

## MORRISON LIZARDS: STRUCTURE, RELATIONSHIPS AND BIOGEOGRAPHY

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Lizards form a rare component of the Morrison vertebrate assemblage and, until recently, were known only from Como Bluff (Quarry 9). They have now been found in the Brushy Basin Member (Kimmeridgian) at Fruita, Colorado, and at Dinosaur National Monument, Utah. In general, the lizard assemblage of the Morrison appears closely similar to that of Jurassic and early Cretaceous localities in Eurasia – most notably in the presence of the scincomorph *Paramacellodus* (including a semiarticulated skull from DNM) and the anguimorph *Dorsetisaurus*. A third genus, recently recognized from DNM, resembles new lizard material from the Middle Jurassic of Britain but is probably generically distinct.

*Keywords:* Lizard; Scincomorph; Anguimorph

### INTRODUCTION

Jurassic lizards are known from several localities across Laurasia. The oldest recorded assemblages are those of the Middle Jurassic (Bathonian) of Britain (Evans 1994a,c, in press; Waldman and Evans, 1994), while Late Jurassic lizards have been found in Germany, France, Portugal, Central Asia (Kazakhstan, Kirghizia) and North America. True lizards were first reported from the Morrison Formation as recently as 1980 when Prothero and Estes recorded the European genera *Paramacellodus* and *Dorsetisaurus* at Quarry 9 (although a possible lizard ilium was described by Hecht and Estes in 1960, and Gilmore [1928] mistakenly identified the

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small choristoderan *Cteniogenys* as a lizard). They have now been recovered from the Brushy Basin Member at Fruita, Colorado (George Callison, personal communication and SEE, pers. obs.), and at Dinosaur National Monument (DNM) (Chure, 1992). The latter material forms the basis of this report.

The specimens from DNM come from three principal localities – DNM 96, 317 and 375 – all in the upper part of the Brushy Basin Member (dated as Kimmeridgian by Turner and Peterson, 1992). Two of these localities, DNM 96 and 375, yield a rich microvertebrate assemblage including abundant frogs in association with sphenodontians, turtles, crocodiles, small theropods and mammals as well as rare lizards and salamanders.

### SYSTEMATIC PALEONTOLOGY

Infraorder Anguimorpha

Family Dorsetisauridae

*Dorsetisaurus* sp.

The genus *Dorsetisaurus*, as its name implies, was first described from Lower Cretaceous microvertebrate horizons within the Purbeck Limestone Formation (PLF) of Dorset, England (Hoffstetter, 1967), and subsequently (under the name *Introrsisaurus*, Seiffert, 1973; Estes, 1983) from Guimarota, Portugal (Oxfordian/Kimmeridgian). It was recorded from the Morrison Formation on the basis of two dentaries found at Quarry 9 (Prothero and Estes, 1980). More recently, dorsetisaur remains have come from Fruita (Callison, work in progress) and DNM (Chure, 1992).

The DNM record is a left dentary, DINO 15915 (Fig. 1) (DNM locality 96), showing the keeled lanceolate teeth typical of the genus. Twelve tooth positions are preserved out of a probable total of 15–16 (which is within the range of *D. purbeckensis*). The teeth are cruciform in cross-section due to the presence of lingual and labial keels (Fig. 1). The weak subdental ridge bears an anteriorly extended splenial facet which is notched, suggesting that the exit foramen for the mylohyoid nerve passed between the dentary and splenial (Hoffstetter's 1967 description of the dentary of the Purbeck form suggests a similar arrangement). A second facet – presumably for an anterior process of the coronoid, overlies the rear end of the subdental ridge.

Comparison with specimens from the PLF shows no significant differences (allowing for the variations in tooth shape – presumably ontogenetic – which occur in this genus), and skull material would be needed to determine specific affinity.

