



A New Freshwater Basal Eucryptodiran Turtle from the Early Cretaceous of Spain

Authors: Adán Pérez-García, Marcelo S. de la Fuente, and Francisco Ortega

Source: Acta Palaeontologica Polonica, 57(2) : 285-298

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: <https://doi.org/10.4202/app.2011.0031>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-o-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

A new freshwater basal eucryptodiran turtle from the Early Cretaceous of Spain

ADÁN PÉREZ-GARCÍA, MARCELO S. DE LA FUENTE, and FRANCISCO ORTEGA



Pérez-García, A., de la Fuente, M.S., and Ortega, F. 2012. A new freshwater basal eucryptodiran turtle from the Early Cretaceous of Spain. *Acta Palaeontologica Polonica* 57 (2): 285–298.

A freshwater turtle from the lithographic limestone of Las Hoyas (Barremian of Cuenca, Spain) is described as a new genus and species of Eucryptodira, *Hoyasemys jimenezi*. The holotype consists of the skull, lower jaw, carapace, plastron, vertebral column, pectoral and pelvic girdle remains, and fore- and hindlimbs. *Hoyasemys jimenezi* gen. et sp. nov. is characterized by three pairs of blind oblique depressions on the ventral surface of the basisphenoid, and a character combination composed, among others, of the articulation between the fourth and fifth cervical vertebrae through a cotyle in the fourth and a condyle in the fifth, amphicoelous caudal centra, and most digits of manus and pes with three elongated phalanges. This study allows clarification of the systematic position of a species of uncertain affinity often identified as “chelydroid” in appearance. A phylogenetic analysis shows *Hoyasemys jimenezi* gen. et sp. nov. forms a monophyletic group with *Judithemys sukhanovi*, *Dracochelys bicuspis*, *Sinemys lens*, and *Ordosemys leios*, collectively the sister group of crown Cryptodira.

Key words: Testudines, Eucryptodira, freshwater turtle, Barremian, Cretaceous, Las Hoyas, Spain.

Adán Pérez-García [paleontologo@gmail.com], Departamento de Paleontología, Facultad de Ciencias Geológicas, Universidad Complutense de Madrid, José Antonio Novais 2, 28040 Ciudad Universitaria, Madrid, Spain;

Marcelo S. de la Fuente [mdelafu@gmail.com], Departamento de Paleontología, Museo de Historia Natural de San Rafael, Parque Mariano Moreno S/N° (5600), San Rafael, Provincia de Mendoza, Argentina;

Francisco Ortega [fortega@ccia.uned.es], Grupo de Biología, Facultad de Ciencias, UNED, Senda del Rey 9, 28040 Madrid, Spain.

Received 25 March 2011, accepted 10 May 2011, available online 11 May 2011.

Introduction

A complete Lower Cretaceous turtle from the Iberian Peninsula has been found in the Barremian fossil site of Las Hoyas (Cuenca). This finding is noteworthy because complete turtle skeletons from the Lower Cretaceous are rare. Sanz et al. (1988) briefly described two specimens from Las Hoyas (MCCM-LH 84 and MCCM-LH 254) and noted the cruciform aspect of the plastron, the presence of hyo-hyoplastral fontanelles and their stylized limbs. These features are only available on MCCM-LH 84 because the other cited specimen is a fragment of carapace. Although Sanz et al. (1988) noted that these characters are present in several testudine families, such as Toxochelyidae, Macrobaenidae, and Chelydridae, they nevertheless referred the Las Hoyas turtles to Toxochelyidae indet. The monophyly of Toxochelyidae has subsequently been rejected (Gaffney and Meylan 1988; Meylan et al. 2000; Averianov 2002). Jiménez-Fuentes (1995) also mentioned these specimens and considered them to be a “toxocheloid” related to Chelonioidea. He recognized the particular elongation of the digits of the manus of MCCM-LH 84 as a shared feature between Las Hoyas specimens and

chelonioids. Nevertheless, this is a common feature among aquatic turtles (Joyce and Gauthier 2004) and the Las Hoyas specimens do not present any synapomorphies diagnostic of the clade Chelonioidea (sensu Joyce 2007). Thereafter, the Las Hoyas specimen was identified as an undetermined basal representative of Centrocryptodira (Ortega et al. 1999) or as an undefined new form with “chelydroid” aspects, but without the autapomorphies of Chelydridae (Lapparent de Broin 2001). Some aspects of the specimens were not available for Sanz et al. (1988) and they suggested that it would be necessary to prepare the skull and the outer surface of the carapace and plastron of the specimen MCCM-LH 84 to analyze it, because most of the characters used for the identification of turtle taxa could not be observed. The specimen has fortunately since been prepared for study. MCCM-LH 84 preserves a large percentage of the elements of the cranial and, especially, postcranial skeleton. The exquisite preservation of this specimen, in a lithographic limestone, therefore allows the description here of a new basal freshwater eucryptodiran genus and species.

Institutional abbreviation.—MCCM, Museo de las Ciencias de Castilla-La Mancha, Cuenca, Spain.

Eucryptodiran turtles in the Upper Jurassic and Lower Cretaceous of Europe

Basal eucryptodiran turtles (*sensu* Joyce 2007) are well represented in the European Jurassic by the endemic littoral Thalassemydidae, Plesiochelyidae, and Eurysternidae (Danilov 2008). Thalassemydidae are present in the Kimmeridgian of Switzerland (Lapparent de Broin et al. 1996) and probably in France (Lapparent de Broin 2001). Eurysternidae range from the upper Kimmeridgian to the lower Tithonian of France, Germany and Switzerland, and are represented by *Achelonia formosa*, *Euryaspis radians*, *Eurysternum wagleri*, *Hydropelta meyeri*, *Idiochelys fitzingeri*, and *Solnhofia parsonsi* (Lapparent de Broin 2001). Several genera of Plesiochelyidae have been recognized in the Upper Jurassic of England, France, Germany, Switzerland, and Portugal: *Plesiochelys*, *Craspedochelys*, *Tropidemys*, and *Tholemys* (Lapparent de Broin 2001). Although there are tentative reports of plesiochelyids from the Valanginian (Lower Cretaceous) of Switzerland (Lapparent de Broin 2001), these turtles are typically thought to be inhabitants of coastlines, disappearing during the Jurassic–Cretaceous transition, when a regression restricted the European epicontinental seas and drastically reduced the habitats for these aquatic reptiles (Bardet 1994). The English taxon *Hylaeochelys* may be close to Plesiochelyidae (Lapparent de Broin 2001) or even a member of this group (Hirayama et al. 2000; Milner 2004). The phylogenetic position of the English *Portlandemys mcdowelli* is difficult to determine (Joyce 2007), although it might to be a plesiochelyid (Milner 2004). Other European Jurassic taxa that could belong to these families or be closely related to them are *Anaphotidemys robusta*, “*Acochelys*” *approximata* or “*Thalassemys*” *marina* (Lapparent de Broin 2001; Joyce 2003), a species perhaps closer to Cryptodira than *Plesiochelys solodurensis* (Joyce 2007).

In the Early Cretaceous of Laurasia, turtles are distributed in three distinct areas: North America, Asia, and Europe (Hirayama et al. 2000). In North America, paracryptodires dominate, in Asia eucryptodires, and in Europe both groups (Hirayama et al. 2000). European and North American faunas comprise the paracryptodiran clades Pleurosternidae and Baenidae, and Solemydidae, another basal pancryptodiran group of uncertain systematic position (Lapparent de Broin 2001; Danilov 2008; Joyce et al. 2011; Lyson and Joyce 2011). The record of basal eucryptodires in the European Cretaceous is limited to *Brodiechelys brodiei*, known from shells from the Barremian of England (Lydekker 1889; Nopcsa 1928). *Brodiechelys* may be closely related to, or a member of, Plesiochelyidae (Lapparent de Broin 2001) or Xinjiangchelyidae, a group from the Middle Jurassic–Early Cretaceous of Central Asia (Hirayama et al. 2000; Danilov 2005, 2008; Danilov and Parham 2007). Cryptodires have also been identified in the European Cretaceous, the dermochelyoid Protostegidae and the

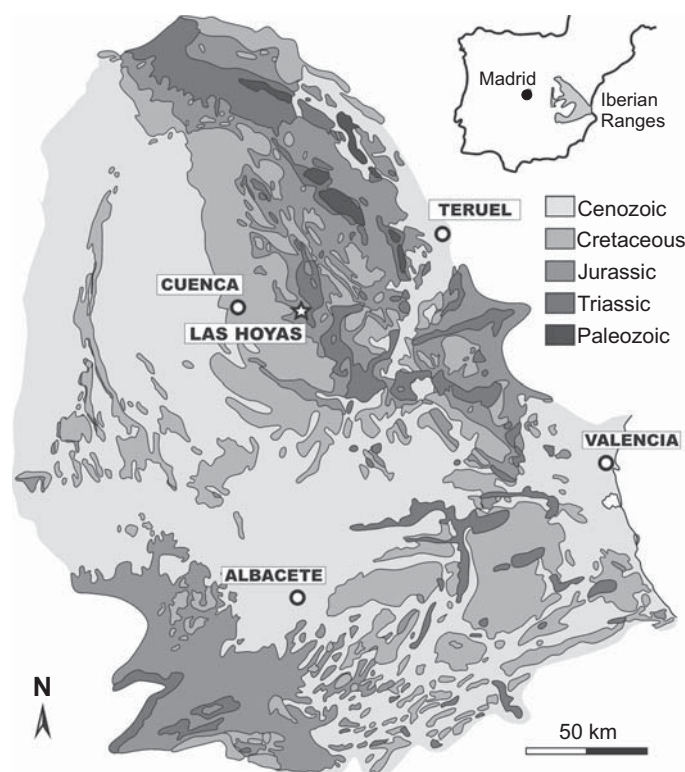


Fig. 1. Geographical and geological location of the fossil site of Las Hoyas (Cuenca, Spain), in the Mesozoic context of the Iberian Ranges.

putative trionychoid *Peltochelys duchastelii*, from Belgium (Meylan 1988; Meylan and Gaffney 1989; Tong et al. 2006; Joyce 2007; Pérez-García 2011). There are others eucryptodiran taxa of uncertain affinity, including *Chitraccephalus dumonii* from Belgium (Dollo 1884), *Salasemys pulcherrima* from Spain (Fuentes Vidarte et al. 2003), and *Sandownia harrisi*, from the Isle of Wight (UK), a taxon that has been assigned to Trionychoidea (Meylan et al. 2000; Lapparent de Broin 2001) or to basal Eucryptodira (Joyce 2007).

