



## Early Cretaceous lizards from Las Hoyas, Spain

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The Lower Cretaceous lithographic limestone locality of Las Hoyas (Cuenca Province, Spain) has yielded a rich terrestrial and freshwater assemblage including early angiosperms, insects, birds, crocodiles, a dinosaur, amphibians and lizards. The Las Hoyas lizards are represented by three distinct taxa, of which one, *Meyasaurus* Vidal 1915, has been described from other Spanish localities of similar age. The Las Hoyas specimens provide the first complete examples of *Meyasaurus*, permitting both a detailed morphological description and a comprehensive analysis of phylogenetic position. *Meyasaurus* is shown to be a lacertoid scincomorph related to teioids. Furthermore, in providing an association between the skull and postcranium, the Las Hoyas specimens of *Meyasaurus* show that the Montsec genus *Ilerdaesaurus* Hoffstetter 1966 is a junior synonym of *Meyasaurus* Vidal 1915.

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ADDITIONAL KEY WORDS: — Squamata – Lacertoidea – palaeontology – morphology – phylogeny.

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## INTRODUCTION

Early Cretaceous lizards have been reported from four Spanish localities: Montsec (Berriasian/Valanginian), Uña (late Barremian), Las Hoyas (late Barremian) and Galve (Barremian/Aptian). The first specimen, a partial postcranial skeleton interpreted as sphenodontian, was described from Santa Maria del Meia, Montsec (Catalonia) by Vidal (1915) who named it *Meyasaurus faurae* (emended to *M. faurai* by von Huene, 1952). In 1963, Hoffstetter, Crusafont and Aquirre reported the discovery of a lizard skull from the same locality. This second specimen was formally described by Hoffstetter (1966) under a new generic name *Ilerdaesaurus*. In the same paper, Hoffstetter also reviewed the position of *Meyasaurus* and showed it to be a lizard. He concluded that *Ilerdaesaurus* was a scincomorph and that *Meyasaurus* showed some scincomorph features, but Estes (1983) placed both genera as *incertae sedis*.

More recently, other early Cretaceous sites — Uña and Las Hoyas in Castilla-La Mancha, and Galve in Teruel — have yielded lizards. The lizards of Uña were described in doctoral work by Annette Richter (1991, 1994a & b) and include cranial and isolated postcranial elements referred to a new species of *Ilerdaesaurus*, two paramacellodids attributable to the genera *Becklesius* and *Paramacellodus*, and a possible new anguimorph, *Cuencasaurus*. Galve has produced dissociated paramacellodid bones, skull elements referred to *Ilerdaesaurus*, and a possible new scincomorph (Estes & Sanchiz, 1982; Richter, 1994b).

At Las Hoyas, an extensive exposure of finely laminated freshwater limestones is currently being worked by an international team coordinated by the Universidad Autónoma de Madrid. Of the nine lizard specimens recovered to date, two represent new genera and will be described elsewhere; one specimen is an assemblage of five or more dissociated individuals and may represent the remains of a faecal or oral pellet; the remaining six are attributable to the genus *Meyasaurus* (Barbadillo & Evans, 1995). These permit a detailed morphological description, a discussion of species relationships and a comprehensive analysis of phylogenetic relationships. In addition, the Las Hoyas material, in combining both cranial and postcranial remains, has also shown that *Ilerdaesaurus* Hoffstetter 1966 (based on a partial skull) is a junior synonym of *Meyasaurus* Vidal 1915 (based on a partial postcranial skeleton (Evans & Barbadillo, in press)).

## THE FOSSIL LOCALITY OF LAS HOYAS

The Lower Cretaceous locality of Las Hoyas is situated some 30 km east of the city of Cuenca in Castilla-la Mancha, Central Spain. It exposes a series of fine-grained (lithographic) limestones (Calizas de la Huérgina Formation, Limestone Unit 3) representing an extensive lacustrine system of late Barremian age deposited under sub-tropical and semi-arid climatic conditions (Gomez-Fernandez & Meléndez, 1991; Fregenal-Martínez & Meléndez, 1993). To date, the site has yielded a diverse and well-preserved terrestrial/freshwater assemblage of plants, invertebrates and vertebrates, including angiosperms, insects, spiders, fish, amphibians, lizards, crocodiles, turtles, an ornithomimosaurid dinosaur and birds (see Sanz *et al.*, 1988; Meléndez, 1995 for a detailed review).

## ABBREVIATIONS

*Institutional abbreviations*

IPFUB – Institute für Paläontologie, Free University Berlin  
 IPPS – Instituto Provincial de Paleontología, Sabadell, Spain  
 LH – Las Hoyas collection.

*Abbreviations used in figures*

AC – astragalocalcaneum	Mx – maxilla
Ar – articular	P – parietal
At.a – atlas arch	Pa – palatine
At.i – atlas intercentrum	Pf – postfrontal
Ax – axis	Pm – premaxilla
Br – braincase	Po – postorbital
ca – cartilage	Pp – postparietal process
ca.e – cartilaginous extension (re-grown tail)	Prf – prefrontal
Cc – coracoid	Pt – pterygoid
Cl – clavicle	Pu – pubis
Co – coronoid	Q – quadrate
di.r – displaced rib	Sa – sacrum
Ec – ectopterygoid	ScC – scapulocoracoid
Ep – epipterygoid	Sl – splenial
Fi – fibula	Sp – sphenoid
Fr – frontal	Sq – squamosal
Hu – humerus	St – sternum
Hyp – hypapophyses	Su – surangular
ICI – interclavicle	Ti – tibia
IL – ilium	1,2,3 (Fig.10D) – cervical ribs
J – jugal	1,5 (Fig.12) – metatarsals
Lj – lower jaw	

## THE MATERIAL

The six specimens attributed to *Meyasaurus* form part of the collection of the Museo de Cuenca (Cuenca, Castilla-Mancha). All are fully articulated and three (LH 370, LH 372, LH 13510) preserve both the skull and postcranial skeleton in association (Figs 1–3), including the remains of cartilaginous elements such as the sternum and suprascapula. The specimens range in size from very small (LH 372, snout-vent 25 mm) to medium-sized (LH 370, LH 14317, snout-vent 52 mm +); LH 33 (snout-vent circa 40 mm) and LH 13510 (snout-vent 51 mm) are intermediate.

*LH 370A + B*

Part and counterpart in which the skull has been split to reveal the underside of the skull roof (LH 370A: Figs 1A, 6B) and the dorsal surface of the palate, braincase and parts of the jaws (LH 370B: Figs 1B, 2, 5A). The characteristic form of the vertebral centra, pectoral girdle, frontal, squamosal and dentition support the attribution of this specimen to *Meyasaurus*.

*LH 372A + B*

Part and counterpart of a very young lizard, as shown by the weak ossification of the vertebrae, skull and limb bones. The head is large in relation to the body (Fig. 3A). In the ankle, the astragalus and calcaneum appear incompletely fused; dt4 and dt3 are present but not fully ossified. The skull is preserved in an inferolateral view, so that the right side of the face is exposed. The pectoral girdle, dentition, frontal and squamosal match that of LH 370 (Fig 8B).

*LH 13510A + B*

Part and counterpart in which the body is curled round on itself (Fig. 3B). The skull, parts of the rib and vertebral series, pectoral girdle and hind limbs are preserved. Frontal and squamosal shape link this specimen to *Meyasaurus* (Fig. 8A).

*LH 33A + B*

Part and counterpart of a partial postcranial skeleton showing perfect preservation of the neck region up to the atlas, but no skull and no forelimb skeleton (Fig. 4A, B). Attribution of this specimen to *Meyasaurus* is based on the structure of the vertebrae and pes.

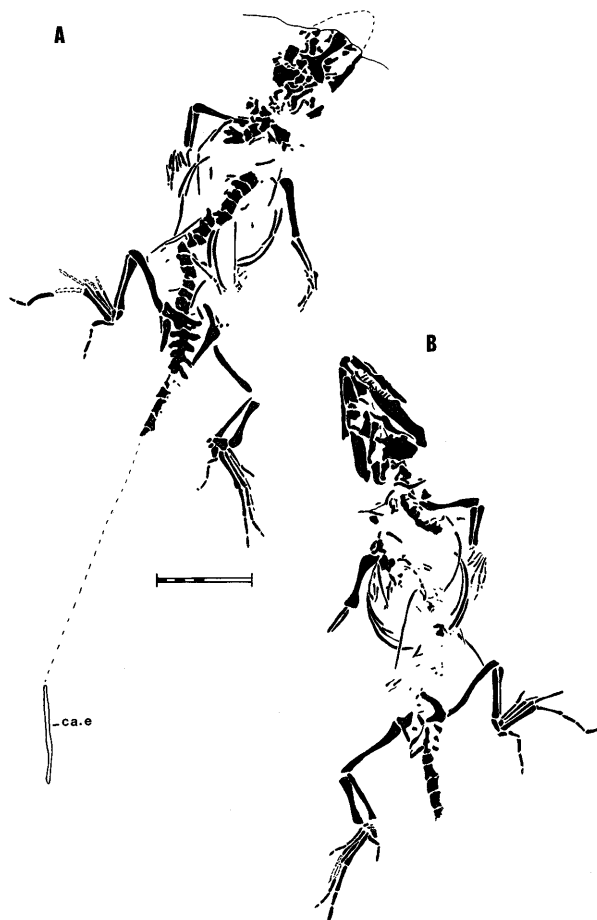


Figure 1. *Meyasaurus diazomerai*, Holotype LH 370, outline figures of A, part and B, counterpart. Scale bar = 1 mm.

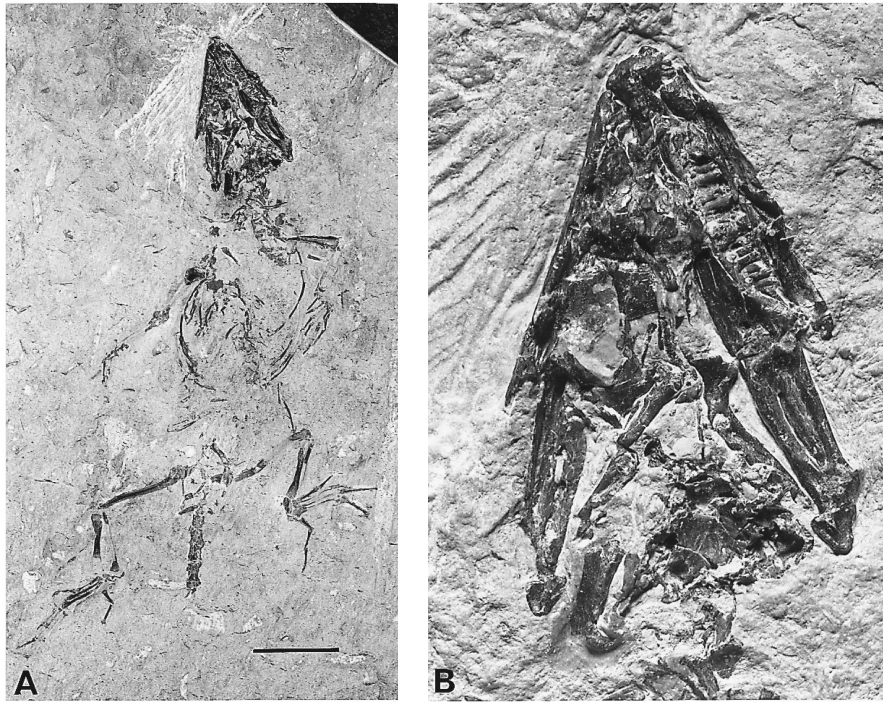


Figure 2. *Meyasaurus diazomeralli*, Holotype LH 370, A, counterpart, B, enlargement of skull showing details of the jaw and dentition. Note the small replacement teeth in the bases of posterior teeth. Scale bar = 10 mm.