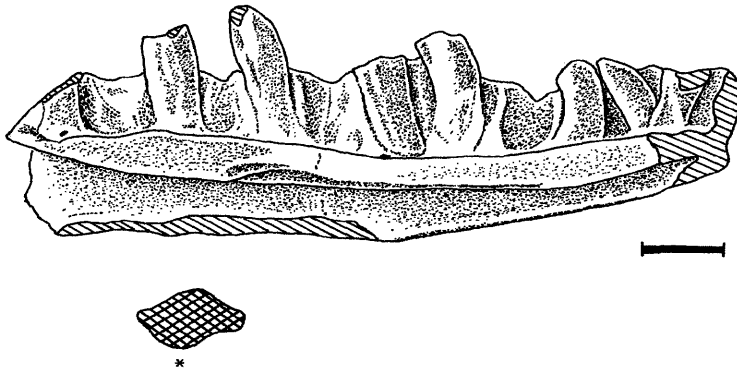


FIGURE 1 Left dentary of *Dorsetisaurus* sp. (DINO 15915) from the Brushy Basin Member at Dinosaur National Monument. Inset shows enlarged cross-section of one of the teeth, with \* marking the lingual margin. Scale bar = 1 mm.

Order Squamata  
 Infraorder Scincomorpha  
 Family Paramacellodidae  
*Paramacellodus* sp.

The family Paramacellodidae was created by Estes (1983) for a group of fossil lizards thought to be related to cordylids (e.g., Hoffstetter, 1967; Estes, 1983). They include *Paramacellodus*, *Becklesius*, *Pseudosaurillus* and, perhaps, *Saurillus* (holotype lost) from the PLF (Hoffstetter, 1967), *Becklesius*, again, from Guimarota (Estes, 1983), *Sharovisaurus* from the Kimmeridgian locality of Michailova (Karatau), Kazakhstan (Hecht and Hecht, 1984), *Mimobecklesisaurus* (Li, 1985) from the Late Jurassic of Gansu, China, unnamed material from Kirghizia (Nessov, 1988) and new material from the Middle Jurassic (Bathonian) of England (Evans, 1994a, in press) and Scotland (Waldman and Evans, 1994).

*Paramacellodus* was described from Quarry 9, Como Bluff, on the basis of a partial skeleton (AMNH 11523 – vertebrae, girdles, a left hind limb, a few skull bones, Prothero and Estes, 1980). There are also jaw fragments amongst Como material held at the National Museum, Washington (SEE, pers. obs.). More recently, paramacellodid remains have been recovered from DNM in the form of a semiarticulated skull (DINO 15914) and, less certainly, a partial postcranial skeleton (DINO 13861) (Chure, 1992).

DINO 15914. This specimen (DNM locality 317) is a small skull, estimated length about 15 mm, preserved in dorsal view (Fig. 2(A)) but subsequently prepared from below to reveal details of the jaws and the underside of the

parietal (Fig. 2(B)). The palate, unfortunately, is sandwiched between the skull roof and lower jaws; the braincase is complete, but it is compressed and provides little morphological information.

The skull will be fully described elsewhere but its main features can be summarized as follows: paired, sculptured frontals with weak orbital crests (deepening anteriorly), little orbital constriction, rugose dorsal sculpture and an irregular midline suture; interdigitated fronto-parietal suture; single parietal with very small, centrally-placed parietal foramen, dorsal sculpture and scale impressions, ventral pit for processus ascendens of braincase set forward from posterior margin of parietal, no midventral crest, lateral borders of parietal straight – grooved ventrally by taenia marginales of chondrocranium; no migration of adductor muscles onto the dorsal surface of parietal, triangular postparietal processes with small posterolateral

