.

Despite their apparent similarity, iguanian and scleroglossan lizards have been separated for as long, or nearly as long, as an egg laying platypus and its human relative (Fig. 8). This deep division is reflected in many features, including the morphology of the skull (patterns of kinesis and temporal fenestration, braincase structure, Fig. 9; e.g. Estes *et al.*, 1988; Arnold, 1998; Schwenk, 1999, 2001, S. E. Evans, in preparation), feeding behaviour (e.g. Delheusy & Bels, 1999; Schwenk, 1999, 2001), and body form (e.g. body elongation and limb loss has occurred repeatedly in scleroglossans, but never in iguanians).

The Triassic was therefore a crucial period for squamate evolution and diversification. The absence of a fossil record for this key period is a major handicap.

(2) **Morphological evolution**

(*a*) *Introduction*

Other small tetrapods are frequently described as ‘lizard-like’ (e.g. the Early Carboniferous *Westlothiana lizzae*; Smithson *et al.*, 1994), the implication being that the lepidosaurian bauplan is a relatively unsophisticated one. However, lepidosaurs, and particularly squamates, show a range of both subtle, but also sometimes dramatic, morphological features that distinguish them from their ancestors.

Although some details of the phylogenetic tree remain unresolved, there is a general consensus on its overall topology. This consensus (Fig. 10) provides a basis from which to begin to map the sequence in which characters appeared, as well as to hypothesize the character state distribution at key stages in lepidosauromorph evolution: notably basal lepidosauromorph (1), a stage roughly corresponding to that of the Permo-Triassic *Paliguana* from South Africa, except that most of its morphology remains unknown; stem lepidosaur (2), a currently unrecorded stage, although probably close morphologically to that of the basal rhynchocephalian *Gephyrosaurus*; stem squamate (3), a stage currently represented, with reservation, by the relict Jurassic genus *Bavarisaurus*; basal iguanian (4), currently unknown; and basal scleroglossan (5), also unknown but perhaps not dissimilar to either *Eichstaettisaurus* or *Ardeosaurus*.

(*b*) *The evolution of skull morphology*

The squamate skull is a complex structure. Its evolution from that of basal diapsids has involved a long series of modifications, only some of which can be documented.

In a lateral view of the skull (Fig. 11), the most obvious changes relate to the decrease in size of the lacrimal and its restriction to the orbital margin; the increase in height of the facial process of the maxilla; and the general reduction in size of elements surrounding the quadrate (although the latter has occurred convergently in some non-squamate lineages). Enlargement of the quadrate conch appeared early (e.g. *Paliguana*), as did reduction of the quadratojugal and loss of the lower temporal bar. With the increase in height of the facial process of the maxilla came a deepening of the pleurodont tooth implantation, a stage first seen in an as yet unnamed lepidosauromorph from the Early Triassic of Poland (Borsuk-Białynicka *et al.*, 1999). Without Triassic stem squamate material, however, the stages in the formation of the typical squamate quadrate suspension (permitting streptostyly) cannot be teased apart.

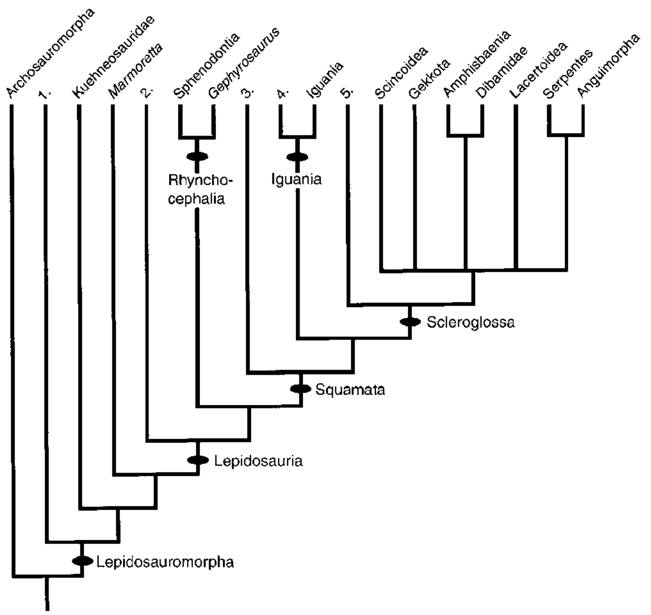

Fig. 10. Consensus phylogeny for Lepidosauromorpha taken mainly from Estes *et al.* (1988), Evans (1988, 1991), Gauthier *et al.* (1988*a*) and Gauthier (1994). The numbered branches represent as yet unknown, and therefore hypothetical, taxa: 1, basal lepidosauromorph; 2, stem lepidosaur; 3, stem squamate; 4, basal iguanian; 5, basal scleroglossan.

Changes in the dorsum of the skull (Fig. 12) were less dramatic, involving mainly consolidation of paired roofing elements and the loss of small bones like the tabulars and postparietals from the posterior margin of the skull roof. The coossification and expansion of the parietals, and the development of a simpler frontoparietal suture may, ultimately, have contributed to the development of squamate mesokinesis. All of the lepidosauromorphs figured show a broadly open upper temporal fenestra but this becomes restricted or closed in many scleroglossans (Fig. 9).

The palatal region underwent more radical alteration (Fig. 13), most notably in the reduction of the palatal dentition and the shortening of the anterior lamina of the pterygoid (although this is reversed in some polyglyphanodont teiids and some acrodont iguanians, presumably for added strength). Kuehneosaurs retained multiple rows of teeth on palatal bones, including those on the pterygoid flange and parasphenoid. Presumably these aided grip. *Marmoretta* and *Gephyrosaurus* (and by implication, therefore, basal lepidosaurs and perhaps stem squamates) conserved the multiple rows, but lost the more primitive pterygoid flange and parasphenoid teeth. Derived sphenodontians and squamates have independently reduced the palatal dentition to a single row or small patches.

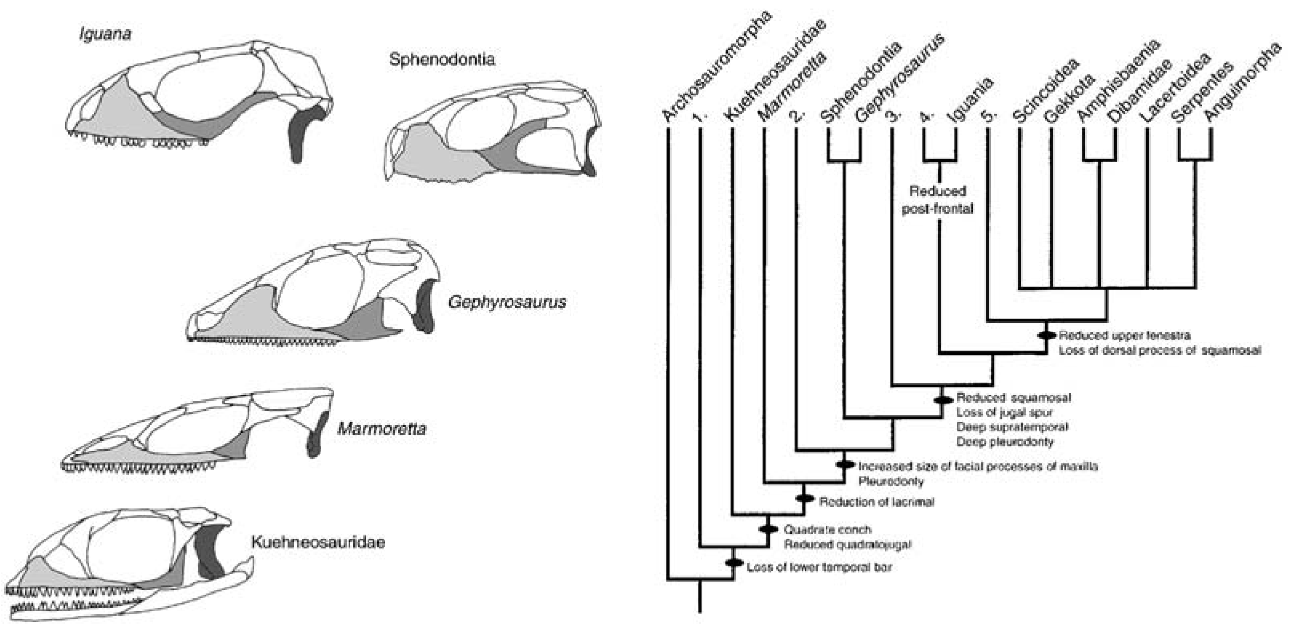

Fig. 11. Consensus phylogeny for Lepidosauromorpha as in Fig. 10 on which are mapped characters of the lateral wall of the skull. Skulls redrawn from Robinson (1967 *a*: *Kuehneosaurus*), Evans (1980: *Gephyrosaurus*), Evans (1991: *Marmoretta*), with originals for *Iguana* and *Sphenodon*. The lacrimal, maxilla, jugal, and quadrate are shown in grey shades of increasing density.

Parallel improvements in jaw structure (shortening the jaw, enlargement of the coronoid process, mechanisms for shearing or propalinal movement, squamate kinesis), and therefore more efficient food manipulation and grip, may have reduced the role of the palatal dentition in both lineages.