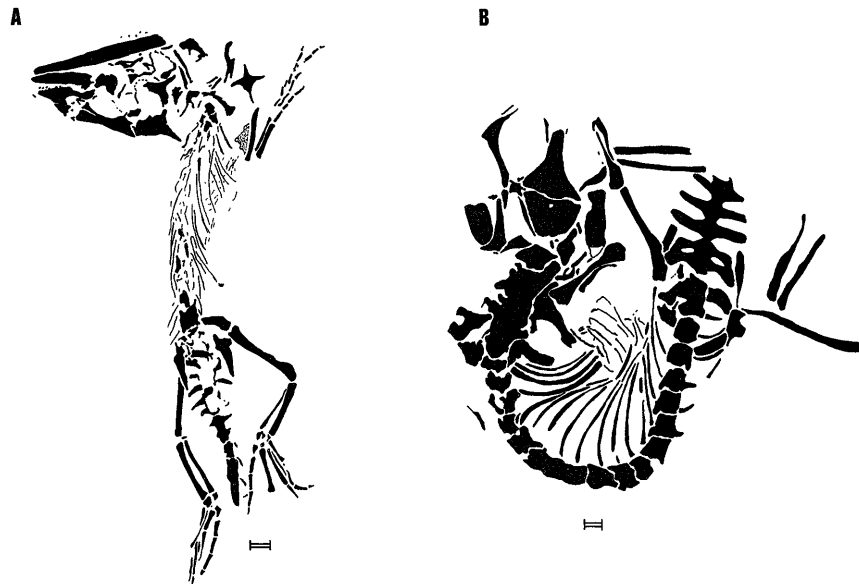


Figure 3. *Meyasaurus diazomeralli*, A, LH 372 (part) and B, LH 13510 (counterpart). Scale bars = 1 mm.

*LH 6026A + B*

Part and counterpart showing the skull, neck and pectoral region – including the distinctive frontals and clavicles (Fig. 7). This specimen also provides the clearest view of the posterolateral surface of the mandible.

*LH 14317A + B*

Part and counterpart of an individual of similar size to LH 370 showing parts of the axial skeleton, pectoral girdle, pelvis and hindlimb. This specimen provides the best information on the tarsus and shows features of the cartilaginous sternum (Figs 11E, 12).

## SYSTEMATIC PALAEOONTOLOGY

## Squamata

## Lacertoidea

*Family indet.**Meyasaurus* Vidal 1915

*Type species.* *Meyasaurus faurai* Vidal 1915 (emend von Huene 1952)

*Range.* Berriasian to Late Barremian or Aptian of Spain.

*Revised and extended generic diagnosis.* Dorsal roofing bones with vermiculate sculpture; premaxilla unpaired, long nasal process, about nine small, unicuspid teeth; maxilla with medial shelf and broad premaxillary process, but no vomerine lappet; dentary long, strong subdental shelf; pleurodont teeth with iguanid replacement pattern; teeth, unicuspid anteriorly, bicuspid posteriorly with strong central cusp and anterior cusplet; small paired nasals, almost or fully separated from the prefrontal by frontomaxillary contact; frontal constricted between orbits, cristae cranii well-developed, deepen anteriorly but do not meet ventrally; frontal with long anterolateral and small anteromedial processes; frontal wide posteriorly, bearing triangular ventral facets for parietal lappets; parietal unpaired, central parietal foramen, strong ventrolateral margins and some development of ventral flanges; postparietal processes long, deep and divergent; jugal with deep anterior process which excludes maxilla from orbital rim, short posterior process, and long orbital process which probably failed to meet the squamosal; postfrontal and postorbital separate; postfrontal small, semilunate with short lateral process to postorbital; postorbital mainly an orbital bone but with strong posterior process; squamosal large with long anterior process, medial flange (= dorsal process) and hooked lateral process; supratemporal present; quadrate with lateral conch but lappet for pterygoid small at best; epipterygoid columnar; pterygoids large, strong oblique suture with palatine, large pterygoid flange; sphenoid with short expanded basiptyergoid processes and ossified rostrum; basioccipital apparently entered lower border of fenestra rotunda; postdentary bones strong; adductor fossa open, quite expanded; slight prearticular crest which excludes angular process; angular process triangular; splenial large; coronoid with deep medial process, short posterior process, anterior process above splenial, and small lateral flange; retroarticular process short; vertebral centra weakly procoelous, rather square centra, last few presacrals shorter than

preceding; 25 presacrals — 8 cervical, 17 dorsal — all but first three bearing free ribs; cervical vertebrae short, the first five at least bearing hypapophyses, with two separate hypapophyses on axis; low neural spines; first three cervical ribs short and expanded; three sternal ribs, two attaching to xiphisternum; remaining ribs sharply divided between six long abdominal ribs and six short presacral ribs; sacrals may be fused distally to enclose a foramen sacrale; anterior caudals with transverse processes; first autotomy septum on caudal vertebra six, passing posterior to transverse process; all posterior caudals autotomous; scapulocoracoid with scapular, scapulocoracoid and two anterior coracoid emarginations; interclavicle cruciform; clavicles perforate, with incomplete medial borders (anterior ramus longest and ending in expansion) and thickened stem; cartilaginous sternal plate rhomboid without sternal fontanelle, bearing attachment points for three sternal and two xiphisternal rib pairs; humerus of moderate length, expanded ends; hands moderately long (around  $1.5 \times$  humeral length), phalangeal formula 2:3:4:5:3; ilium with long slender blade; pubis with obturator foramen and short triangular pubic tubercle, proximally placed but with

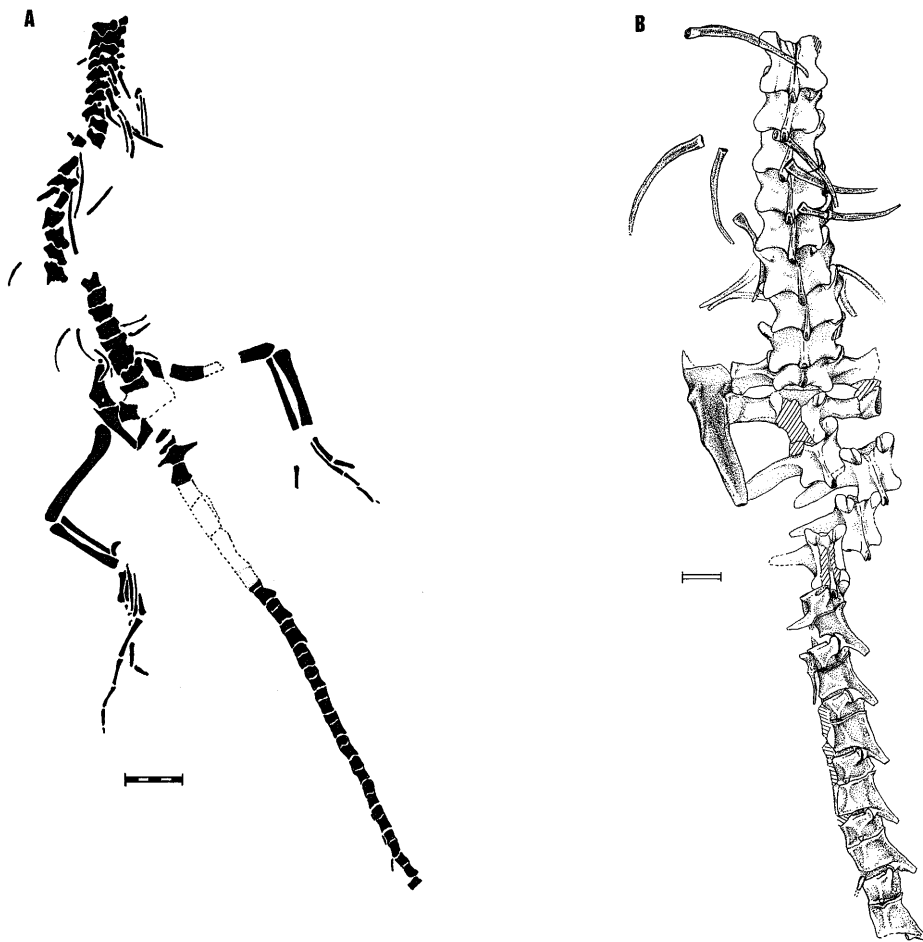


Figure 4. *Meyasaurus diazomeralli*, LH 33, A, outline of part, B, counterpart. Scale bars = 1 mm.

some ventral displacement; femur robust, tibia and fibula shorter; astragalocalca-  
neum fused in adult, bearing proximal crest which articulates with notched distal  
tibial epiphysis; large dt4, smaller dt3, dt2 apparently absent; mt5 short and hooked  
in two planes; long metapodials, mt4 equal or subequal in length to mt3; pedal  
phalangeal formula 2:3:4:5:4.

***Meyasaurus diazromerali* sp.nov.**

(Figs 1–8, 10–12)

*Derivation of name.* To honour Señor Armando Diaz-Romeral of Cuenca who  
collected many of the important specimens from Las Hoyas.

*Holotype.* LH 370, part and counterpart (Figs 1, 2, 6), Museo de Cuenca, Cuenca,  
Spain.