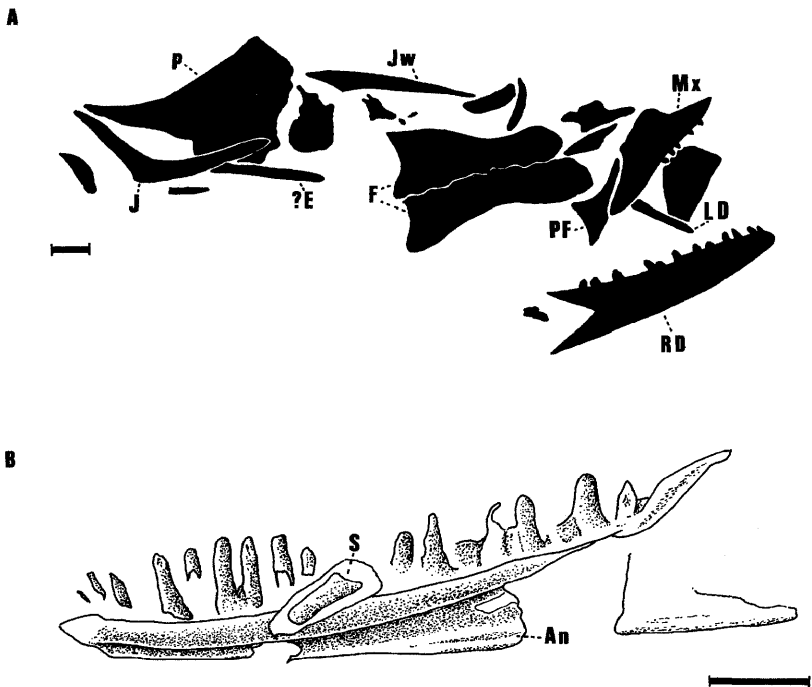


FIGURE 2 Paramacellodid skull (DINO 15914) from Dinosaur National Monument. (A) outline of bones as preserved in dorsal view; (B) enlargement showing medial surface of right dentary as exposed ventrally. Scale bars = 1 mm. Abbreviations: An, angular; E, epipterygoid; F, frontals; Jw, accessory jaw bones; LD, left dentary; Mx, maxilla; P, parietal; PF, prefrontal; RD, right dentary; S, skull fragment.

angulation and facets for supratemporals; upper temporal fenestra probably open but reduced; squamosal long and slender and typically scleroglossan, with curved posterior tip; jugal sickle-shaped with small posterior angle, strong orbital process probably excluded maxilla from orbital margin; shape and orientation of processes and facets of jugal and squamosal suggest they were not in contact; maxilla with at least 15 pleurodont teeth, broad facial process perforated by a single line of large sensory foramina, strong palatal flange, vertical narial margin; premaxillae unknown; braincase with short broad paroccipital processes, weak supraoccipital crest and no trace of strong ventral muscle tubera or crests, no expansion of occipital recess; bones of braincase apparently coossified.

The dentary is gracile with 22–23 pleurodont tooth positions supported by a weak subdental ridge; anterior teeth smallest. Meckelian groove open medially and ventrally, weak splenial and angular facets, inferior alveolar canal opening below roughly 19th tooth position; teeth slender, cylindrical, with tapered tips that tilt slightly towards the rear and are faintly striated lingually; dentary with lateral row of foramina and weak ventral muscle scar; dentary strongly forked posteriorly, upper ramus slightly broader but shorter than ventral one; post-dentary bones slender and elongate; angular strap-like, curves upward on lateral face of mandible; retroarticular process parallel-sided, no strong torsion and no angular process.

In comparison with paramacellodid material from European localities, the Morrison skull most closely resembles specimens of the genus *Paramacellodus*. The teeth of *Becklesius* are characterized by their expanded and robust tips, while those of *Pseudosaurillus* are distinguished by their relatively smaller size. In addition, the skull bones of *Pseudosaurillus* bear a distinctive pustulate sculpture which differs from that on the Morrison skull. DINO 15914 shares with *Paramacellodus* the shape and detailed morphology of the teeth; tooth number and jaw shape in general; the shape of the angular; and the shape of the facial process of the maxilla with its vertical narial border. Unfortunately, the skulls cannot be compared in any greater detail. The skull roof is, as yet, unknown in the Purbeck *Paramacellodus* and neither the palate nor premaxilla can be described in the Morrison specimen. The jaws of DINO 15914 are more gracile than those of the Purbeck holotype, and the skull would be about half the size (Prothero and Estes' 1980 figures suggest a similar size disparity for the Quarry 9 specimen), but this is within the range of variation for the European *Paramacellodus*. The Morrison *Paramacellodus* may be specifically distinct, but without comparable material for the rest of the skull, there is no basis for a diagnosis.