Further alterations occurred in the braincase, leading to elaboration of the squamate perilymphatic system, and in the lower jaw and dentition. Above all, fundamental changes took place in the palatoquadrate region and dermatocranium in relation to the evolution and development of squamate cranial kinesis.

(*c*) *Cranial kinesis – terms and definitions*

The amniote cranium has three primary components – the dermatocranium (bones developed within the skin and mostly forming roofing, palatal and facial elements), the chondrocranium (endocranium) or braincase (mostly cartilage-derived bones) and the viscerocranium (ossifications in and around the pharyngeal arches, most importantly Meckel's cartilage of the lower jaw and the palatoquadrate of the upper jaw) (De Beer, 1937). Cranial kinesis involves movements within or between these skull components.

Metakinesis provides an accommodation between the braincase (and thus also the vertebral column) and the surrounding dermatocranium (Fig. 14). It involves five primary contact points: the supraoccipital and parietal in the midline; the paroccipital processes and skull roof bilaterally; and the basipterygoid processes and palate (pterygoids) bilaterally. Initially, at least, metakinesis may have helped to protect the brain against external stresses, but may later have contributed to more controlled head positioning and, perhaps, increased gular width (Frazzetta, 1962).

Streptostyly is a movement of the quadrate in relation to the dermatocranium (Fig. 15). In squamates the translation is usually described as anteroposterior, although the mediolateral potential has been little investigated. Dorsally, squamate streptostyly typically involves a special joint surface provided by a reduced squamosal, a slender supratemporal, and the paroccipital process of the braincase (Robinson, 1967 *a*: in different proportions in different groups). Ventrally, it requires accommodation between the quadrate and the palate. This may be accomplished by a complete loss of bony contact between the quadrate and pterygoid (e.g. the hyperstreptostyly of some acrodont iguanians: Iordansky, 1990), or by a linked mechanism by which anterior quadrate movement results in protraction of the pterygoid (Frazzetta, 1962), and thus of the antorbital skull. As such, it would also be an intrinsic part of the third kinetic mechanism – mesokinesis (see below), although the universality of this linkage mechanism in lizards is disputed (e.g. Smith, 1978,

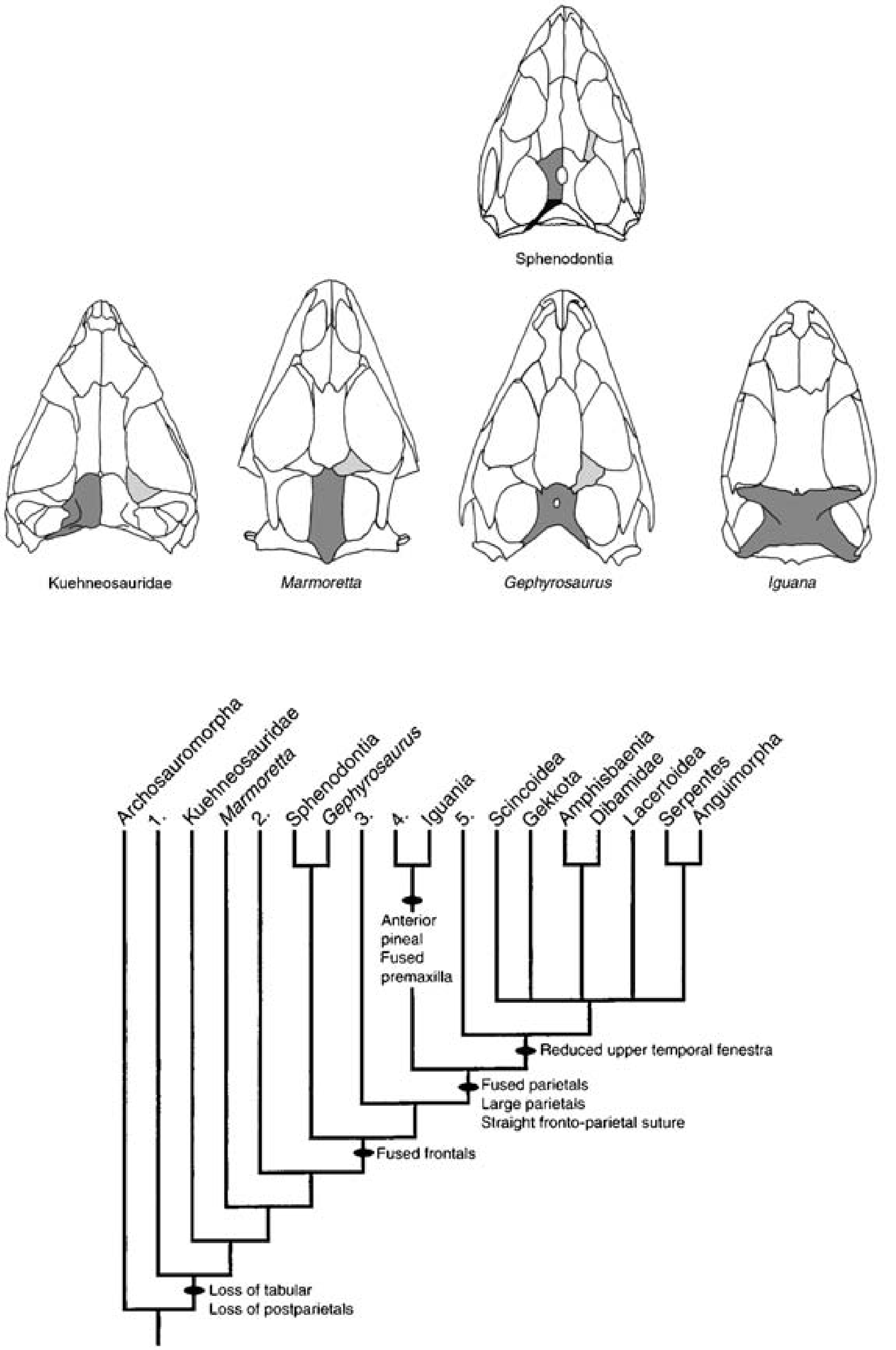

Fig. 12. Consensus phylogeny for Lepidosauromorpha as in Fig. 10 on which are mapped characters of the skull roof. The premaxilla, postfrontal, and parietal are shown in grey shades of increasing density.

1980, 1982; Smith & Hylander, 1985; Schwenk, 1999, 2001).

Both metakinesis and streptostyly involve elements derived primarily from the cartilaginous chondrocranium. The synovial joints between them are, as Rieppel (1978) showed, lined with cartilages of viscerocranial origin. Mesokinesis (lizards) or prokinesis (snakes) (Fig. 15) differs in occurring at syndesmotic joints between dermatocranial elements. Lizard mesokinesis requires a hinge between the frontal and parietal bones of the skull roof, with compensatory hinges in the palate and postorbital region. Snake prokinesis is similar but the primary hinge is further anterior, between the frontal (integrated with the braincase) and

