

## Late Jurassic lizards from Como Bluff, Wyoming and their palaeobiogeographic significance

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Fossils from the late Jurassic Morrison Formation, Como Bluff, Wyoming (Tithonian, ~140 Myr ago) show that three genera of European lizards from the later Jurassic of England and Portugal (*Ctenioagenys*, *Paramaceliodus*, *Dorsetisaurus*) also inhabited North America. These specimens corroborate evidence from mammal and other terrestrial vertebrate faunal similarities that western Europe and western North America had a continuous land connection in the late Jurassic. Some of this similarity, however, is pre-Tithonian, indicating that widespread mid-Jurassic transgressive seas in Europe were no barrier to vertebrate dispersal.

Between 1968 and 1970, a joint American Museum of Natural History-Yale University expedition made new collections at Quarry Nine, the famous 'mammal quarry', in the Upper Jurassic Morrison Formation at Como Bluff, Wyoming. The expedition collected many mammalian specimens described elsewhere<sup>1</sup>, as well as dinosaur material, glyptopsid turtles<sup>2</sup>, crocodiles, sphenodontids, frogs, lungfish, amioid fish and lizards. A review of this and previously known lizard material from the Morrison Formation has resulted in the identification of at least three genera of lizards. Only one, *Ctenioagenys antiquus* Gilmore 1928, was known previously from North America; it has been shown to be an eolacertilian<sup>3</sup>.

Hecht and Estes<sup>4</sup> reported an ilium of what they believed to be a true lacertilian from previous Quarry Nine collections, but did not name it. Lacertilian ('true') lizards are known from the late Jurassic of Europe and China<sup>5,6</sup>. A presumed lacertilian was described from the late Triassic of China<sup>6</sup>, but one of us (R.E.) believes it to be an eolacertilian. The new material from the Morrison Formation not only verifies the occurrence of both eolacertilians and lacertilians in the late Jurassic of North America, but also shows for the latter group a well-established, derived, 'autarchoglossan' organization at this early time, which is in agreement with previous identifications of some Jurassic European forms as scincomorphs. The three lizard species identified in the Morrison Formation are classified as follows:

Order Squamata  
Suborder Lacertilia  
Infraorder Eolacertilia  
*Ctenioagenys antiquus* Gilmore 1928

The new collection includes two jaws referable to this species. (Other jaws, including the type specimen, were found in the original Marsh collections made at Como Bluff in 1879 and 1880.) *Ctenioagenys* was later identified by Seiffert<sup>3</sup> from the late Jurassic (Kimmeridgian) fauna from Guimarota, Portugal. We agree with Seiffert's identification of *Ctenioagenys* as an eolacertilian, closely related to the 'flying lizards', or kuehneosaurs, known from the late Triassic of Europe<sup>7</sup> and North America<sup>8</sup>. *Ctenioagenys* is known from jaws, maxillae and parietals. The other species are true lacertilians, of which the first is:

Infraorder Lacertilia  
*Paramaceliodus* sp.

*Paramaceliodus oweni* was first described from the late Jurassic Purbeck Formation of England, and allied with the cordyloid

scincomorphs<sup>9</sup>. Several jaws referable to *Paramaceliodus* (including two from the new collection) occur at Quarry Nine (Fig. 1a,b); they may represent the same species but the material is insufficient to determine this. Some postcranial material, possibly referable to *Paramaceliodus* also occurs in the new collection. The specimen (AMNH 11523) consists of a left prefrontal, a left scapulocoracoid, one trunk vertebra, a partial pelvis, seven caudal vertebrae, and a nearly complete left hind limb. The hind limb, pelvis and sacral vertebrae are articulated. All other elements are disarticulated, but closely associated on the block of matrix.