DINO 13861. This specimen (locality DNM 96) comprises the hind limbs, part of one manus, and a series of ribs and vertebrae (Fig. 3) from a small lizard (estimated SV length 90 mm). The limb bones are associated but the bones of the crus have been driven down through the feet and are partially obscured. The distal femoral epiphyses remain unfused and the astragalus and calcaneum are separate, both conditions suggesting immaturity. At least five posterior dorsal vertebrae and their ribs are preserved. The vertebrae are fully procoelous with no remnant of the notochordal pit. The neural spines are low, the zygapophyses broad and there is little development of a zygosphene/zygantral system. The rib facets are small and oval, as expected of posterior dorsals, and the centra bear slight ventral keels.

The hindlimbs are well-developed, with a strong, slender femur and gracile crus. The propodial/epipodial proportions ( $Ti/Fe = 0.77$ ) are similar to those of the modern scincid *Mabuaya*, but the foot is relatively longer ( $Foot/Fe = 1.5$ ). The displacement of the crural bones has disrupted the tarsals which are scattered but there were at least two distal tarsals – probably more. The primary metatarsals are elongate but the fifth, as expected, is short and hooked. The foot is strongly asymmetrical with digits 1 and 2 markedly shorter than digits 3 and 4, and a phalangeal formula of 2:3:4:5:3. The claws are strong and recurved. Two small digits of the manus are preserved at the top of the block.

A series of geometrical bone fragments lying to the side of the limbs and vertebrae may be ventral osteoscutes. This would support the attribution of DINO 13861 to *Paramacellodus* (or to a close relative). By comparison with Purbeck material (e.g., BMNH R8208), the limbs of the Morrison specimen are relatively longer and more slender (even allowing for immaturity) – adding to the general impression that the Morrison paramacellodid was more gracile than its European counterpart.

#### Squamata: incertae sedis

Two further specimens from DNM (DINO 14720 and DINO 14734: DNM locality 375) cannot be referred to either *Paramacellodus* or *Dorsetisaurus* and represent a new generic record for the Morrison.

DINO 14720. This specimen bears the disarticulated skeleton of a small lizard (estimated SV length 80–90 mm). The specimen has been preserved within a very thin bedding plane through which the block (and therefore most of the skeleton) has been split. Figure 4 is based on both part and counterpart, but only the more complete elements have been included. Many are indecipherable.