*Horizon and locality.* Las Hoyas fossil site, Cierva Township, Cuenca Province,

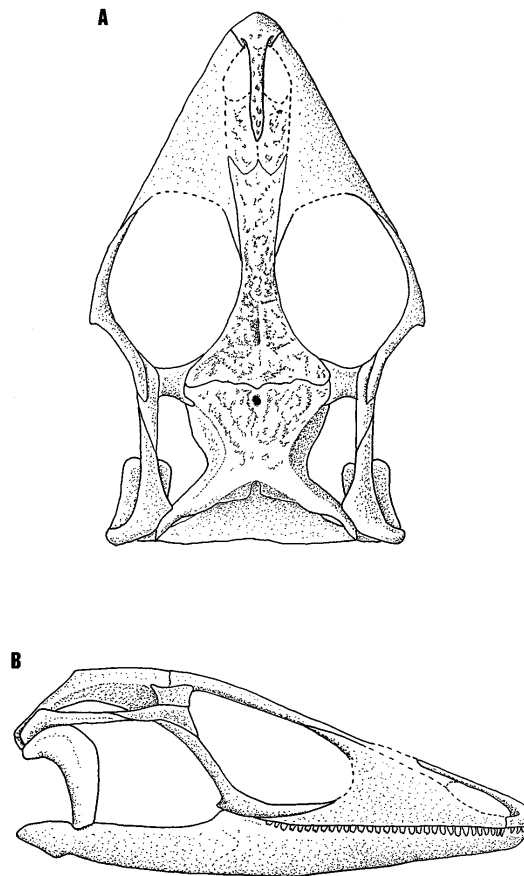


Figure 5. *Meyasaurus diazromerali*, reconstruction of the skull in A, dorsal and B, lateral views. Scale bar = 1 mm.



Castilla-La Mancha, Spain. Calizas de la Huérguina Formation (Limestone Unit III), Early Cretaceous (Barremian).

*Referred specimens.* Museo de Cuenca LH 372, LH 33, LH 13510, LH 6026, LH 14317.

*Specific diagnosis.* A species of *Meyasaurus* which is distinguished from other known species by the possession of a frontals sharply constricted between the orbits while retaining jaws bearing 30 tooth positions (see also discussion below).

#### DESCRIPTION

##### *Skull*

The skull is narrow with large orbits and open upper temporal fenestrae (Figs 5–8). The dermal roofing bones bear a vermiculate sculpture pattern, with occasional deep grooves marking the original positions of large overlying head scales (Fig. 8A).

In the skull roof, the nasals remain poorly known, but fragmentary remains in LH

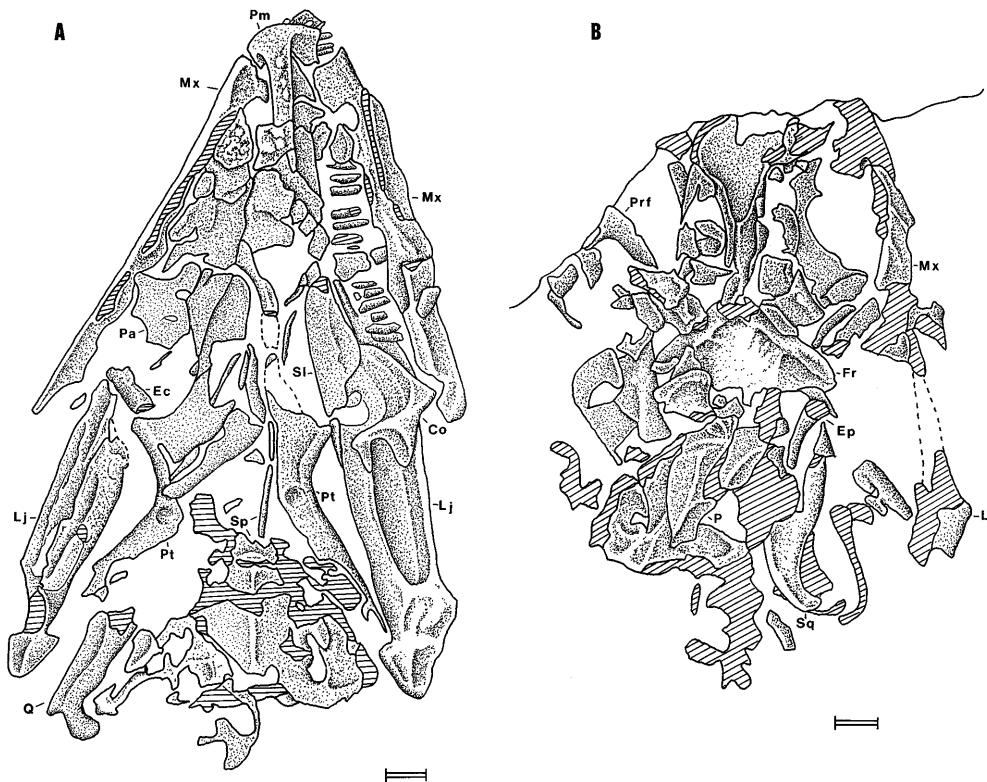


Figure 6. *Meyasaurus diazomerai*, Holotype LH 370, skull, A, counterpart and B, part. Scale bar = 1 mm.

370 show sculpturing. The holotype of '*Ilerdaesaurus*' shows the naso-frontal suture to be trifurcate, with anterolateral processes restricting or precluding contact between the nasals and prefrontals. The frontals appear paired in very young animals (LH 372), but later fused, leaving a dorsal midline groove (LH 13510) but no trace ventrally (LH 370, LH 6026). The adult frontal is distinctive in being relatively broad at the frontoparietal suture, but strongly constricted between the orbits (Figs 7, 8A) and remaining narrow anteriorly. Ventrally, the cristae cranii (olfactory processes) are strongly developed between the orbits and contributed to the orbitonasal septum. They decrease in size posteriorly where each flanks a triangular facet for the anterior process of the parietal.

The adult parietal (Figs 7, 8B) has a roughly square body, pierced anteriorly by a small parietal foramen. The sculptured dorsal surface is sharply delimited from the

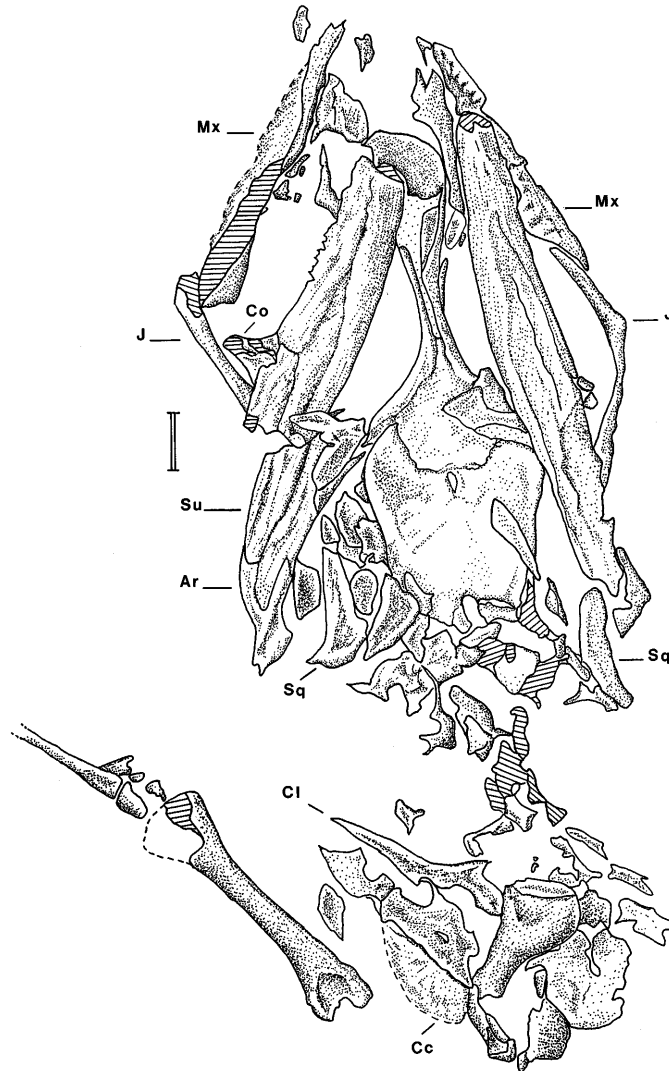


Figure 7. *Meyasaurus diazomeralli*, LH 6026, skull and anterior skeleton. Scale bar = 1 mm.

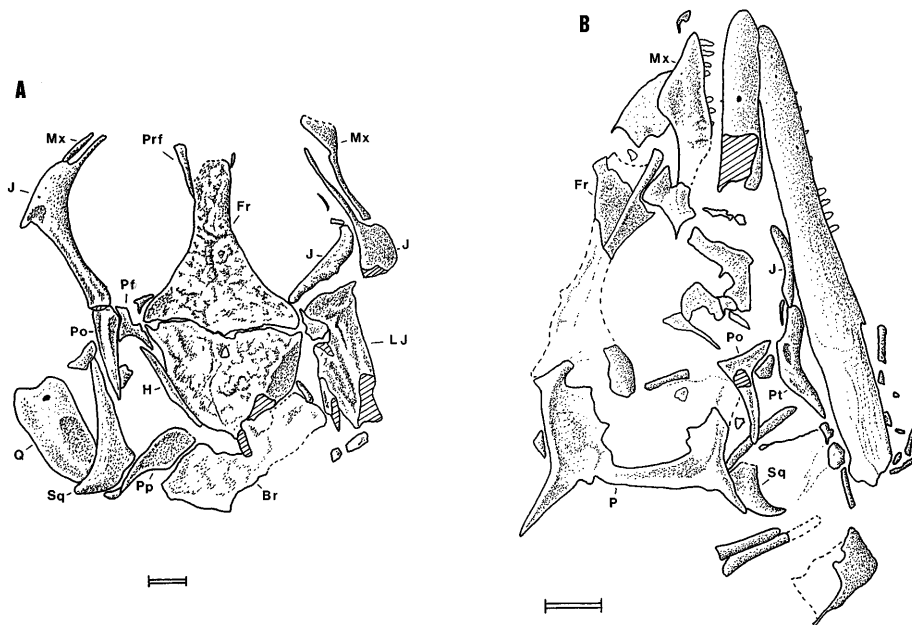


Figure 8. *Meyasaurus diazomeralli*, skull, A, LH 13510B and B, LH 372A. Scale bars = 1 mm.

smooth lateral borders, and the latter are extended ventrally into small descending flanges. The postparietal processes are long, deep and divergent. Between them is a deep central recess for the process ascends of the supraoccipital, flanked by small posterior flanges. The juvenile parietal (LH 372, Fig. 8B) appears relatively shorter, broader and flatter (i.e. without the lateral borders and flanges), with short postparietal processes. As in the young of living lizards, there appears to be an unossified anterior region around the parietal foramen.

The prefrontal is poorly exposed in all specimens, and the presence or absence of a lacrimal remains uncertain. The postfrontal, postorbital and jugal are distinct (Fig. 8A). The postfrontal is semilunate, its anteromedial and posteromedial rami bridging the frontoparietal suture, and its short lateral process meeting the postorbital. The latter is primarily an orbital bone despite its strong posterior squamosal process. The jugal is triradiate, with a short posterior spur and a narrow, columnar dorsal process which met the postorbital but probably not the squamosal. The deeper anterior process bears a strong ventrolateral facet for the maxilla, which was excluded, or nearly excluded, from the orbital margin.

