

The Early Cretaceous lizards of Montsec (Catalonia, Spain)

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RESUMEN

EVANS, S.E. y BARBADILLO, L.J. Los lagartos del Cretácico Inferior del Montsec (Cataluña, España).

Los depósitos del Cretácico Inferior del Montsec (Cataluña, España) han proporcionado restos pertenecientes a dos ejemplares de lagartos. El primero está representado por un esqueleto postcranial incompleto que fue descrito por Vidal (1915) como *Meyasaurus fauræ*. El segundo, representado por un cráneo, fue descrito como *Ilerdaesaurus crusafonti* por Hoffstetter (1966). Hasta la fecha, debido a la inexistencia de materiales craneales y postcraneales asociados, no había podido determinarse si ambos restos podían ser atribuidos al mismo género. Sin embargo, el descubrimiento de nuevos restos de lagartos procedentes de los depósitos lacustres del Cretácico Inferior de las Hoyas en Cuenca (Castilla-La Mancha, España) han dado repuesta a dicha cuestión. Los lagartos de Las Hoyas permiten asociar el cráneo de *Ilerdaesaurus* con el esqueleto postcranial de *Meyasaurus*. *Meyasaurus* Vidal 1915 tiene clara prioridad sobre *Ilerdaesaurus* Hoffstetter 1966, convirtiéndose así éste en un sinónimo de aquél.

Palabras clave: Lagartos, Squamata, Cretácico Inferior, Barremiense, Montsec, Cataluña, España.

ABSTRACT

The Lower Cretaceous deposits of Montsec (Catalonia, Spain) have yielded two lizard specimens. One, a partial postcranial skeleton, was named *Meyasaurus fauræ* by Vidal (1915). The second, a skull, was named *Ilerdaesaurus crusafonti* by Hoffstetter (1966). There has always been the possibility that the skull and postcranial skeleton belonged to a single genus, but without associated material, the question remained open. New lizard material from the Lower Cretaceous (Late Barremian) lacustrine deposits at Las Hoyas, near Cuenca (Castilla-La Mancha, Spain), provides the answer. The Las Hoyas lizards combine the skull of *Ilerdaesaurus* with the postcranial skeleton of *Meyasaurus*. *Meyasaurus* Vidal 1915 clearly has priority over *Ilerdaesaurus* Hoffstetter 1966, and the latter becomes a junior synonym.

Key words: Lizards, Squamata, Cretaceous, Barremian, Montsec, Catalonia, Spain.

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INTRODUCTION

The Lower Cretaceous lithographic limestones of Montsec (province of Lleida, Catalonia) have yielded a varied freshwater assemblage including insects, frogs, birds, crocodiles and lizards (Buscalioni & Sanz, 1991), although the latter are rare and are restricted to two specimens from Santa Maria de Meià. Vidal (1915) produced the first detailed description of the Montsec vertebrate assemblage, then thought to be of late Jurassic age. He described and named a small partial reptilian postcranium as *Meyasaurus fauræ* (correctly emended to *M. faurai* by von Huene, 1952), interpreting the animal as a sphenodontian on the basis of, supposedly, amphicoelous vertebrae. Cocude-Michel (1963) reviewing Jurassic lizards and sphenodontians accepted his interpretation, but Hoffstetter (1966) did not. Hoffstetter argued, correctly, that the presence of procoelous (not amphicoelous) vertebrae, the absence of gastralia and the conspicuous presence of scapulocoracoid emarginations and a perforate clavicle placed *Meyasaurus* within lizards not sphenodontians. He suggested *Meyasaurus* might be a scincomorph of some form.

In the same paper, Hoffstetter described and named a second lizard specimen from Montsec. This specimen, a skull (Fig. 2A), had been discussed in a preliminary account by Hoffstetter, Crusafont & Aguirre (1965). Hoffstetter (1966) named it *Ilerdaesaurus*. Clearly comparison between *Meyasaurus* and *Ilerdaesaurus* was impossible but, at least in print, Hoffstetter did not consider the possibility that the skull and postcranium might belong to the same genus. In order to establish this, it would be necessary to find specimens in which the head and body were preserved in association. At the lithographic limestone locality of Las Hoyas (province of Cuenca, Castilla-La Mancha), associated lizard specimens of late Barremian age have now been recovered. They permit a reconsideration of the status of the Montsec genera.