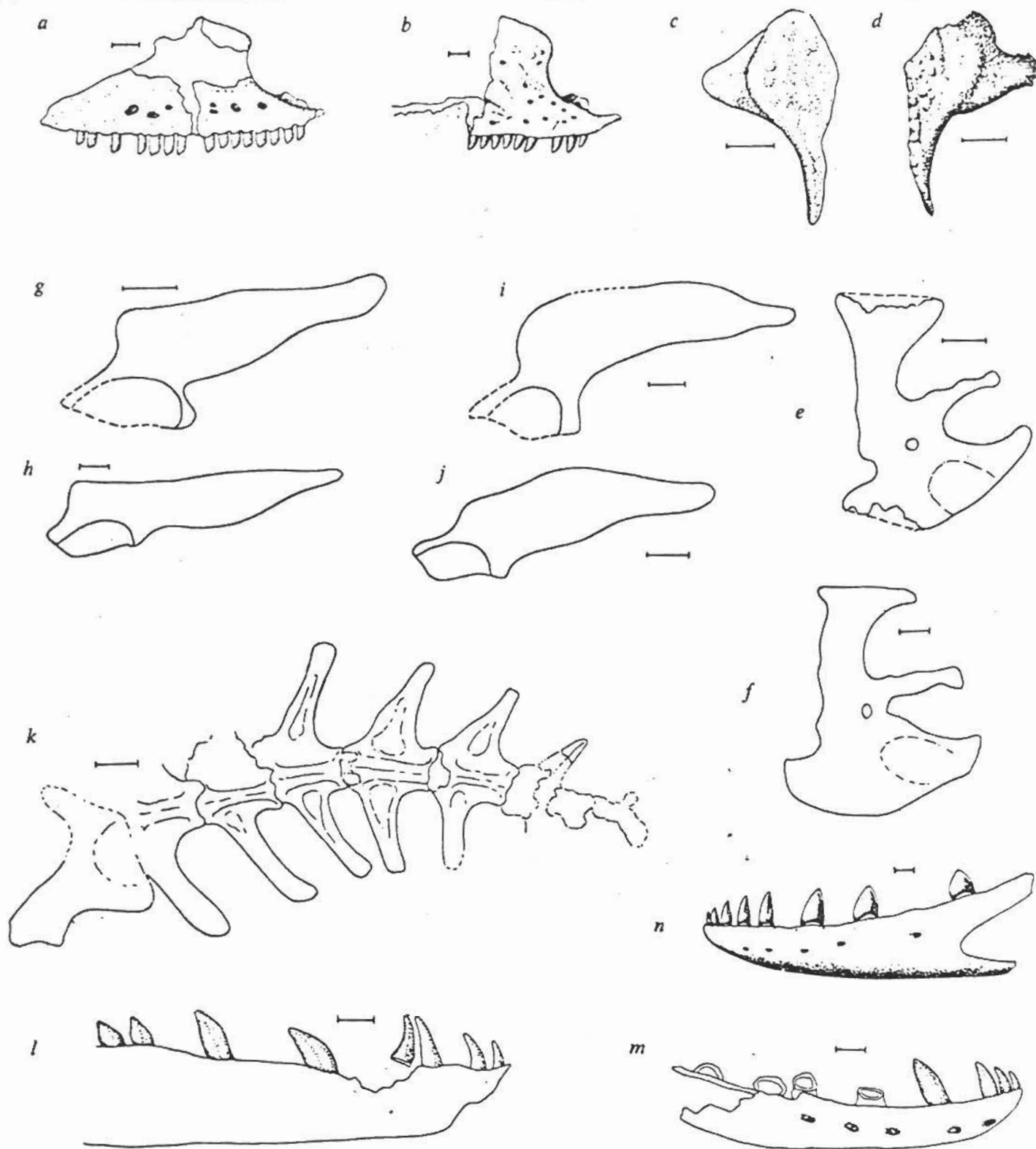
A detailed description of this material is in preparation, but the important features of AMNH 11523 can be summarized as follows. The prefrontal has a sculpture pattern like that of an unidentified Jurassic specimen from Portugal (Fig. 1c,d)<sup>3</sup> and may possibly represent the prefrontal of *Paramaceliodus*. The scapulocoracoid (Fig. 1e,f) is fully lacertilian, with expanded coracoid region that resembles the derived condition in cordyloid lizards. In the pubis, the iliac blade differs in shape from the ilium described by Hecht and Estes<sup>4</sup>, but both are generally similar in morphology to the ilia of some cordyloid lizards (Fig. 1g-j). In the tail (Fig. 1k), the transverse process of the sixth vertebra may show an autotomic septum, implying fragility of the tail. If so, the septum would split the vertebra into two parts as in many lizards. Comparison of AMNH 11523 with recent lizard skeletons showed that this autotomic configuration is very similar to that of comparably sized lizards belonging to several families, particularly some scincids; cordyloids have the autotomic plane anterior to the transverse process. The third species is:

Family Dorsetisauridae  
*Dorsetisaurus* sp.