The large squamosal has a distinctive shape, with a strong tapering anterior process and a broader posterior body. The latter expands medially into a dorsal parietal process and laterally into a hook-like process for the quadrate (Figs 5, 6B, 7–9). A supratemporal lies wedged between the squamosal and parietal, but its shape is unclear. The quadrate is seen most clearly in LH 13510, where it is exposed in anterior view (Fig. 8A). There is a moderate-sized lateral conch, but little development of a medial flange. A slight swelling on the medial border probably marks the point of articulation with the pterygoid.

The premaxilla is an unpaired element bearing about nine small monocuspid

teeth below a broad palatal shelf. Its sculptured nasal process is long (Fig. 5A). The maxillae are incompletely known and an accurate tooth count is not possible. Laterally, each bone has a short broad premaxillary process, a long orbital process and a broad facial process, with a strong medial shelf above the tooth row.

The palate is best preserved in LH 370 (Fig. 6A), but details are limited. The vomers are obscured by overlying bones and the palatines are damaged. The pterygoids show no distinguishing features. Each has a long quadrate process, strong pterygoid flange and long palatal plate. The latter extends well forward and has an oblique suture with the palatine. The ectopterygoid is only partially visible, appearing as a transverse bar between the quadrate process and the jugal.

The braincase is poorly preserved in all available specimens. In LH 370, it has been split horizontally, leaving an internal view of the braincase floor (Fig. 6A). The sphenoid carries a long ossified parasphenoid rostrum between short divergent

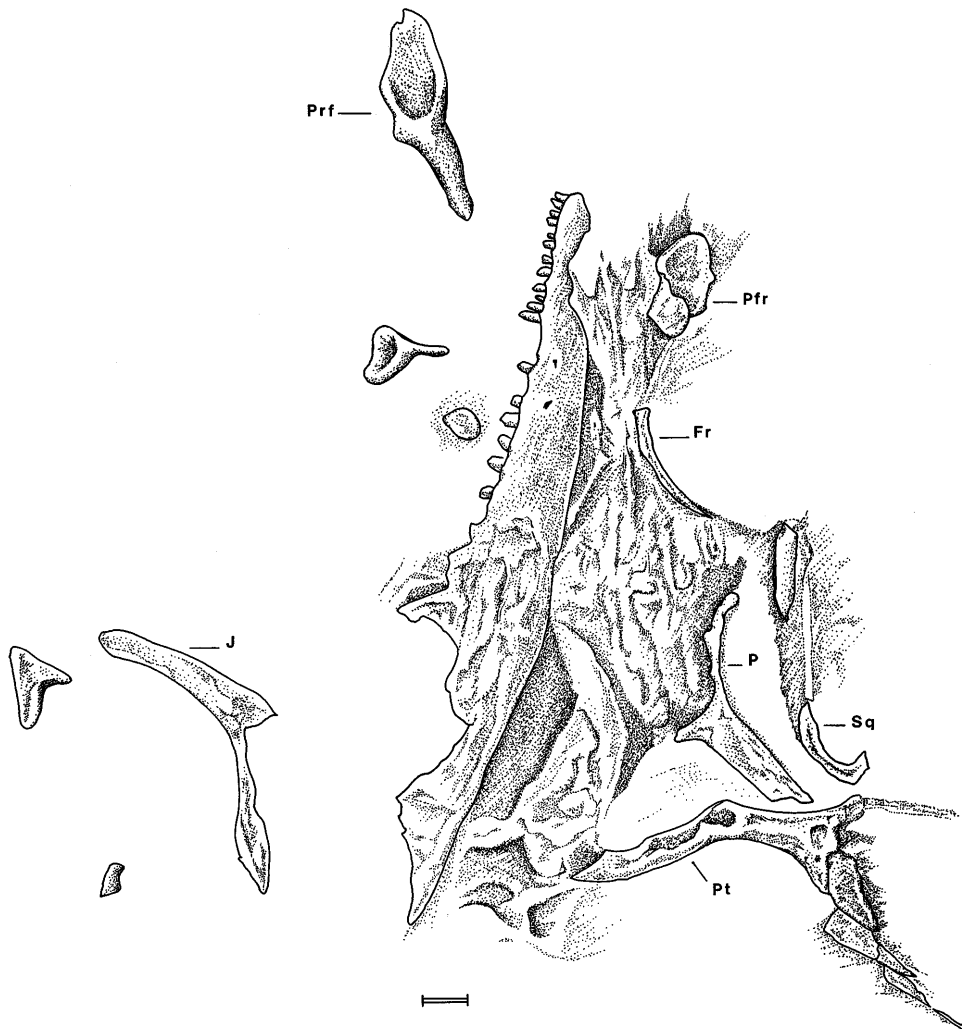


Figure 9. *Meyasaurus (Ilrdaesaurus) crusafonti*, IPPS Montsec 10, skull.

basipterygoid processes, but no details of nerve foramina or hypophysial fossa are preserved. The sphenoccipital suture is not visible and the bones of the braincase may be coossified. The basioccipital appears to contribute to the lateral opening of the recessus scala tympani, but there is no development of a deep occipital recess.

The lower jaw is best preserved in LH 370 (Figs 2B, 6A) and LH 6026 (Fig. 7). The dentary is deep, and bears a strong subdental shelf above an open Meckelian fossa. As visible, the lateral surface is smooth and pierced by eight or nine sensory nerve foramina, but the presence or absence of a ventral muscle scar cannot be

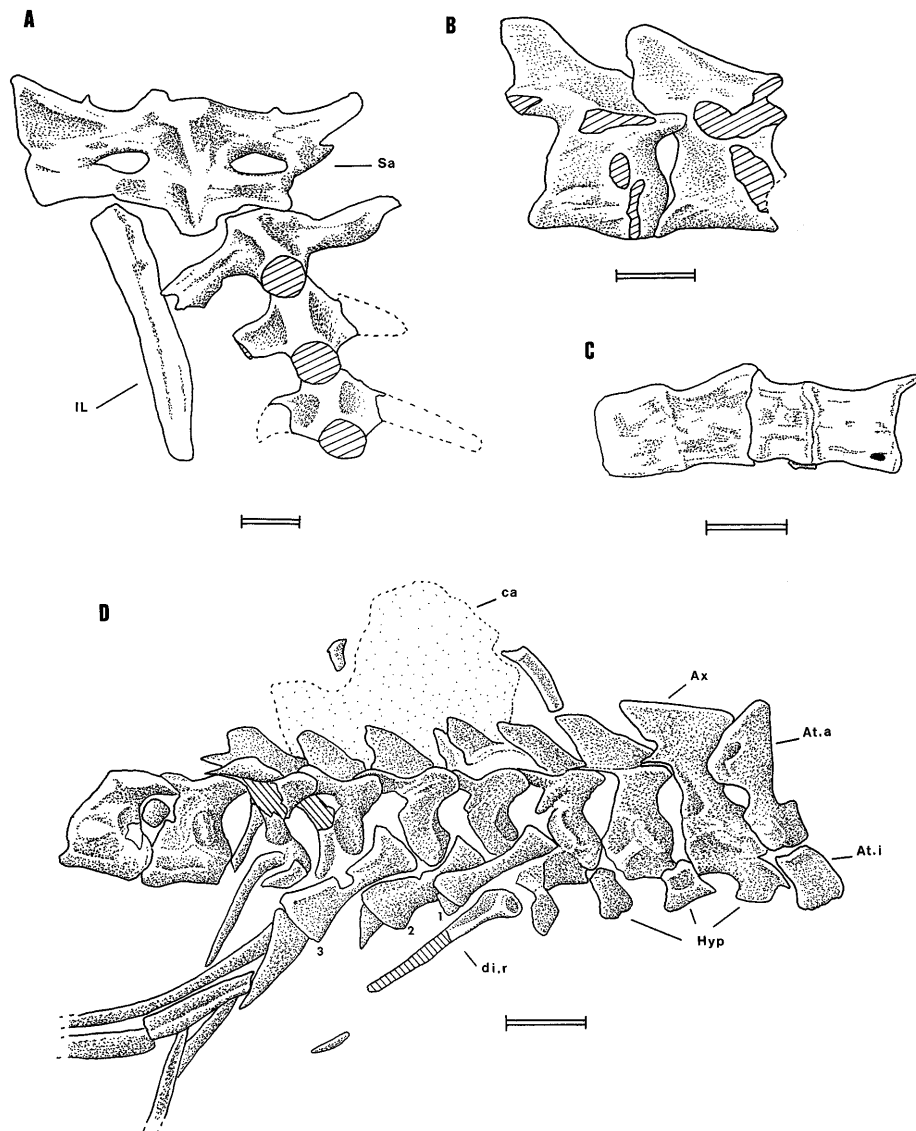


Figure 10. *Meyasaurus diazomeralli*, vertebrae. A,B, LH 370A, A, sacral and anterior caudals in ventral view, and B, dorsal vertebrae, lateral view; C, LH 33A caudal vertebrae in left lateral view; D, LH 33A, cervical vertebrae in right lateral view. Scale bars = 1 mm.