MATERIAL

Meyasaurus

The genus *Meyasaurus* was named by Vidal (1915) on the basis of a partial postcranial skeleton now housed in the collections of the Museu de Geologia de Barcelona (MGB 534, Fig. 1A). The skeleton includes most of the presacral vertebral column and ribs, parts of the pectoral girdles and forelimbs and fragments of the braincase, exposed in ventral view. Hoffstetter reviewed the specimen in 1966. For the most part, his published description and figures are accurate but his interpretation of the vertebral sequence, and of the dermal pectoral girdle require revision.

Hoffstetter counted a total of 26 presacral vertebrae, 8 cervicals and eighteen dorsals. Under his interpretation, the first rib was associated, somewhat unusually for lizards, on the fifth vertebrae, leaving three vertebrae (5-7) with short ribs and only one (8) with a long rib (usually there are two). However, the first few cervical vertebrae are very poorly preserved and their individual boundaries are unclear. The small element labelled 1 by Hoffstetter appears to be an isolated atlas arch, leaving the

remainder of the atlas unaccounted for. His axis is very short particularly allowing for an attached odontoid. It is much more likely that Hoffstetter's vertebra 3 is the axis and the small structure immediately anterior to it is the odontoid. The joint between these two parts is masked by an intercentrum. Under this interpretation, the short ribs are on cervicals 4-6, and there are two long cervical ribs, as in the majority of living lizards. The three short ribs increase in length from first to last and are characterised by their distal expansion. The first is short, robust and shows some distal widening. The second is greatly expanded. The third has a longer, more gracile shaft. These three short ribs are followed by the two prethoracic ribs. The first two sternal ribs are of similar length, but the following eight are robust and elongated—giving a barrel-like appearance to the thorax and abdomen. Further posteriorly, there is a sharp change leaving seven (or more) short, slender ribs before the sacrum, which is off the block.

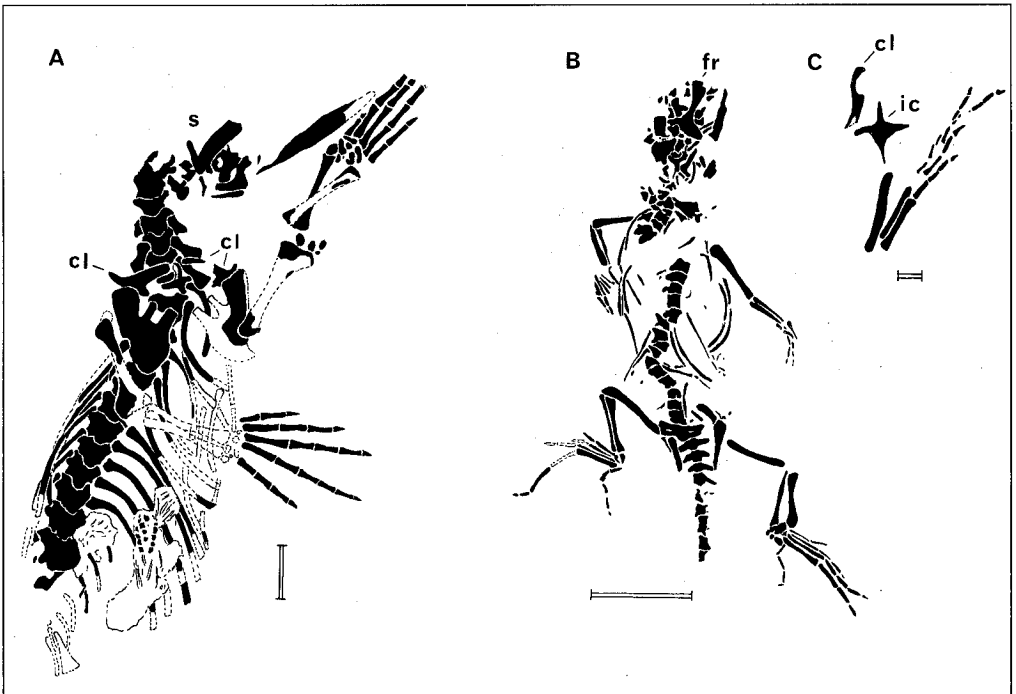


Figure 1: *Meyasaurus*.