A relatively abundant record of basal eucryptodires is known from the Upper Jurassic of the Iberian Peninsula (Sauvage 1898; Antunes et al. 1988; Lapparent de Broin et al. 1996; Pérez-García et al. 2008b). Non-marine basal eucryptodires are reported from North and South America, central Asia, and Australia, but not yet from Europe (Gaffney et al. 2007). Thus, the new Las Hoyas turtle *Hoyasemys jimenezii* gen. et sp. nov. confirms the presence of this group of turtles in the Early Cretaceous of Europe. Other specimens from the Cretaceous of Spain could belong to this node, such as the turtle specimens from the Maestrazgo Basin or from the Cameros Basin (Pérez-García et al. 2008a; Pérez-García and Ortega 2009).

Geological setting

The Las Hoyas fossil site is a well-known Lower Cretaceous Konservatlagerstätte located in the southern part of the Serra-

nía de Cuenca (Southwestern Iberian Ranges, Eastern Spain) (Fig. 1). The fossiliferous deposits, the La Huérguina Formation (upper Barremian), are composed of laminated limestone and rare marlstone beds. The depositional environment was a freshwater subtropical carbonate wetland that overlay a low-relief karstic terrain (Buscalioni and Fregenal-Martínez 2010). The Las Hoyas biota consists mainly of obligate aquatic organisms, such as osteichthyan fishes, decapod crustaceans, belostomid insects, charophytes, the aquatic plant *Montsechia* (Buscalioni et al. 2008). Amphibious forms (crocodiles, turtles, and lissamphibians) are much less abundant, and terrestrial/arboreal forms, such as insects, lizards, and basal birds, are rare as well. Large animals including dinosaurs are exceptional finds (Buscalioni and Fregenal 2006). The terrestrial macroflora is dominated by conifers (Cheirolepidiaceae) and ferns (Mantoniaceae and Schizaeaceae) (Escaso et al. 2005).

Systematic palaeontology

Testudines Batsch, 1788

Eucryptodira Gaffney, 1975a

Genus *Hoyasemys* nov.

Type species: Hoyasemys jimenezi sp. nov., see below.

Etymology: From Spanish *hoyas*, the source of the specimen; and Greek *emys*, for freshwater turtle.

Diagnosis.—As for monotypic type species.

Hoyasemys jimenezi sp. nov.

Figs. 2–4.

Etymology: In honour of Dr. Emiliano Jiménez Fuentes for his contribution to the knowledge of Spanish fossil turtles.

Holotype: MCCM-LH 84, an almost complete skeleton, missing the dorsal portion of the skull. The specimen is preserved on two slabs. One shows the ventral view of the skull, the five proximal cervical vertebrae, some dorsal vertebrae, some fragments of the peripherals and of the lateral part of the costal plates, the plastron, sacral and caudal vertebrae and the appendicular skeleton. The other slab preserves the partial carapace and some bones of the hindlimb.

Type locality: Las Hoyas site, La Cierva township, Cuenca Province, Spain.

Type horizon: Calizas de La Huérguina Formation, Upper Barremian, Lower Cretaceous (Sanz et al. 1988; Diéguez et al. 1995).

Diagnosis.—Small basal eucryptodiran turtle with three pairs of oblique depressions on ventral surface of the basisphenoid. Differing from the rest of basal Eucryptodira in the following character combination: rear contact of the pterygoids with the basioccipital; basisphenoid large and narrower than basioccipital; basioccipital wider than long; cervicals two to four opisthocoelous; single transverse processes on the anterior edge of the centrum of the cervical vertebrae; cervical ribs absent; caudal vertebrae amphicoelous; small chevrons poorly developed, along the posterior caudals; shell low, longer than wide; nuchal plate relatively broad, without anterior or posterior notch; first neural plate longer than the second; two suprapygal plates; anterior pairs

of peripherals guttered; mediolaterally expanded posterior peripherals; marginals overlapping onto the whole surface of the peripherals; plastral buttresses reaching only peripherals; posteriorly elongated inguinal process; anals scutes near the border of the hypo-xiphiplastron; most digits of manus and pes with three elongated phalanges.

Description

The anatomical terminology of the cranium follows Gaffney (1972), and of the bones and scutes of the carapace and plastron follows Zangerl (1969).

Skull.—All available cranial information was seen in ventral view (Fig. 2). The cranial length is about a third of the plastral length.

Rostral elements: In ventral view, the labial ridge of both premaxillae and maxillae are visible. *Hoyasemys jimenezi* lacks a medial hook along the labial margin of the premaxillae. On the left maxilla the labial ridge extends posteriorly forming a straight and sharp edge. The triturating surface and lingual ridge could be preserved, but they are hidden by the left branch of the lower jaws. A part of the upper edge of the maxilla can be observed delimiting the left orbit. A partial left jugal is preserved.

Palatoquadrate elements: The long processus articularis of the right and particularly the left quadrate are well preserved. The right condylus mandibularis is not fully visible, while the left one is partly hidden by the posterior area articularis mandibularis of the lower jaw, showing the lateralmost articular facet. The quadrate-ptyergoid suture is hidden by the hyoid elements. Only a part of the left quadratojugal can be seen in ventral view. It contacts the squamosal posteriorly.

The anterior portions of both pterygoids are missing or are at least represented only by minute fragments. The posterior portion of the left pterygoid and especially the right one are broken in fragments that are slightly displaced from their original position. On the right side, the pterygoid-basisphenoid suture runs between bony fragments. Likewise, the left pterygoid bone is sagittally displaced and its medial margin overlaps the lateral edge of the basisphenoid and basioccipital.

Braincase elements: The basisphenoid lies between the pterygoids. It lacks the anteriormost portion. The available ventral surface of the basisphenoid suggests it was subtriangular in shape. The preserved ventral surface of the basisphenoid is ornamented by three pairs of oblique and parasagittal depressions. The two posterior pairs of depressions have a prominent and crenulated ridge on the anterior edge. The anterior depression is the deepest. A blunt crest is situated anterior to the rear depressions. At least two posterior pairs of grooves, and likely also one other, are blind depressions, not related to the development of any cranial foramina.

The basioccipital presents an anterior, transverse contact with the basisphenoid and an anterolateral contact with the pterygoids. The basioccipital is notably broader than the posterior end of the basisphenoid. The basioccipital has a slight midventral ridge. This bone forms a short and robust con-