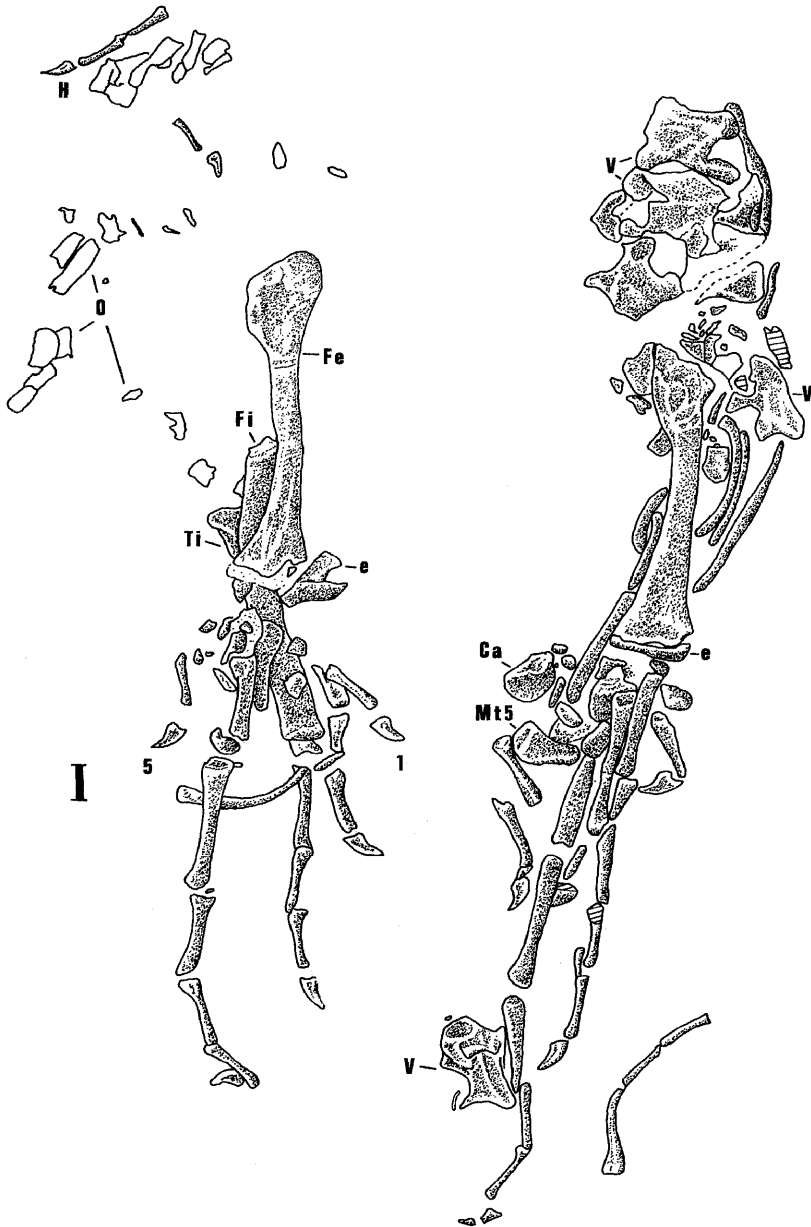


FIGURE 3 Paramacelloidid hind limbs (DINO 13861) from Dinosaur National Monument. Scale bar = 1 mm. Abbreviations: Ca, calcaneum; e, femoral epiphysis; Fe, femur; Fi, fibula; Mt5, fifth metatarsal; O, osteoscutes; Ti, tibia; V, vertebrae; 1-5, digits.

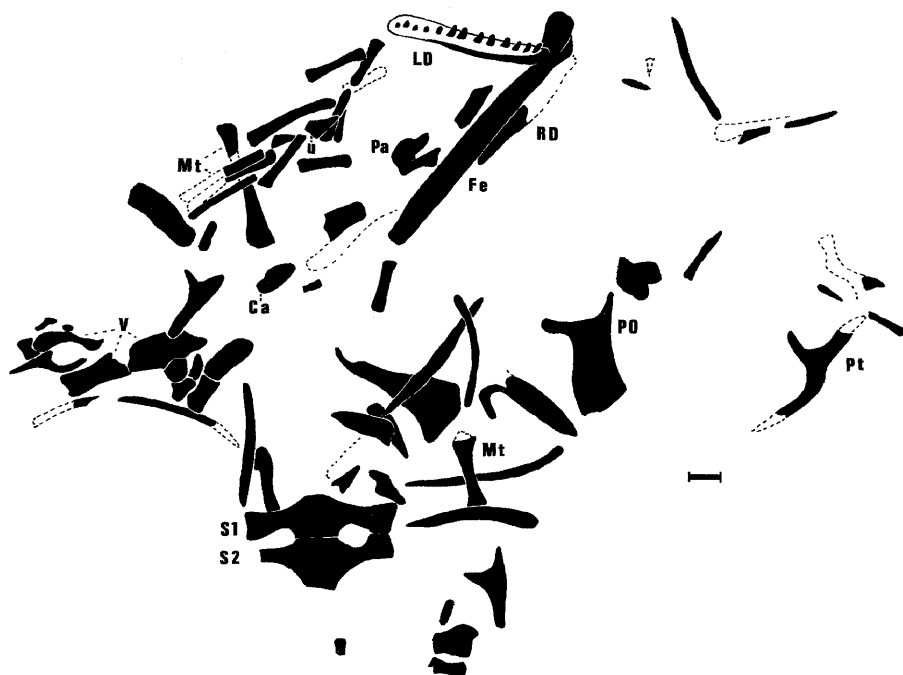


FIGURE 4 Disarticulated skeleton of a small lizard from Dinosaur National Monument (DINO 14720). Scale bar = 1.0 mm. Abbreviations: Ca, calcaneum; Fe, femur; LD, left dentary; Mt, metatarsals; Pa, palatine; PO, postorbitofrontal; Pt, pterygoid; RD, right dentary; S1,2, sacral vertebrae; u, ungual; V, vertebrae.

