

The Origin and Early Diversification of Squamates

SUSAN E. EVANS

2.1 Introduction

Squamata, the group that encompasses snakes, lizards, and amphisbaenians, is the largest (>10,500 sp.) and most disparate group of modern reptiles. Extant squamates are distributed over all but the coldest parts of the world; range in size (snout-vent length, SVL) from millimetres to metres; and show a diversity of diets, shapes, locomotor patterns, and reproductive strategies. Snakes (Serpentes) account for roughly 35 per cent of all extant squamate species and their origin and relationships, which have long intrigued herpetologists, are the focus of this volume. This chapter aims to provide a foundation for subsequent chapters, by reviewing what is currently known of the early stages of squamate evolution and diversification.

Most researchers recognize eight extant major squamate clades (Fig. 2.1): Dibamidae; Gekkota; Scincoidea (=Scinciformata [1]), encompassing Xantusiidae, Scincidae, and Cordyliformes; Lacertoidea (=Laterata [1]), encompassing Lacertidae and Teiioidea; Amphisbaenia; Iguania; Anguimorpha; and Serpentes. Although Camp [2] considered Gekkota to be primitive squamates (part of his Ascalabota), the first comprehensive cladistic analysis [3], based on morphological characters, placed Iguania as the sister group of other squamates (Scleroglossa). Within Scleroglossa, Estes et al. [3] united Scincoidea + Lacertoidea in Scincomorpha, and Scincomorpha + Anguimorpha as Autarchoglossa. The position of three limb-reduced clades, Dibamidae, Amphisbaenia, and Serpentes, was unresolved within Scleroglossa. The topology of Estes et al. [3] remained the working hypothesis for most herpetologists until 2004 with the publication of phylogenies based on molecular data [4, 5]. The molecular trees placed Gekkota rather than Iguania as the sister group of other squamates (invalidating Scleroglossa), with Scincoidea, and then Lacertoidea (including Amphisbaenia) as successive outgroups to a Toxicofera that

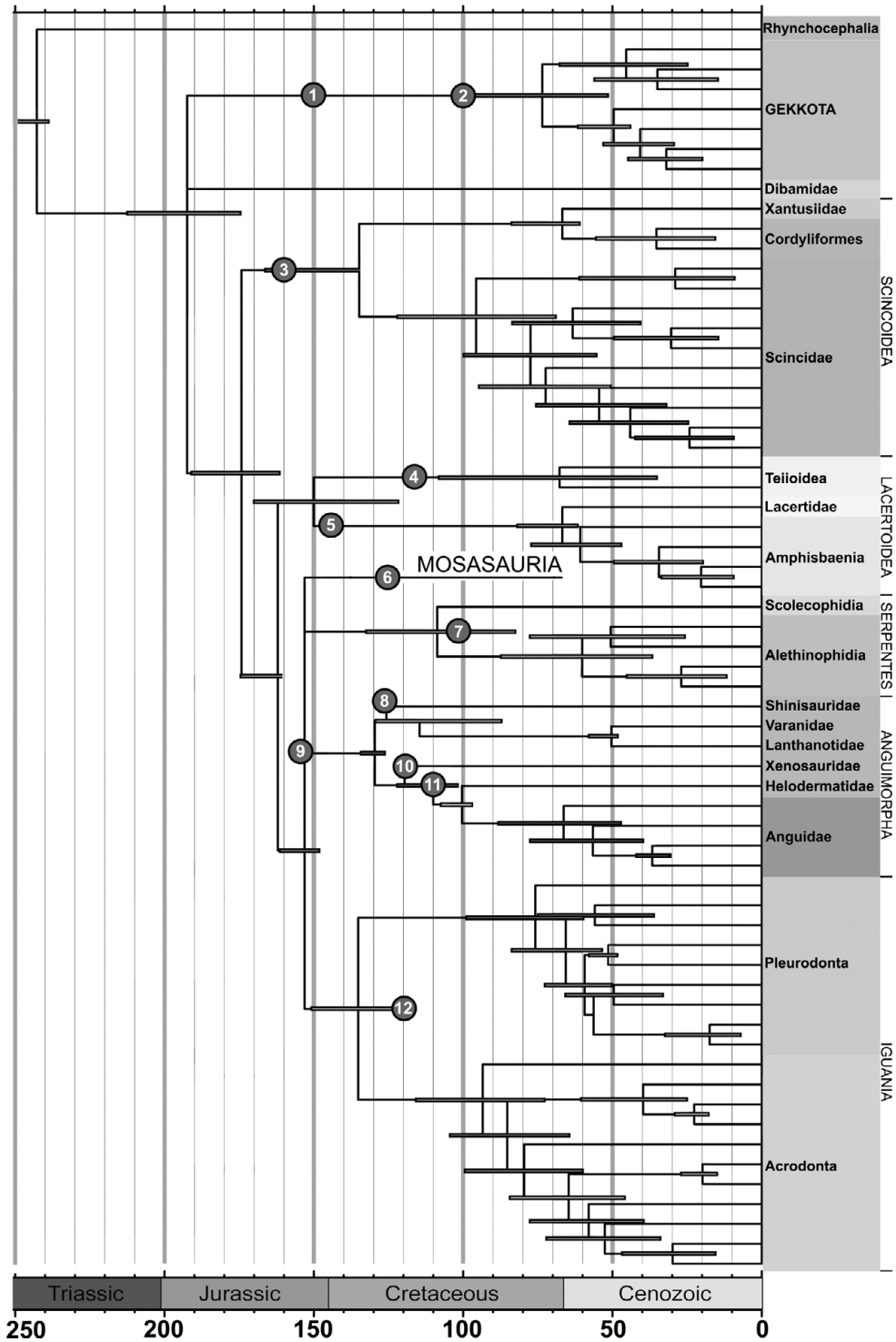


Figure 2.1 Molecular time tree for Squamata, redrawn and simplified from Jones et al. [14], showing putative early representatives of major clades discussed in the text. (1) *Eichstaettisaurus*

encompassed Iguania, Anguimorpha, and Serpentes [1]. Although morphological data sets (e.g., [6]) tend to replicate the Estes et al. [3] tree, subsequent molecular and combined evidence analyses [7–13] agree with those of Townsend et al. [4] and Vidal and Hedges [5]. The molecular tree is therefore used as the phylogenetic framework herein (Fig. 2.1).

2.2 The Early Squamate Fossil Record

Within Lepidosauria, Squamata is the sister group of Rhynchocephalia. Rhynchocephalia is represented today only by the genus *Sphenodon* (New Zealand), but the group has a relatively good fossil record through much of the Mesozoic. The occurrence of a primitive rhynchocephalian in the Middle Triassic of Germany [14] provides a latest possible age for the division of the lepidosaurian stem, although that division, and thus the origin of Squamata, probably occurred in the Early Triassic [12, 14]. However, although there are many records of Triassic rhynchocephalians, there are currently no unequivocal records of Triassic squamates. Those described last century have all been re-assigned to other reptile groups or to the lepidosaurian stem [15, 16].

Tikiguana estesi, represented by a single jaw with an acrodont dentition collected from Upper Triassic deposits in India [17], was shown to be a modern intrusion [18]. More recently, Simões et al. [19] placed three monotypic genera, *Sophineta cracoviensis* (Lower Triassic, Poland, [20]), *Megachirella wachtleri* (Upper Triassic, Italy [21]), and *Marmoretta oxoniensis* (Middle Jurassic, UK [22]) into Squamata. However, re-analyses, based on new data for *Marmoretta* [23], do not support a squamate attribution for either *Marmoretta* or *Sophineta*, and leave the position of *Megachirella* as equivocal.

Paikisaurus indicus is based on two jaw fragments from the Lower–Middle Jurassic Kota Formation of India [24]. The designated holotype bears two teeth, neither of which is obviously pleurodont, whereas the referred specimen bears a single tooth with little resemblance to that of the holotype. *Bharatagama rebbanensis*, also from the Kota Formation, is represented by multiple jaws bearing both pleurodont and acrodont teeth [25]. It was described as a possible acrodont iguanian but could also be an aberrant rhynchocephalian [18, 26].