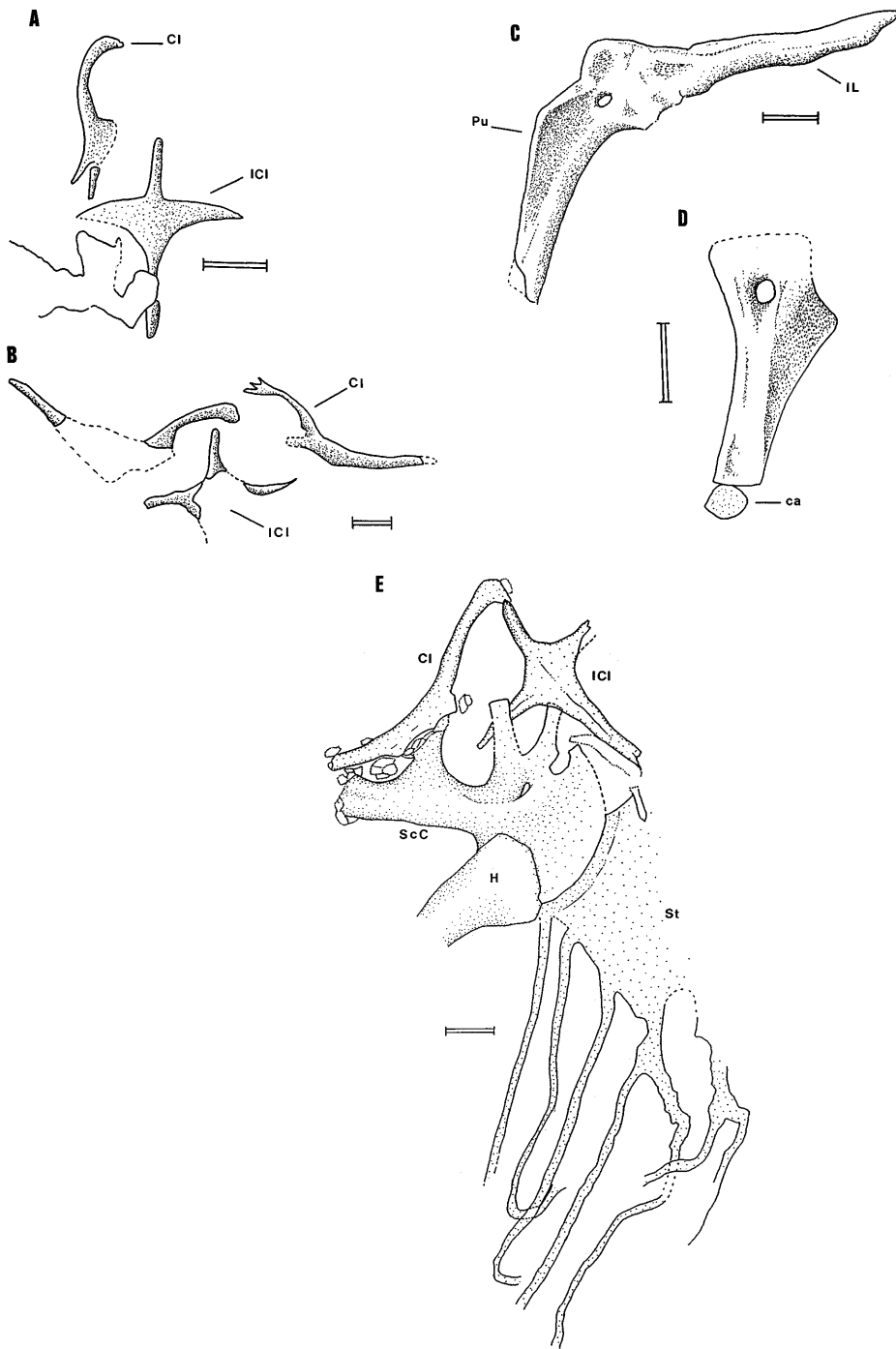


Figure 11. *Meyasaurus diazromerali*, girdles. A,B, dermal pectoral girdle of A, LH 372A and B, LH 370B; C,D, pelvic girdle, C, left pubis and ilium of LH 370A and D, left pubis of OH 33A; E, LH 14317, right pectoral girdle and sternal plate in ventrolateral view. Scale bars = 1 mm.

determined. There are about 30 teeth, monocuspid at the front and bicuspid at the rear. The bicuspidy is particularly marked in the young LH 372, as in the juveniles of extant lacertids. In LH 370, many of the teeth are undergoing replacement in a clearly iguanid pattern (Fig. 2B) — fully lingual not posterolingual (contra Richter, 1994a).

Of the accessory bones, the coronoid is divided into a rather small dorsal process, a deep medial process, a small anterior process and a short surangular process. There is also a small lateral flange (Fig. 7). The surangular is relatively deep and, with the prearticular and dentary, bounds an adductor fossa which is broad but appears to lack the lateral extension seen in most lacertoid lizards. The articular is short, with a transverse articular surface, a short strong retroarticular process and a triangular angular process. The splenial is large and a narrow, ventrally placed angular curves up onto the posterolateral surface.

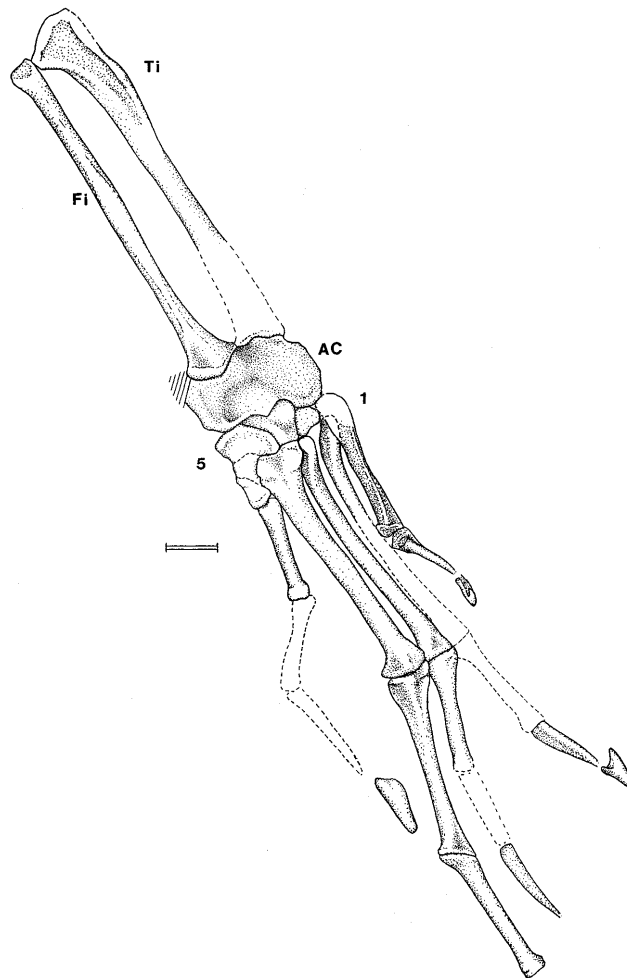


Figure 12. *Meyasaurus diazromerai*, LH 14317, right crus and pes, plantar view. Scale bar = 1 mm.

*Postcranial skeleton*

*Vertebrae and ribs.* The axial skeleton appears to consist of 25 presacral vertebra, two sacrals and an unknown number of caudals. The vertebrae are procoelous, with a broad but relatively short condyle. Ribs begin on the fourth cervical (contra Hoffstetter, 1966), and extend through the length of the presacral series; intercentra are present only in the neck (hypapophyses) and tail (haemal arches).

There are eight cervical vertebrae (CV) with short keeled centra and relatively long neural spines decreasing in height posteriorly. The region is best preserved in LH 33A (Fig. 10D). It shows clearly the presence of well-developed hypapophyses associated on at least the first five vertebrae (behind this, the intercentral region is obscured by the expanded ribs). These hypapophyses are attached intercentrally, with the second hypapophysis of the axis sending a small process forward beneath that bone. Each cervical bears a small lateral process, presumably for muscle attachment, but the first rib is attached to CV4. Using the standard criterion of the first rib attached to the sternum, the first dorsal vertebra is presacral nine. Dorsals (Figs 4B, 10B) are generally longer than cervicals, with rectangular centra that bear ventral longitudinal ridges and grooves. The arch bears a short neural spine and accessory facets (zygosphene-zygantrum system). All dorsal vertebrae are rib bearing. The sacral vertebrae can be fused at their expanded tips to enclose a foramen sacrale (LH 370), the anterior vertebra slightly larger than the posterior one (Fig. 10A). The anterior caudals are non-autotomous and bear well-developed caudal ribs, decreasing in length quite rapidly from the first to the sixth (very small) (Fig. 4B). Autotomy septa being on or about the sixth caudal (LH 33B) and extend to the tip of the tail. The septa divide the vertebrae into unequal halves (anterior shortest) and, in more anterior caudals, lie behind a single small process. In both LH 370 and LH 14317, most of the original tail had been autotomised during life and the specimens bears a trace of the cartilaginous replacement (ca.e, Fig. 1A).

The first three cervical ribs, on CV4-6, are short, increasing in length from first to last, and expanded distally (especially on CV5). In LH 33 (Fig. 10D), these ribs are seen to bear cartilaginous extensions. The next two ribs closely resemble those of the dorsal series, except that they are slightly shorter. Dorsal ribs are seen mostly clearly on LH 14317. They can be divided into three groups: the first five pairs met the sternum (three) and xiphisternum (two); they are followed by a series of six rib pairs which are longer and give the body a rather barrel-like appearance (Figs 1B, 2A); these, in turn, are then followed by a final group of 6 pairs of shorter ribs on the posterior dorsals (Fig. 3B).

*Pectoral girdle and forelimb.* The pectoral girdle is preserved in LH 370, LH 372, LH 14317 and LH 6026 (Figs 7, 11A,B,E), but is incomplete in LH 13510 and LH 33. Where preserved, the scapulocoracoid shows a series of anterior emarginations — one within the scapula, one at the scapulocoracoid junction, and one clearly within the coracoid at the level of the coracoid foramen. In LH 14317 (Fig. 11E), there appears to be a second coracoid emargination but the lower border is incomplete and may not have been fully ossified. In this respect, the scapulocoracoid of the Las Hoyas lizard resembles that of *Meyasaurus faurii* from Montsec. Despite Hoffstetter's (1966) reconstruction, it is not clear from the specimen that the lower margin of the coracoid is complete and there is a clear notch in this margin. In the Las Hoyas lizards, the scapula blade is elongate and fairly narrow; it contains an emargination within a recess. In the much larger *Meyasaurus faurii*, the recess is



present but is filled by a thin lamina of bone. The difference therefore may be age/size related.

The interclavicle is cruciform with slender anterior and lateral processes supporting a clavicle of distinctive shape (Fig. 11A,B,E). The proximal portion of the clavicle is expanded and fenestrate, but its margins are incomplete medially, giving a curious bifurcate structure similar to that found in some living lacertid lizards. The anterior limb is longest and ends medially in a small posteriorly directed knob; the posterior limb is short. The distal part of the clavicle has an expanded stem which then narrows as it curves laterally. All specimens preserve remnants of the cartilaginous sternum, but the element is seen most clearly in LH 14317 (Fig. 11E). The sternal plate is rhomboid and there is no trace of a sternal fontanelle. There are four points of costal insertion on each side. The first three supported sternal ribs (*sensu stricto*); the fourth has the structure of a short rod (xiphisternum) which bifurcates to provide insertion points for two further ribs (Fig. 11E).

The humerus is a sturdy element (70% femur) with expanded proximal and distal ends: the distal epiphyses bearing the joint surfaces are sometimes detached at the elbow (as in *Meyasaurus faura*). None of the specimens show the ectepicondyle clearly enough to show whether it is perforate. Radius and ulna are shorter (average 65% humerus) and gracile without notable features. The carpus is not clearly visible on any specimen. The hand is relatively large ( $1.5 \times$  humerus length) with long metacarpals (MC3 and MC4 roughly equal in length) and a phalangeal formula of 2:3:4:5:3. The distal phalanges are not clearly elongated, and the claws are short but robust.

*Pelvic girdle and hindlimb.* The ilium has a long slender blade which reaches back to the level of the first anterior caudal (caudosacral) (Fig. 10C). The pubis long and slender with a proximal obturator foramen and a small triangular pubic tubercle (pectineal process) in a proximal position but with some ventral displacement (Fig. 10C,D).

Like the humerus, the femur is robust and of moderate length (roughly 20% snout-vent length). The tibia and fibula are shorter (65–75% femur with the lower values in the youngest specimens). In the ankle, the astragalus and calcaneum appear incompletely ossified in LH 372 but are fused in LH 370 and LH 14317 (Fig. 12). The combined bone forms the strong proximal part of the tarsus, widest medially where it carries a proximal crest which articulates with a notch in the distal tibial epiphysis. Distally, the bone is notched to accommodate an enlarged distal tarsal (dt) four (Fig. 12).