There are two dentaries of *Dorsetisaurus* sp.<sup>5</sup>. Neither specimen is well preserved (Fig. 1l-n), and both are visible only in lateral view. The elongated, flattened, blade-like teeth, some of which are antero-posteriorly expanded, make this identification clear. Hoffstetter, who originally described *Dorsetisaurus*, placed it in its own family Dorsetisauridae, with which we agree. He also included the family in the Anguimorpha; if so, dorsetisaurus would be very primitive members of that group.

The presence of three genera of small lizards in both North America and Europe in the late Jurassic is an indication of the close faunal affinities of the two regions at that time. Continental reconstructions show that the North American plate was still in contact with Europe at the end of the late Jurassic<sup>11,12</sup>. Como Bluff, Wyoming, and southern England were approximately 2,500 km apart, equivalent to the present distance between San Francisco, California and St Louis, Missouri. Some recent lizards have ranges larger than this. In addition, several other small animals apparently ranged from England to the present western United States. These include four genera of shrew-sized mammals<sup>13,14</sup> (*Docodon*, *Amblotherium*, *Ctenacodon*, *Trioracodon*), the crocodile *Goniopholis*<sup>15</sup>, the dinosaur *Campiosaurus*<sup>16</sup>, and the amioid fish *Ophiopsis*<sup>17</sup>. Also, most of the Morrison mammal taxa have their closest sister-groups in Europe, and a cladogram of therian mammals shows no separation of the taxa into European and American clusters, as might be expected if long-term endemism had taken place<sup>1</sup>.

Direct comparisons have not been made in other groups, but most other elements in the Morrison fauna have their closest relatives in the European later Jurassic. Turtles from the early Cretaceous of England<sup>18</sup> and sphenodontids from the Kimmeridgian of Portugal<sup>19</sup> have been examined recently, and are most closely related to Morrison taxa. Complete faunal lists of the Kimmeridgian Guimarota fauna of Portugal have not yet been published, but the partial one given by Kühne<sup>19</sup> is very similar to that from the Purbeck and Morrison Formations. To date, the mammals<sup>13,14</sup>, dinosaurs<sup>20</sup>, crocodilians<sup>21</sup>, turtles<sup>22</sup> and lizards<sup>3</sup> have been described, and most forms show their closest



**Fig. 1** *a*, *Paramacellodus* sp., right maxilla, Morrison Fm. *b*, *Paramacellodus oweni*, right maxilla, Purbeck Fm<sup>5</sup>. *c*, AMNH 11523, left prefrontal, Morrison Fm. *d*, GU1. 157, right prefrontal, Guimarota Beds<sup>3</sup>. *e*, AMNH 11523, left scapulocoracoid, Morrison Fm. *f*, Left scapulocoracoid of recent *Cordylus polyzonus* for comparison. *g*, AMNH 11523, left ilium, Morrison Fm, comparable with *h*, recent *Platysaurus guttatus*. *i*, YPM 1568, left ilium, Morrison Fm, comparable with *j*, recent *Cordylus warreni*. The fossil iliac blades show some differences, but are within the range of variation of modern cordyloid lizards. *k*, AMNH 11523, caudal vertebrae. *l-m*, *Dorsetisaurus* sp., dentary, Morrison Fm. Both specimens are badly broken. *n*, *Dorsetisaurus purbeckensis*, dentary, Purbeck Fm<sup>5</sup>. All scale bars, 1 mm.

affinities with forms from the Morrison and Purbeck Formations. Kimmeridgian sauropods from Portugal (*Apatosaurus*, *Brachiosaurus*) are congeneric with Morrison taxa<sup>21</sup>. Pre-Kimmeridgian Jurassic dinosaur faunas in both North America and Europe are highly similar<sup>24-26</sup>. Bathonian (middle Jurassic) mammals from England<sup>27</sup> and Scotland<sup>28</sup> show close affinities with Morrison mammals<sup>1</sup>.

These strong faunal resemblances between western Europe and western North America seem to indicate a continuous land connection between these regions throughout the Jurassic. Yet reconstructions by Ager<sup>29</sup>, Hallam<sup>30</sup>, and Hallam and Sellwood<sup>31</sup> show both southern England and Portugal submerged or surrounded by seaways during most of the Jurassic. The maximum extent of Jurassic epicontinental seas was during the Oxfordian and Kimmeridgian (early late Jurassic)<sup>30</sup>. During the Tithonian, widespread tectonism uplifted large areas of land, reconnecting Europe and North America<sup>30,31</sup>. The amount of exposed land in the late Tithonian reached a maximum level matched only by the earliest Jurassic (Sinemurian-Pliensbachian) regression<sup>30</sup>.