Skull bones are scattered across the block and include parts of the mandibles and palate (palatine, pterygoids). Of the postcranial bones, elements of the hind limbs and sacrum are preserved, with further damaged vertebrae and ribs across the block. The femur is long and gracile by comparison with DNM 13861, as are the visible elements of the pes (particularly metatarsals 3 and 4), although the claws are relatively deeper. A calcaneum lies in association with the pes but its medial edge is obscured. It appears to be separated from the astragalus, but this is not certain. The ends of the bones, as preserved, are rounded but have a porous quality which suggests that ossification was incomplete. This may indicate that the animal, though of roughly adult size, was not fully mature.

Two elements in particular – the mandible and the sacrum – are noteworthy. The dentary is small and shallow, with subparallel borders. The teeth are fully pleurodont and there are 24–26 tooth positions undergoing



rapid replacement. At their base is a strong lingual gutter. The Meckelian groove is open. The two sacral vertebrae are in articulation but neither has a posterior condyle. Furthermore, the broken surface of the first centrum suggests that the notochordal canal was open – a conclusion supported by some of the other scattered centra. The sacral ribs meet at their tips and were apparently fused. There is no trace of an intercentrum, but this does not preclude the possibility that such elements were present in the trunk.

Clearly this small lizard cannot be referred to either *Paramacellodus* or *Dorsetisaurus*. In comparison with known European genera, the dentary of DINO 14720 bears a resemblance, principally in terms of general shape, shallow build and the lingual gutter, to a small dentary (BMNH R12689) from the Bathonian of Oxfordshire, England (Evans, in press). Tentatively associated with the Oxfordshire jaw are a series of amphicoelous vertebrae like those on DINO 14720.

On the basis of jaw shape, the lingual gutter and the vertebrae, the Bathonian form was interpreted as a possible primitive gekkotan (Evans, in press) but this is tentative. One skull element in DINO 14720 has been interpreted as a postorbitofrontal (Fig. 4, PO) and appears to have a strongly concave orbital margin and a long broad posterior flange. This flange, from its size and shape, could have closed the upper temporal fenestra – an unlikely (though not impossible) feature for a primitive gekkotan where the trend is towards reduction of ossification leading to loss of the skull arches. There is, admittedly, very little material for comparison but *Eichstaettisaurus* from Solnhofen, a possible Jurassic gekkotan (Estes, 1983; Evans, 1994a), retains an open fenestra and separate post-orbital and postfrontal bones.

DINO 14734. This second specimen has recently been identified, but has yet to be prepared. It comes from the same locality as DINO 14720 and represents an animal of similar size. The skeleton is fragmentary but some elements of the skull (frontal) and postcranial skeleton (vertebrae, ribs, humerus, fibula and part of a femur/tibia) are identifiable. The frontal is lightly built and unsculptured – precluding attribution of this specimen to either *Paramacellodus* or *Dorsetisaurus*. The limb elements, as preserved, are long and gracile and the vertebrae appear to be amphicoelous. On this basis, it seems likely that DINO 14734 is related to DINO 14720.

As yet, we know too little about these two small lizards to be certain of their phylogenetic position. DINO 14720 (with or without DINO 14734) certainly represents a new generic and family record for the Morrison. If the British Bathonian form and the Morrison lizards are related, they are probably not congeneric. The teeth differ: those of the Morrison lizard

being slender, sharply pointed cones in contrast to the proportionally shorter teeth with expanded tips seen in the British form. A more detailed description and formal classification of these Morrison lizards will be given elsewhere when the material has been fully prepared.