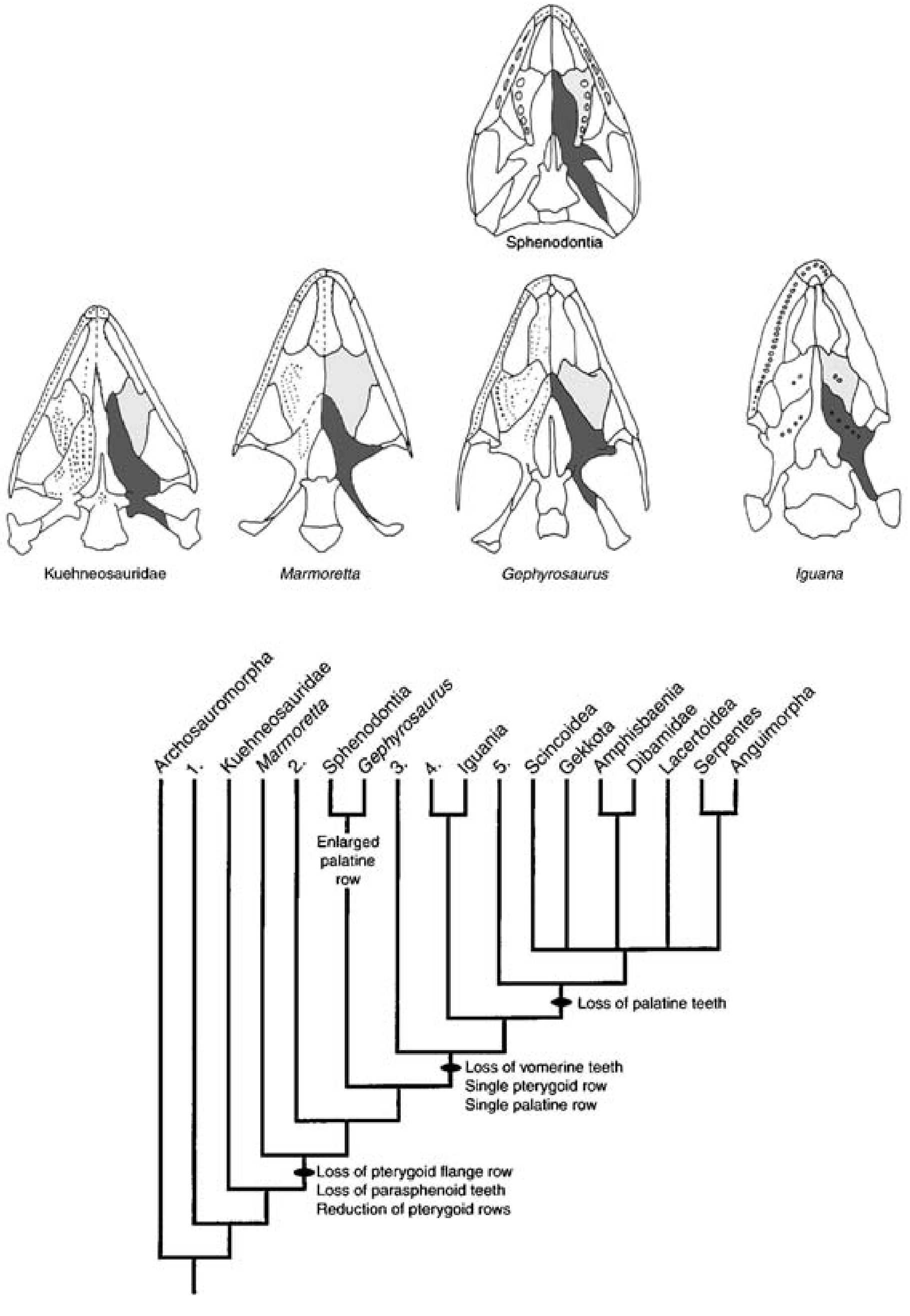

Fig. 13. Consensus phylogeny for Lepidosauromorpha as in Fig. 10 on which are mapped characters of the palate. The palatine is pale grey, the pterygoid a darker shade.

nasal bones. As part of the quadric-crank mechanism of Frazzetta (1962, 1986), quadrate protraction supposedly effects an elevation of the muzzle unit about the frontoparietal hinge; retraction has the opposite effect. However, these movements have proved difficult to observe and may be very subtle (e.g. Condon, 1987, 1989), resulting in considerable discussion as to their extent (e.g. Throckmorton, 1976, 1980; Throckmorton & Clark, 1981; Smith & Hylander, 1985; Condon, 1987, 1989) and function (e.g. Condon, 1987, 1989; De Vree & Gans, 1989). Gekkotans, snakes, and many varanid lizards are certainly highly kinetic (e.g. Condon, 1987, 1989; De Vree & Gans, 1987, 1989; Herrel *et al.*, 1999; Cundall & Greene, 2000), iguanians perhaps so only to a limited degree (e.g. Schwenk & Throckmorton, 1989; Schwenk, 1999, 2001; Wagner & Schwenk, 2000). Kinesis almost certainly improves food handling and bite efficiency (Condon, 1987,

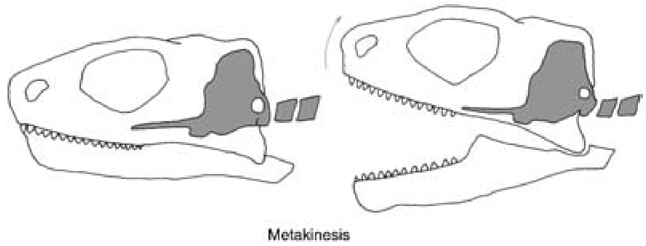

Fig. 14. Diagrammatic representation of a diapsid skull, based on *Sphenodon*, illustrating the movement involved in metakinesis. The braincase is in grey.

1989; Sinclair & McNeil Alexander, 1987; Schwenk, 1999), but is also likely to play an important role in dissipating the strains resulting from biting and muscle activity, since this is a key function of cranial articulations generally (Herring, 1972, 1993; Jaslow, 1990; Herring & Mucci, 1991; Herring *et al.*, 1996; Rafferty & Herring, 1999; Herring & Teng, 2000).

(*d*) *Cranial kinesis – evolution*

Cranial kinesis has always dominated discussions of squamate evolution, from rather simplistic early ideas on the development of streptostyly (see above), to the more complex ones on linkage mechanisms and skull function. How did a fully diapsid, akinetic, skull evolve into the highly kinetic cranium of, for example, geckos, varanids, and snakes?

Based on the condition in crownward taxa (e.g. *Paliguana*, *Kuehneosaurus*), we may conclude that the ancestral lepidosauromorph had already reduced the lower temporal bar, while retaining a small quadratojugal attached to the anterolateral edge of an expanded quadrate (Fig. 15). Early discussions of squamate evolution focused on streptostyly due to a belief that loss of the lower temporal bar 'freed' the quadrate (e.g. Parrington, 1935; von Huene, 1956; Robinson, 1962, 1967*a*). In fact, with or without the bar, the quadrate was still held in place by the strong descending process of the squamosal, where present (e.g. *Gephyrosaurus*), and also by the overlapping wing of the pterygoid (e.g. *Kuehneosaurus*).

Whether or not functional metakinesis existed in early tetrapods (e.g. Versluys, 1912; De Beer, 1937) remains unclear, but the close connections between the skull and braincase in early amniotes (e.g. Berman, 2000) must have limited kinetic potential. Small postparietals still lay across the metakinetic axis in the Early Triassic *Paliguana* (Carroll, 1975, 1977; S. E. Evans, personal observation), but they had been lost in kuehneosaurs (Robinson, 1967*a*) and lepidosaurs. Robinson (1967*a*) characterized *Kuehneosaurus* as lacking metakinesis, and the structure of the braincase/pterygoid articulation supports this. The living *Sphenodon* also lacks metakinesis, but it retains a synovial joint (+interarticular cartilage) between the basipterygoid process and the pterygoid, as well as rudiments of the constrictor dorsalis (Ostrom, 1962; Gorniak, Rosenberg & Gans, 1982), a muscle group active in metakinetic lizards. Together, these features suggest that akinesis, like the lower temporal bar, may be secondary in *Sphenodon*. Certainly, the structure of the sphenoid/pterygoid joints in *Gephyrosaurus* (S. E. Evans, personal observations) gives the impression that basal rhynchocephalians, and therefore presumably basal lepidosaurs, were metakinetic, although this metakinesis may have been less sophisticated than that of modern lizards (see below).

The subsequent elaboration of squamate kinesis required further changes including: reduction of the squamosal; a deeper position for the supratemporal; expansion of the distal tips of the supratemporal and paroccipital process to support the quadrate; reduction of the pterygoid/epipterygoid/quadrate overlap; simplification of the frontoparietal suture in association with mesokinesis; modification of the bones of the postorbital bar and palate to accommodate bending; the development of a synovial joint between the pterygoid and epipterygoid (in place of the more primitive suture) (Fig. 15); and the development of a specialized joint between the supraoccipital and parietal (whereby the anterior processus ascendens of the supraoccipital fits into a notch or recess in the posteroventral margin of the parietal). The last two of these changes (relating to the epipterygoid and parietal) have been associated with the evolution of squamate metakinesis (e.g. De Beer, 1937; Bellairs & Kamal, 1981), suggesting a functional change by comparison with other groups.

The absence of a Triassic fossil record for squamates limits discussion of the sequence in which these character states were acquired. However, if the Late Jurassic *Bavarisaurus* is genuinely primitive (see above), then it provides an obvious starting point. The quadrate is unknown, but the suspensorium was already typically squamate (Evans, 1994*c*) and the posterior ramus of the pterygoid is gracile – indicating a weak connection with the quadrate. There is therefore little doubt that *Bavarisaurus* had achieved streptostyly of the type found in living lizards. The earliest known (Middle Jurassic) lizards already had a mobile joint between the epipterygoid and pterygoid, as evidenced by the presence of the fossa columellae, a small round pit in the dorsal surface of all pterygoids (Evans, 1998*c*), while some parietals show evidence of a recess for the