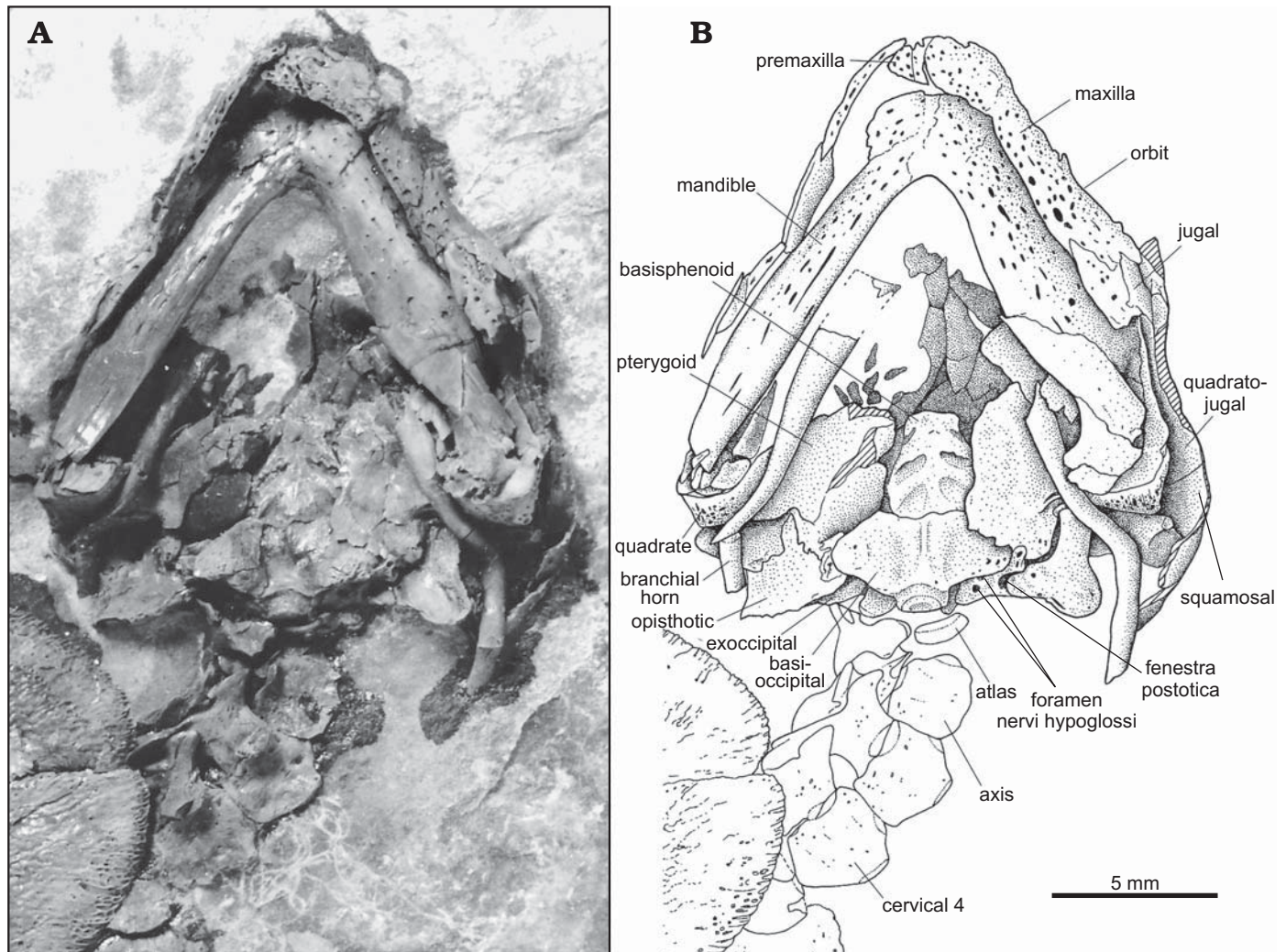


Fig. 2. Skull and cervical vertebrae of the eucryptodiran turtle *Hoyasemys jimenezi* gen. et sp. nov. (MCCM-LH 84) from the Early Cretaceous of Las Hoyas, Spain. Photograph (A) and explanatory drawing (B).

dylus occipitalis, likely with lateral contributions from the exoccipitals.

Portions of the opisthotics are present on both sides. The contact of the opisthotic with the exoccipital is visible postero-medially and the contact of the opisthotic with the quadrate anterolaterally.

The exoccipitals are preserved on both sides, the left being more complete than the right. Two foramina nervi hypoglossi are located in a unique depression close to the base of the condylus occipitalis. The foramen jugulare posterius is not entirely formed by bone and confluent with the fenestra postotica.

Lower jaw.—Both mandibular rami are preserved and articulated with the skull (Fig. 2). The dentary is the dominant element of the lower jaw. A dentary-articular sutural line is not evident in the posteroventral view of mandible. There is no evidence of a retroarticular process. The jaw joint is located well anterior relative to the basioccipital condyle.

Hyoid apparatus.—The hyoid apparatus is represented by a single pair of branchial horns, which consist of ossified rods

extending from the middle of the palate to the posterolateral corner of the skull (Fig. 2).

Vertebral column.—It is possible to identify some cervical and thoracic vertebrae, in addition to all sacral and some caudal vertebrae.

Cervical vertebrae: Remains of the atlas, axis, third, fourth and the anterior portion of the fifth cervical vertebrae are preserved (Fig. 2). The atlas preserves its right neural arch, part of the left one and the crescentic atlantal intercentrum. The axis, and third and fourth cervical vertebrae are relatively short. The third and fourth cervicals are slightly larger than the axis. The transverse processes are well-developed, single, and placed slightly cranially. The neurocentral suture divides the transverse processes. The vertebrae are located in lateral view. A low ridge represents the neural spine. The centra of the axis, third, and fourth cervical vertebrae are opisthocoelous, having a well-formed anterior condyle. The fifth cervical vertebra is caudally hidden by the left epiplastron, but its badly preserved anterior end seems to be convex too. There are well developed midventral keels from the axis to the fifth centrum. These

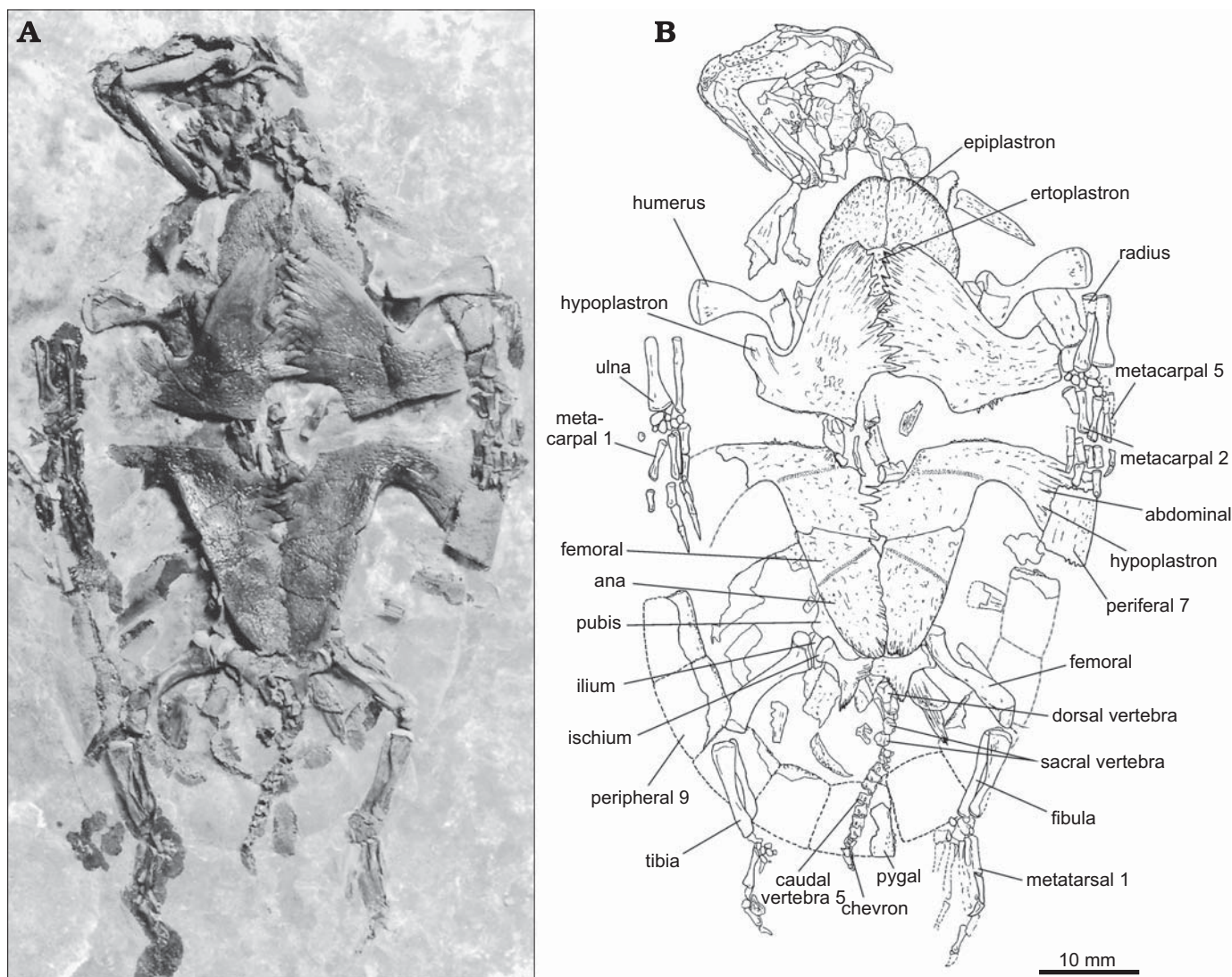


Fig. 3. Ventral view of the eucryptodiran turtle *Hoyasemys jimenezi* gen. et sp. nov. (MCCM-LH 84) from the Early Cretaceous of Las Hoyas, Spain. Photograph (A) and explanatory drawing (B).

keels are more developed cranially, decreasing to the rear part, showing a convex ventral outline. This convexity gradually increases from the second to the fifth vertebrae.

The base of the high neural arch of the second cervical vertebra is broken and is partially displaced. The prezygapophysis of the third cervical vertebra is situated near the broken base of the second neural arch. The zygapophyses are long; particularly the postzygapophyses are well developed. In the third cervical vertebra, the peduncle that bears the postzygapophyses is as longer as the vertebral centrum. No ribs are present along the preserved cervical series.