The earliest unequivocal squamates are from the Middle Jurassic (Bathonian) of the United Kingdom, Russia, Kyrgyzstan, and Morocco. One of the most productive Bathonian

Figure 2.1 (cont.) (Upper Jurassic, Germany); (2) *Hoburogekko* (Lower Cretaceous, Mongolia); (3) Paramacellodidae and *Saurillodon* (Upper Jurassic, Portugal); (4) *Asagaolacerta*, *Kuwajimalla*, Polyglyphanodontia (Lower Cretaceous, Japan); (5) *Purbicella* (Lower Cretaceous, UK); (6) *Kaganaias* (Lower Cretaceous, Japan); (7) ‘*Coniophis*’ (Albian–Cenomanian, North America) and terrestrial + aquatic snakes (Albian–Cenomanian, Algeria); (8) *Dalinghosaurus* (Lower Cretaceous, China); (9) *Dorsetisaurus* (Upper Jurassic to Lower Cretaceous, Pan-Laurasia); (10) ?*Xenostius* (Early Cretaceous, Mongolia); (11) *Primaderma* (Albian–Cenomanian, North America); (12) ?*Hoyalacerta* (Early Cretaceous, Spain). See Supplementary Figure 2.S1 for terminal taxon labels in full. (A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.)

localities has been Kirtlington Quarry (UK, [27, 28]). In addition to the lepidosauromorph *Marmoretta*, Kirtlington yielded five named squamate genera: *Balnealacerta*, *Bellairsia*, cf. *Saurillodon*, *Oxiella*, and *Parviraptor*. Squamate bones were also reported from roughly contemporaneous deposits on the Isle of Skye, Scotland [23], and new fieldwork on Skye has yielded both isolated elements and associated material, including specimens referable to the Kirtlington genera *Balnealacerta*, *Bellairsia*, and *Parviraptor* [29]. These specimens both validate the original associations [27, 28], *contra* Caldwell et al. [30], and add new morphological data for phylogenetic analysis. Work on this material is in progress, but it highlights the clear morphological gap between lepidosaurian stem taxa, like *Marmoretta*, and squamates from the Middle Jurassic onward that show derived features including biradiate squamosals, loss of quadrate-ptyergoid fixation, loss of quadratojugal, a synovial epiptyergoid-ptyergoid joint, and subdivision of the metotic fissure in the braincase.

Among other Middle Jurassic records, *Changetisaurus estesi* (Bathonian, Kyrgyzstan [31]) is a partial skeleton attributed to Squamata, but it requires re-study. Squamate remains are also recorded from the Bathonian Berezovsk Mine, western Siberia (a possible paramacellodid, two ‘scincomorphs’: [32]) and from similar aged deposits in Morocco (‘scincomorphs’, ‘*Parviraptor*-like’ taxon [33]). An osteoderm-covered lizard was briefly described from Callovian-Oxfordian age deposits at Shishougou (Junggar Valley, China [34]), but a detailed description and analysis has yet to be published. Roughly contemporaneous deposits at Daohugou, Chinese Inner Mongolia, have also yielded associated lizard skeletons, one of general proportions and the other with elongate limbs [35, 36], but both are immature and the preservation is poor. More recently, however, a complete lizard skeleton was recovered from Daohugou equivalent deposits at Guancaishan, Liaoning Province (*Hongshanxi xiei*, [37]).

Moving into the Upper Jurassic, squamate material is known from several additional Laurasian localities, notably: Portugal (Oxfordian, Guimarota [38]), Kazakhstan (Oxfordian–Kimmeridgian, Karabastau Formation [39]), North America (Kimmeridgian, Morrison Formation [40–42]), Germany (Tithonian, Solnhofen and neighbouring localities [26, 43–48]) and France (Kimmeridgian, Cerin [49]). Unfortunately, the only contemporaneous Gondwanan record is a ‘paramacellodid’ osteoderm from the Tendaguru Formation of Tanzania [50], but this identification is unconfirmed.

The squamate fossil record improves substantially in the Early to Middle Cretaceous (i.e., Berriasian–Cenomanian), with specimens from Europe, Africa, the Middle East, Asia, and the Americas. Concurrent with this apparent global expansion, Early Cretaceous (Barremian) specimens include some of the first known occurrences of squamate gliding [51], body elongation with limb reduction [52], viviparity [53], herbivory [54], and specialist climbing [55, 56].

2.3 The First Records of Crown-Group Squamates

Most recent molecular divergence estimates date the first radiation of crown-group squamate lineages to the Early–Middle Jurassic [12–14], with further splitting of major

lineages in the Late Jurassic. As yet, however, none of the known Middle Jurassic taxa, and relatively few of those from the Late Jurassic, can be placed unequivocally into crown lineages (Fig. 2.1). There is some improvement in the Early Cretaceous, but many lizards from this period are phylogenetically problematic and behave as wild cards in analyses.

2.3.1 Gekkota

Given that gekkotans are now considered to be one of the first of the major branches to diverge from the ancestral crown squamate, they should be well represented in early squamate assemblages. Their apparent absence could be due to preservational or ecological constraints, or a failure of identification due to a lack of distinctive gekkotan characters in their early history. Several Late Jurassic and Early Cretaceous genera (notably *Ardeosaurus*, *Bavarisaurus*, *Eichstaettisaurus*, *Palaeolacerta*, *Yabeinosaurus*) were originally attributed to Gekkota (e.g., [44]), but a majority of these have been re-assigned. One exception is *Eichstaettisaurus* (Upper Jurassic, Germany [43]; Lower Cretaceous, Spain, Italy [57, 58]) which is frequently placed on the gekkotan stem (e.g., [6, 12, 59]), albeit with limited evidence. The first unequivocal stem gekkotan is *Hoburogekko suchanovi* (Aptian–Albian, Höövor, Mongolia [60, 61]) although *Norellius nyctisaurops* (Aptian–Albian, Mongolia [62, 63]) has also been assigned to Gekkota (e.g., [12], but see [9]), based primarily on the combination of notochordal vertebrae and paired parietals. In recent years, Cretaceous amber has offered an important window into gekkotan history because it is able to preserve small, delicate skeletons, often with exquisite soft tissues (e.g., *Cretaceogekko burmae* [56]). The Albian–Cenomanian amber deposits of north-western Myanmar are particularly rich in gekkotans and stem gekkotans from a rarely sampled tropical forest ecosystem [64, 65].

2.3.2 Dibamidae

The phylogenetic position of this small, specialized, and biogeographically disparate clade (*Dibamus*, South East Asia, New Guinea, Philippines; *Anelytropsis*, Mexico) has long been problematic (e.g., [3, 66]). Molecular analyses have provided greater clarity but there remains uncertainty as to whether dibamids are sister to all other squamates including gekkotans [10, 11], to gekkotans alone [13], or to all squamates except gekkotans [12]. Unfortunately, the group has no Mesozoic record. The only putative fossil dibamid is *Hoekosaurus mongoliensis* from the Oligocene of Mongolia [67].

2.3.3 Scincoidea

Estes et al. [3] grouped scincoids and lacertoids within Scincomorpha. Consequently, many fossil lizard remains are classified simply as ‘scincomorphs’, making them difficult to attribute to any clade. Scincoidea is probably represented by the Jurassic–Cretaceous Paramacellodidae [68] with their body covering of rectangular osteoderms, and possibly by short-jawed Jurassic–Cretaceous taxa like *Saurillodon* (Fig. 2.1). *Saurillodon* (*S. proraformis*, *S. henkeli*) was first described from Guimarota (Oxfordian, Portugal) based on short robust dentaries with a few large conical teeth [38, 69], resembling the jaws of limb-reduced modern scincids and amphisbaenians. Similar jaws were reported from

Anoual (Lower Cretaceous, Morocco, *Tarratosaurus anoualensis* [70]) and from Kirtlington (Middle Jurassic, UK [28]). The Kirtlington specimens were referred to *Saurillodon*, and tentatively associated with unusual elongated vertebrae. If the association is correct, then this Middle Jurassic taxon would be of considerable interest as an early long-bodied, and presumably limb-reduced, squamate. *Balnealacerta*, also from Kirtlington [28] was attributed to Paramacellodidae based on similarities in jaw and tooth structure, as were dentaries from contemporaneous localities on Skye [23]. However, no osteoderms were recovered from among the many kilos of residue from Kirtlington sorted by the author, nor are they known from Skye (e.g., in association with the new material of *Balnealacerta* [29]), and therefore attribution of these Middle Jurassic remains to Paramacellodidae remains tentative. Nonetheless, paramacellodids (including osteoderms) are recorded from Upper Jurassic deposits including those from Guimarota (Oxfordian [38, 71]), Kazakhstan (Kimmeridgian, *Sharovisaurus* [39]), and the Morrison Formation, USA (Kimmeridgian [40, 41]), as well as from the Lower Cretaceous of the United Kingdom [72], China [73], Russia [74], Spain [75], Morocco [75], and North America [76]. Most recently, a partial lizard skeleton, *Neokotus sanfranciscanus* (Valanginian, Brazil), was described as a possible Gondwanan paramacellodid [77], but no osteoderms are associated with the skeleton and the attribution is based mainly on dental morphology.