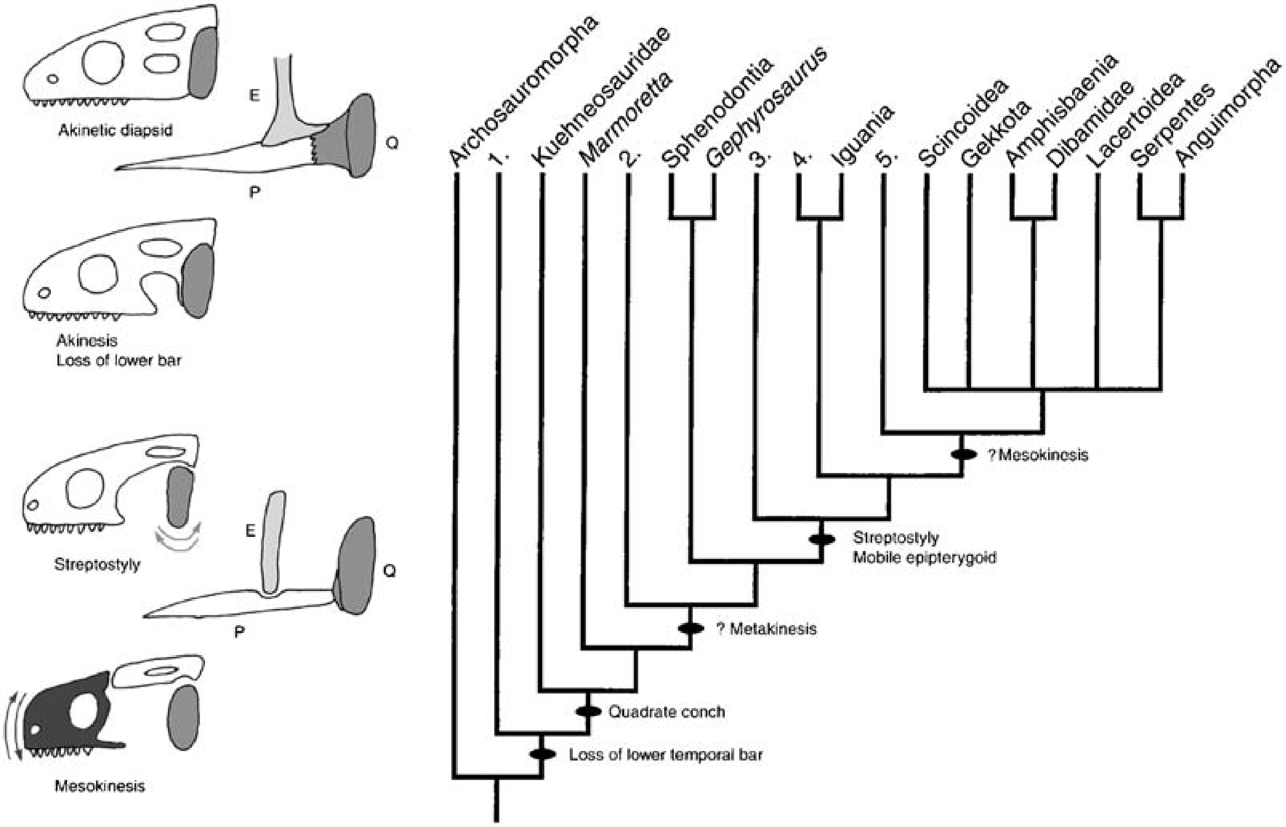

Fig. 15. Consensus phylogeny for Lepidosauromorpha as in Fig. 10 on which are mapped characters relating to cranial kinesis. The epipterygoid (E) is pale grey; the quadrate (Q) in darker grey; the pterygoid (P) is uncoloured. The dark grey colour of the lowest mesokinetic skull shows the antorbital maxillary segment.

processus ascendens of the supraoccipital. This implies squamate-style metakinesis. These regions are not clearly preserved in *Bavarisaurus*, but there is a clear fossa columellae in the Early Cretaceous (Barremian) *Hoyalacerta* (Evans & Barbadillo, 1999) which is also been placed on the squamate stem.

Mesokinesis is unknown outside Squamata, but there is an ongoing debate as to whether or not it was present in basal members of the clade (e.g. Arnold, 1998; Schwenk, 1999, 2001). If Frazzetta's (1962) 'quadric-crank' model applies to all squamates, then mesokinesis is integral to squamate kinesis, including streptostyly, and should have been present in basal taxa. However, Frazzetta's linked kinesis has been unambiguously documented only in insectivorous geckos (De Vree & Gans, 1987; Herrel *et al.*, 1999) and in species of the predatory *Varanus* (Condon, 1987, 1989). It has not been demonstrated in any iguanian (e.g. Throckmorton, 1976, 1980), leading Schwenk (1999, 2001) and Wagner & Schwenk (2000) to argue that mesokinesis was absent in basal squamates and arose within Scleroglossa to improve jaw mobility. Unlike *Sphenodon* and iguanians, which are primarily lingual feeders (taking at least small prey with the tongue), scleroglossans rely strongly on jaw prehension (Schwenk, 1999, 2001).

Mesokinesis involves simplification (reduction of overlap/interdigitation) of the frontoparietal suture, the development of a corresponding hypokinetic joint in the palate, and the presence of an accommodation point either within the postorbital bar, or between the postorbital bar and the temporal region. Iguanians have a simple straight frontoparietal joint, but they lack a hypokinetic joint. Interestingly, however, the iguanian postorbital region is modified and differs from that of both scleroglossans and basal squamates (Arnold, 1998; S. E. Evans, personal observations). Iguanians reduce or lose the postfrontal, and reduce the contact between the postorbital bone and the parietal (Fig. 9). This is suggestive of mesokinetic accommodation, but if mesokinesis has never evolved in Iguania, an alternative explanation is needed.

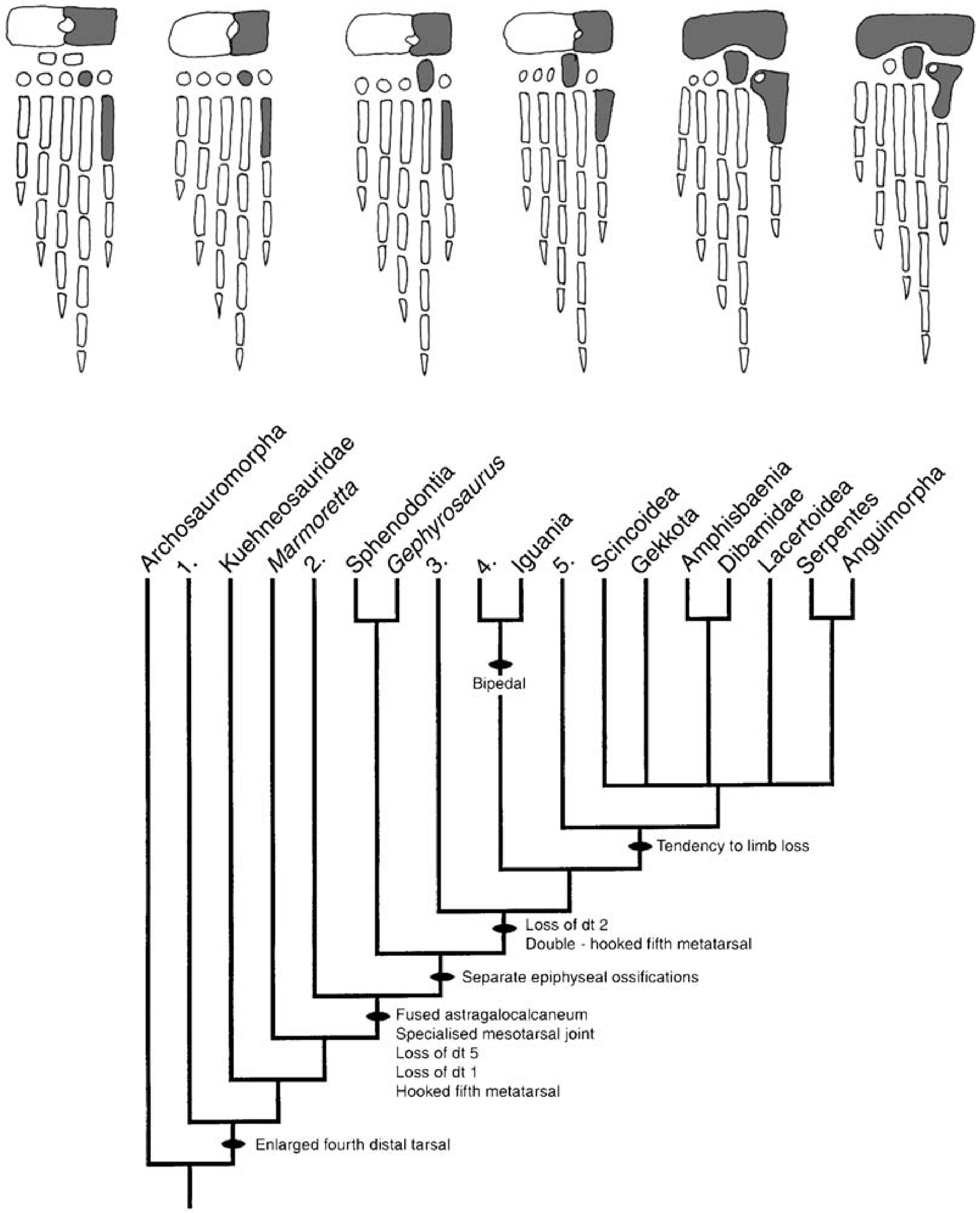

Fig. 16. For legend see opposite page.

In scleroglossans, the postfrontal, postorbital and squamosal form a more integrated unit, with an accommodation point lying between this and the ventrally placed jugal. The sickle-shaped postfrontal clasps the frontal weakly, permitting hingeing to occur (Fig. 9).

In *Bavarisaurus*, the frontoparietal suture is irregular (as it is in *Hoyalacerta*) and the bones of the postorbital bar retain a primitive configuration. Mesokinesis is therefore unlikely. By contrast, the contemporaneous *Eichstaettisaurus* has a simple, fairly straight, frontoparietal suture, a sickle-shaped postfrontal, and lightly built palatal bones, all of which are found in mesokinetic lizards. If the morphological interpretation is sound, the argument with respect to the antiquity of mesokinesis would then hinge on whether *Eichstaettisaurus* is a basal squamate or a basal scleroglossan. Clearly we need more material.