Dorsal, sacral, and caudal vertebrae: Three dorsal centra are exposed throughout the central fontanelle of the plastron (Fig. 3), but just one of them is antero-posteriorly complete. Its centrum is elongate and possesses a ventral sagittal ridge. All available articular surfaces are slightly concave. The cranial articular surface of the most caudal of these vertebrae is exposed. It is dorso-ventrally depressed and has a subtriangular outline.

Four precaudal vertebrae are visible in the sacral area, of which two or three may be sacral vertebrae. The two anterior preserved precaudal vertebrae have low and wide centra with a strong midventral keel. The anterior articular surface of the first vertebra is platycoelous and mediolaterally elongated. The posterior one is not visible. The two posterior precaudal (sacral) vertebrae have low, wide centra with a low midventral keel.

The preserved portion of the tail is about a quarter of the plastral length. Twelve caudal vertebrae with amphicoelous centra are visible. The first four caudal vertebrae have transverse processes that are as long as their centra. The length of the transverse processes decreases posteriorly and disappears at the level of the eighth caudal vertebra. Starting with the fourth caudal vertebra, slightly developed articular surfaces for haemal arches are apparent. Small chevrons are attached to the sixth-seventh, seventh-eighth and eighth-ninth caudal vertebrae. The caudal vertebrae 9 to 12 are rotated with respect to the anterior ones and their haemal arches,

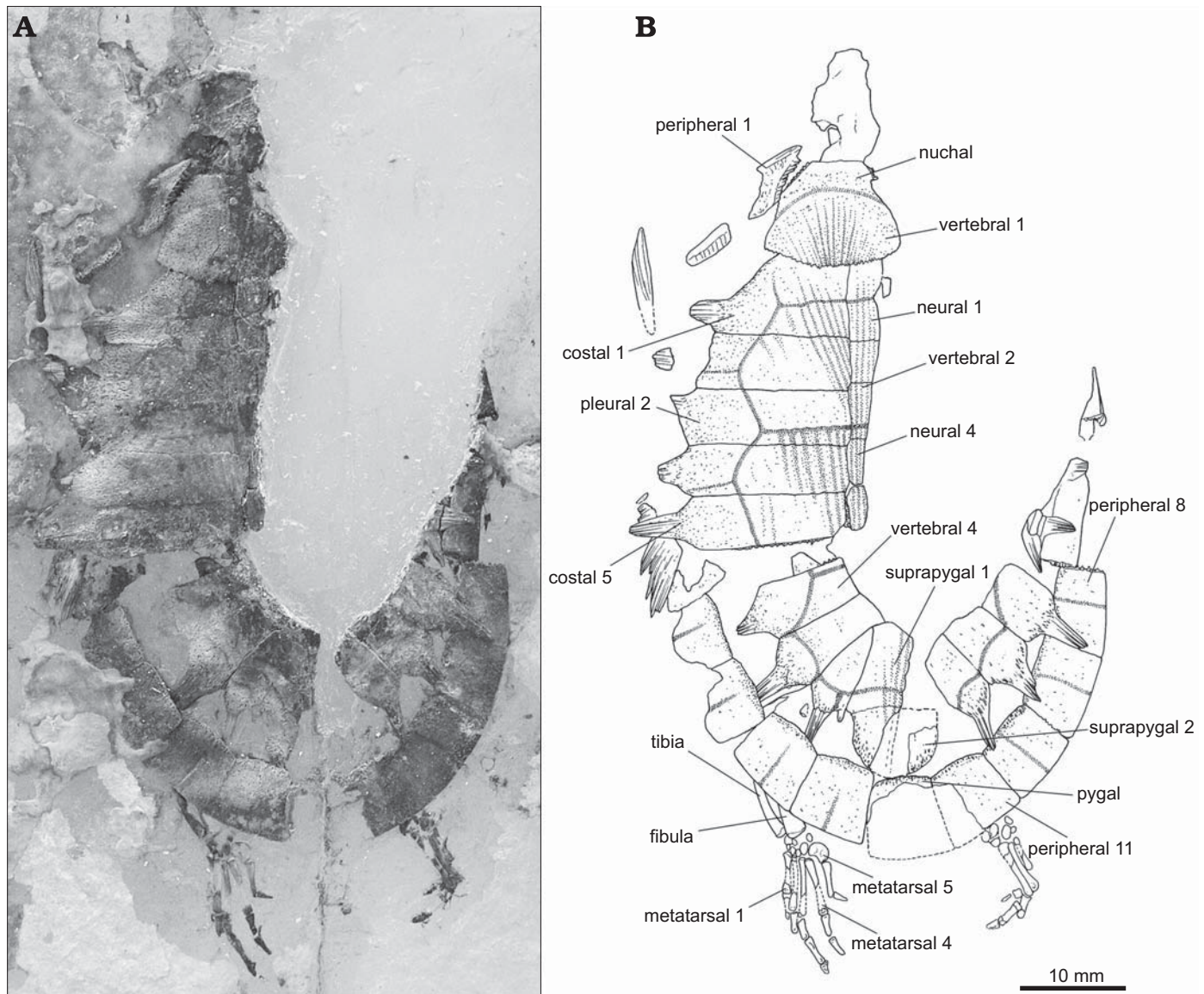


Fig. 4. Dorsal view of the eucryptodiran turtle *Hoyasemys jimenezi* gen. et sp. nov. (MCCM-LH 84) from the Early Cretaceous of Las Hoyas, Spain. Photograph (A) and explanatory drawing (B).

when present, are slightly displaced from their natural positions. The neural arches of these vertebrae are strongly modified and its neural spines taper forwardly and overlap the prezygapophyses.

Carapace.—The carapace is oval and low, and elongate in shape (Fig. 4). Unfortunately most of its right side is not preserved and the anterior left side is slightly displaced. The dorsal surface of the vertebral scutes is weakly sculptured by grooves radiating forwards and laterally from a midpoint on the posterior edge of the vertebral scutes.

Plates: The nuchal is a large plate slightly displaced from the midline of the carapace. It is trapezoidal in shape, lacking the posterior notch for articulation with the first neural. This plate also lacks an anterior emargination.

The specimen preserves the first five plates of the neural series. The first two neurals are rectangular, while from the third to fifth they become hexagonal with short anterolateral

edges. The first neural is the largest in the preserved series and despite its rectangular shape, it has contacts with two pairs of costals. The second neural plate by contrast contacts only with one costal (costal 2).

Hoyasemys jimenezi has two suprapygals. The specimen shows half of the left side of both suprapygal plates, a small part of the right region of this later, and the proximal margin of the pygal, quadrangular in shape. A cast of the pygal plate suggests that no posterior notch is present. The complete left costal series is preserved. The right costal series is composed of the lateral ends of the four posterior plates, slightly displaced and overlapping onto the peripheral bones.

The posterior costal plates form lateral fontanelles with the peripheral bones. These fontanelles are apparently larger than they probably were due to compaction and disarticulation of the specimen and the relative displacement of some of the plates of the carapace.

As it is typical in other turtles, *Hoyasemys jimenezi* likely had eleven pairs of peripherals. However, only two left peripheral plates of the anterolateral margin and the last five pairs of peripherals from both sides of the posterolateral margin are preserved. Among these bones is a fragment of a trapezoidal and elongated first left peripheral plate. It is laterally displaced from its contact with the nuchal. The anterolateral margin of this peripheral is upturned. Several fragments of the second left peripheral, also guttered, represent the remainder antero-lateral margin. Peripheral plates from eight to eleven are mediolaterally expanded.

Scutes: In the anterior region of the nuchal plate the limits of the scutes are not visible, so it is unknown if *Hoyasemys jimenezi* has one or more cervical scutes on this plate. The first vertebral scute covers the posterior portion of this plate. Most of the first, second, third, fourth and fifth vertebral scutes can be recognized. They are hexagonal, wider than long, and with lateral angled edges.

The contact between the first and second vertebral scutes is located on the first costal and neural plates, the contact between the second and third vertebral scutes on the third costal and neural plates, the contacts between the third and fourth on the sixth costal and probably sixth neural, and the contact of the last vertebral scutes over the last pair of costals and the first suprapygal.

Apparently, the marginal scutes are at least as wide as peripheral plates, but the contact between pleurals and marginals is not evident.

Plastron.—The length of the plastron is about the 70% of the carapace. It has a narrow bridge, with deeply concave axillary and inguinal notches, and with a subtriangular posterior lobe (Fig. 3). The plastron is slightly shifted in relation to its original position. The distal regions of the right hyoplastra or hypoplastra are not preserved and the lateral left margin is located below the peripheral plates. There therefore is no contact between the plastron and the carapace, and the nature of the plastron/carapace connection is unclear. The plastral buttresses only reach the peripheral plates.

There is a rounded mid-sized central plastral fontanelle between the hyoplastra and hypoplastra. Preservation does not allow identification of lateral bridge fontanelles, but if these existed they would have been very small.

Plates: The epiplastra are large, broad and elongate, giving a rounded outline to the anterior lobe of the plastron. Between the epiplastra and the hyoplastra there is a long, probably ligamentous attachment. The entoplastron is narrow and barely protrudes from between the hyoplastra. The hyoplastra meet each other in the plastral midline and with the entoplastron along an interfingering contact. This anterior half of the plastron is partially disarticulated likely due to compaction.