A, Holotype of *Meyasaurus faurai* Vidal, 1915 (MGB 534); B, immature specimen from Las Hoyas (LH 370), hands and tail incomplete; C, pectoral girdle and right forearm of juvenile specimen from Las Hoyas (LH 372).

Scale bars for A-B = 10 mm; scale bar for C = 1 mm. Abbreviations: cl, clavicle; fr, frontal; ic, interclavicle.

Figura 1: *Meyasaurus*.

A, Holotipo de *Meyasaurus faurai* Vidal, 1915 (MGB 534); B, espécimen inmaduro de Las Hoyas (LH 370), manos y cola incompletos; C, pectoral y antebrazo derecho de un espécimen juvenil de Las Hoyas (LH 372).

Escalas de A-B= 10 mm; escala de C= 1 mm. Abreviaturas: cl, clavícula; fr, frontal; ic, interclavícula.

The vertebrae themselves are procoelous, although the condyles are weak and, apparently, partially cartilaginous. Most cervical vertebrae are too poorly preserved to distinguish keels or hypapophyses, but the last two have shallow keels. Dorsal vertebrae lack these keels and have robust, almost rectangular centra which are rugose in surface structure and bear longitudinal grooves. The rib facets are prominent and each vertebra also has a slight posterior expansion.

The pectoral girdle is well-preserved on the left side. The scapulocoracoid, as described by Hoffstetter (1966), has two emarginations in its posterior border, a typically lizard condition. The supposed suture between scapula and coracoid (Hoffstetter, 1966) is less convincing and is probably an artefact. The scapula blade is narrow and subrectangular in outline.

The clavicles are divided into a S-shaped lateral portion and an expanded, perforate medial part. The borders of this medial section, however, are incomplete (Figs. 1A, 3A). What Hoffstetter interpreted as a medial region of contact between the two clavicles is better interpreted as part of a cruciform interclavicle (Fig. 3A). The medial part of the clavicle is therefore bifurcate, with a long anterior limb which ends in a curved knob and a shorter posterior limb (Fig. 3A). The right clavicle is seen to have a broad base to the lateral stem; this section is obscured on the left by the scapula.

The forelimb is robust with a strong humerus which possesses an expanded entepicondyle. There may be an ectepicondylar foramen (Hoffstetter, 1966) represented by a small lateral depression, but this is uncertain. The ends of the long bones are unfinished and (as noted by Hoffstetter, 1966) there are detached epiphyses from the humerus and ulna in the elbow region. The hand is large (as long as the humerus) with the third and fourth digits of similar length. The third metacarpal is longer than the fourth, but the fourth digit contains an additional phalanx phalangeal formula - 2.3.4.5.3. In the digits, the ends of both metacarpals and phalanges are capped by cartilage.

The block is broken at the level of the 25th presacral (26th on Hoffstetter's numbering). Close to this point there is an impression, labelled x by Hoffstetter (1966) and interpreted as a hind limb element. However, from its shape and position, and a possible proximal foramen, this may be the ventral ramus of the pubis.

Ilerdaesaurus

A second lizard specimen – a skull – was recovered from Montsec in 1964, and is housed in the Institut de Paleontologia “M. Crusafont” de Sabadell (MIPS, Montsec 10). It was described in a preliminary note by Hoffstetter, Crusafont and Aguirre (1965), and then discussed in more detail by Hoffstetter (1966) who named it *Ilerdaesaurus crusafonti*. The principal features of the skull were an unpaired parietal, frontals which are constricted between the orbits, an open upper temporal fenestra bounded by a posteriorly expanded and hooked squamosal, separate postorbital and postfrontal bones, and a dentition in which the anterior teeth were monocuspid and the posterior teeth bicuspid (Fig. 2A).

Hoffstetter interpreted *Ilerdaesaurus* as an autarchoglossan, probably, but not certainly, an anguimorph.