Other than paramacellodids, the well-preserved *Tepexisaurus tepexii* (Albian, Mexico [78]) may also be a scincoid [6], but other attributions have less support. Talanda [48] argued that *Ardeosaurus* (Upper Jurassic, Germany) was a scincid, but this was based on an interpretation of cranial ornamentation as representing compound osteoderms. By contrast, Simões et al. [47] recovered *Ardeosaurus* as a gekkotan, whereas other researchers (e.g., [12]) found *Ardeosaurus* to be a wild-card taxon in analyses. Finally, *Calanguban alamoii* is known from a poorly preserved skeleton from Brazil (Aptian–Albian, Crato Formation [79]). It was recovered within Cordyliformes in an analysis using the Conrad [59] matrix, but unresolved using Gauthier et al.'s [6] matrix. Neither analysis attempted to use a molecular constraint.

2.3.4 Lacertoidea

Lacertoidea encompasses lacertids, amphisbaenians, teiids and gymnophthalmids, and may be represented by *Purbicella ragei* from the Lower Cretaceous of England (Berriasian, Purbeck Limestone Group [80]). *Meyasaurus* spp. (Barremian, Spain) was proposed to lie on the teioid stem by Evans and Barbadillo [81], but within anguimorphs by Richter [82] and Conrad [59]. *Tijubina ponteii* (Aptian–Albian, Crato Formation, Brazil) was originally attributed to Teiidae [83], but subsequent researchers either failed to place it securely within the squamate crown [84, 85] or suggested that it and a second Brazilian species (*Olindalacerta brasiliensis* [86]) might be polyglyphanodonts [79]. Until recently, Polyglyphanodontia were classified as teioids (e.g., [68, 87, 88]), a position also recovered by Pyron [12] using a combined morphological [59] and molecular matrix. However, Gauthier et al. [6] recovered polyglyphanodonts on the stem of 'Scleroglossa', whereas Pyron [12], combining the Gauthier et al. [6] matrix with a molecular dataset, found polyglyphanodonts to be the sister group of Iguania. The position of this large and important fossil group therefore remains problematic, but it is attributed to Teiioidea in

Figure 2.1. The earliest attributed polyglyphanodonts are *Kuwajimalla kagaensis* [54] and *Asagaolacerta tricuspidens* [89] from the Tetori Formation (Barremian–Aptian, Japan). An unnamed lizard specimen preserved in amber (Albian–Cenomanian, Myanmar) was also described as a crown lacertoid [64], but this attribution was based primarily on comparison with polyglyphanodonts.

Molecular divergence estimates (e.g., [12]) date the separation of stem amphisbaenians and lacertids to the Late Jurassic–Early Cretaceous, but the earliest unequivocal record of amphisbaenians is from the Palaeocene [90]. *Hodzhakulia magna* (Albian, Uzbekistan [91]; Mongolia [92]) and *Sineoamphisbaena hexatabularis* (Santonian–Campanian, China [93]) were originally classified as stem amphisbaenians, but *Hodzhakulia* is fragmentary ('scincomorph' [92]) and *Sineoamphisbaena* may be related to polyglyphanodonts [12]. The limb-reduced *Slavoia darevskii* has also been proposed as a candidate stem amphisbaenian [94]. The type material is from the Campanian of Mongolia, but older 'slavoiids' were reported from the Albian Mongolian locality of Höövor [95].

2.3.5 Anguimorpha

Parviraptorids (Middle Jurassic–Early Cretaceous, UK [27]) were originally attributed to Anguimorpha, based on jaw and tooth morphology. This attribution will be tested by new, in progress, analyses based on associated material from Skye (Middle Jurassic). The Middle Jurassic *Changetisaurus* (Bathonian, Kyrgyzstan) was also attributed to Anguimorpha [31], but this taxon needs re-examination. Currently, the earliest generally accepted anguimorph is *Dorsetisaurus purbeckensis*. As its name suggests, this taxon was first described from the Lower Cretaceous (Berriasian) Purbeck Limestone Group of England [72], but dorsetisaurus have subsequently been reported from the Upper Jurassic of Portugal (Guimarota, Oxfordian [38, 71] and the USA (Morrison Formation, Kimmeridgian [40]), as well as the Early Cretaceous of Mongolia (Aptian–Albian, *Paradoretisaurus postumus* [96] (Fig. 2.1). Additionally, a small lizard skeleton (*Indrasaurus wangi* [97] found as gut contents within an Early Cretaceous Chinese *Microraptor* has a dorsetisaurus-like dentition and may be related to dorsetisaurus.

Further anguimorph taxa are recorded from the Lower Cretaceous of Mongolia (Aptian–Albian, *Xenostius futilis*, crown xenosaur [95]); Uzbekistan (Albian, xenosaur [98]); Thailand (Barremian, eggs with embryos [99]); China (Barremian, *Dalinghosaurus longidigitus*, stem shinisaur [100]); North America (Albian–Cenomanian, *Primaderma*, stem monstersaur [101, 102]); England (Wealden, indet. [103]); and Spain (Barremian–Aptian, *Arcanosaurus ibericus*, 'varanoid' [104]), although many of these records are based on isolated elements. The tiny attenuate *Barlochersaurus winhtini* from the mid-Cretaceous amber of Myanmar was also tentatively attributed to Anguimorpha [105], but a more mature specimen is needed to verify this because the skull is poorly preserved.

The relationships of mosasaurians, also frequently grouped within Anguimorpha, are discussed separately (§ 2.3.7).

2.3.6 Iguania

This major squamate clade, comprising both pleurodont and acrodont jawed taxa, is first recorded with certainty from the Late Cretaceous (e.g., Mongolia, North America [68]). Some

analyses (e.g., [59]) recovered *Hoyalacerta sanzi*, a short-limbed lizard from the Lower Cretaceous of Spain (Barremian, Las Hoyas [106]) on the iguanian stem but further specimens are needed to test this attribution. Conrad [59] also recovered the enigmatic *Huehuecuetzpalli mixtecus* (Albian, Mexico [107]) as a stem iguanian, although other researchers (e.g., [6, 107]) inferred that it lies on the squamate stem. *Huehuecuetzpalli* combines primitive characters (e.g., notochordal vertebrae, trunk intercentra, retained second distal tarsal) with derived ones (e.g., retracted nares, anterior parietal foramen). A stem-iguanian position was also recovered by Pyron [12], evaluating both the Conrad [59] and the Gauthier et al. [6] matrices using time calibration and combined evidence. Such major inconsistencies in tree position are, unfortunately, rather common for Jurassic–Early Cretaceous taxa.

Xianglong zhaoui, a gliding lizard from the Lower Cretaceous (Barremian) of China was described as an acrodontan [51], but this was based on the misinterpretation of the jagged broken edge of the crushed juvenile skull as an acrodont jaw (pers. obs.). Its affinities remain unknown. The Albian–Cenomanian amber of Myanmar has also yielded possible acrodontans [64], but this attribution is based on postcranial material and needs to be confirmed from well-preserved skulls. A stem chameleon described from the same deposits [64] is actually an albanerpetontid amphibian [108]. *Jeddaherdan aleadonta*, a partial dentary from the Cenomanian of Kem Kem, in Morocco, is possibly an early acrodontan [109], but *Gueragama sudamerica* (Turonian–Campanian, Brazil [79]) is a partial dentary with teeth like those of scincoids or teiids, and is unlikely to be an acrodontan as proposed.

2.3.7 Mosasauria

This group encompasses the Mosasauroidea (Late Cretaceous mosasaurs and aigialosaurs), and several smaller, long-necked, long-bodied taxa ('dolichosaurs') from the Early–Late Cretaceous. Mosasaurians are included briefly in this review chapter for completeness (see the relevant chapters in this volume for a more detailed discussion).

Generally considered close relatives of varanids and/or lanthanotids within Anguimorpha (e.g., [110, 111; Chapter 9]), several subsequent cladistic analyses distanced mosasaurians from varanids, albeit to varying degrees (e.g., [6, 112–114]). The proposal that mosasaurians were closely related to snakes (e.g., [113, 115, 116] and subsequent papers by the same authors and their collaborators) led Lee and Caldwell [117] to resurrect Cope's [118] name Pythonomorpha for their mosasaurian + snake clade, and generated the associated, and more controversial, suggestion of a marine origin for snakes [117, 119] (see also Chapter 7).