Mesoplastra are absent. The posterior half of the plastron is also displaced from its natural position. Consequently there is a large gap between the hyoplastra and hypoplastra. Hyoplastra are shorter than hypoplastra. The suture between the hypoplastra and xiphiplastra is medially directed toward

the rear, with a small notch laterally. The xiphiplastra are elongate and lack anal notch.

Scutes: The morphology of the scutes of the anterior half of the plastron is not known because the sulci are not discernible. Inframarginal scutes are not preserved. The sulci between the abdomino-femoral and femoro-anal scutes are clearly visible. The abdomino-femoral sulci, restricted to the hypoplastra, articulated along a line that extends from the deepest point of the inguinal notch to the posterior part of the hyo-hyoplastral fenestra. The femoral-anal sulcus is oblique, tends sagittally to reach the hypoplastra-xiphiplastra contact, but remains restricted to the xiphiplastron.

Pectoral girdle and forelimbs.—Pectoral girdle: Most of the elements of the left and right scapular girdles lie under the hyoplastra and can only be partially described. Only the glenoid cavity is visible on both sides where the humeri are articulated. The articular surface is slightly convex.

Humerus: Both humeri are exposed in ventral view. The axis of the humeri presents a slightly sigmoidal shape and a strong medial constriction. The medial process is about twice as large as the lateral process. Between them, a shallow intertubercular fossae is present. The proximal end is slightly cranio-caudally wider than the distal one. The articular surface of the distal end is directed ventrally. The radial and ulnar condyles are only lightly developed.

Radius and ulna: These elements are relatively well preserved on both sides. The radius is slightly longer, and more columnar and slender than the ulna. The ulna is about two-thirds the length of the humerus and is flattened dorso-ventrally, with a convex proximal end. The olecranon fossa is not well developed.

Carpus and manus: The right and left carpi are partially preserved and the relative position of the elements has suffered some distortion. Both carpi are exposed in dorsal view. The preserved bones of the proximal carpus are difficult to determine because of slightly disarticulation. However, the ulnare, the intermedium and the centrale can be recognized in both forelimbs. The five distal carpals are preserved in both carpi. They are rounded elements. Distal carpals I to III are subequal in size, while distal carpal IV is the largest and the V is the smallest.

The metacarpals are relatively long elements. As usual, the first metacarpal is relatively short and broad in comparison with the other metacarpals. The proximal end of metacarpal I has an expanded base that is broader than the rest of the bone. Metacarpals II to IV are similar in general size and shape, while the V is the shortest. This metacarpal is preserved in bad conditions on both manus.

The phalanges are exposed mainly in lateral or dorsal views. They are preserved on the right manus in digits I to IV and in the left one in all the digits but not complete. The first digit has two phalanges, the second and the third have three. Digit IV probably had three phalanges, but there is no evidence to ensure that this number is not higher. Digit V has two preserved phalanges, the first and the claw.

Pelvic girdle and hindlimbs.—Pelvic girdle: Partially preserved and slightly distorted pelvic elements are present. Just a small part of the acetabular portion of the right ilium is available. The articular surface is narrow and concave. Most of the pubis lies under the visceral surface of the plastron. The proximal region of both pubes is partially exposed around the acetabulum. The pubis is a thin blade, as can be seen in the available portion of the right one. The ischia are caudally displaced and sagittally articulated, almost completely exposed. The lower end is expanded.

Femur: Both femora are preserved articulated with the acetabulum. They are slightly S-shaped, and slightly longer than the humeri. The rounded femoral head forms an angle of approximately 120° from the main axis of the bone. The right femur is exposed in lateral view, while the left one is exposed in latero-ventral view. The femur expands distally forming a large tibial condyle. A small fibular condyle is placed on the posteroventral margin.

Tibia and fibula: The tibia and fibula are equal in size and slightly shorter than the femur. They articulate with one other. The tibia has an expanded proximal end. Its broad proximal articular surface articulates with much of the tibial condyle of the femur. The medial edge of the tibia is concave and the lateral edge is nearly straight. Distally, the tibia expands slightly. The fibula is a slender bone with a head scarcely wider than its shaft, while the distal end is broader and flatter than the proximal end.

Tarsus and pes: Both tarsi are partially preserved. As in the carpi, the proximal elements are somewhat disarticulated. It is not possible to identify the different bones of the right tarsi. Two elements of the left tarsi probably correspond to the astragalus and calcaneum. The element interpreted as the astragalus is larger than the calcaneum, and proximally articulates with the tibia and fibula.

The distal tarsals are oval in shape. In the left hindlimb five metatarsals are recognized, which increase in length from I to IV and decrease in the last one. The metatarsals are slender and long. Metatarsal V is characterized by a flat L-shape.

Digits I to V are relatively well preserved. Digit I has two phalanges. In the digit II there is only one preserved phalanx. Digit III has three phalanges. The first phalanx and the proximal region of the second phalanx are observed in digits IV and V. Therefore, the total number of phalanges in these two digits is not known.

Stratigraphic and geographic range.—Known only from the type locality.

Phylogenetic analysis

In order to determine the systematic position of *Hoyasemys jimenezi*, we used the data matrix from Joyce (2007), consisting of 56 taxa and 136 characters. Because of the variation shown by characters 73 (vertebral B: shape of the vertebrae)

and 76 (plastron B: central plastral fontanelle) during ontogenetic development, we chose not to code these for *Hoyasemys*. Since the state of character 99 (anal A: plastral scale set 7, anals) in MCCM-LH 84 is intermediate between the conditions coded as 0 and 1, it also was not coded. Finally, it should be noted that for character 132 (manus A: phalangeal formula of manus and pes), the scoring was the reverse of that in Joyce (2007). All in all, *Hoyasemys jimenezi* was scored for 51 of the characters from Joyce (2007) (see Appendix 1).

The phylogenetic analysis was conducted using the TNT v. 1.0 program (Goloboff et al. 2008), with *Proganochelys quenstedti* as outgroup. Considering that *Hoyasemys* is an unequivocal pancryptodire, we used a reduced version of the data matrix in which all representatives of Panpleurodira and three of Joyce's (2007) rogue taxa (*Portlandemys mcdowellii*, *Sandownia harrisi*, *Mongolemys elegans*) were excluded. The most parsimonious trees were found using the heuristic tree search, performing 1000 replicates of Wagner trees (using random addition sequences) followed by TBR branch swapping (holding 10 trees per replicate). All characters were considered unordered and equally weighted.

The phylogenetic analysis resulted in 20 most parsimonious trees (MPTs) of 297 steps (CI = 0.569, RI = 0.863). The majority rule tree (Fig. 5) shows the same topology as found by Joyce (2007). *Hoyasemys jimenezi* gen. et sp. nov. is placed as a basal member of Eucryptodira, forming a monophyletic group with the “Macrobaenidae” and “Sinemydidae”. Here we found, as did Joyce (2007), that the “Macrobaenidae” and “Sinemydidae” are non-monophyletic groups more derived than *Xinjiangchelys latimarginalis*, but not including Cryptodira. The node “Macrobaenidae” + “Sinemydidae” + Crypto-

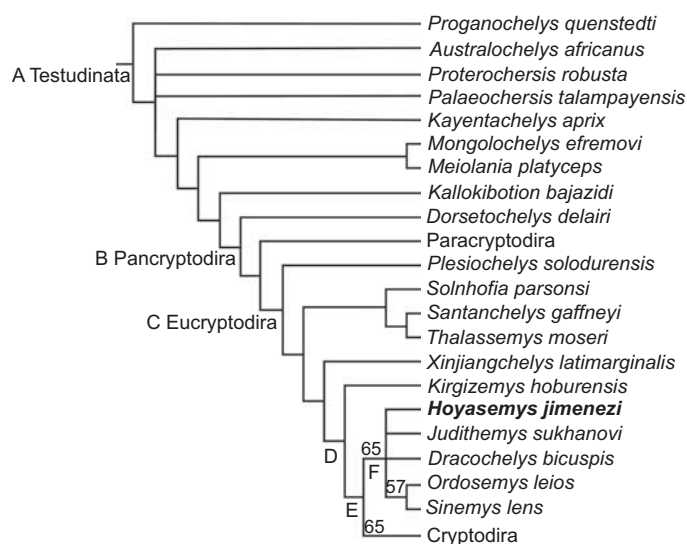


Fig. 5. Majority rule tree from the 87 maximum parsimonious trees produced by the cladistic analysis of *Hoyasemys jimenezi* in the modified data set of Joyce (2007). Retention index (RI) = 0.863 and consistency index (CI) = 0.569. Values refer percentages under 100% obtained in the majority rule analysis. Branches with percentage under 50% are collapsed. Letters refer to the nodes mentioned in the text.

dira (Fig. 5: node D) is diagnosed by the following synapomorphies: epiplastra elongate in shape, with long postero-medial contact with the hyoplastra (Joyce 2007: character 83); extragular scutes absent (character 92); posterior cervicals with strongly developed ventral keels (character 103); and presence of cervical central articulations (character 105). The node consisting of all these taxa except *Kirgizemys hoburensis* (Fig. 5: node E) is diagnosed by the absence of parietal–squamosal contact because the upper temporal emargination is well developed (character 11).