If the similarity of land faunas were restricted to the late Tithonian, then rapid migration during the maximum phase of regression would be sufficient to explain the lack of endemism. But the similarity persists throughout the Jurassic, indicating that the submergence was not continuous or effective enough to be a barrier to vertebrate migration. Hallam (personal communication) has suggested that the epicontinental seas were so shallow that the numerous short-term regressions occurring throughout the Jurassic<sup>30</sup> would create transient land corridors. Migration then reached a peak during the Tithonian when dry land connection extended across Europe and North America.

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## Green anole in Dominican amber

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A lizard of the iguanid genus *Anolis* enclosed in amber of Oligocene or Miocene age from the Dominican Republic represents the first complete vertebrate fossil in amber as well as the oldest and only complete fossil of its genus. The fossil *Anolis* is very closely related to a recent form and will shed some light on the evolution of its genus which otherwise has a poor fossil record.

The evolution of the iguanid genus *Anolis* on the Caribbean islands serves as a model for the ecology of colonization and speciation on small islands<sup>1,2</sup>. The evolution of the Caribbean *Anolis* has been reconstructed by Etheridge on the basis of osteology and by Gorman *et al.* on the basis of cytology. Their findings have been summarized by Williams<sup>3</sup>. Etheridge was able to divide the genus into an  $\alpha$  and a  $\beta$  section.  $\alpha$  *Anolis* lacks transverse processes on the caudal vertebrae whereas they are present on  $\beta$  *Anolis*. A striking result of Etheridge's analysis is that the  $\alpha$  *Anolis carolinensis* from the south-eastern United States is not related to the  $\beta$  anoles from Mexico, but it has Caribbean affinities, being related to the species of the *carolinensis* complex of the western Caribbean. *Anolis carolinensis* invaded the continent from a tropical island. The geographic centre of the *carolinensis* complex today is Cuba. Some slightly more primitive  $\alpha$  anoles occur on Hispaniola. Of these, members of the 'green anole species group' as defined by Williams<sup>3</sup>, such as *A. chlorocyanus* or *A. coelestinus*, were found by Etheridge to be most closely related to and possibly ancestral to the *carolinensis* complex.

This phylogenetic scenario is usually assumed to have taken place during the Pleistocene. The genus *Anolis* is thought to have colonized the Caribbean islands after the Early Miocene inundation<sup>4</sup>, but no fossil remains of these lizards older than the latest Pleistocene age have been reported, either from the Caribbean islands or from the southeastern United States. The oldest fossil *Anolis* remains are skin fragments enclosed in amber of Oligocene or Miocene age from Mexico<sup>4</sup>.

In 1979, Dr C. Baroni-Urbani from the Natural History Museum in Basel obtained a more or less completely preserved specimen of *Anolis* in amber from the Mina 'La Toca', Cordillera Septentrional, Dominican Republic (Fig. 1). Dominican amber is thought to be of middle Oligocene or early Miocene age<sup>5</sup>. The generic affinities of the fossil lizard are indicated by the structure of the toes, which bear scansorial pads on the lower surface of their expanded distal parts (Fig. 1). X-ray analysis revealed an incompletely preserved skeleton. Important characters such as the structure of the pectoral girdle or the number of presacral vertebrae cannot be determined. However, caudal vertebrae can be shown to lack transverse processes, a feature characteristic of  $\alpha$  anoles (Fig. 2).

In view of its uniqueness I propose to name the fossil anole:

*Anolis dominicanus* n. sp.

**Holotype:** Natur. History Museum Basel, Department of Entomology collection no. P 52. Mina 'La Toca', Cordillera Septentrional, Dominican Republic.

**Diagnosis:** A member of the  $\alpha$  section of the genus *Anolis*; ventral scales hexagonal, subimbricate, smooth; scales on tail imbricate, keeled, arranged in verticils comprising 4-5 middorsal scales; 22-24 lamellae under fourth toe.

**Description:** The fossil *Anolis* has a total length of approximately 71 mm; the head is 9.2 mm long; snout-vent length is 26.5 mm; the tail is complete and not regenerated. The left front limb is difficult to measure because of three-dimensional

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