There is a smaller dt3 but apparently no dt2. The foot (Fig. 12) is long ( $1.2 \times$  femoral length). The metatarsals match the usual lizard condition. The fifth is very short and hooked. The remaining metatarsals are long (3 subequal to 4) and slender, with expanded ends. The phalangeal formula is 2:3:4:5:4, with the fifth digit of greater length than the second. The claws are strong.

#### COMPARISON WITH OTHER SPECIMENS OF *MEYASAURUS*

*Meyasaurus* (including *Ilerdaesaurus*) has been described from four localities in Spain: Montsec (Berriasian-Valenginian, Catalonia); Uña (Barremian, Cuenca Province, Castilla-La Mancha), Galve (Barremian/Aptian, Teruel Province) and, now, Las Hoyas (Barremian, Cuenca Province, Castilla-La Mancha). These lizards show a

broad general resemblance in features of the skull, dentition and postcranial skeleton (especially allowing for differences in size/age, e.g. in the scapula), but show more subtle differences in features such as tooth numbers and the shape of the frontals.

The holotype of *M. (I) crusafonti* (IPPS Montsec 10) is a skull with both frontals and dentition (Fig. 9). The specimens from Uña, Galve and Las Hoyas all differ from *M. (I) crusafonti* in having a frontal in which the interorbital region is much narrower relative to the posterior width. Richter (1994a) erected a new species *M. (I) unaensis* for the Uña specimens on the basis of a number of character states:

1. *The high number of teeth* – about 40 on the dentary.
2. *The fact that the posterior teeth are always bicuspid, not tricuspid*, where those of the *M. (I) crusafonti* holotype are said to approach tricuspidy (a feature that more recent damage to the tooth crowns in *M. (I) crusafonti* makes difficult to confirm). However, in living lacertids, this feature can vary along the tooth row and with the age of the individual, with one or more tricuspidate teeth appearing at the end of the row in older specimens.
3. *Higher number of lateral foramina in the dentary (7)*. The dentary of *M. (I) crusafonti* shows 5 foramina, but a recent survey by one of our students (Tim Kerr UCL) showed that there is variation in this feature within taxa, and even between right and left sides of the same animal. Thus, for example, one specimen of *Amphibolurus barbatus* had seven foramina on the right and five on the left; a specimen of *Cnemidosaurus* had nine on the right and six on the left; and a series of *Varanus griseus* ranged from 5–7. A difference in number of two foramina is therefore of questionable significance at the specific level.
4. *Presence of a ventral facet (scar) for the pterygomandibularis*. This region is not visible on the holotype of *M. (I) crusafonti* and cannot be used to distinguish the species.
5. *Prefrontal with a sharp crest*. Again, this aspect is not visible on the holotype of *M. (I) crusafonti*, but there is no trace of it on the impression.
6. *Unpaired, fully fused frontal*. In the Las Hoyas specimens, this feature varies with age/size.
7. *Extreme waisting of the frontal*. The frontals of the Uña specimens are certainly much narrower in the orbital region than the frontal of *M. (I) crusafonti*.
8. *Shallow, but clear, ornamentation on the frontal*. Since the dorsal surface of *M. (I) crusafonti* is known only in impression, the degree of ornamentation is difficult to judge, but the preserved impression shows an irregular surface suggestive of ornament.
9. *Very gracile jugal with a row of foramina*. Foramina for zygomatic branches of the maxillary division of the trigeminal nerve are a general feature in jugals. Their absence in *M. (I) crusafonti* reflects surface damage to the bone. Allowing for the fact that the anterior process is broken in *M. (I) crusafonti*, jugal shape is also an uncertain criterion.
10. *Zygomatic process of jugal very small and pointed*. The back of the jugal is broken in *M. (I) crusafonti*.

Of these features, frontal shape and tooth number are most reliable. The specimens from Uña have smaller and more numerous teeth than those from any other locality. This, in combination with the frontal shape, distinguishes them from *M. (I) crusafonti* at the specific level. The Las Hoyas lizards resemble *M. (I) unaensis* in frontal shape, but differ in retaining the lower tooth count. The difference in tooth number is greater than that found within modern lizard species (lacertids for example), and supports the erection of a second new species for the Las Hoyas

*Meyasaurus*. The Galve lizards resemble those from Uña and Las Hoyas on frontal shape, but without the dentition, their specific relationship cannot be determined.

*M. (I) crusafonti* is from the same locality as *M. faurai* and is probably conspecific with it, but without an associated specimen from Montsec, a degree of uncertainty remains (Uña and Las Hoyas are geographically close yet have different species, and more than one species of the living *Lacerta* may be found together). It is proposed, therefore, that the specific name *faurai* be restricted to the generic holotype, and that in the absence of evidence to the contrary, the name *M. crusafonti* be retained for the skull specimen which can be compared directly with specimens from other localities.

*Meyasaurus faurai* Vidal 1915, emend von Huene 1952

*Type and only specimen.* No. 534, Museu Geologia Municipal, Barcelona.

*Locality.* Rubies, Santa Maria del Meia, Montsec, Catalonia, Spain.

*Type horizon.* Pedrera de Rubies, Berriasian-Valenginian (Lacasa, 1981).

*Diagnosis.* As for genus; skull unknown.

*Meyasaurus crusafonti* (Hoffstetter 1966)

*Type and only specimen.* Institute of Paleontology, Sabadell, Montsec 10 (Fig. 9).

*Locality.* Rubies, Santa Maria de Meia, Montsec, Catalonia, Spain.

*Type horizon.* Pedrera de Rubies, Berriasian – Valenginian.

*Diagnosis.* Species of *Meyasaurus* in which the frontals, though constricted between the orbits, are less markedly so than in other species; 30 tooth positions in each jaw ramus.

*Meyasaurus unaensis* (Richter 1994)

*Type specimen.* IPFUB Uña L.4a.

*Locality.* South-west of Uña, Cuenca Province, Castilla-La Mancha, Spain.

*Type horizon.* Limnic lignites in Wealden facies, *Atopochara trivolis triquetra* Zone (Upper Barremian).

*Diagnosis.* A species of *Meyasaurus* in which the frontals are greatly constricted between the orbits and in which there are in excess of 40 teeth in each jaw ramus.

THE TAXONOMIC POSITION OF *MEYASAUROS* VIDAL 1915

Hoffstetter (1966) shows clearly that *Meyasaurus* was a lizard and not a rhynchocephalian. The question is that of the taxonomic position of *Meyasaurus* within Squamata.

Most recent workers on squamate relationships accept the hypothesis that there

are four major groups of modern lizards: Iguania, Gekkota, Scincomorpha and Anguimorpha. Of these, Iguania stands as the sister taxon to the other three which together constitute the Scleroglossa. Within Scleroglossa, Gekkota is the sister taxon of Scincomorpha + Anguimorpha (Autarchoglossa) (e.g. Estes *et al.*, 1988).

Hoffstetter (1966) observed that *Meyasaurus* and '*Ilerdaesaurus*' showed a mixture of scincomorph and anguimorph features, though this was partly based on a misinterpretation of the neck region in *Meyasaurus* (Evans & Barbadillo, in press). Estes (1983) was uncertain as to their position but thought Scincomorpha most probable, while Richter (1991, 1994a), on the basis of her Uña specimens, proposed that *Meyasaurus* (*Ilerdaesaurus*) was a primitive anguimorph. However, this conclusion rested primarily on the presence of a small intramandibular septum (found also in some iguanians), medial striae on the tooth tips (not restricted to anguimorphans) and what was described as anguimorph tooth replacement, a problematic interpretation that we have been unable to confirm. Richter's (1994a) description seems to be based mainly on the anterior symphyseal region of the jaw where the teeth are closely packed and twisted in relation to the jaw axis. The normally implanted teeth in the central section of the jaws in *M. diazomeralli* show a clear pattern of medial replacements (iguanaid type) (Fig. 2B).

In order to make a comprehensive reevaluation of the phylogenetic position of *Meyasaurus*, we have compared its character distribution against that of modern lizard families using the 148 characters listed by Estes *et al.* (1988). One amendment has been made to the character list; this splits character 124 (the shape of the pubis) into two parts — the first is retained as character 124, the second part forms character 149 at the end of the data set (Appendix 1 and 2).

The resulting matrix (Appendix 2) was run on Hennig 86 (Farris, 1988) using mHennig and bb (branch and bound) programmes. Preliminary runs included snakes, amphisbaenids and dibamids, but their removal had no effect on the relative positions of other taxa, and in subsequent runs they were omitted. The combination of mHennig and bb programmes yielded six equally parsimonious trees of length 313 (ci51, ri58). With respect to *Meyasaurus* the only difference between the trees was that the fossil genus alternated from a position as sister taxon to Teiidae alone to a position as sister taxon to Teiidae + Gymnophthalmidae. The Nelson consensus tree left the three terminal taxa in a trichotomy. Running the character states unordered shortened the tree slightly (length 298) but had little effect on its consistency (ci 53, ri 56). The position of *Meyasaurus* with respect to other scincomorphs remained unchanged. The application of successive weighting (Farris, 1969; Carpenter, 1988) yielded a single, very much longer (length 889 steps) but more consistent (ci 84, ri 87) tree in which *Meyasaurus* was placed as the sister taxon of Teiidae + Gymnophthalmidae (Fig. 13). Whatever the merits or demerits of weighting, the process did not significantly alter the position of any taxon. *Meyasaurus* is securely nested within Scincomorpha, and its position within Lacertoidea is strongly supported.

#### MEYASAURUS AND THE FOSSIL RECORD OF SCINCOMORPHA

Living scincomorphs form a large and successful group with a worldwide distribution from the Arctic Circle to Tasmania. Of all lizard groups, scincomorphs also have the best fossil record with a range of taxa documented from the Jurassic as well as the Cretaceous (Estes, 1983; Evans, 1993). Estes *et al.*'s (1988) review of

modern lizard relationships divided Scincomorpha between two major groups: the Scincoidea (scincids and cordylids) and the Lacertoidea (xantusiids, lacertids, teiids and gymnophthalmids). Our runs of the lizard data matrix generally agree with this, although trees with cordylids and scincids as successful outgroups to the Lacertoidea were equally parsimonious.

Within Scincoidea (*sensu* Estes *et al.*, 1988), scincids are recorded from the late Cretaceous (e.g. Estes, 1983), with possible acontines from the Aptian/Albian of Mongolia (Alifanov, 1993). Cordylid osteoscutes have been described from the late Cretaceous of India and Madagascar (Gao, 1994), but if the Jurassic and early Cretaceous paramacellodids are part of this lineage—as their rectangular osteoscutes suggest (e.g. Estes, 1983)—then the scincid-cordylid dichotomy occurred prior to the Middle Jurassic.