(*e*) *Postcranial morphology*

Although cranial modifications have attracted most attention in discussions of lepidosaurian evolution, there were also significant changes in the postcranial skeleton that improved terrestrial locomotion and may have facilitated the exploitation of different locomotor strategies. Amongst the most easily followed of these changes are those of the axial skeleton, girdles and limbs.

Vertebral modifications include increasing consolidation of the vertebrae, with gradual loss of free intercentra; conjoined rib articulations; the development of stronger and more sophisticated joints between neural arches (including the evolution of accessory zygosphenes) and centra; and the development of mid-vertebral fracture planes in caudal vertebrae, permitting the tail to be shed as an escape mechanism (caudal autotomy). In basal diapsids, the vertebral centrum is amphicoelous forming a cylinder of bone around the notochordal canal. In the lepidosauromorphs *Kuehneosaurus* and *Marmoretta*, the centrum has become solid with flattened surfaces (platycoelous), but amphicoely appears again in early rhynchocephalians. The basal lepidosaurian condition is therefore difficult to reconstruct. Procoely (anterior cotyle, posterior condyle) is probably the original condition for crown-group squamates, although amphicoely has been regained in many higher (i.e. non-eublepharine) gekkotans, presumably in association with paedomorphy. Amongst living squamates, amphicoely is thus a unique derived feature of gekkonids. This led earlier workers (e.g. Hoffstetter, 1962; Estes, 1983*a*) to refer amphicoelous taxa like *Bavarisaurus* to the Gekkota, despite the overall differences in morphology. It now seems that several basal squamates were also amphicoelous (Evans, 1994*a*; Reynoso, 1998).

The structure of the limb girdles is broadly similar throughout the Lepidosauromorpha, the primary changes being the emargination of the anterior border of the scapulocoracoid in squamates, and the development of the thyroid fenestra in the pelvis (between pubis and ischium). A small, fully enclosed, fenestra exists in the kuehneosaur *Icarosaurus* (Colbert, 1970), but perhaps not in *Kuehneosaurus* (S. E. Evans, personal observation). It becomes further enlarged in lepidosaurs and then expands to separate the pubis and ischium more completely in squamates.

There were also important changes in the structure of the foot and ankle (Fig. 16), most notably: consolidation of the proximal tarsals to form a single astragalocalcaneum; loss of the centrale; reduction of the distal tarsal number and enlargement of the fourth distal tarsal; and the development and elaboration of the fifth metatarsal. Together, the astragalocalcaneum and enlarged distal tarsal four create a specialized mid-tarsal joint (analogous to the sub-talar joint of mammals) that aids movement over rough ground (Brinkman, 1980). The hooking of the fifth metatarsal in first one plane and then two permits the fifth digit to be rotated posteriorly and used in a manner analogous to that of the mammalian calcaneal heel (Robinson, 1975). A hooked (hamate) fifth metatarsal is not unique to lepidosaurs however; it is found also in turtles and many archosauromorphs, although not in the double-hooked morphology of squamates. Again, the polarity of the character is problematic, but the bone appears to be simple in kuehneosaurs (P. L. Robinson, unpublished manuscript) suggesting that the lepidosaurian morphology could be novel.

(*f*) *Character complexes*

Character mapping of the kind illustrated above has the potential to yield insights into the sequence in which the complex morphological characters of

Fig. 16. Consensus phylogeny for Lepidosauromorpha as in Fig. 10 on which are mapped characters of the ankle and pes, with diagrammatic representations of the ankle and pes from, left to right, basal lepidosauromorph to squamate. In each figure, the fifth metatarsal, fourth distal tarsal and calcaneum (or fused astragalocalcaneum) are in grey.

squamates have arisen, and to document the possible co-evolution of these characters. This, in turn, may promote increased dialogue between developmental biology, functional morphology, and phylogenetic analysis, and foster a more synthetic approach to the evolution of squamate morphology. In order to succeed, however, we need to fill not only the gaps in the fossil record, but also those in our knowledge of modern squamate development, morphology, and function.

(*g*) *Ecomorphological diversification*

Like the majority of living lizards, basal squamates were probably tetrapodal, terrestrial and insectivorous. Subsequently, however, some squamates modified this body plan in subtle, or not so subtle, ways, in order to invade a variety of new niches. Some of the innovations involve soft part structures or behavioural attributes that cannot be inferred from fossils (e.g. reproductive strategies or skin structure). Others affect the skull and skeleton, most notably those relating to diet and locomotion.

(i) *Dietary adaptation*

The teeth of basal lepidosaurs (e.g. those of *Gephyrosaurus*) are conical with a small degree of apical faceting or striation. Alterations to this pattern occur within many living and fossil groups: labiolingual compression and increased cuspidy in some herbivores (e.g. living iguanas); enlargement, greater robusticity, and additional bone of attachment in durophages (e.g. the teiid *Dracaena guianensis*); compression and marginal serration in carnivores (many varanid lizards); grooving (venomous helodermatids); and, ultimately, the development of hollow fangs (venomous advanced snakes) that act as miniature hypodermic syringes. To date, most examples of such specialisation within squamates date back no further than the Early Cretaceous. Lizard material from the Valanginian-Hauterivian (approximately 130 Ma) of Japan includes rare jaws with a cuspidate dentition similar to that of a modern iguana (Evans & Manabe, 2000), while durophagy is suggested by the blunt posterior teeth of the contemporaneous Japanese *Sakurasaurus* (Evans & Manabe, 1999) and the early polyglyphanodont teiid, *Dicothodon*, from the mid-Cretaceous of Utah (Nydam, 1999).

(ii) *Climbing*

Most lizards climb with varying degrees of skill, but only geckos, chamaeleons, and a few iguanians (e.g. anoles) show clear specialisation. The earliest chamaeleons are Miocene in age (Rieppel, Walker & Odhiambo, 1992), while the earliest certain gekkotan (but skull fragments only) is from the Albian of Mongolia (Alifanov, 1989*b*). Modern climbing specialists tend to have feet with a greater degree of digital symmetry than those of terrestrial relatives, while some scansorial geckos show elongation of the penultimate phalanges (S. E. Evans, personal observation). The Solnhofen genus *Eichstaettisaurus* resembles some modern climbers in having rather short legs, long toes, but quite symmetrical feet. More striking, however, is the Early Cretaceous *Scandensia* (Las Hoyas, Spain: Evans & Barbadillo, 1998), a lizard with extraordinarily long penultimate digits matched only by those of some living arboreal gekkotans with digital climbing pads.

(iii) *Aquatic adaptations*

As the major continental blocks began to move apart in the Early Cretaceous, wide areas of shallow coastal sea provided new niches for marine tetrapods. From at least the mid-Cretaceous onwards, this seems to have catalysed a remarkable diversification of marine varanoid lizards (e.g. Carroll & De Braga, 1992; Dal Sasso & Pinna, 1997; Lee & Caldwell, 2000), and, at some stage and by some, as yet undetermined, route, early eel-like pachyophid snakes (e.g. Lee & Caldwell, 1998; Rage & Escuillié, 2000; Tchernov *et al.*, 2000; Caldwell & Albino, 2001). Later came the mosasaurs, increasing in size until they were the top marine predators of the Late Cretaceous seas (Russell, 1967; Bell, 1997*a*, *b*). Many living lizards will swim if the need arises, but few show obvious specialisations (except for some bilateral flattening of the tail, and the possession of salt glands in the Marine Iguana, *Amblyrhynchus cristatus*, of the Galapagos). The only putative example of a freshwater swimmer currently available is the Early Cretaceous *Meyasaurus* from Spain (e.g. Vidal, 1915; Evans & Barbadillo, 1996, 1997). At Las Hoyas, this is by far the most common lizard in a largely wetland assemblage (fish, frogs, salamanders), while the holotype (from the locality of Montsech; Vidal, 1915; Evans & Barbadillo, 1996) has a small freshwater fish within the abdominal cavity, suggesting it may have fed at or beyond the margins of the lake.

(iv) *Burrowing, elongation and limb reduction*

A serpentine body form is estimated to have occurred independently more than 60 times within scleroglossans (e.g. Gans, 1962; Greer, 1991; Coates & Ruta, 2000) – culminating in the evolution of the Amphisbaenia ('worm-lizards') and Serpentes (snakes). With the possible exception of the problematic *Tamaulipasaurus* (Clark & Hernandez, 1994: see above), the earliest known occurrence of this clearly successful bauplan comes from the Middle Jurassic (Bathonian) deposits of Kirtlington Quarry, Oxfordshire, England. Material tentatively attributed to the short-jawed scincomorph *Saurillodon* includes exceptionally elongated trunk vertebrae that clearly came from a serpentiform animal (Evans, 1998*a*). Elongation more frequently occurs by an increase in vertebral number as seen in the serpentiform marine varanoids, pachyophid snakes, and possible basal amphisbaenians of the later Cretaceous (Wu *et al.*, 1993, 1996; Dal Sasso & Pinna, 1997; Lee & Caldwell, 1998; Rage & Escuillié, 2000; Tchernov *et al.*, 2000).