There is general agreement as to the monophyly of Mosasauroidea, but not of Aigialosauridae ([113] versus [115, 120, 121; Chapter 8]). Both groups have their earliest representatives in the Cenomanian [122]. 'Dolichosaurs' are more problematic, mainly because their skulls are poorly known. Recent papers, often with overlapping groups of authors, disagree as to whether 'dolichosaurs' are monophyletic (e.g., [123; Chapter 9]) or paraphyletic (e.g., [122, 124]), how they are defined and diagnosed (contrast [125] with [123, 124]), and whether they are closer to snakes (forming the Ophidiomorpha of [122, 125]) or to mosasauroids [123]. Most 'dolichosaur' genera were recovered from shallow marine

deposits associated with either the remnant Tethys seaway (Slovenia, Croatia, Kazakhstan, Lebanon, Palestine, United Kingdom, Germany, France, Spain) or the Western Interior Seaway (North America) [122]. However, the earliest accepted ‘dolichosaurs’ are from freshwater deposits: in Spain (Barremian, vertebrae originally identified as snake [126]), Japan (Barremian–Albian *Kaganaias* [52]); and Australia (Albian [127]). The enigmatic snake-like *Tetrapodophis amplexus* (Albian, Brazil [128]), also from a freshwater deposit, was recovered by Paparella et al. [123] on the stem of a Mosasauroidae + Dolichosauridae clade that is proposed to be the sister group of snakes (see also Chapter 8).

2.3.8 Pan-Serpentes

The morphological specializations of the snake skeleton and the lack of early fossil representatives have hampered attempts to resolve the relationships of snakes to extant lizards. McDowell and Bogert [110] argued that snakes were related to anguimorphs, particularly varanids and/or lanthanotids, and several cladistic analyses (e.g., [115, 116, 123, 124, 129]) supported this (snake–mosasaurian relationships notwithstanding). However, convergence between snakes and other limbless squamates (e.g., amphisbaenians, dibamids, limbless scincids, and anguids) tends to confound analyses based solely on phenotypic data (e.g., [6, 59, 116, 130]), leading to artificial groupings. Molecular and combined evidence analyses avoid this problem, and unite Serpentes, Anguimorpha, and Iguania within Toxicofera (e.g., [1]). Most analyses find Serpentes + [Iguania + Anguimorpha] (e.g., [1, 8, 10, 11, 13, 131]) but the sister-group relationship between Iguania and Anguimorpha is not strongly supported. Furthermore, this does not resolve the position of mosasaurians with respect to snakes, because their common placement within an extended Anguimorpha (e.g., [115, 116, 123, 124, 132]) is incompatible with the molecular results. Pyron [12] ran combined evidence analyses using either the matrix of Conrad [59] or that of Gauthier et al. [6] for the morphological component. Predictably, he obtained very different results. His optimal tree for the Conrad matrix placed mosasaurians as sister to varanids (i.e., within Anguimorpha) and only distantly related to snakes, whereas the equivalent tree for the Gauthier et al. [6] matrix placed mosasaurians as the sister group of snakes, as did Reeder et al. [9] (see Augusta et al. and Zaher et al., this volume, for further discussion of snake and mosasaurian relationships).

The first unequivocal snake fossils are isolated vertebrae from the Lower Cretaceous of Algeria (Albian–Cenomanian [133, 134]), reportedly from both terrestrial (*Lapparentophis* sp.) and aquatic taxa [135], and isolated vertebrae referred to ‘*Coniophis*’ sp. from North America (terrestrial, Aptian–Cenomanian [136]). A much more extensive suite of snake fossils is recorded from the Cenomanian. This Cenomanian record is dominated (and biased) by aquatic taxa from the widespread shallow marine deposits of this period, notably the simoliophiids (or pachyophiids; see Zaher et al., this volume): *Simoliophis* spp. (France, Portugal, Egypt, Morocco, western Europe and North Africa [135, 137]), *Pachyophis woodwardi* (Bosnia-Herzegovina [138]), *Pachyrhachis problematicus* (Palestine [139–142]); *Eupodophis descouensi* (Lebanon [143]), and *Haasiophis terrasanctus* (Palestine [144]), as well as the enigmatic aquatic *Lunaophis aquaticus* (Venezuela [145]). The current Cenomanian record of terrestrial snakes is more limited, but this is likely to be a gross

underestimate considering the global distribution of these taxa: *Pouitella pervetus* (France [146]), *Xiaophis myanmarensis* (Myanmar [147]), *Najash rionegrina* (Argentina [148, 149]), *Seismophis septentrionalis* (Brazil [150]), and *Norisophis begaa* (Morocco [151]).

Snakes had clearly diversified, both ecologically and geographically, by the mid-Cretaceous. This is consistent with molecular divergence estimates that place the separation of stem snakes from other toxicoferans during the Jurassic (e.g., [10, 12]). Nonetheless, there remains a significant gap in the fossil record. Filling this gap, Caldwell et al. [30] re-interpreted specimens referred to the Middle Jurassic–Early Cretaceous lizard *Parviraptor* [27] as stem snakes. Based only on jaw fragments, Caldwell et al. [30] named *Eophis underwoodi* (Middle Jurassic, UK, dentary symphysis), *Diablophis gilmorei* (Upper Jurassic, Morrison Formation, USA, maxilla), and *Portugalophis lignites* (Upper Jurassic, Portugal, maxilla). However, this revision excluded most of the non-dental elements originally attributed to *Parviraptor* [27], based on the claim that *Parviraptor* as originally described was a chimaera of several different lizard taxa. New associated parviraptorid material from the Middle Jurassic of Skye confirms the original attribution of elements, both the preserved association on the Lower Cretaceous holotype block and the inferred association from Kirtlington (Middle Jurassic). These elements include paired frontals and parietals, the latter enclosing a parietal foramen, short palatines, and vertebrae that are notochordal and amphicoelous in immature individuals, becoming procoelous with maturity [27]. Work on the new Skye material and other parviraptorids is ongoing but *Parviraptor* as originally diagnosed is not a chimaera, and phylogenetic analyses must therefore include all of the attributed skeletal elements, rather than selecting only those (maxillae, dentaries) consistent with a particular hypothesis. Preliminary analyses (work in progress) do not support the inclusion of parviraptorids within Pan-Serpentes, and the Middle Jurassic age of the first recorded parviraptorid should therefore not be used to date snake origins in molecular divergence estimates (e.g. [152]).

2.4 Discussion and Conclusion

Although the squamate stem probably extended back into the Early Triassic, morphologically diagnosable squamates are currently unknown prior to the Middle Jurassic of Eurasia and North Africa. Molecular divergence estimates predict that major squamate clades had arisen by this time but, as yet, none of the currently known Middle Jurassic squamates can be placed confidently into the crown. A few Late Jurassic taxa, notably the dorsetisaurs (Anguimorpha), the paramacellodids (Scincoidea), and perhaps *Eichstaettisaurus* (Gekkota), may lie on the stems of crown clades, but the first unequivocal snake fossils currently date from the mid Cretaceous. The near global distribution of both terrestrial (France, USA, Gondwana) and aquatic (mostly Tethyan) snakes by the Cenomanian provides strong evidence of an earlier origin, but recent reports of Jurassic snake fossils [30] are based on misconception (see above). Given the close relationship between iguanians, anguimorphs and snakes, as strongly supported by molecular data, stem iguanians and stem anguimorphs have the potential to shed light on the expected morphology of the

earliest stem snakes – given that stem toxicoferans presumably resembled one another morphologically until they diverged. Taxa like the dorsetisaur, *Huehucuetzpalli*, *Hoyalacerta*, and perhaps *Parviraptor* may therefore provide insights into early toxicoferan morphology, and may help to refine ideas on ancestral traits (e.g., [153]). Moreover, if mosasaurians (in total or in part) are genuinely the sister group of snakes (but see Augusta et al. and Zaher et al., this volume), then stem members of that clade also need to be identified, probably from terrestrial and/or freshwater deposits.

Further progress in unravelling the early history of squamates generally, and snakes in particular, will therefore require a combination of new fossil material; accurate (and objective) re-description of existing material using CT scan technology where possible; and a concerted effort to recover early squamate material from biogeographically and ecologically diverse deposits. Unfortunately, most Jurassic and Early Cretaceous squamate taxa are phylogenetically unstable when analysed in matrices combining living and extinct taxa. The topographic position of Mesozoic squamates is sensitive to analysis variables like data input (character choice and definition, ingroup and outgroup taxa sampled, incorporation of temporal data), and the use of ordering, weighting, or molecular constraints. Moreover, apomorphic skeletal features that characterize individuals of modern clades may be absent in early or stem representatives of those clades, further complicating their phylogenetic placement, especially when incomplete. Improving tree resolution is not simply a question of adding more phenotypic characters. We need to develop a greater understanding of those characters, and of the developmental and functional relationships between them.