NEW MATERIAL

For many years, these two specimens remained the only record of lizards from the early Cretaceous of Spain. More recently, however, lizard remains have been recovered from additional localities, most notably the late Barremian lithographic limestones of Uña and Las Hoyas, both in Cuenca province, Castilla-La Mancha.

Uña and Galve

The locality of Uña (Cuenca province, Castilla-La Mancha) has yielded a variety of small vertebrates including a mammal, frogs, crocodiles, lizards and an early snake

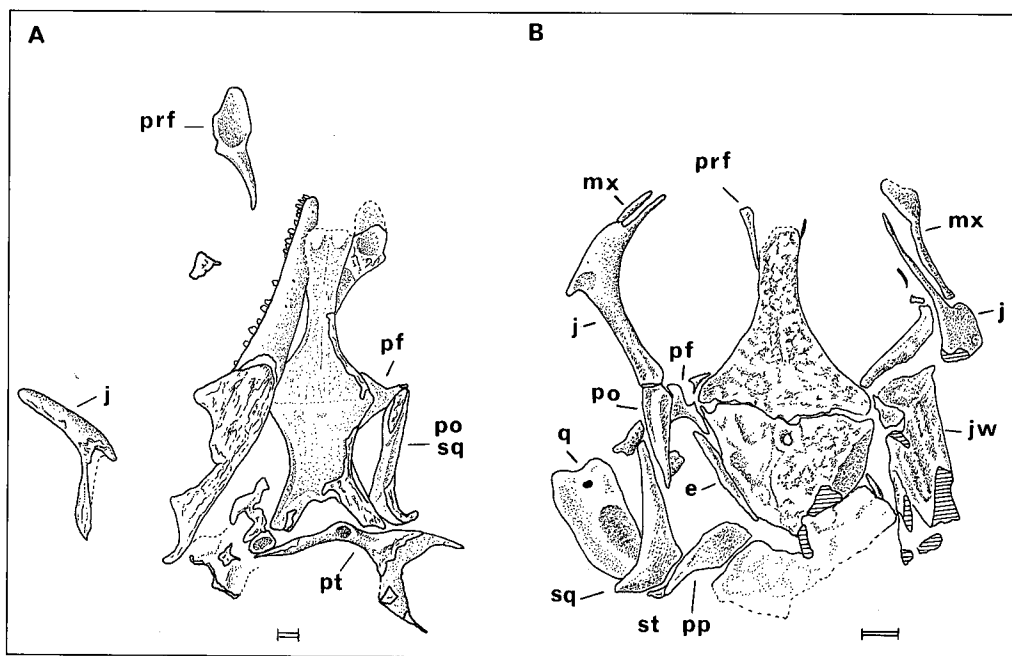


Figure 2: Skull.

A, Holotype of *Ilerdaesaurus crusafonti* Hoffstetter, 1966 (MIPS, Montsec 10); B, Las Hoyas 13510. Scale bars = 1 mm.

Abbreviations: e, ?epipterygoid; j, jugal; jw, jaw; mx, maxilla; pf, postfrontal; po, postorbital; posq, impression representing postorbital and squamosal; pp, posterior process of parietal; prf, prefrontal; pt, pterygoid; q, quadrate; sq, squamosal; st, supratemporal.

Figura 2: Cráneo.

A, Holotipo de *Ilerdaesaurus crusafonti* Hoffstetter, 1966 (MIPS, Montsec 10); B, Las Hoyas 13510. Scala= 1mm.

Abreviaturas: e, ?epipterigoide; j, yugal; jw, mandíbula; mx, maxilar; pf, postfrontal; po, postorbital; posq, impresión representando el postorbital y el escamoso; pp, proceso posterior del parietal; prf, prefrontal; pt, pterigoide; q, cuadrado; sq, escamoso; st, supratemporal.

(Richter 1991, 1994a&b). According to Richter (1994b), the lizards include four taxa, *Ilerdaesaurus*; two paramaceloidids (cordyloid scincomorphs known from a range of late Jurassic and early Cretaceous assemblages) representing the genera *Becklesius* and *Paramacelodus*; and a possible new anguimorph, *Cuencasaurus* (Richter, 1994a&b). The material assigned to *Ilerdaesaurus* includes an associated skull (Richter, 1991, 1994a) and a number of blocks bearing isolated cranial elements, a pelvic girdle and some vertebrae. While it adds to our knowledge of the cranial morphology of the genus, this material does not contribute to discussion of the relationship between *Meyasaurus* and *Ilerdaesaurus*.