## DISCUSSION

Over the last decade, our knowledge of Jurassic lizards has been improved and clarified by the description of new material and the reassessment of existing material. At present, the squamate record begins in the Middle Jurassic (Bathonian) of Britain (Evans, 1994a,c, in press; Waldman and Evans, 1994). These assemblages are already diverse and provide evidence of an, as yet unrecorded, Triassic and Early Jurassic history. They also provide a base from which to review known Late Jurassic assemblages – leading to some reinterpretations, most notably of some of the supposed gekkotans from Solnhofen, Germany (Evans, 1994a,b). Although the relationships of some taxa have yet to be resolved, Jurassic and Early Cretaceous assemblages across Laurasia (Fig. 5) appear to show both temporal and geographical similarity (Table I). They are dominated by scincomorphs, particularly paramacellodids, with anguimorphs but no iguanians and, at best, extremely rare gekkotans.

Jurassic lizard horizons fall mostly into one of two distinct categories: those that yield well-preserved, but rare, articulated specimens (e.g., Solnhofen, Cerin, Karatau); and microvertebrate horizons permitting bulk sampling in which the bones are disarticulated, but in larger numbers. The first type of horizon provides information on the morphology, and hence the systematics, of the individual genera; the second, in addition to morphological information, gives a clearer insight into the composition of the assemblage as a whole. The Purbeck Limestone Formation of Dorset is valuable because it yields not only articulated specimens but also horizons suitable for bulk sampling (e.g., Ensom, Evans and Milner, 1991). The horizons recently identified in the Morrison Formation suggest a similar potential. They also provide an opportunity to compare different localities within a single Formation, as a means of gauging the effects of local environmental/depositional factors.

Table II shows taxon distribution in four assemblages with comparable material – Kirtlington and Skye (Bathonian, Britain), the Lignite Beds of Guimarota, Portugal (Oxfordian/Kimmeridgian, Milner and Evans, 1991),

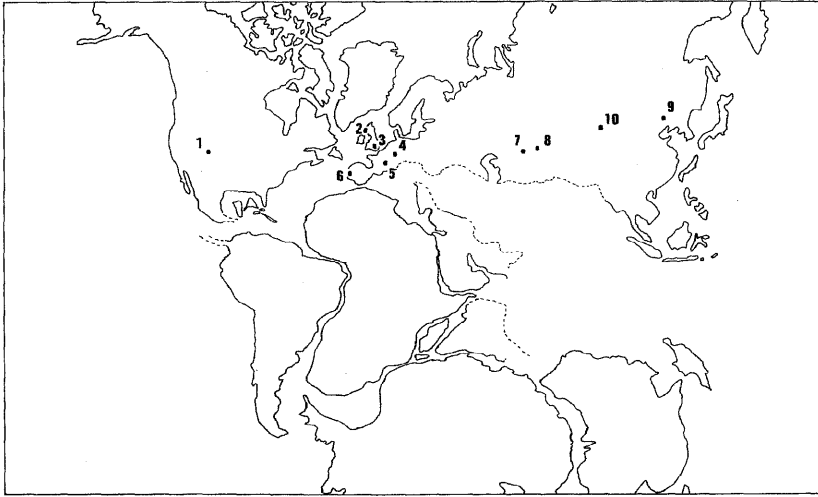


FIGURE 5 Early lizard assemblages: map showing position of continents in the Late Jurassic (simplified from Smith and Briden 1977) with lizard localities marked - 1, Morrison Formation (Kimmeridgian); 2, Skye, Scotland (Bathonian); 3, Kirtlington (Bathonian) and Purbeck (Berriasian), England; 4, Solnhofen, Germany (Tithonian); 5, Cerin, France (Kimmeridgian); 6, Guimarota, Portugal (Oxfordian, Kimmeridgian); 7, Kirghizia (Kimmeridgian); 8, Karatau, Kazakhstan (Kimmeridgian); 9, Liaoning, China (Tithonian); 10, Gansu, China (Late Jurassic).