Acknowledgements

My thanks to David Gower and Hussam Zaher for the invitation to participate in the symposium and this volume, and to the many colleagues around the world who have worked with me on fossil lepidosaurs. My particular thanks to Professor Roger Benson, University of Oxford, who is coordinating the research on the new material from the Middle Jurassic of Skye, and to Nick Fraser and an anonymous reviewer whose comments improved the manuscript. Bruno Navarro (University of São Paulo, Brazil) drafted Fig. 2.1.

References

1. N. Vidal and S. B. Hedges, The phylogeny of squamate reptiles (lizards, snakes, and amphisbaenians) inferred from nine nuclear protein-coding genes. *Comptes Rendus Biologies*, 328 (2005), 1000–1008.
2. C. L. Camp, Classification of the lizards. *Bulletin of the American Museum of Natural History*, 48 (1923), 289–481.
3. R. Estes, K. De Queiroz, and J. Gauthier, Phylogenetic relationships within Squamata. In R. Estes, and G. Pregill, eds., *Essays Commemorating Charles L. Camp. Phylogenetic Relationships of the Lizard Families* (Stanford, CA: Stanford University Press, 1988), pp. 119–281.
4. T. M. Townsend, A. Larson, E. Louis, and J. R. Macey, Molecular phylogenetics of

- Squamata: the position of snakes, amphisbaenians, and dibamids, and the root of the squamate tree. *Systematic Biology*, 53 (2004), 735–757.
5. N. Vidal and S. B. Hedges, Molecular evidence for a terrestrial origin of snakes. *Proceedings of the Royal Society of London, series B: Biological Sciences*, 271 (2004), suppl: S226–S229.
 6. J. A. Gauthier, M. Kearney, J. A. Maisano, O. Rieppel, and A. D. B. Behlke, Assembling the squamate tree of life: perspectives from the phenotype and the fossil record. *Bulletin of the Peabody Museum of Natural History*, 53 (2012), 3–308.
 7. J. J. Wiens, C. R. Hutter, D. G. Mulcahy, et al., Resolving the phylogeny of lizards and snakes (Squamata) with extensive sampling of genes and species. *Biology Letters*, 8 (2012), 1043–1046.
 8. R. A. Pyron, F. T. Burbrink, and J. J. Wiens, A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evolutionary Biology*, 13 (2013), 93.
 9. T. W. Reeder, T. M. Townsend, D. G. Mulcahy, et al., Integrated analyses resolve conflicts over squamate reptile phylogeny and reveal unexpected placements for fossil taxa. *PLoS ONE*, 10 (2015), e0118199.
 10. Y. Zheng and J. J. Wiens, Combining phylogenomic and supermatrix approaches, and a time-calibrated phylogeny for squamate reptiles (lizards and snakes) based on 52 genes and 4162 species. *Molecular Phylogenetics and Evolution*, 94 (2016), 537–547.
 11. J. W. Streicher and J. J. Wiens, Phylogenomic analyses of more than 4000 nuclear loci resolve the origin of snakes among lizard families. *Biology Letters*, 13 (2017), 20170393.
 12. R. A. Pyron, Novel approaches for phylogenetic inference from morphological data and total-evidence dating in squamate reptiles (lizards, snakes, and amphisbaenians). *Systematic Biology*, 66 (2017), 38–56.
 13. F. T. Burbrink, F. G. Grazziotin, R. A. Pyron, et al., Interrogating genomic-scale data for Squamata (lizards, snakes, and amphisbaenians) shows no support for key traditional morphological relationships. *Systematic Biology*, 69 (2020), 502–520.
 14. M. E. H. Jones, C. L. Anderson, C. A. Hipsley, et al., Integration of molecules and new fossils supports a Triassic origin for Lepidosauria (lizards, snakes, and tuatara). *BMC Evolutionary Biology*, 13 (2013), 208.
 15. S. E. Evans, At the feet of the dinosaurs: the origin, evolution and early diversification of squamate reptiles (Lepidosauria: Diapsida). *Biological Reviews*, 78 (2003), 513–551.
 16. S. E. Evans and M. E. H. Jones, The origins, early history and diversification of lepidosauromorph reptiles. In S. Bandyopadhyay, ed., *New Aspects of Mesozoic Biodiversity, Lecture Notes in Earth Sciences 132* (Berlin, Germany: Springer-Verlag, 2010), pp. 27–44.
 17. P. M. Datta and S. Ray, Earliest lizard from the Late Triassic (Carnian) of India. *Journal of Vertebrate Paleontology*, 26 (2006), 795–800.
 18. M. N. Hutchinson, A. Skinner, and M. S. Y. Lee, *Tikiguana* and the antiquity of squamate reptiles (lizards and snakes). *Biology Letters*, 8 (2012), 665–669.
 19. T. R. Simões, M. W. Caldwell, M. Talanda, et al., The origin of squamates revealed by a Middle Triassic ‘lizard’ from the Italian Alps. *Nature*, 557 (2018), 706–709.
 20. S. E. Evans and M. Borsuk-Białynicka, A small lepidosauromorph reptile from the Early Triassic of Poland. *Palaontologica Polonica*, 65 (2009), 179–202.
 21. S. Renesto and R. Posenato, A new lepidosauromorph reptile from the Middle Triassic of the Dolomites (Northern Italy). *Rivista Italiana di Paleontologia e Stratigrafia*, 109 (2003), 463–474.
 22. S. E. Evans, A new lizard-like reptile (Diapsida: Lepidosauromorpha) from the Middle Jurassic of Oxfordshire. *Zoological*

- Journal of the Linnean Society*, 103 (1991), 391–412.
23. E. F. Griffiths, D. P. Ford, R. B. J. Benson, and S. E. Evans, New information on the Jurassic lepidosauromorph *Marmoretta oxoniensis*. *Papers in Palaeontology*, 7:4 (2021), 2255–2278
 24. P. Yadagiri, Lower Jurassic lower vertebrates from Kota Formation, Pranhita-Godavari valley, India. *Journal of the Palaeontological Society of India*, 31 (1986), 89–96.
 25. S. E. Evans, G. V. R. Prasad, and B. Manhas, Fossil lizards from the Jurassic Kota Formation of India. *Journal of Vertebrate Paleontology*, 22 (2002), 299–312.
 26. J. L. Conrad, A new lizard (Squamata) was the last meal of *Compsognathus* (Theropoda: Dinosauria) and is a holotype in a holotype. *Zoological Journal of the Linnean Society*, 183 (2018), 584–634.
 27. S. E. Evans, A new anguimorph lizard from the Jurassic and Lower Cretaceous of England. *Palaeontology*, 37 (1994), 33–49.
 28. S. E. Evans, Crown group lizards from the Middle Jurassic of Britain. *Palaeontographica, Abt.A* 250 (1998), 123–154.
 29. E. Pancirioli, R. B. J. Benson, S. Walsh, et al., Diverse vertebrate assemblage of the Kilmaluag Formation (Bathonian, Middle Jurassic) of Skye, Scotland. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 111 (2020), 135–56.
 30. M. W. Caldwell, R. L. Nydam, A. Palci, and S. Apesteguia, The oldest known snakes from the Middle Jurassic–Lower Cretaceous provide insights on snake evolution. *Nature Communications*, 6 (2015), 5996.
 31. P. V. Fedorov and L. A. Nessov, A lizard from the boundary of the Middle and Late Jurassic of north-east Fergana, *Bulletin of St. Petersburg University, Geology and Geography*, 3 (1992), 9–14 [In Russian].
 32. A. Averianov, T. Martin, P. P. Skutschas, et al., Middle Jurassic vertebrate assemblages of Berezovsk coal mine in western Siberia, (Russia). *Global Geology*, 19 (2016), 187–204.
 33. H. Haddoumi, R. Allain, S. Meslouh, et al., Guelb el Ahmar (Bathonian, Anoual Syncline, eastern Morocco): first continental flora and fauna including mammals from the Middle Jurassic of Africa. *Gondwana Research*, 29 (2016), 290–319.
 34. J. L. Conrad, Y. Wang, X. Xu, R. A. Pyron, and J. Clark, Skeleton of a heavily armoured and long-legged Middle Jurassic lizard (Squamata, Reptilia). *Journal of Vertebrate Paleontology Supplement, Annual Meeting Abstracts*, 73 (2013), 108.
 35. S. E. Evans and Y. Wang, A juvenile lizard from the Late Jurassic/Early Cretaceous of China. *Naturwissenschaften*, 94 (2007), 431–439.
 36. S. E. Evans and Y. Wang, A long-limbed lizard from the Upper Jurassic/Lower Cretaceous of Daohugou, Inner Mongolia, China. *Vertebrata Palasiatica*, 47 (2009), 21–34.
 37. L. P. Dong, Y. Wang, L. Mou, G. Zhang, and S. E. Evans, A new Jurassic lizard from China. *Geodiversitas*, 41 (2019), 623–641.
 38. J. Seiffert, Upper Jurassic lizards from Central Portugal. *Memoria, Serviços Geológicos de Portugal*, 22 (1973), 1–85.
 39. M. K. Hecht and B. M. Hecht, A new lizard from Jurassic deposits of Middle Asia. *Paleontological Journal*, 18 (1984), 133–136.
 40. D. R. Prothero and R. Estes, Late Jurassic lizards from Como Bluff Wyoming, and their palaeobiogeographic significance. *Nature*, 286 (1980), 484–486.
 41. S. E. Evans and D. C. Chure, Paramacellodid lizard skulls from the Jurassic Morrison Formation at Dinosaur National Monument, Utah. *Journal of Vertebrate Paleontology*, 18 (1998), 99–114.
 42. S. E. Evans and D. C. Chure, Morrison lizards: structure, relationships and biogeography. *Modern Geology*, 23 (1998), 35–48.