Hoyasemys jimenezi forms an unnamed clade with *Judithemys sukhanovi*, *Dracochelys bicuspis*, *Sinemys lens*, and *Ordosemys leios*. The members of this clade (Fig. 5: node F) share the absence or underdevelopment of chevrons (character 117). This clade is the sister group of crown-group Cryptodira (Joyce 2007).

Hoyasemys jimenezi has three autapomorphies in this cladistic analysis: articulation between fourth and fifth cervicals through a cotyle in the fourth and a condyle in the fifth (character 108); all caudal centra amphicoelous (character 119); most digits of manus and pes with three elongate phalanges (character 132).

Comparisons

Because of its systematic position in the cladistic analysis (Fig. 5), *Hoyasemys jimenezi* is compared with some species traditionally attributed to “Macrobaenidae” and “Sinemydidae”, primitive eucryptodires from the Cretaceous to the Paleocene of Asia and North America (Parham and Hutchinson 2003; Lee et al. 2009): *Kirgizemys hoburensis* (considered a subjective senior synonym of *Hangaemys hoburensis* sensu Danilov et al. 2006), *Judithemys sukhanovi*, *Dracochelys bicuspis*, *Ordosemys leios*, *Sinemys lens*, *Anatolemys oxensis*, *Macrobaena mongolica*, and *Wuguia efremovi*. “Macrobaenidae” or “Sinemydidae” may both be paraphyletic (Parham and Hutchinson 2003; Gaffney et al. 2007), a view supported by our study. Other basal eucryptodires are also compared: *Plesiochelys solodurensis*, *Plesiochelys etalloni*, *Solnhofia parsonsi*, *Thalassemys moseri*, *Brodiechelys brodiei*, and *Xinjiangchelys latimarginalis*.

Skull.—As in most turtles, in *Hoyasemys jimenezi* the quadratojugal is present. The only basal eucryptodire in which this bone is absent is *Sinemys*, both *S. lens* and *S. gamera* (Joyce 2007).

In *Hoyasemys jimenezi* the pterygoids contact the basioccipital, as in *Kirgizemys hoburensis*, *Judithemys sukhanovi*, *Dracochelys bicuspis*, and *Ordosemys leios* but also in other basal eucryptodires, such as *Portlandemys mcdowellii*, *Plesiochelys etalloni*, and *Solnhofia parsonsi* (Joyce 2007). However, there is no contact between these bones in other taxa, including *Sinemys lens* (Brinkman and Peng 1993b; Sukhanov 2000; Sukhanov and Narmandakh 2006). The sagittal contact of the pterygoids in *Hoyasemys jimenezi* is shared with all

basal eucryptodires except *Kirgizemys hoburensis*, which has lost this contact (Danilov et al. 2006; Joyce 2007).

A pair of pits on the posterior region of the ventral surface of the basisphenoid is present in several primitive pancryptodires, such as *Sinemys lens*, *Kirgizemys hoburensis*, *Ordosemys leios*, and *Judithemys sukhanovi* (Brinkman and Peng 1993b; Brinkman and Wu 1999; Tong et al. 2004; Danilov et al. 2006; Gaffney et al. 2007; Joyce 2007). This pair of pits is absent in *Macrobaena mongolica*, and other basal eucryptodires such as *Portlandemys mcdowellii*, *Plesiochelys etalloni*, and *Solnhofia parsonsi* (Danilov et al. 2006), but they are present in members of the paraphyletic group that includes all pancryptodires more derived than *Xinjiangchelys latimarginalis*, but excluding Cryptodira (Joyce 2007). This pair of pits is likely associated with insertions of major ligaments from the neck onto the base of the skull, allowing neck retraction (Brinkman and Peng 1993b; Joyce 2007). However, the presence of two pairs of blind depressions on this bone is not shared with any other representative of this node.

The triangular shape of the basisphenoid in *Hoyasemys jimenezi* is shared by some basal eucryptodires such as *Portlandemys mcdowellii*, *Plesiochelys etalloni*, and *Dracochelys bicuspis* (Gaffney 1976; Gaffney and Ye 1992; Gaffney et al. 2007), but not by *Ordosemys leios* or *Kirgizemys hoburensis*, in which it is rectangular (Gaffney et al. 2007).

As in most other pancryptodires, the basisphenoid of *Hoyasemys jimenezi* is narrower than the basioccipital. However, in *Plesiochelys etalloni* and *Portlandemys mcdowellii* the width of the rear end of the basisphenoid is the same of the basioccipital (Gaffney 1976; Rieppel 1980). The long basisphenoid of *Hoyasemys jimenezi*, as in *Plesiochelys etalloni*, contrasts with the condition in other taxa such as *Solnhofia parsonsi*, in which it is very short (Lapparent de Broin et al. 1996).

The relatively short and wide basioccipital of *Hoyasemys jimenezi* is shared with *Ordosemys leios*, but it is longer than wide in other taxa such as *Kirgizemys hoburensis* and *Dracochelys bicuspis* (Brinkman and Wu 1999; Gaffney et al. 2007).

Vertebral column.—The transverse processes on the anterior edge of the centrum of the cervical vertebrae in *Hoyasemys jimenezi* is shared with the basal eucryptodires *Kirgizemys hoburensis*, *Judithemys sukhanovi*, and *Xinjiangchelys latimarginalis* (Gaffney et al. 2007). However, other representatives of this group show the transverse processes in the middle of the centrum, such as *Dracochelys bicuspis* and *Solnhofia parsonsi* (Gaffney et al. 2007).

The articulations of the cervical vertebrae of *Hoyasemys jimenezi* are formed as in *Kirgizemys hoburensis*, *Judithemys sukhanovi*, and *Ordosemys leios*. This condition, also present in Cryptodira, differs from that observed in other basal eucryptodires, with amphicoelous vertebrae, such as *Solnhofia parsonsi*, *Thalassemys moseri*, and *Xinjiangchelys latimarginalis* (Joyce 2007).

The presence of at least the three opisthocoelous cervicals seen in *Hoyasemys jimenezi* (from the second to the fourth) is shared with *Sinemys lens* and *Dracochelys bicuspis*, with

opisthocoelous cervicals 2–7 and a biconvex 8 (Brinkman and Wu 1999; Brinkman 2001). This differs from the character in most Pancryptodira, with the fourth cervical biconvex, separating the opisthocoelous anterior vertebrae from the procoelous posterior cervicals (Parham and Hutchinson 2003). The fourth cervical vertebra is biconvex in taxa such as *Judithemys sukhanovi*, *Ordosemys leios*, and *Kirgizemys hoburensis* (Brinkman and Wu 1999; Joyce 2007; Gaffney et al. 2007).

As in *Solnhofia parsonsi*, all caudal centra in MCCM-LH 84 are amphicoelous (Gaffney et al. 2007; Joyce 2007). *Dracochelys bicuspis*, *Kirgizemys hoburensis*, *Ordosemys leios*, and *Judithemys sukhanovi* have a biconcave third caudal vertebra, with procoelous anterior and opisthocoelous posterior caudals (Brinkman and Peng 1993a; Brinkman and Wu 1999; Hirayama et al. 2000; Parham and Hutchinson 2003; Gaffney et al. 2007; Joyce 2007).

The small, poorly developed chevrons in the last preserved vertebrae of *Hoyasemys jimenezi* are like those of *Judithemys sukhanovi* and *Ordosemys leios* (Parham and Hutchinson 2003; Joyce 2007). However, many basal eucryptodires have well-developed chevrons in nearly all caudals, such as *Solnhofia parsonsi* (Brinkman and Wu 1999; Hirayama et al. 2000; Gaffney et al. 2007; Joyce 2007).

Carapace.—The longer than wide carapace of *Hoyasemys jimenezi* is seen in almost all basal eucryptodes, but not in *Ordosemys leios*, in which it is as wide as long, or in some specimens of *Sinemys*, such as *Sinemys lens* or *Sinemys gamera*, in which the width of the carapace can be greater than or equal to its length (Brinkman 2001; Parham and Hutchinson 2003; Danilov and Sukhanov 2006; Danilov et al. 2006).

The absence of emargination in the anterior margin the nuchal plate of *Hoyasemys jimenezi* is shared with *Wuguia efremovi* or *Anatolemys oxensis*, taxa in which this emargination is weak or absent. *Judithemys sukhanovi*, *Kirgizemys hoburensis*, *Ordosemys leios*, and *Sinemys lens* have a small emargination. On the contrary, in *Dracochelys bicuspis* the emargination is well developed (Sukhanov 2000; Parham and Hutchinson 2003; Matzke et al. 2004a; Danilov et al. 2006; Danilov and Sukhanov 2006; Sukhanov and Narmandakh 2006; Danilov and Parham 2008).

Hoyasemys jimenezi shares with other primitive eucryptodires, such *Kirgizemys hoburensis*, *Ordosemys leios*, and *Wuguia efremovi*, the dorsal thickening of the lateral edges in the anterior peripherals (Brinkman and Peng 1993a, b; Peng and Brinkman 1993; Parham and Hutchinson 2003; Matzke et al. 2004b; Danilov and Sukhanov 2006; Danilov and Parham 2008). Guttered peripherals are absent in other taxa such as *Dracochelys bicuspis*, *Judithemys sukhanovi*, or *Sinemys lens* (Peng and Brinkman 1993a, b; Matzke et al. 2004b; Danilov and Sukhanov 2006).