(3) Palaeobiogeography

Any discussion of squamate evolution and diversification inevitably leads to questions concerning centres of origin for major clades, or patterns and times of colonization for different landmasses. Estes (1983*b*) presented the first comprehensive examination of squamate palaeobiogeography, but he was limited by the paucity of the fossil record, especially for Gondwana, and by problems of identification (especially for Late Triassic and Jurassic taxa, e.g. Evans, 1988, 1993, 1994*b*). Nearly 20 years on, these problems still constrain discussion.

Estes' (1983*b*) main proposition in relation to early squamate history was that an early Pangaean stem-squamate assemblage had undergone vicariance as a result of the separation of Laurasia and Gondwana during the Jurassic (Fig. 17), with northern populations evolving into scleroglossans and southern ones into iguanians. Later continental contacts permitted north–south migration of these groups. Estes' hypothesis was challenged by a series of discoveries of iguanian fossils in the mid and Late Cretaceous of Asia (e.g. Alifanov, 1989*a*, 1993*c*; Borsuk-Białynicka & Alifanov, 1991; Gao & Hou, 1995; Gao & Nessov, 1998), leading to an alternative consensus on Laurasian ancestry for Iguania, although this hypothesis relies heavily on the absence of data from Gondwana. Molecular data (Macey *et al.*, 2000), however, tend to support a southern origin for Acrodonta, at least, and the new material from the Kota Formation of India corroborates this. If Iguania and Scleroglossa had already separated before the fragmentation of Pangaea, as the evidence suggests, then the pattern of distribution of daughter lineages on the two continents was probably far more complex than Estes envisaged – as evidenced by the reported occurrence of scincomorph paramacellodids in the Jurassic of Tanzania (Broschinski, 1999) and of iguanians in the mid-Cretaceous of Mongolia and central Asia (Alifanov, 1993*c*; Gao & Nessov, 1998), as well as those in India.

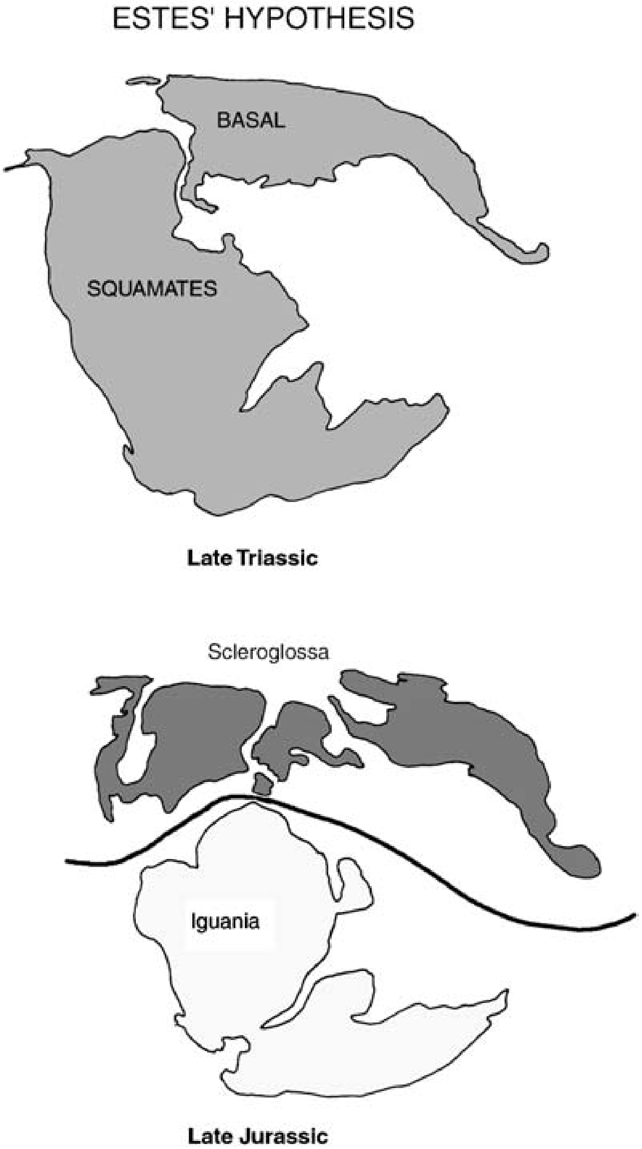

Fig. 17. Diagrammatic illustration of Estes' (1983*b*) model of early squamate vicariance. Maps are from Smith *et al.* (1994).

The discussion is currently hampered by the information bias towards northern continents, and this probably says more about the geographical distribution of palaeontologists than of lizards. The situation is beginning to change (e.g. Bonfim-Júnior & Marques, 1997; Evans & Yabumoto, 1998; Martill & Frey, 1998; Bonfim-Junior, 1999; Broschinski, 1999; Ross *et al.*, 1999; Evans *et al.*, 2000, 2001, 2002; Rauhut, Lopez-Arbarella & Puerta, 2001: Figs 6 and 18), but although we know that lizards were present in

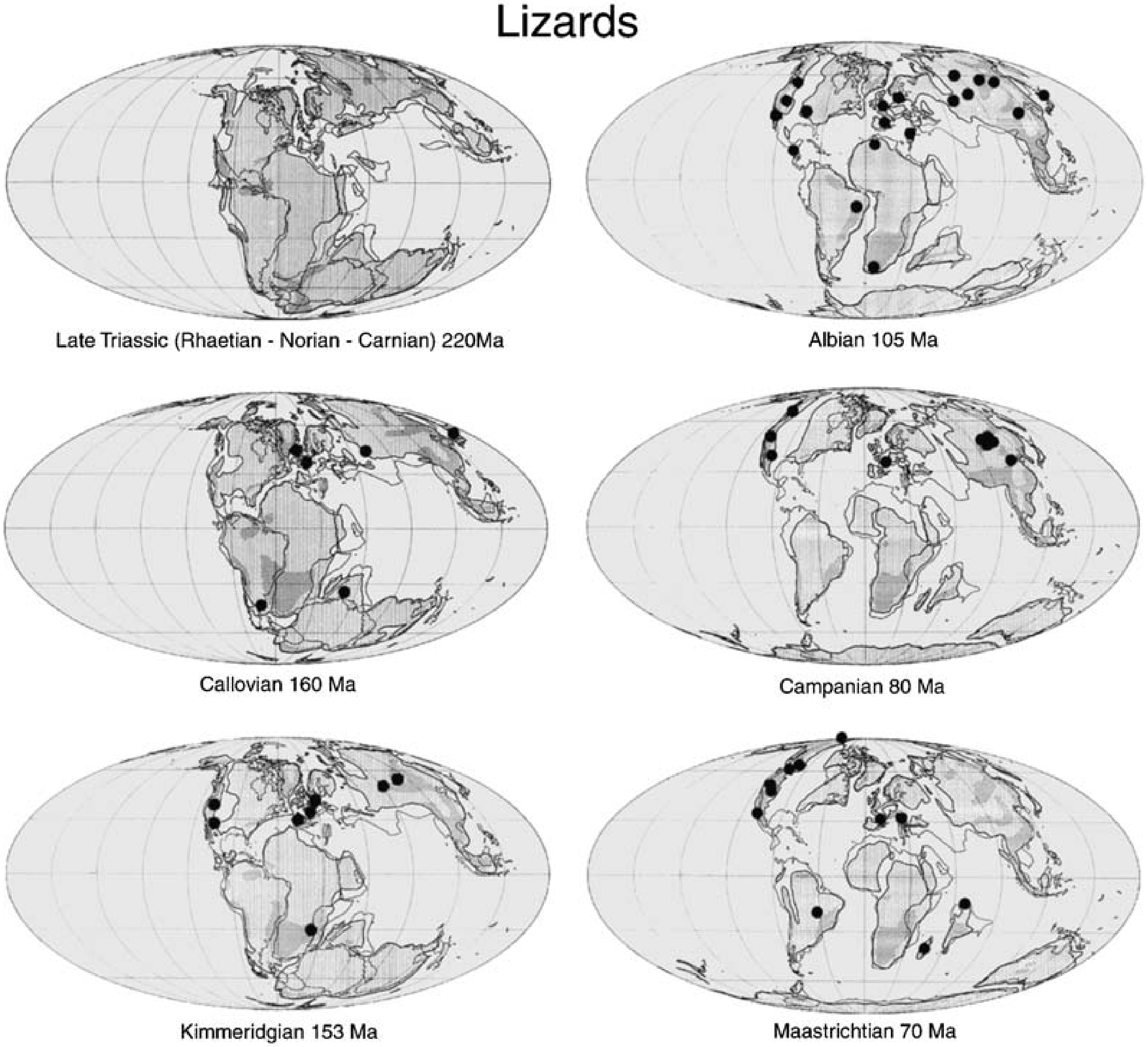

Fig. 18. Palaeogeographic maps showing approximate continental positions through the Triassic, Jurassic and Cretaceous, with known locations of fossil lizards shown. Data from the same sources as listed in Figs 5 and 6. Maps are from Smith *et al.* (1994). The Callovian map has been used for all early or middle Jurassic taxa; the Albian map represents all Early Cretaceous genera. Neither snakes nor marine varanoids are included.