43. M. Cocude-Michel, Les rhynchocéphales et les Sauriens des Calcaires Lithographiques (Jurassique supérieur) d'Europe Occidentale. *Nouvelles Archives du Muséum d'Histoire naturelle de Lyon*, 7 (1963), 1–187.
44. R. Hoffstetter, Les Sauria du Jurassique supérieur et spécialement les Gekkota de Bavière et de Mandchourie. *Senckenbergiana Biologie*, 45 (1964), 281–322.
45. N. J. Mateer, Osteology of the Jurassic lizard *Ardeosaurus brevipes* (Meyer). *Palaeontology*, 25 (1982), 461–9.
46. S. E. Evans, The Solnhofen (Jurassic: Tithonian) lizard genus *Bavarisaurus*: new skull material and a reinterpretation. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 192 (1994), 37–52.
47. T. R. Simões, M. W. Caldwell, R. L. Nydam, and P. Jimenez-Huidabro, Osteology, phylogeny, and functional morphology of two Jurassic lizard species and the early evolution of scansoriality in geckoes. *Zoological Journal of the Linnean Society*, 180 (2017), 216–241.
48. M. Talanda, An exceptionally preserved Jurassic skink suggests lizard diversification preceded the fragmentation of Pangaea. *Palaeontology*, 61 (2018), 659–677.
49. S. E. Evans, A re-evaluation of the late Jurassic (Kimmeridgian) reptile *Euposaurus* (Reptilia: Lepidosauria) from Cerin, France. *Geobios*, 27 (1994), 621–631.
50. W. Zils, C. Werner, A. Moritz, and C. Saanane, Tendaguru, the most famous dinosaur locality of Africa. Review, survey and future prospects. *Documenta naturae, Munich*, 97 (1995), 1–41.
51. P. P. Li, K. Q. Gao, L. H. Hou, and X. Xu, A gliding lizard from the Early Cretaceous of China. *Proceedings of the National Academy of Sciences of the U.S.A.*, 104 (2007), 5507–5509.
52. S. E. Evans, M. Manabe, M. Noro, S. Isaji, and M. Yamaguchi, A long-bodied lizard from the Lower Cretaceous of Japan. *Palaeontology*, 49(6) (2006), 1143–1165.
53. Y. Wang and S. E. Evans, A gravid lizard from the Early Cretaceous of China: insights into the history of squamate viviparity. *Naturwissenschaften*, 98 (2011), 739–743.
54. S. E. Evans and M. Manabe, A herbivorous lizard from the Early Cretaceous of Japan. *Palaeontology*, 51 (2008), 487–498.
55. S. E. Evans and L. J. Barbadillo, An unusual lizard (Reptilia, Squamata) from the Early Cretaceous of Las Hoyas, Spain. *Zoological Journal of the Linnean Society*, 124 (1998), 235–266.
56. E. N. Arnold and G. Poinar, A 100 million year old gecko with sophisticated adhesive toepads preserved in amber from Myanmar. *Zootaxa*, 1847 (2008), 62–68.
57. S. E. Evans, A. Lacasa-Ruiz, and J. Erill Rey, A lizard from the Early Cretaceous (Berriasian-Hauterivian) of Montsec. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 215 (1999), 1–15.
58. S. E. Evans, P. Raia, and C. Barbera, New lizards and rhynchocephalians from the Early Cretaceous of southern Italy. *Acta Palaeontologica Polonica*, 49 (3) (2004), 393–408.
59. J. L. Conrad, Phylogeny and systematic of Squamata (Reptilia) based on morphology. *Bulletin of the American Museum of Natural History*, 310 (2008), 1–182.
60. V. R. Alifanov, The oldest gecko (Lacertilia: Gekkonidae) from the Lower Cretaceous of Mongolia. *Paleontological Journal*, 23 (1990), 128–131.
61. J. D. Daza, A. M. Bauer, and E. D. Snively, On the fossil record of Gekkota. *Anatomical Record*, 297 (2014), 433–462.
62. J. L. Conrad and M. A. Norell, High-resolution X-ray computed tomography of an early Cretaceous gekkonomorph (Squamata) from Öösh (Övörkhangai: Mongolia). *Historical Biology*, 18 (2006), 405–431.
63. J. L. Conrad and J. D. Daza, Naming and re-diagnosing the Cretaceous gekkonomorph (Reptilia, Squamata) from Öösh (Övörkhangai, Mongolia). *Journal of*

- Vertebrate Paleontology*, 35 (2015), e980891.
64. J. D. Daza, E. L. Stanley, P. Wagner, A. Bauer, and D. A. Grimaldi, Mid-Cretaceous amber fossils illuminate the past diversity of tropical lizards. *Science Advances*, 2 (2016), e1501080.
 65. G. Fontanarrosa, J. D. Daza, and V. Abdala, Cretaceous fossil gecko hand reveals a strikingly modern scansorial morphology: qualitative and biometric analysis of an amber-preserved lizard hand. *Cretaceous Research*, 84 (2018), 120–133.
 66. A. E. Greer, The relationships of the lizard genera *Anelytropsis* and *Dibamus*. *Journal of Herpetology*, 19 (1985), 116–156.
 67. A. Cernansky, The first potential fossil record of a dibamid reptile (Squamata; Dibamidae): a new taxon from the early Oligocene of Central Mongolia. *Zoological Journal of the Linnean Society*, 187 (2019), 782–799.
 68. R. Estes and Sauria, *Amphisbaenia. Handbuch der Paläoherpetologie/ Encyclopedia of Paleontology*, Part 10A (Stuttgart: Gustav Fischer, 1983).
 69. R. Kosma, The dentitions of recent and fossil scincomorph lizard (Lacertilia, Squamata). Systematics, functional morphology, palaeoecology. Unpublished PhD Thesis, University of Hannover (2004).
 70. A. Broschinski and D. Sigogneau-Russell, Remarkable lizard remains from the lower Cretaceous of Anoual (Morocco). *Annales de Paléontologie (Vert.-Invert.)*, 82 (1996), 147–175.
 71. A. Broschinski, The lizards from the Guimarota mine. In T. Martin and B. Krebs, eds., *Guimarota. A Jurassic Ecosystem* (Munich: Dr. Friedrich Pfeil, 2000), pp. 59–68.
 72. R. Hoffstetter, Coup d’oeil sur les Sauriens (Lacertiliens) des couches de Purbeck (Jurassique Supérieur d’Angleterre). *Problèmes Actuels de Paleontologie (Evolution des Vertébrates)*, *Colloques Internationaux du Centre National de la Recherche Scientifique*, 163 (1967), 349–371.
 73. J.-L. Li, A new lizard from the late Jurassic of Subei, Gansu. *Vertebrata Palasiatica*, 23 (1985), 13–18.
 74. A. O. Averianov and P. P. Skutchas, Paramacellodid lizard (Squamata, Scincomorpha) from the Early Cretaceous of Transbaikalia. *Russian Journal of Herpetology*, 6 (1999), 115–117.
 75. A. Richter, Lacertilia aus der Unteren Kreide von Uña und Galve (Spanien) und Anoual (Marokko). *Berliner geowissenschaftliche Abhandlungen*, 14 (1994), 1–147.
 76. R. L. Nydam and R. L. Cifelli, Lizards from the Lower Cretaceous (Aptian-Albian) Antlers and Cloverley Formations. *Journal of Vertebrate Paleontology*, 22 (2002), 286–298.
 77. J. S. Bittencourt, T. R. Simões, M. W. Caldwell, and M. C. Langer, Discovery of the oldest South American fossil lizard illustrates the cosmopolitanism of early South American squamates. *Communications Biology*, 3 (2020), 201.
 78. V. H. Reynoso and G. Callison, A new scincomorph lizard from the Early Cretaceous of Puebla, Mexico. *Zoological Journal of the Linnean Society*, 130 (2000), 183–212.
 79. T. R. Simões, E. Wilner, M. W. Caldwell, L. C. Weinschutz, and A. W. A. Kellner, A stem-acrodontan lizard in the Cretaceous of Brazil revises early lizard evolution in Gondwana. *Nature Communications*, 6 (2015), 9149.
 80. S. E. Evans, M. E. H. Jones, and R. Matsumoto, A new lizard skull from the Purbeck Limestone Group of England. *Bulletin of the Geological Society of France*, 183 (2012), 517–524.
 81. S. E. Evans and L. J. Barbadillo, Early Cretaceous lizards from las Hoyas, Spain. *Zoological Journal of the Linnean Society*, 119 (1997), 23–49.
 82. A. Richter, Der problematische Lacertilier *Ilerdaesaurus* (Reptilia: Squamata) aus der Unter-Kreide von Uña und Galve. *Berliner geowissenschaftliche Abhandlungen*, 13 (1994), 135–161.