the Brushy Basin Member (Kimmeridgian) of the Morrison Formation (data from several localities combined) and microvertebrate horizons in the Purbeck Limestone Formation – once thought to be roughly contemporaneous with the Morrison (e.g., Simpson, 1926; Kermack, 1975) but now considered as early Cretaceous (Berrisian) in age (Allen and Wimbledon, 1991). The squamate assemblage is broadly similar across the chart and some of the apparent differences, e.g., the absence of the anguimorph *Parviraptor* (Evans, 1994c) and the paramacellodid *Becklesius* (Estes, 1983) from the Morrison, may disappear when there is more material. Amongst the non-squamate small reptiles, the absence of the early choristodere *Cteniogenys* (Evans, 1989; 1990) from Purbeck, and of the lepidosauromorph *Marmoretta* (Evans, 1991) from both the Morrison Formation and Purbeck is interesting. At Kirtlington and Guimarota, *Marmoretta* and *Cteniogenys* are found together in large numbers (and have been confused – e.g., Seiffert, 1973). *Cteniogenys* jaws are relatively common in material from Quarry 9, but there is no trace of *Marmoretta* in any collection (i.e., Yale, Smithsonian, AMNH); there is equally no trace of *Cteniogenys* among the

TABLE I The distribution and relationships of early lizard genera on the basis of recent work

Locality: Age:	Kirrlington Bathonian	Guimarota Oxfordian	Morrison Kimmeridgian	Cerin Kimmeridgian	Kazakhstan Kimmeridgian	Solnhofen Tithonian	China Tithonian	Purbeck Berriasian	Spain Barremian
Iguania:	—	—	—	—	—	—	—	—	—
Gekkota:	—	—	—	—	—	<i>Eichstettisaurus</i>	—	—	—
Scinco- morpha	parama- celloid	—	<i>Paramaceloidus</i>	—	—	? <i>Ardeosaurus</i>	<i>Mimobecklesis- saurus</i>	<i>Para- maceloidus</i>	<i>Para- maceloidus</i> <i>Becklesius</i>
	—	<i>Becklesius</i> <i>Saurillus</i>	—	—	—	—	—	<i>Becklesius</i>	<i>Becklesius</i>
	—	—	—	—	—	—	—	<i>Pseudo- saurillus</i>	—
Angui- morpha	new genus <i>Saurillodon</i>	—	new genus	—	—	—	—	—	—
	—	<i>Saurillodon</i>	—	—	—	—	—	—	—
	—	<i>Dorsetisaurus</i>	<i>Dorsetisaurus</i>	—	—	—	—	<i>Durotrigia</i> <i>Dorsetisaurus</i>	<i>Meyasaurus</i>
	—	—	—	—	—	—	—	—	<i>Cuencasaurus</i>
Spheno- dontids	<i>Parviraptor</i> rare	<i>Parviraptor</i> absent	—	—	absent	common	absent	rare	absent

TABLE II Detailed comparison of small reptile genera from Jurassic and Lower Cretaceous

Locality	Kirlington/ Skye	Guimarota	Morrison	Purbeck	Notes
Age:	Bathonian	Oxfordian/ Kimmeridgian	Kimmeridgian	Berriasian	
Non-squamate:					
<i>Marmoretta</i>	X	X	O	O	Lepidosauromorph (Evans, 1991)
<i>Cteniogenys</i>	X	X	X	O	Choristoderan (Evans, 1990)
Squamate:					
<i>Saurillodon</i>	X	X	O	O	
<i>Parviraptor</i>	X	X	O	O	
new gracile genus	X	O	X	O	
<i>Paramacellodus</i>	X	O	X	X	
<i>Becklesius</i>	O	X	O	X	
<i>Dorsetisaurus</i>	O	X	X	X	
<i>Durotrigia</i>	O	O	O	X	related form in Barremian of Spain?
<i>Pseudosaurillus</i>	O	O	O	X	

hundreds of small bones from Purbeck. Whether these differences are temporal (extinctions) or due to differences of environment is a question that has yet to be resolved.

### Acknowledgments

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### *Note Added in Proof*

The anguimorph genus *Parviraptor* has now been recognised from the Morrison Formation at Fruita, Colorado (Evans, 1996).

Evans, S.E. (1996) *Parviraptor* (Squamata: Anguimorpha) and other lizards from the Morrison Formation at Fruita, Colorado. In Morales, M. (Ed.) *The Continental Jurassic*. *Mus. N. Arizona Bull.*, **60**, 243–248.