Frontals matching those of *Ilerdaesaurus* have also been recovered from the locality of Galve (Barremian, Teruel) (Richter, 1994a).

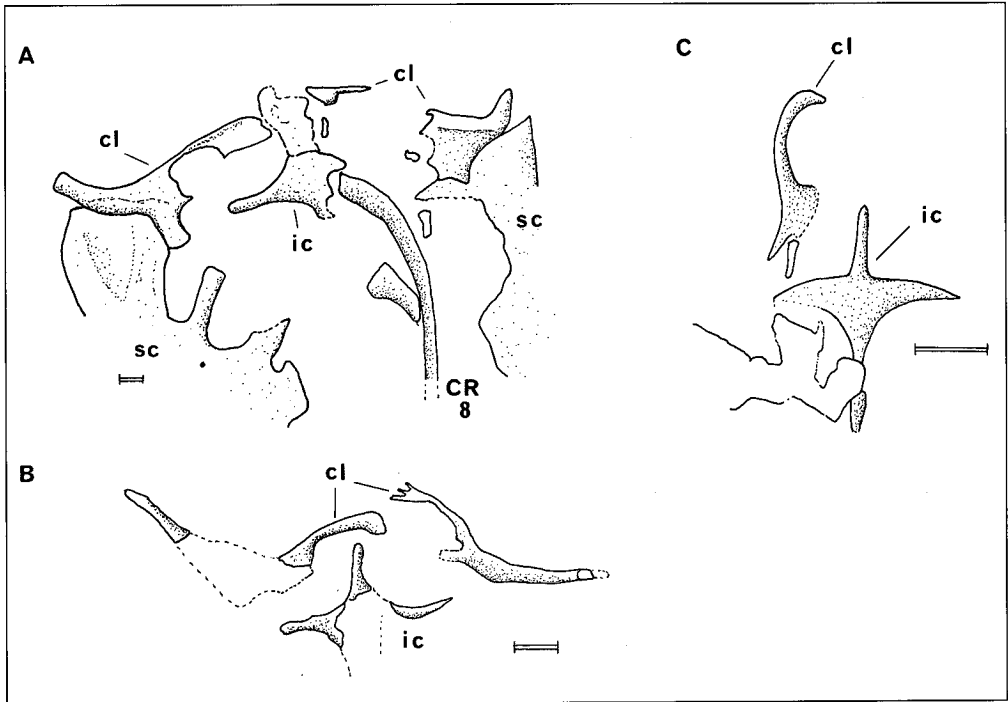


Figure 3: Clavicles and interclavicles.

A, Holotype of *Meyasaurus faurai* Vidal, 1915 (MGB 534); B, LH 370; C, LH 372.

Scale bars = 1mm.

Abbreviations: c, clavicle; CR, cervical rib; ic, interclavicle; sc, scapulocoracoid.

Figura 3: Clavículas e interclavículas.

A, Holotipo de *Meyasaurus faurai* Vidal, 1915 (MGB 534); B, LH 370; C, LH 372.

Escalas= 1 mm. Abreviaturas: cl, clavícula; CR, costilla cervical; ic, interclavícula; sc, escapulocoracoides.

Las Hoyas

The locality of Las Hoyas lies close to Uña, and its deposits may represent part of the same lacustrine system. Las Hoyas is currently being worked by a multidisciplinary international team, coordinated by the Universidad Autónoma de Madrid and funded by the European Community. To date, the deposits have yielded a broad range of vertebrates and invertebrates. The tetrapod component includes frogs, salamanders, turtles, crocodiles, lizards, birds and an ornithomimosaurid dinosaur. To date, seven lizard specimens have been recovered. Of these, one is an assemblage of dissociated specimens (probably a faecal or oral pellet) and two appear to belong to distinct and novel taxa. Of the remainder, four (Museo de Cuenca LH 33, 370, 372, 13510) are of relevance to the Montsec lizards.