83. F. C. Bonfim-Junior and R. B. Marques, Um novo lagarto do Cretáceo do Brasil (Lepidosauria, Squamata, Lacertilia – formação Santana, Aptiano da Bacia do Araripe). *Anuario do Instituto de Geociencias*, 20 (1997), 233–240.
84. F. C. Bonfim-Junior and L. D. S. Avila, Phylogenetic position of *Tijubina pontei* Bonfim and Marques 1997 (Lepidosauria, Squamata), a basal lizard from the Santana Formation, Lower Cretaceous of Brazil. *Journal of Vertebrate Paleontology*, 22 (Supplement to 3) (2002), 37A–38A.
85. T. R. Simões, Redescription of *Tijubina pontei*, and Early Cretaceous lizard (Reptilia; Squamata) from the Crato Formation of Brazil. *Anais da Academia Brasileira de Ciências*, 84 (2012), 1.
86. S. E. Evans and Y. Yabumoto, A lizard from the Early Cretaceous Crato Formation, Araripe Basin, Brazil. *Neues Jahrbuch für Paläontologie und Geologie, Monatshefte* 1998 (1998), 349–364.
87. V. R. Alifanov, New lizards of the Macrocephalosauridae (Sauria) from the Upper Cretaceous of Mongolia, critical remarks on the systematics of the Teiidae (sensu Estes, 1983). *Paleontological Journal*, 27 (1993), 70–90.
88. R. L. Nydam, J. G. Eaton, and J. Sankey, New taxa of transversely-toothed lizards (Squamata; Scincomorpha) and new information on the evolutionary history of ‘teiids’. *Journal of Paleontology*, 81 (2007), 538–549.
89. S. E. Evans and R. Matsumoto, An assemblage of lizards from the Early Cretaceous of Japan. *Palaeontologica Electronica*, 18.2.36A (2015), 1–36.
90. R. M. Sullivan, A new middle Paleocene (Torrejonian) rhineurid amphisbaenian, *Plesiorhineura tsentasi* new genus, new species, from the San Juan Basin, New Mexico. *Journal of Paleontology*, 59 (1985), 1481–1485.
91. L. A. Nessov, Rare bony fishes, terrestrial lizards and mammals from the lagoonal zone of the litoral lowlands of the Cretaceous of the Kyzylkumy. *Yearbook of the All-Union Palaeontological Society, Leningrad*, 28 (1985), 199–219.
92. V. R. Alifanov, Lizards of the family Hodzhakuliidae (Scincomorpha) from the Lower Cretaceous of Mongolia. *Paleontological Journal*, 50 (2016), 504–513.
93. X.-C. Wu, D. B. Brinkman, and A. P. Russell, *Sineoamphisbaena hexatabularis*: an amphisbaenian (Diapsida: Squamata) from the Upper Cretaceous redbeds at Bayan Mandahu (Inner Mongolia, People’s Republic of China), and comments on the phylogenetic relationships of the Amphisbaenia. *Canadian Journal of Earth Sciences*, 33 (1996), 541–577.
94. M. Talanda, Cretaceous roots of the amphisbaenian lizards. *Zoologica Scripta*, 45 (2015), 1–8.
95. V. R. Alifanov, Lizards of the families Eoxantidae, Ardeosauridae, Globauridae, and Paramacellodidae (Scincomorpha) from the Aptian-Albian of Mongolia. *Paleontological Journal*, 53 (2019), 74–88.
96. V. R. Alifanov, Lizards of the families Dorsetisauridae and Xenosauridae (Anguimorpha) from the Aptian–Albian of Mongolia. *Paleontological Journal*, 53 (2019), 183–193.
97. J. M. O’Connor, X. Zheng, L. Dong, et al., *Microaptor* with ingested lizard suggests non-specialized digestive function. *Current Biology*, 29 (2019), 2423–2429.
98. K. Q. Gao and L. A. Nessov, Early Cretaceous squamates from the Kyzylkum Desert, Uzbekistan. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 207 (1998), 289–309.
99. V. Fernandez, E. Buffetaut, V. Suteethorn, et al., Evidence of egg diversity in squamate evolution from Cretaceous anguimorph embryos. *PLoS ONE*, 10 (2015), e0128610.
100. S. E. Evans and Y. Wang, The Early Cretaceous lizard *Dalinghosaurus* from China. *Acta Palaeontologica Polonica*, 50 (2005), 725–742.

101. R. L. Cifelli and R. L. Nydam, Primitive, helodermatid-like platynotan from the Early Cretaceous of Utah. *Herpetologica*, 51 (1995), 286–291.
102. R. L. Nydam, A new taxon of helodermatid-like lizard from the Albian-Cenomanian of Utah. *Journal of Vertebrate Paleontology*, 20 (2000), 285–294.
103. S. C. Sweetman and S. E. Evans, Lepidosaurs (lizards). In D. J. Batten, ed., *Palaeontological Association Field Guide to Fossils*, 14. *English Wealden Fossils* (London: The Palaeontological Association, 2011), pp. 264–284.
104. A. Houssaye, J.-C. Rage, F. T. Fernandez-Baldor, et al., A new varanoid squamate from the Early Cretaceous (Barremian-Aptian) of Burgos, Spain. *Cretaceous Research*, 41 (2013), 127–135.
105. J. D. Daza, A. M. Bauer, E. L. Stanley, et al., An enigmatic miniaturized and attenuate whole lizard from the mid-Cretaceous amber of Myanmar. *Breviora*, 563 (2018), 1–18.
106. S. E. Evans and L. J. Barbadillo, A short-limbed lizard from the Lower Cretaceous of Spain. *Special Papers in Palaeontology*, 60 (1999), 73–85.
107. V. H. Reynoso, *Huehucuetzpalli mixtecus* gen. et sp. nov.: a basal squamate (Reptilia) from the early Cretaceous of Tepexi de Rodríguez, Central Mexico. *Philosophical Transactions of the Royal Society of London, Biological Sciences*, 353 (1998), 477–500.
108. R. Matsumoto and S. E. Evans, The first record of albanerpetontid amphibians (Amphibia, Albanerpetontidae) from East Asia. *PLoS ONE*, 13 (2018), e0189767.
109. S. Apesteguía, J. D. Daza, T. R. Simões, and J.-C. Rage, The first iguanian lizard from the Mesozoic of Africa. *Royal Society Open Science*, 3 (2016), 160462.
110. S. B. McDowell and C. M. Bogert, The systematic position of *Lanthanotus* and the affinities of the anguimorph lizard. *Bulletin of the American Museum of Natural History*, 105 (1954), 1–142.
111. R. L. Carroll and M. De Braga, *Aigialosaurus*: mid-Cretaceous varanoid lizards. *Journal of Vertebrate Paleontology*, 12 (1992), 66–86.
112. M. W. Caldwell, R. L. Carroll, and H. Kaiser, The pectoral girdle and forelimb of *Carsosaurus marchesetti* (Aigialosauridae) with a preliminary phylogenetic analysis of mosasauroids and varanoids. *Journal of Vertebrate Paleontology*, 15 (1995), 516–531.
113. M. W. Caldwell, Squamate phylogeny and the relationships of snakes and mosasauroids. *Zoological Journal of the Linnean Society*, 125 (1999), 115–147.
114. T. R. Simões, O. Vernygora, I. Paparella, P. Jimenez-Huidobro, and M. W. Caldwell, Mosasauroid phylogeny under multiple phylogenetic methods provides new insights on the evolution of aquatic adaptations in the group. *PLoS ONE* 12 (2017), e0176773.
115. M. S. Y. Lee, The phylogeny of varanoid lizards and the affinities of snakes. *Philosophical Transactions of the Royal Society, Biological Sciences*, 352 (1997), 53–91.
116. M. S. Y. Lee, Convergent evolution and character correlation in burrowing reptiles: towards a resolution of squamate phylogeny. *Biological Journal of the Linnean Society*, 65 (1998), 369–453.
117. M. S. Y. Lee and M. W. Caldwell, *Adriosaurus* and the affinities of mosasaurs, dolichosaurs, and snakes. *Journal of Paleontology*, 74 (2000), 915–37.
118. E. D. Cope, On the reptilian orders, Pythonomorpha and Streptosauria. *Proceedings of the Boston Society of Natural History*, 12 (1869), 250–66.
119. M. S. Y. Lee, Molecular evidence and marine snake origins. *Biology Letters*, 1 (2005), 227–230.
120. M. W. Caldwell, On the aquatic squamate *Dolichosaurus longicollis* Owen, 1850 (Cenomanian, Upper Cretaceous), and the evolution of elongate necks in squamates. *Journal of Vertebrate Paleontology*, 20 (2000), 720–735.
121. A. R. Dutchak, A review of the taxonomy and systematics of aigialosaurs.