The angled lateral edges of the vertebral scutes of *Hoyasemys jimenezi* are more like those of *Dracochelys bicuspis* than *Kirgizemys hoburensis*, where the vertebral scutes have nearly parallel sides (Brinkman 2001).

Plastron.—In *Hoyasemys jimenezi* the plastral buttresses reach only the peripherals, as in *Sinemys lens*, *Kirgizemys hoburensis*, *Dracochelys bicuspis*, *Ordosemys leios*, *Judithemys sukhanovi*, *Xinjiangchelys latimarginalis*, *Solnhofia parsonsi*, and *Brodiechelys brodiei* (Hirayama et al. 2000; Gaffney et al. 2007; Joyce 2007). In *Plesiochelys solodurensis* and *Thalassemys moseri* the plastral buttresses reach the costals (Lapparent de Broin et al. 1996; Hirayama et al. 2000; Gaffney et al. 2007; Joyce 2007).

The broad epiplastra of *Hoyasemys jimenezi* are also seen in *Xinjiangchelys latimarginalis*, but *Sinemys lens*, *Dracochelys bicuspis*, *Kirgizemys hoburensis*, and *Ordosemys leios* have narrow epiplastra (Brinkman and Wu 1999). The elongate epiplastra of *Hoyasemys jimenezi*, with a long postero-medial contact with the hyoplastra, are similar to *Kirgizemys hoburensis*, *Judithemys sukhanovi*, and *Dracochelys bicuspis*, but different from the squarish epiplastra with a minor posterior contact with the hyoplastra in *Plesiochelys solodurensis*, *Solnhofia parsonsi*, and *Xinjiangchelys latimarginalis* (Joyce 2007).

Appendicular skeleton.—The hook-shaped fifth metatarsal of *Hoyasemys jimenezi* is the general condition in turtles (Brinkman 2001). The complete phalangeal formula of the pes of *Hoyasemys jimenezi* is not known, but is compatible with the primitive formula for Pancryptodira, 2-3-3-3-3, present in eucryptodiran taxa such *Judithemys sukhanovi* (Parham and Hutchinson 2003).

Discussion

Adult basal eucryptodes can exhibit several characters seen in juveniles of other groups of turtles. In particular, the large size of the skull in relation to the carapace, the ornamentation on the vertebral scutes, the presence of fontanelles, the presence of broad vertebral scutes, or the interdigitating interhyoplastral and interhypoplastral sutures observed in the type of *Hoyasemys jimenezi* are shared with other adult eucryptodires.

The ratio of the length of the skull to the carapace in *Hoyasemys jimenezi* is about 25%, similar to *Idiochelys fitzingeri* and *Eurysternum wagleri* (Lapparent de Broin et al. 1996). *Solnhofia parsonsi* is diagnosed by a skull that is 40% the length of the carapace (Joyce 2000).

The ornamentation of forward-radiating ridges on the vertebral scutes in *Hoyasemys jimenezi* is present in adults of some basal eucryptodires. *Xinjiangchelys qiguensis*, *X. tianshanensis*, and *X. radiplicatus* show this dorsal ornamentation of the carapace, but the pattern and intensity is different, being weakest in *X. qiguensis* and strongest in *X. radiplicatus* (Matzke et al. 2004b). This pattern is also present in some Eurysternidae such as *Eurysternum wagleri* (Lapparent de Broin 2001). In some “Macrobaenidae” such as *Kirgizemys hoburensis*, the carapace is also sculptured by grooves (Brinkman and Peng 1993a).

Peripheral fontanelles are present in adult specimens of Eurysternidae, *Dracochelys bicuspis*, *Ordosemys brinkmania*, undetermined representatives of *Sichuanchelys*, *Xinjiangchelys chowi*, and some species of *Sinemys* such as *S. gamera* (Brinkman and Peng 1993b; Lapparent de Broin et al. 1996; Joyce 2000; Brinkman 2001; Maisch et al. 2003; Matzke et al. 2005; Sukhanov and Narmandakh 2006; Danilov and Parham 2007, 2008), but are absent in other taxa such as *Kirgizemys hoburensis*, *Sichuanchelys chowi*, *Sinemys lens*, and *Xinjiangchelys qiguensis* (Brinkman and Peng 1993a, b; Maisch et al. 2003; Matzke et al. 2004b; Danilov and Parham 2008).

The fenestrated plastron is primitive for Eucryptodira (Brinkman and Peng 1993b). A central fontanelle in the plastron is present in *Ordosemys leios*, *Solnhofia parsonsi*, and *Eurysternum wagleri*. However, other basal Eucryptodira lack this fontanelle, such as *Judithemys sukhanovi*, *Kirgizemys hoburensis*, *Brodiechelys brodiei*, and *Xinjiangchelys latimarginalis* (Hirayama et al. 2000; Joyce 2000; Sukhanov 2000; Danilov and Parham 2008). In other turtles, including Plesiochelyidae and *Sinemys lens*, this fontanelle can be retained or absent in adults (Bräm 1965; Gaffney 1975b; Lapparent de Broin et al. 1996; Gaffney et al. 2007).

The broad vertebral scutes of *Hoyasemys jimenezi* represent the primitive condition for Eucryptodira, observed in taxa such as Eurysternidae, Plesiochelyidae, Xinjiangchelyidae, *Ordosemys leios*, *Dracochelys bicuspis*, and *Judithemys sukhanovi* (Gaffney 1975c; Brinkman and Peng 1993a; Lapparent de Broin et al. 1996; Hirayama et al. 2000; Joyce 2000; Sukhanov 2000; Matzke et al. 2004b; Danilov et al. 2006). In some of these taxa, the vertebral scutes are considerably wider than in *Hoyasemys jimenezi*, extending to the peripheral plates in the case of *Xinjiangchelys qiguensis* (Matzke et al. 2004b).

The strongly interdigitating interhyoplastral and partial interhypoplastral sutures of *Hoyasemys jimenezi* are similar to those observed in adults of other taxa such as *Xinjiangchelys qiguensis*, *Dracochelys bicuspis*, or *Macrobaena mongolica* (Brinkman 2001; Maisch et al. 2003; Matzke et al. 2004b; Tong et al. 2004).

These comparisons mean it is impossible to determine the ontogenetic age of *Hoyasemys jimenezi*. For this reason, some characters were not coded for *Hoyasemys jimenezi* in the cladistic analysis, nor taken into account in the diagnosis of this new taxon. In this analysis, *Hoyasemys jimenezi* is considered to be a member of Eucryptodira more derived than *Xinjiangchelys latimarginalis*, but primitive relative to Cryptodira (Fig. 5).

The Uña locality (Cuenca, Spain) is the closest fossil site both spatially and temporally, and it has yielded a rich vertebrate fauna. Turtles are represented by shell fragments, including a “chelydroid-like” turtle (after Broin in Krebs 1995), which might be *Hoyasemys jimenezi*, although diagnostic characters are lacking.

Although some basal eucryptodires more primitive than *Hoyasemys jimenezi*, such as Thalassemydidae, Plesiochelyidae and Eurysternidae, are interpreted as coastal chelonians

(Danilov 2008), closer relatives of *Hoyasemys jimenezi*, such as “Macrobaenidae” and “Sinemydidae”, may have been freshwater forms. In fact, *Kirgizemys hoburensis*, *Dracochelys bicuspis*, *Sinemys lens*, and *Ordosemys leios* are interpreted as adapted to freshwater environments, and described as “chelydroid” in appearance (Renous et al. 2008). *Judithemys sukhanovi* was a more specialized swimmer (Parham and Hutchinson 2003). The Las Hoyas deposits were formed in a shallow and permanent lacustrine system (Fregenal-Martínez and Meléndez 1995), and the fauna is largely freshwater (Buscalioni et al. 2008).

The adaptation of turtles to an aquatic life involves modifications both in shell shape and in the limbs (Renous et al. 2008). An incomplete and reduced shell, like that in this group of Eucryptodira, seems to be adequate in aquatic environments (Renous et al. 2008). The low shell is hydrodynamically efficient (Claude et al. 2003; Parham and Hutchinson 2003). The reduced fenestrated and cruciform plastron of the aquatic “Macrobaenidae” and “Sinemydidae” (Brinkman and Peng 1993a) allows good leg mobility. However, a reduced plastron could also facilitate other functions such as cutaneous respiration over a greater surface area, so it does not always imply an adaptation to swimming (Parham and Hutchinson 2003).

Adaptation to different modes of aquatic life has led to significant changes in the limbs of turtles. *Hoyasemys jimenezi* lacks the adaptations of marine forms, in which the forelimbs are much longer than the hindlimbs and are modified into rigid flippers and the hindlimbs into semi-rigid paddles. This is achieved by an increase in the length of the metacarpals and phalanges, the loss of articulations between these, similar length of the femur and humerus, a peculiar morphology of the pisiform, and flattened limb bones (Pace et al. 2001; Renous et al. 2008). *Hoyasemys jimenezi*, as well as the rest of basal Eucryptodira, clearly lacks these characters. However, the limbs of *Hoyasemys jimenezi* are similar to those of semi-aquatic and highly aquatic freshwater forms (Pace et al. 2001; Renous et al. 2008), in that the femur is a little longer than the humerus, the paddles are small and consist of mobile digits, long claws on all digits, and a typical phalangeal formula of 2-3-3-3-3. In contrast, in highly aquatic freshwater forms such as Trionychidae and Carettochelyidae the paddles are more developed, with long mobile digits, hyperphalangy in phalanges IV and V, and claws only in the first three digits (Joyce 2007; Renous et al. 2008). Although the exact number of phalanges of the last two digits of the hands or feet are not known in *Hoyasemys jimenezi*, the fifth digit of the hand has no more than three phalanges, the last being a claw, as in semiaquatic turtles. Therefore, the carapace and limbs suggest *Hoyasemys jimenezi* was an inhabitant of freshwater, compatible with the environment where it was found.