These specimens range in size from very small (LH 372, snout-vent length 26mm), to medium-sized (LH 370, snout-vent 58mm) and three (except LH 33) preserve elements of both skull and postcranial skeletons.

The skull (Fig. 2B, LH 13510) is distinctive -mostly notably in the presence of the long frontals which are sharply constricted between the orbits, a single parietal with an anteriorly placed foramen, a posteriorly expanded and distinctly hooked squamosal, a slender jugal with a small posterior process, separate postfrontal and postorbital bones, and a dentition in which the anterior teeth are monocuspid and the posterior teeth bicuspid (LH 370, 372). In these features, the Las Hoyas lizards match specimens of *Ilerdaesaurus* from both Montsec and Uña.

In the postcranial skeleton, the Las Hoyas lizards also show a number of significant features: a cervical series of eight vertebrae in which the fourth to the six? bear short expanded ribs -the first of which is small and thick; the second is broader; the third is longer, expanded distally but waisted in the shaft. The vertebrae are procoelous, but weakly so with cartilage remaining over the condyle. The vertebrae in the thoracic region have centra with grooved surfaces and a subrectangular appearance. With the exception of the first two, the thoracoabdominal ribs are very long (Fig. 1B), but there is a marked change in length on the last 7/8 presacrals to create a discrete lumbar region. In the pectoral girdle, the clavicles are perforated but the borders are incomplete- a long anterior arm ends in a curved knob, the posterior arm is short (Figs. 1C, 3B-C). The lateral part is flanged and S-shaped. The scapulocoracoids have two anterioemarginations and a narrow scapula blade. The hands are long, with the third metacarpal longer than the fourth, and the fourth digit has five phalanges. In all of these features, except size (the largest Las Hoyas lizard, LH 370, is less than half the size of the Montsec skeleton), the Las Hoyas lizards match *Meyasaurus*. Although many of these are general features found in a number of modern lizards, the specific similarities in the shape of the clavicle, the appearance of the vertebral centra and the proportions of the ribs suggest a close relationship between *Meyasaurus* and the Las Hoyas lizards.

CONCLUSIONS

The Las Hoyas lizards combine the skull of *Ilerdaesaurus* with the postcranial skeleton of *Meyasaurus*. This provides a clear indication that the two Montsec lizards

belong to a single genus. *Meyasaurus* Vidal 1915 has priority over *Ilerdaesaurus* Hoffstetter 1966; the latter should be considered a junior synonym of *Meyasaurus*. *Meyasaurus* is thus known from a series of Lower Cretaceous localities in Spain (Montsec, Uña, Las Hoyas, Galve), and ranges in age from Berriasian/Valangian to late Barremian. It is also possible that *Durotrigia* Hoffstetter 1967, based on an enigmatic jaw fragment from the Purbeck Limestone Formation (Berriasian) of Britain, is a related form.

The associated skeletons of *Meyasaurus* from Las Hoyas (which will be described in detail elsewhere, Evans and Barbadillo, MS) have permitted a more rigorous evaluation of the systematic position of the genus. Cladistic analysis (Hennig 86) using 149 derived character states to compare *Meyasaurus* with living lizard groups and *Sphenodon* (Evans and Barbadillo MS), places *Meyasaurus* unequivocally in the Scincomorpha, nested within Lacertoidea (teiids, gymnophthalmids, lacertids and xantusiids). There is little basis for regarding *Meyasaurus* as an anguimorph (Hoffstetter 1966, Richter 1991, 1994a).

Within the abdominal cavity of the Montsec specimen, there are one or more small fish skeletons. This observation led Vidal (1915) to suggest that *Meyasaurus* might be fully or partially aquatic. This hypothesis receives some support from the relative abundance of lizard specimens at the Las Hoyas locality, where terrestrial vertebrates are generally rare.

ACKNOWLEDGEMENTS

This work was supported by EC Capital and Mobility Programme grant CHRX CT93 0164 which funds work on the Las Hoyas locality and its assemblage. Thanks are also due to Dr Julio Gómez-Alba at the Museu de Geologia de Barcelona, for access to the holotype of *Meyasaurus faurai*.

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