- Netherlands Journal of Geosciences*, 84 (2005), 221–229.
122. M. C. Mekarski, S. E. Pierce, and M. W. Caldwell, Spatiotemporal distributions of non-ophidian ophidiomorphs, with implications for their origin, radiation, and extinction. *Frontiers in Earth Science*, 7 (2019), article 24.
 123. M. Paparella, A. Palci, U. Nicosia, and M. W. Caldwell, A new fossil marine lizard with soft tissues from the Late Cretaceous of southern Italy. *Royal Society Open Science*, 5 (2018), e172411.
 124. S. E. Pierce and M. W. Caldwell, Redescription and phylogenetic position of the Adriatic (Upper Cretaceous; Cenomanian) dolichosaur *Pontosaurus lesinensis* (Kornhuber, 1873). *Journal of Vertebrate Paleontology*, 24 (2004), 373–386.
 125. A. Palci and M. W. Caldwell, Redescription of *Acteosaurus tommasinii* Von Meyer 1860, and a discussion of evolutionary trends within the clade Ophiodiomorpha. *Journal of Vertebrate Paleontology*, 30 (2010), 94–108.
 126. J.-C. Rage and A. Richter, A snake from the lower Cretaceous (Barremian) of Spain: the oldest known snake. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 1995 (1995), 561–565.
 127. J. D. Scanlon and S. A. Hocknull, A dolichosaurid lizard from the latest Albian (mid-Cretaceous) Winto Formation, Queensland, Australia. In M. J. Everhard, ed., *Proceedings of the Second Mosasaur Meeting, Fort Hays Studies Special Issue*, 3 (2008), 131–136.
 128. D. M. Martill, H. Tischlinger, and N. R. Longrich, A four-legged snake from the Early Cretaceous of Gondwana. *Science*, 349 (2015), 416–419.
 129. M. S. Y. Lee, Squamate phylogeny, taxon sampling, and data congruence. *Organisms, Diversity, and Evolution*, 5 (2005), 25–45.
 130. T. R. Simões, M. W. Caldwell, and A. W. A. Kellner, A new Early Cretaceous lizard species from Brazil, and the phylogenetic position of the oldest known South American squamates. *Journal of Systematic Palaeontology*, 13 (2015), 601–614.
 131. D. G. Mulcahy, B. P. Noonan, T. Moss, et al., Estimating divergence dates and evaluating dating methods using phylogenomic and mitochondrial data in squamate reptiles. *Molecular Phylogenetics and Evolution*, 65 (2012), 974–991.
 132. M. S. Y. Lee, Hidden support from unpromising data sets strongly unites snakes with anguimorph ‘lizards’. *Journal of Evolutionary Biology*, 22 (2009), 1308–1316.
 133. R. Hoffstetter, Un serpent terrestre dans le Crétacé inférieur du Sahara. *Bulletin de la Société Géologique de France*, 1 (1959), 897–902.
 134. G. Cuny, J. J. Jaeger, M. Mahboubi, and J.-C. Rage, Les plus anciens serpentes (Reptilia, Squamata) connus. Mise au point sur l’âge géologiques des Serpents de la partie moyenne du Crétacé. *Comptes rendus des séances de l’Académie des Sciences Paris, Series 2*, 311 (1990), 1267–1272.
 135. J.-C. Rage and F. Escuillié, The Cenomanian: stage of hind-limbed snakes. *Notebooks on Geology*, (1) (2003), (CG2003 A01 JCR-FE).
 136. J. D. Gardner and R. L. Cifelli, A primitive snake from the Cretaceous of Utah. *Special Papers in Palaeontology*, 60 (1999), 87–100.
 137. J.-C. Rage and D. B. Dutheil, Amphibians and squamates from the Cretaceous (Cenomanian) of Morocco. A preliminary study. *Palaeontographica Abteilung A*, 286 (2008), 1–22.
 138. M. S. Y. Lee, M. W. Caldwell, and J. D. Scanlon, A second primitive marine snake: *Pachyophis woodwoodi* from the Cretaceous of Bosnia-Herzegovina. *Journal of Zoology*, 248 (1999), 509–520.
 139. G. Haas, On a new snake-like reptile from the lower Cenomanian of Ein Jabrud, near Jerusalem. *Bulletin du Muséum National*

- d'Histoire Naturelle de Paris*, 1 (1979), 51–64.
140. M. W. Caldwell and M. S. Y. Lee, A snake with legs from the marine Cretaceous of the Middle East. *Nature*, 386 (1997), 705–709.
 141. H. Zaher, The phylogenetic position of *Pachyrachis* within snakes (Squamata, Lepidosauria). *Journal of Vertebrate Paleontology*, 18 (1998), 1–3.
 142. H. Zaher and O. Rieppel, The phylogenetic relationships of *Pachyrachis problematicus* and the evolution of limblessness in snakes (Lepidosauria, Squamata). *Comptes Rendus de l'Académie de Sciences, Series IIA – Earth and Planetary Science*, 329 (1999), 831–837.
 143. J.-C. Rage and F. Escuillié, Un nouveau serpent bipède du Cénomani (Crétacé). Implications phylétiques. *Comptes Rendus de l'Académie des Sciences, Series IIA – Earth and Planetary Science*, 330 (2000), 513–520.
 144. E. Tchernov, O. Rieppel, H. Zaher, M. J. Polcyn, and L. L. Jacobs, A fossil snake with limbs. *Science*, 287 (2000), 2010–2012.
 145. A. Albino, J. D., Carillo-Briceno, and J. M. Neenan, An enigmatic aquatic snake from the Cenomanian of northern South America. *PeerJ*, 4 (2016), DOI [10.7717/peerj.2027](https://doi.org/10.7717/peerj.2027)e2027.
 146. J.-C. Rage, Un serpent primitif (Reptilia, Squamata) dans le Cénomani (base du Crétacé supérieur). *Comptes rendus de l'Académie des Sciences, Paris*, 307 (1988), 1027–1032.
 147. L. Xing, M. W. Caldwell, R. Chen, et al., A mid-Cretaceous embryonic-to-neonate snake in amber from Myanmar. *Science Advances*, 4 (2018), eaat5042.
 148. S. Apesteguía and H. Zaher, A Cretaceous terrestrial limbed snake with robust hindlimbs and sacrum, *Nature*, 440 (2006), 1037–1040.
 149. F. F. Garberoglio, S. Apesteguía, T. R. Simões, et al., New skulls and skeletons of the Cretaceous legged snake *Najash*, and the evolution of the modern snake body plan. *Science Advances*, 5 (2019), eaax5833.
 150. A. S. Hsiou, A. M. Albino, M. A. Medeiros, and R. A. B. Santos, The oldest Brazilian snakes from the Cenomanian (early Late Cretaceous). *Acta Palaeontologica Polonica*, 59 (2013), 635–642.
 151. C. G. Klein, N. R. Longrich, N. Ibrahim, S. Zouhri, and D. M. Martill, A new basal snake from the mid-Cretaceous of Morocco. *Cretaceous Research*, 72 (2017), 134–141.
 152. S. M. Harrington and T. W. Reeder, Phylogenetic inference and divergence dating of snakes using molecules, morphology and fossils: new insights into convergent evolution of feeding morphology and limb reduction. *Biological Journal of the Linnean Society*, 121(2017), 379–394.
 153. F. O. Da Silva, A.-C. Fabre, Y. Savriama, et al., The ecological origins of snakes as revealed by skull evolution. *Nature Communications*, 9 (2018), 376.