Of lacertoids, gymnophthalmids are unknown in the fossil record and lacertids are unrecorded prior to the Palaeocene (Rage & Auge, 1993). Xantusiids are known from the Palaeocene (North America, Estes, 1983), but have also been reported from the early (Aptian/Albian) and late Cretaceous of Mongolia (Alifanov, 1993). In

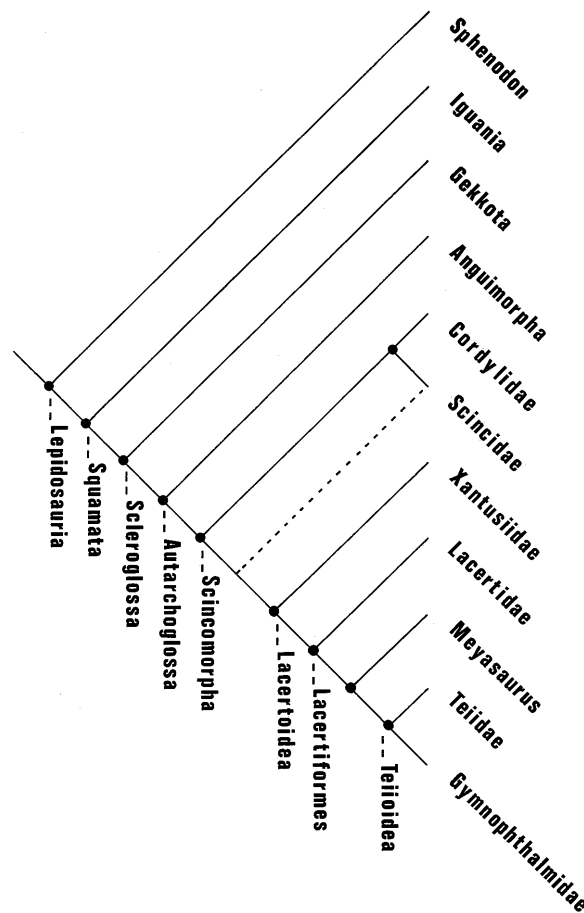


Figure 13. Cladogram showing hypothesis of relationships for *Meiasaurus* within Squamata, based on the data matrix in Appendix 2, and using data and characters taken from Estes *et al.*, 1988.

addition, Borsuk-Bialynicka (1988) has described several late Cretaceous non-teiid lacertoids (e.g. *Eoxanta*, *Globaura*) from Mongolian localities. Teiids have by far the best Mesozoic record (with a sharp decline at the K-T boundary) and a diversity of late Cretaceous taxa (mostly the large polyglyphanodonts) are documented from China, Mongolia and North America (Borsuk-Bialynicka, 1991; Alifanov, 1993; Gao, 1990; Gao & Fox, 1991). Before that the record is poor, but the interpretation of *Meyasaurus* as a teioid relative, and new finds of possible teioids in the early Cretaceous of Japan (Dr Makoto Manabe, pers. comm. and work in progress), suggests an early (Jurassic) differentiation of lacertoids as well as scincoids. Work on new middle and late Jurassic scincomorphs (SEE) should shed further light on the early history of the group.

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## APPENDIX 1

*Characters used in phylogenetic analysis*

Characters and states used in the construction of the data matrix in Appendix 2, with condition in *Meyasaurus* shown in *italic*. Characters from Estes *et al.*, 1988, with a division of state 124 to give an additional character: 149.

1. Ontogenetic fusion of premaxillae: (0) paired well into postembryonic ontogeny or (1) fused in embryo – *apparently, 1*
2. Bony external nares extent – *relatively small, 0*
3. Ontogenetic fusion of nasals: (0) paired well into postembryonic ontogeny or (1) fused in embryo – *probably, 0*
4. Nasal-prefrontal contact: (0) present or (1) absent, with anterior process of frontal separating them – *from M. crusafonti probably little or no contact, 1*
5. Prefrontal contact with posterior orbital bones: (0) does not contact posterior orbital bones or (1) does contact above orbit – *no contact, 0*
6. Ontogenetic fusion of frontals: (0) paired well into postembryonic ontogeny or (1) fused in embryo or early posthatchling – *LH 372 suggests not fully fused in hatchling, 0*
7. Lateral borders of frontals: (0) more or less parallel or (1) strongly constricted between orbits – *clearly, 1*
8. Frontal shelf: (0) lacking broad shelf below nasals or (1) broad shelf with frontals often exposed dorsolaterally as wedges or spikes – *apparently, 1*
9. Descending processes of frontals: (0) weakly developed and prefrontals broadly participate in orbitonasal fenestra or (1) strongly developed and replace prefrontals – *LH 370, LH 372 and LH 6026 show that the cristae cranii deepen anteriorly, 1*
10. Median contact of descending processes of frontals: (0) – none or (1) in contact below olfactory tracts – *no contact, 0*
11. Frontal tabs: (0) no tabs or (1) frontal tabs project posteriorly over parietal – *no obvious projecting tabs, 0*
12. Postfrontal: (0) present, separate at some stage or (1) absent – *from LH 13510, 0*
13. Postfrontal forking: (0) subtriangular, not forked medially or (1) semilunate, forked medially – *LH 13510 has a postfrontal which is forked but subtriangular; the trend is therefore towards 1*
14. Postfrontal fusion: (0) separate or absent or (1) fused to postorbital – *separate, 0*
15. Postfrontal size: (0) extensive, not confined to orbital rim or (1) reduced and confined – *from LH 13510, 0*
16. Postorbital: (0) present or (1) absent – *from LH 372 and LH 13510, 0*
17. Postorbital contribution to posterior border of orbit: (0) forms about one half of orbital border and is mainly an orbital bone or (1) forms less than one half and is mainly a temporal bone – *from LH 372 and LH 13510, definitely in orbit, but less than half; then extends back in temporal region, 1*
18. Jugal-squamosal contact: (0) no contact, bones widely separately or (1) contact or approach closely – *LH 372 and LH 13510 suggest the jugal and squamosal did not meet, but LH 6026 gives the impression that they were not widely separated, 1*
19. Supratemporal fenestra: (0) open or restricted by postfrontal or (1) restricted mainly by postorbital – *open but restricted posteriorly by squamosal, 0*
20. Supratemporal fenestra: (0) open or restricted mainly by postorbital or (1) restricted by postfrontal – *as before, 0*
21. Ontogenetic fusion of parietals: (0) paired well into postembryonic ontogeny or (1) fused early – *fused in LH 372, 1*
22. Parietal tabs: (0) absent or (1) present as thin triangular structures extending into fossae below frontal – *from LH 370 and LH 6026, 1*
23. Parietal downgrowths: (0) absent or (1) pointed ventral downgrowths – *visible, although incomplete, in LH 13510, 1*
24. Parietal table: (0) extensive posterior table covers most of braincase, postparietal processes short or (1) table short, braincase exposed, postparietal processes long – *from LH 6026, some extension of parietal table to each side of the processus ascendens of the supraoccipital, but the postparietal processes are long and the braincase would have been exposed, 1*
25. Parietal foramen: (0) within parietal or (1) at frontoparietal suture or (2) in frontal – *in parietal behind frontoparietal border, 0*
26. Parietal foramen: (0) present or (1) absent – *present, 0*
27. Posterior extent of maxilla: (0) extends well back under orbits or (1) only just beyond anterior edge of orbit – *clearly, 0*
- 28–30. Lacrimal – *no data on lacrimal (-)*
31. Anteroventral border of orbit: (0) formed by maxilla with jugal confined to medial surface or (1) formed by jugal – *LH 13510 suggests, 1*
32. Jugal/postorbital bar: (0) jugal large, bar complete or (1) jugal reduced or absent – *clearly, 0*
33. Squamosal: (0) present or (1) absent – *0*
34. Dorsal process of squamosal: (0) present or (1) absent – *present – like that of many teiids, 0*
35. Supratemporal: (0) present or (1) absent – *present, 0*
36. Palpebral ossifications – *no data (-)*
37. Pterygoid lappet of quadrate: (0) present or absent (1) – *very small lappet present, coded 0*
- 38–39. Vomers – *no data (-)*
- 40–42. Septomaxilla – *no data (-)*
- 43–45. Details of palate – *no data (-)*
46. Ectopterygoid size and restriction of suborbital fenestra: (0) ectopterygoid relatively slender, fenestra widely open, or (1) ectopterygoid enlarged medially, restricting suborbital fenestra – *from LH 370, fenestra widely open, 0*
47. Epipterygoid: (0) present or (1) absent – *0*