Gondwana during the Jurassic and Cretaceous, most of the material is either too fragmentary to assign to known lineages, or has yet to be adequately described. Until there is a comparable level of knowledge for the Mesozoic assemblages of both Gondwana and Laurasia, it is premature to reconstruct centres of origin or dispersal on the basis of fossil data alone.

The difficulties of palaeobiogeographic reconstruction are further emphasized by more recent molecular data showing that long-distance oceanic dispersal has occurred repeatedly in lizards. Carranza *et al.* (2000), for example, demonstrated that some species of Cuban geckos (*Tarentola* sp.) have their closest relatives in North Africa, requiring a journey of at least 6000 km on trans-Atlantic currents. Similarly, the scincid genus *Mabuya* probably colonized Madagascar from Africa over the deep Mozambique Channel (Mausfeld *et al.*, 2000). If currents can carry small reptiles across major oceans, then hypotheses of vicariance and past dispersal patterns become more problematic.

IV. CONCLUSIONS

(1) Squamates are a large and successful group of reptiles diagnosed by a suite of derived characters. They are the sister group of Rhynchocephalia, within a monophyletic Lepidosauria. Snakes and amphisbaenians ('worm-lizards') arose from within lizards, leaving lizards as a paraphyletic group that cannot be diagnosed to the exclusion of other squamates. Formal terms like Lacertilia and Sauria should therefore not be used to encompass lizards alone. The major dichotomy with squamates is between Iguania and Scleroglossa, the latter embracing all other squamates including Serpentes (snakes) and Amphisbaenia.

(2) Although none of the Triassic genera previously identified as squamates actually belongs to this group, indirect evidence suggests that squamates and rhynchocephalians had diverged by the Middle Triassic, and that stem squamates had already begun to diversify prior to the end of the Triassic. Iguania and Scleroglossa have probably been separate since this time, and therefore split before the fragmentation of the Pangaean supercontinent. The current absence of Triassic squamate fossils is best explained as an artefact of either preservation or sampling. There is no evidence that squamates originated from rhynchocephalians despite the disparity in their Triassic records.

(3) In addition to the major temporal gap in the squamate record (i.e. that of the Triassic and earliest Jurassic), there is also a major biogeographic one. Very little is known of the Mesozoic history of squamates in southern continents (Gondwana), and this constrains discussion of centres of origin, and of patterns of diversification and colonisation. It seems likely, however, that ancestral populations of both iguanians and scleroglossans may have been present on both Laurasia and Gondwana at the time of separation, but their subsequent history in Gondwana remains largely unknown. Allowing for the vagaries of the record, Laurasian lizard assemblages were dominated by scincomorphs, with fewer anguimorphs, and still fewer representatives of other groups. We do not yet know whether southern faunas show a different combination, but there is some evidence that snakes may have been more widely distributed and more diverse in Gondwana.

(4) Despite some lack of resolution, the current phylogenetic consensus permits us to begin mapping of characters against phylogeny. While the exercise is constrained by the limited record for Permian and Triassic stem taxa, it does suggest some patterns of character co-evolution (e.g. the concomitant increase in the facial process of the maxilla, reduction of the lacrimal, deepening of the pleurodont implantation; or reduction of palatal teeth, shortening of the jaw, increase in size of the coronoid process) that need to be explored in greater detail with respect to functional, developmental, and phylogenetic implications. Cranial kinesis was clearly a key innovation in squamate evolution, but even in living squamates, it remains poorly understood. Better data from the early squamate record as to the sequence of evolution of component parts of the system might well shed new light on this difficult but interesting problem.

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VII. APPENDIX: EARLY LIZARD TAXA (TO MID-CRETACEOUS) DESCRIBED IN THE LITERATURE

(Key: An, anguimorph; G, gekkotan; Ig, iguanian; P, paramacellodid; Sc, scincomorph; ?, position unknown)

Permo-Triassic, Triassic and Jurassic pseudolizards

1. *Palaeagama* (Carroll, 1975, 1977) – indeterminate diapsid (Evans, 1988).
2. *Paliguana* (Carroll 1975, 1977) – probably basal lepidosauromorph (Evans, 1988).
3. *Saurosternon* (Carroll 1975, 1977) – possible basal lepidosauromorph (Evans, 1988).
4. *Colubrifer* (Carroll, 1982) – procolophonian (Evans, 2001).
5. *Kudnu* – Arcadia Formation, Australia (Bartholomai, 1979) – possible juvenile prolacertiform (S. E. Evans, personal observations).
6. *Santaisaurus* – China (Sun *et al.*, 1992) – procolophonian (Evans, 2001).
7. *Blomosaurus* – Russia (Tatarinov, 1978) – probable procolophonian (Evans, 2001).
8. *Kuehneosaurus*, *Kuehneosuchus* – Upper Triassic fissure fillings, England (Robinson, 1967*a*, *b*) – lepidosauromorphs.
9. *Icarosaurus* – Newark Supergroup, USA (Colbert, 1969, 1970) – lepidosauromorph.
10. '*Perparvus*' – Upper Triassic fissure fillings, England (Carroll, 1988) – rhynchocephalian (informal name given by Pamela L. Robinson, but never published, for a genus subsequently described by Whiteside, 1986, as *Diphydontosaurus*: Frances Mussett personal communication to S. E. Evans, 1993).
11. *Protolacerta* – Lower Jurassic, Argentina (Casimequela, 1975) – fish, (Estes, 1983*a*).
12. *Cteniogenys* – Bathonian-Kimmeridgian (Seiffert, 1973; Estes, 1983*a*) – choristoderan reptile (Evans, 1991).
13. '*Tedorosaurus*' – Oxfordian, Japan (Shikama, 1969; Asuma & Tomida, 1995) – indeterminate ?reptile described from a private specimen (schematic figure) and not available to science.

(*a*) *Early or Middle Jurassic*

1. Indeterminate pleurodont lizard – Kota Formation, India (Evans *et al.*, 2000, 2001, 2002).
2. Acrodont lizard (*Bharatagama*) (Ig) – Kota Formation, India (Evans *et al.*, 2000, 2001, 2002).
3. *Bellairsia* (Sc) – Kirtlington, Oxfordshire, Bathonian (Evans, 1998*b*).
4. *Balnealacerta* (Sc) – Kirtlington, Oxfordshire, Bathonian (Evans, 1998*b*).

5\. Indet scincomorphs – Skye, Scotland, Bathonian (Waldman & Evans, 1994).

6\. *Oxiella* (?) – Kirtlington, Oxfordshire, Bathonian (Evans, 1998*b*).

7\. *Parviraptor* (An) – Kirtlington, Oxfordshire, Bathonian (Evans, 1994*a*).

8\. cf. *Saurillodon* (Sc, reduced limbed) – Kirtlington, Oxfordshire, Bathonian (Evans, 1998*b*).

9\. ? Indeterminate Squamata or possible gekkotan – Kirtlington, Oxfordshire, Bathonian (Evans, 1998*b*).

10\. *Changetisaurus* (Sc/An) – Fergana, Kirghizia, Callovian (Fedorov & Nessov, 1992); indeterminate Squamata – Fergana, Kirghizia Callovian (Nessov, 1985).

11\. Indeterminate Squamata – Patagonia, Argentina, ?Bathonian (Rauhut *et al.*, 2001).

12\. ?Squamata – Kayenta Formation, USA, ?Pliensbachian (Meszoely, 1987).

(*b*) *Late Jurassic*

1\. *Parviraptor* (An) – Guimarota, Portugal, Kimmeridgian (Broschinski, 2000); Morrison Fm USA, Kimmeridgian (Evans, 1996; Evans & Chure, 1998*a*, 1999).

2\. *Saurillodon* (Sc) – Guimarota, Portugal, Kimmeridgian (Estes, 1983*a*; Broschinski, 2000); Morrison Fm USA, Kimmeridgian (Evans, 1996; Evans & Chure, 1998*a*, 1999).

3\. *Dorsetisaurus* (An) – Guimarota, Portugal, Kimmeridgian (Seiffert, 1973; Broschinski, 2000); Morrison Formation USA, Kimmeridgian (Evans, 1996; Evans & Chure, 1998*a*, *b*, 1999).

4\. *Paramacellodus* (Sc, P) – Morrison Formation USA, Kimmeridgian (Evans, 1996; Evans & Chure, 1998*a*, *b*, 1999); Tendagaru, Tanzania (Broschinski, 1999).

5\. *Becklesius* (Sc, P) – Guimarota, Portugal, Kimmeridgian (Seiffert, 1973; Broschinski, 2000).

6\. *Mimobecklesius* (Sc, P) – Gansu, China, Late Jurassic (Li, 1985).

7\. *Sharovisaurus* (Sc, P) – Karatau, Kazachstan, Kimeridgian (Hecht & Hecht, 1984).

8\. *Euposaurus* (?) – Cerin, France, Kimmeridgian (Jourdan, 1862).