48. Pyriform recess: (0) narrow throughout or (1) broad – *LH 370 suggests, 0*
- 49–53. Braincase details – *no data (-)*
54. Jaw adductors: (0) extend onto dorsal surface of parietal or (1) ventral – *LH 13510 shows attachment surfaces on the lateral margins of the parietal, 0*
55. Meckels canal: (0) open or (1) closed with or (2) without suture *open, 0*
56. Intramandibular septum – *Richter (1991, 1994a) records as present on the basis of Uña material; no data from Montsec or Las Hoyas, 1*
57. Meckelian canal: (0) medially for whole length or (1) ventral anteriorly – *LH 370 suggests 0*
58. Subdental shelf: (0) small or absent or (1) large – *large, 1*
59. Subdental shelf: (0) present or (1) absent – *present, 0*
60. Dorsal extension of coronoid process of dentary: (0) small or absent or (1) large extending onto coronoid – *LH 372 and LH 6026 suggest 0*
61. Lateral view of disarticulated surangular: (0) tapers anteriorly, pointed distally, (1) expanded anterodorsally and nearly vertical at anterior margin, (2) as in state 1, but anterior end of surangular terminates relatively closer to level of coronoid eminence on surangular – *LH 6026 suggests 0*
62. Prearticular shape – *insufficient data (-)*
63. Posterolateral dentary shape: (0) no surangular or coronoid notches or (1) notches present or (2) notches reduced – *no notch, 0*
64. Dentary/postdentary: (0) much overlap or (1) overlap reduced – *overlap, 0*
65. Splenial reduction: (0) splenial extends anterior to mid tooth row or (1) shorter or (2) absent – *LH 370 suggests 0*
66. Splenial posteriorly: (0) posterior to apex of coronoid process or (1) not posterior to coronoid process or (2) limited overlap posteriorly – *LH 370 suggests it reaches level of apex of coronoid, 0*
67. Splenial-dentary suture: (0) extensive bone to bone contact or (1) reduced, much connective tissue present – *unclear, but LH 370 suggests 0*
68. Coronoid with lateral lappet: (0) absent or covered by dentary or (1) present – *from LH 370 and LH 6026 small lappet, 1*
69. Coronoid process anteriorly: (0) curves smoothly onto dentary or (1) anterior border levels out before reaching dentary producing long low extension – *LH 370 and LH 6026 suggest 0*
70. Anterior end of coronoid: (0) clasps dentary overlapping medially and laterally or (1) abuts against dentary – *LH 370 suggests 0*
71. Restriction of lateral process of coronoid: (0) unrestricted or (1) restricted by dentary and surangular so limited – *unrestricted, 0*
72. Angular: (0) present or (1) absent – *from LH 370 present, 0*
73. Preaticular crest: (0) absent or (1) present or (2) prominent with embedded angular process – *from LH 370, small crest but angular process not embedded, 1*
74. Retroarticular process: (0) dorsal surface with sulcus or pit or (1) none – *there is a pit in LH 370, 0*
75. Retroarticular process direction: (0) posterior or (1) inflected medially – *small medial inflexion, 0*
76. Retroarticular process medial margin: (0) smooth or (1) tubercle or flange – *smooth, 0*
77. Retroarticular process offset: (0) no offset or (1) offset with lateral notch – *no obvious offset, 0*
78. Retroarticular process: (0) tapered or parallel-sided or (1) broader posteriorly – *tapered, 0*
79. Retroarticular process torsion: (0) no posterior torsion or (1) posterior torsion – *there appears to be some degree of torsion but the preservation of the specimens makes it difficult to judge (-)*
80. Finger-like angular process: (0) absent or (1) present – *as defined by Estes et al. (1988), this character is problematic. A finger-like angular process is a derived state of many iguanians. In the Las Hoyas lizards, the angular process is not finger-like – it is a broad-based triangle. However, this feature shows both inter- and intraspecific variation in living taxa. In some iguanians (e.g. Acanthosaura, JB pers. obs.), the process resembles that of the Las Hoyas lizard. For this reason, Meyasaurus has been coded (1) – but trial runs on Hennig 86 shows that changing the polarity of this state does not affect the topology of the resulting tree*
81. Adductor fossa: (0) small or moderate or (1) expanded and inflated – *an expanded, and inflated (i.e. with a large lateral recess) adductor fossa is a derived character of lacertids and teiids. The adductor fossa of the Las Hoyas lizards is large but, as preserved, appears to lack the lateral inflation. It has therefore been coded (0)*
- 82–83. Palate teeth – *no data (-)*
84. Marginal teeth: (0) pleurodont or (1) acrodon – *pleurodont, 0*
85. Replacement: (0) iguanid type or (1) posterolingual – *iguanid type, 0*
86. Plicidentine: (0) absent or (1) present – *absent, 0*
87. Step or offset in tooth margin of maxilla: (0) absent or (1) present – *unclear (-)*
- 88–91. Scleral ossicles and hyoid – *no data, (-)*
92. Vertebral condyle: (0) not oblique or (1) oblique – *visible, not oblique, 0*
93. Vertebral centrum: (0) amphicoelous or (1) procoelous – *procoelous, 1*
94. Centrum constricted before condyles: (0) not or (1) constricted – *not, 0*
95. Zygosphene and zygantrum development: (0) weakly developed or absent (1) strongly developed – *from LH 13510, strongly developed, 1*
96. Zygosphene and zygantrum: (0) present or (1) absent – *from LH 13510, present, 0*
97. Cervical intercentra attachment 1: (0) intervertebral or fixed under anterior part of following centrum, (1) sutured to posterior part of preceding centrum, (2) fused to posterior part of preceding centrum – *from LH 11006, intervertebral, 0*

98. Cervical intercentra attachment 2: (0) intervertebral or fixed under posterior part of preceding vertebra, (1) sutured to anterior part of following centrum, (2) fused to anterior part of following centrum – *intervertebral, 0*
99. Trunk intercentra: (0) present or (1) absent – *absent, 1*
100. Transverse processes on caudal vertebrae: (0) single pair of processes or two pairs of converging processes or (1) two pairs of diverging processes – *single pair of processes, 0*
101. Transverse processes of caudal vertebrae: (0) single pair of processes, (1) two pairs of diverging processes, (2) anterior pair of processes absent – *single pair of processes, 0*
102. Location of autotomy septa in caudal vertebrae: (0) within a single pair of transverse processes, between two pairs of transverse processes, or anterior to a single pair of processes, (1) posterior to a single pair of transverse processes – *from LH 14317, behind a single pair of processes, 1*
103. Autotomy septa: (0) present or (1) absent – *present, 0*
104. Number of presacrals: (0) 23 or more or (1) fewer – *25, 0*
105. Number of presacrals: (0) 25 or fewer or (1) more – *25, 0*
106. Number of presacrals: (0) 26 or fewer or (1) 27 or more – *0*
107. Number of cervicals: (0) 8 or more or (1) fewer than 8 – *8, 0*
108. Number of cervicals: (0) 8 or fewer or (1) more than 8 – *0*
109. Number of rib attachments on sternum: (0) 5 or (1) 4 or (2) 3 or (3) 2 or fewer – *from LH 14317 there are four attachment points, 1*
110. Postxiphisternal inscriptional ribs: (0) none continue midventrally or (1) at least some do – *none, 0*
111. Scapular emargination: (0) absent or (1) present – *present, 1*
112. Anterior primary coracoid emargination: (0) absent or (1) present – *from LH 13510 present, 1*
113. Posterior secondary emargination: (0) absent (1) present – *from LH 14317 probably present, 1*
114. Epicoracoid cartilage – *no data (-)*
115. Clavicle: (0) present or (1) absent – *present, 0*
116. Clavicle angulation: (0) simple curved rods or (1) angle away from scapulocoracoid – *angled, 1*
117. Clavicle meets: (0) scapula or suprascapula (1) – *not clear, (-)*
118. Interclavicle: (0) present or (1) absent – *present, 0*
119. Interclavicle lateral process: (0) present or (1) absent – *present, 0*
120. Interclavicle: (0) T-shaped or (1) cruciform – *cruciform, 1*
121. Sternal fontanelle: (0) absent or (1) present – *from LH 14317, absent, 1*
122. Ectepicondylar foramen: (0) present or (1) absent – *uncertain, (-)*
123. Notching of distal tibial epiphysis: (0) absent or (1) present – *from LH 14317, present, 1*
124. (Modified somewhat from Estes *et al.*, 1988, see also 149) ventral view of pubis: (0) pubis short or only moderately elongated with symphyseal process ventrally directed, (1) pubis very long with symphyseal process elongate and anteriorly directed – *pubis moderately elongated, 0*
125. Postcloacal bones: (0) absent or (1) present – *no trace, 0*
126. Ventral body osteoderms: (0) absent or (1) present – *no trace, 0*
127. Dorsal body osteoderms: (0) absent or (1) present – *no trace, 0*
128. Cephalic osteoderms: (0) absent or (1) present – *from LH 13510, absent, 0*
129. Dermal rugosities: (0) absent or (1) present not vermiculate or (2) present, vermiculate – *vermiculate with scale impressions, shown clearly in LH 13510, 2*
130. Epiphysis fusion: (0) at same time or after fusion of braincase elements or (1) prior to fusion of braincase elements – *braincase too poorly preserved to know if fused or not, however presence of unfused epiphyses in all specimens, including Montsec suggests 0*
- 131–148. Soft part characters – *no data (-)*
149. (Extension of character 124) pubis tubercle position: (0) tubercle posterodorsally placed, (1) tubercle anteroventrally placed – *tubercle appears anteroventrally placed, 1*

## APPENDIX 2

Matrix of character states for extant lizard groups and *Meyasaurus*. Character states and data on modern lizards and *Sphenodon* taken mostly from Estes *et al.*, 1988. Where variation occurs within extant group, the primitive condition for that group has been used

Sphenodon										
00000	00000	00100	00000	00010	00000	00001	00000	00000	00100	00000
00010	01002	32000	00000	00000	00000	00000	00000	00000	00000	00010
00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000
Iguania										
10000	11100	00001	00100	10011	00000	10000	00000	00000	00101	10000
00000	00000	00000	00000	00001	00000	00100	00100	00010	00000	00000
01000	01000	00000	00000	00000	01000	00002	0000			
Gekkota										
00000	10011	00100	1----	0001-	101-0	01010	01011	10010	00110	11012
00100	00001	00100	00011	01110	01100	00000	00000	10000	01001	00010
11000	11001	00101	00001	00001	01111	10000	1001			
Cordylidae										
10000	00010	00100	01010	10100	00000	00010	01011	10010	00110	10010
00101	00000	00102	10001	11010	01000	00100	00100	00010	00000	00000
01000	11001	00110	11121	00110	01102	00012	1101			
Scincidae										
00010	00010	00100	01101	10010	00000	10010	10011	10110	00110	10010
00101	00000	00102	10011	10110	01000	00100	00100	01010	0001	10010
Xantusiidae										
10010	00010	0111-	01010	01100	01--0	00010	01111	10011	10110	11012
00101	00001	12002	11100	00000	01000	00101	00100	10001	00001	00010
01000	11001	00110	00021	11110	01212	00012	1101			
Lacertidae										
10010	00010	01100	01001	11000	00000	00010	10011	10010	00010	10110
00100	00000	00100	00100	00000	11000	01100	00101	00011	00000	00010
01010	11001	10110	00121	11110	03221	00002	1101			
Teiidae										
10000	00000	00100	01100	11110	00000	10000	00011	10011	10010	10000
00100	00000	00100	00200	00000	11000	01100	00101	00111	00000	00010
01100	11001	11100	00021	11110	04211	01102	1101			
Gymnophthalmidae										
10000	10011	10100	01000	1111-	10000	10010	00011	10010	00010	10000
00000	00000	00100	00200	00000	11000	01101	00101	00111	00000	00010
01100	11001	11110	00021	1111-	0421-	11102	1101			
Anguidae										
10000	00010	00100	01000	10010	00000	10010	11011	10010	00110	10100
11000	00100	00100	00011	00110	00001	00100	10100	12010	10001	10010
01000	11001	00110	11121	00010	12100	10002	1101			
Xenosauridae										
10000	01000	00100	01100	10000	00000	10000	11011	10010	00110	10000
11000	00100	00100	00010	00010	01001	00101	10100	12010	00001	00010
01000	11000	00100	01121	00110	12100	00002	1001			
Helodermatidae										
10001	00011	00100	1----	1001-	11000	10010	00011	10011	00110	10110
11010	10111	11110	00011	00010	00002	10110	11100	11010	0-101	10010
00010	1101-	00100	01111	00110	13100	01102	1001			
Varanus										
111-0	00011	00110	01000	10010	01001	11010	11011	11011	00110	10000
11010	21210	11010	00011	00010	01102	10001	11110	11010	0-101	10120
01110	11000	00100	00001	01110	151-0	01002	1000			
Lanthanotus										
11101	00010	00100	1----	1001-	11001	10010	01011	11011	00110	10100
11010	21210	21011	00011	00010	00002	10111	11110	11010	0-101	10130
01010	11001	00100	01101	001--	1410-	01002	1001			
Meyasaurus										
10010	01110	00100	01110	11110	00---	10000	-0---	-----	000--	---00
10100	0-000	00100	00100	000-1	0--00	0-----	-0101	00010	01000	00010
111-0	1-001	1-100	00020	-----	-----	-----	---1			