9\. *Schilleria* (?) – Morrison Formation, USA, Kimmeridgian (Evans & Chure, 1999).

10\. *Eichstaettisaurus* (?) – Solnhofen, Germany, Tithonian (Broili, 1938).

11\. *Bavarisaurus* (?) – Solnhofen, Germany, Tithonian (Wagner, 1852).

12\. *Ardeosaurus* (?) – Solnhofen, Germany, Tithonian (Meyer, 1860).

13\. *Palaeolacerta* (?) – Solnhofen, Germany, Tithonian (Cocude-Michel, 1961).

14\. '*Proaigialosaurus*' (?) – Solnhofen, Germany, Tithonian (Kuhn, 1958) – private specimen now lost.

(*c*) *Early Cretaceous* (*Berriasian – Hauterivian*)

1\. *Tarratosaurus* (Sc) – Anoual, Morocco, Berriasian (Broschinski & Sigogneau-Russell, 1996).

2\. *Saurillus* (Sc) – Purbeck, England, Berriasian (Owen, 1854; Hoffstetter, 1967; Evans & Searle, 2002).

3\. *Pseudosaurillus* (Sc) – Purbeck, England, Berriasian (Hoffstetter, 1967; Evans & Searle, 2002).

4\. *Becklesius* (Sc) – Purbeck, England, Berriasian (Hoffstetter, 1967; Estes 1983*a*; Evans & Searle, 2002); Anoual, Morocco, Berriasian (Broschinski & Sigogneau-Russell, 1996).

5\. *Paramacellodus* (Sc) – Purbeck, England, Berriasian (Hoffstetter, 1967; Evans & Searle, 2002); Anoual, Morocco, Berriasian (Broschinski & Sigogneau-Russell, 1996).

6\. *Parasaurillus* (Sc) – Purbeck, England, Berriasian (Hoffstetter, 1967; Evans & Searle, 2002).

7\. Undescribed or indeterminate paramacellodid – Shiramine, Japan, Hauterivian/Valanginian (Evans & Manabe, 2000); Sussex, England (Milner & Evans, 1998).

8\. *Durotrigia* (Sc) – Purbeck, England, Berriasian (Hoffstetter, 1967; Evans & Searle, 2002).

9\. *Parviraptor* (An) – Purbeck, England, Berriasian (Hoffstetter, 1967; Evans & Searle, 2002).

10\. *Dorsetisaurus* (An) – Purbeck, England, Berriasian (Hoffstetter, 1967; Evans & Searle, 2002); Sussex England (Milner & Evans, 1998; S. E. Evans, in preparation).

11\. *Meyasaurus* (Sc) – Montsech, Spain, ?Berriasian (Vidal, 1915; Evans & Barbadillo, 1996).

12\. *Eichstaettisaurus* (?) – Montsech, Spain, ?Berriasian (Evans *et al.*, 2000).

13\. *Sakurasaurus* (Sc) – Shokawa, Shiramine, Japan, Valanginian/Hauterivian (Evans & Manabe, 1999).

14\. *Yabeinosaurus* – Liaoning, China, age uncertain (in the range of Upper Jurassic to mid-Cretaceous) (Endo & Shikama, 1942).

15\. Two undescribed anguimorphs – Shokawa, Shiramine, Japan, Valanginian/Hauterivian (Evans & Manabe, 1999, 2000, in preparation).

16\. Three undescribed scincomorphs – Shiramine, Japan, Valanginian/Hauterivian (Evans & Manabe, 1999); two unnamed scincomorphs, Isle of Wight, England (S. E. Evans, P. Barrett and D. Ward, submitted manuscript); indeterminate scincomorph – Borholm, Denmark (Rees, 2000).

17\. Undescribed ?iguanian – Shiramine, Japan, Valanginian/Hauterivian (Evans & Manabe, 2000, in preparation).

18\. Indeterminate Squamata – Kirkwood Formation, South Africa, Valanginian (Ross *et al.*, 1999); three unnamed Purbeck dental morphotypes (Evans & Searle, 2002).

(*d*) *Mid-Cretaceous* (*Barremian-Albian*)

1\. *Meyasaurus* (Sc) – Una, Galve, Las Hoyas, Spain, Barremian (Vidal, 1915; Richter, 1994*a*; Evans & Barbadillo, 1997).

2\. *Scandensia* (?) – Las Hoyas, Spain, Barremian (Evans & Barbadillo, 1997).

3\. *Hoyalacerta* (?) – Las Hoyas, Spain, Barremian (Evans & Barbadillo, 1997).

4\. *Eichstaettisaurus* (?) – Pietraroja, Italy, Albian (S. E. Evans, P. Raia, C. Barbera, in preparation); ?Eichstaettisauridae – Höövör (Khobur), Mongolia, Aptian-Albian (Alifanov, 2000).

5\. *Chometochadmon* (?) – Pietraroja, Italy, Albian (Costa, 1864; Barbera & Macuglia, 1988, 1991).

6\. *Costasaurus* – Pietraroja, Italy, Albian (Costa, 1851; Estes, 1983*a*).

7\. *Paramacellodus* – (ScUna, Galve, Spain, Barremian (Richter, 1994*b*); Mogoito, Transbaikal, Russia, Barremian-Aptian (Averianov & Skutchas, 1999); Oklahoma, USA, Aptian-Albian (Nydam & Cifelli, 2002*b*).

8\. *Becklesius* (Sc) – Una, Galve, Spain, Barremian (Richter, 1994*a*).

9\. Indeterminate Paramacellodidae – Texas, Oklahoma, Utah, USA, Aptian-Albian (Winkler *et al.*, 1990; Cifelli *et al.*, 1997, 1999); Höövör (Khobur), Mongolia, Aptian-Albian (Alifanov, 2000); Siberia (Leshchinskiy *et al.*, 2001).

10. *Primaderma* (An) – Utah, USA Albian-Cenomanian (Cifelli *et al.*, 1999, Nydam, 2000).

11. *Dicothodon* (Sc) – Utah, USA Albian (Nydam, 1999).

12. Undescribed Teiidae (Sc) – Texas, Oklahoma, Utah, USA, Aptian-Albian (Winkler *et al.*, 1990; Cifelli *et al.*, 1997; Nydam, 1999).

13. *Huehuecuetzpalli* (?) – Tepexi de Rodriguez, Mexico (Reynoso, 1998).

14. *Tepexisaurus* (Sc) – Tepexi de Rodriguez, Mexico, Aptian/Albian (Reynoso & Callison, 2000).

15. '*Patricosaurus*' (?An) – Cambridgeshire, England, Albian (Seeley, 1887; Barrett & Evans, 2002).

16. *Olindalacerta* (?) – Crato Formation, Brazil (Evans & Yabumoto, 1998).

17. *Oxia* (An) – Uzbekistan, Albian (Nessov, 1985; Gao & Nessov, 1998).

18. *Hoburogekko* (G) – Höövör (Khobur), Mongolia, Aptian-Albian (Alifanov, 1989*b*).

19. Undescribed iguanians – Höövör (Khobur), Mongolia, Aptian-Albian (Alifanov, 2000); Kirghizia, Uzbekistan, Kazachstan (Gao & Nessov, 1998).

20. *Hodzhakulia* (?) – Höövör (Khobur), Mongolia, Aptian-Albian (Alifanov, 1993*a*, 2000); Uzbekistan, Aptian-Albian (Nessov, 1985; Gao & Nessov, 1998).

21. cf. *Dorsetisaurus* (An) – Höövör (Khobur), Mongolia, Aptian-Albian (Alifanov, 2000).

22. ?Mongolochamopidae (Sc) – Höövör (Khobur), Mongolia, Aptian-Albian (Alifanov, 2000).

23. cf. *Slavoia* (Sc) – Höövör (Khobur), Mongolia, Aptian-Albian (Alifanov, 1993*b*, 2000).

24. *Cuencasaurus* (?) – Una, Spain (Richter, 1994*a*).

25. *Pachygenys* (?Sc) – China, Barremian (Gao & Cheng, 1999).

26. cf. *Penetius* (Sc) – Utah, USA, Albian-Cenomanian (Cifelli *et al.*, 1999).

27. Undescribed Scincomorpha – Crato Formation, Brazil, Albian (Bonfim-Júnior, 1999; Bonfim-Júnior & Marques, 1997), Uzbekistan, (Gao & Nessov, 1998); Oklahoma, Utah, USA, Aptian-Albian (Cifelli *et al.*, 1997, 1999).

28. ?Necrosauridae (An) – Utah, USA Albian-Cenomanian (Cifelli *et al.*, 1999).

29. Indeterminate Xenosauridae (An) – Siberia, Aptian-Albian (Leshchinskiy *et al.*, 2001).

30. *Bicuspidon* (Sc) – Utah, USA, Albian-Cenomanian (Nydam & Cifelli, 2002*a*).

31. *Atokasaurus* (Sc) – Oklahoma, USA, Aptian-Albian (Nydam & Cifelli, 2002*b*).

32. *Ptilotodon* (Sc) – Oklahoma, USA, Aptian-Albian (Nydam & Cifelli, 2002*b*).