Acknowledgements

We thank Walter Joyce (University of Tübingen, Germany) and Juliana Sterli (Museo Paleontológico Egidio Feruglio, Trelew, Argentina) for

comments and suggestions. Maximiliano Lezcano (San Carlos de Bariloche, Argentina) drew the figures. APG is funded by the FPU subprogramme of the “Ministerio de Ciencia e Innovación” (ref. AP2007-00873). The Willi Hennig Society sponsors TNT cladistics software.

References

- Antunes, M.T., Becquart, D., and Broin, F. de 1988. Découverte de “*Plesiochelys*”, Chélonien marin-littoral, dans le Kimméridgien d’Alcoçaba, Portugal. *Ciências da Terra* 3: 179–195.
- Averianov, A.O. 2002. Review of Mesozoic and Cenozoic sea turtles from the former USSR. *Russian Journal of Herpetology* 9: 137–154.
- Bardet, N. 1994. Extinction events among Mesozoic marine reptiles. *Historical Biology* 7: 313–324.
- Bräm, H. 1965. Die Schildkröten aus dem oberen Jura (Malm) der Gegend von Solothurn. *Schweizerische Paläontologische Abhandlungen* 83: 1–190.
- Brinkman, D.B. 2001. New material of *Dracochelys* (Eucryptodira: Sine-mydiidae) from the Juggar Basin, Xinjiang, People’s Republic of China. *Canadian Journal of Earth Sciences* 38: 1645–1651.
- Brinkman, D.B. and Peng, J.H. 1993a. *Ordosemys leios* n. gen. a new turtle from the early Cretaceous of the Ordos Basin, Inner Mongolia. *Canadian Journal of Earth Sciences* 30: 2128–2138.
- Brinkman, D.B. and Peng, J.H. 1993b. New material of *Sinemys* (Testudines, Sine-mydiidae) from the Early Cretaceous of China. *Canadian Journal of Earth Sciences* 30: 2139–2152.
- Brinkman, D.B. and Wu, X.-C. 1999. The skull of *Ordosemys*, an Early Cretaceous turtle from Inner Mongolia, People’s Republic of China, and the interrelationships of Eucryptodira (Chelonia, Cryptodira). *Paludicola* 2: 134–147.
- Buscalioni, A.D. and Fregenal-Martínez, M.A. 2006. Archosaurian size bias in Jurassic and Cretaceous freshwater ecosystems. In: P.M. Barrett and S.E. Evans (eds.), *Ninth International Symposium on Mesozoic Terrestrial Ecosystems and Biota*, 9–12. Natural History Museum, London.
- Buscalioni, A.D. and Fregenal-Martínez, M.A. 2010. A holistic approach to the palaeoecology of Las Hoyas Konservat-Lagerstätte (La Huerguina Formation, Lower Cretaceous, Iberian Ranges, Spain). *Journal of Iberian Geology* 36: 297–326.
- Buscalioni, A.D., Fregenal, M.A., Bravo, A., Poyato-Ariza, F.J., Sanchiz, B., Báez, A.M., Cambra Moo, O., Marín Closas, C., Evanz, S. E., and Marugán Lobón, J. 2008. The vertebrate assemblage of Buenache de la Sierra (Upper Barremian of Serranía de Cuenca, Spain) with insights into its taphonomy and palaeoecology. *Cretaceous Research* 29: 687–710.
- Claude, J., Paradis, E., Tong, H., and Auffray, J.-C. 2003. A geometric morphometric assessment of the effects of environment and cladogenesis on the evolution of the turtle shell. *Biological Journal of the Linnean Society* 79: 485–501.
- Danilov, I. 2005. Die fossilen Schildkröten Europas. In: U. Fritz (ed.), *Handbuch der Reptilien und Amphibien Europas. Schildkröten (Testudines) II*, 329–448. Aula-Verlag, Wiebelsheim.
- Danilov, I. 2008. An overview of fossil non-marine turtles of Europe. In: C. Corti (ed.), *Herpetologia Sardiniae, VII Congresso Nazionale, Societas Herpetologica Italica*, 184–187. Edizioni Delvedere, Latina.
- Danilov, I.G. and Parham, J.F. 2007. The type series of “*Sinemys*” *wuerhensis*, a problematic turtle from the Lower Cretaceous of China, includes at least three taxa. *Palaentology* 50: 431–444.
- Danilov, I.G. and Parham, J.F. 2008. A reassessment of some poorly known turtles from the middle Jurassic of China, with comments on the antiquity of extant turtles. *Journal of Vertebrate Paleontology* 28: 306–318.
- Danilov, I.G. and Sukhanov, V.B. 2006. A basal eucryptodiran turtle “*Sinemys*” *efremovi* (= *Wuguia efremovi*) from the Early Cretaceous of China. *Acta Palaeontologica Polonica* 51: 105–110.
- Danilov, I.G., Averianov, A.O., Skutchas, P.P., and Rezvyi, A.S. 2006. *Kirgizemys* (Testudines, Macrobaenidae): new material from the Lower Cretaceous of Buryatia (Russia) and taxonomic revision. *Fossil Turtle Research* 1: 46–62.
- Diéguez, C., Martín-Closas, C., Meléndez, N., Rodríguez-Lázaro, J., and Trincão, P. 1995. Biostratigraphy. In: M.N. Meléndez (ed.), *Las Hoyas, a lacustrine Konservat-Lagerstätte, Field trip guide book, II International Symposium on Lithographic Limestones, Lleida-Cuenca*, 77–89. Universidad Complutense de Madrid, Madrid.
- Dollo, M.L. 1884. Première note sur les cheloniens de Bernissart. *Bulletin du Musée Royal d’Histoire Naturelle de Belgique* 3: 63–79.
- Escaso, F., Sanz, J.L., and Ortega, F. 2005. Un Konservat-Lagerstätte del Cretácico Inferior de Europa: Las Hoyas. *Boletín de la Real Sociedad Española de Historia Natural (Sección Geológica)* 100: 221–33.
- Fregenal-Martínez, M.A. and Meléndez, N. 1995. Paleotectonic controls of the origin of the Las Hoyas fossil site (Serranía de Cuenca, Spain). In: *Extended Abstract, II International Symposium on Lithographic Limestones, Lleida-Cuenca, Lleida-Cuenca*, 71–74. Ediciones de la Universidad Autónoma de Madrid, Madrid, Spain.
- Fuentes Vidarte, C., Meijide Calvo, M., and Meijide Fuentes, F. 2003. Nueva tortuga para el Cretácico Inferior de Salas de los Infantes (Burgos, España): *Salasemys pulcherrima* n. gen. n. sp. *Studia Geologica Salmantica* 39: 109–123.
- Gaffney, E.S. 1972. An illustrated glossary of turtle skull nomenclature. *American Museum Novitates* 2486: 1–33.
- Gaffney, E.S. 1975a. A phylogeny and classification of higher categories of turtles. *Bulletin of the American Museum of Natural History* 155: 387–436.
- Gaffney, E.S. 1975b. A taxonomic revision of the Jurassic turtles *Portlandemys* and *Plesiochelys*. *American Museum Novitates* 2574: 1–19.
- Gaffney, E.S. 1975c. *Solnhofia parsoni*, a new cryptodiran turtle from the Late Jurassic of Europe. *American Museum Novitates* 2576: 1–25.
- Gaffney, E.S. 1976. Cranial morphology of the European Jurassic turtles *Portlandemys* and *Plesiochelys*. *Bulletin of the American Museum of Natural History* 157: 488–543.
- Gaffney, E.S. and Meylan, P. 1988. A phylogeny of turtles. In: M.J. Benton (ed.), *The Phylogeny and Classification of the Tetrapods, Vol. 1 Amphibians, Reptiles and Birds. Systematics Association, Oxford, Special Volume 35A*: 157–219.
- Gaffney, E.S. and Ye, X. 1992. *Dracochelys*, a new cryptodiran turtle from the Early Cretaceous of China. *American Museum Novitates* 3048: 1–13.
- Gaffney, E.S., Rich, T.H., Vickers-Rich, P., Constantine, A., Vacca, R., and Kool, L. 2007. *Chubutemys*, a new eucryptodiran turtle from the Early Cretaceous of Argentina, and the relationships of Meiolianiidae. *American Museum Novitates* 3599: 1–36.
- Goloboff, P.A., Farris, J.S., and Nixon, K.C. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24: 774–786.
- Hirayama, R., Brinkman D.B., and Danilov I.G. 2000. Distribution and biogeography of non-marine Cretaceous turtles. *Russian Journal of Herpetology* 7: 181–198.
- Jiménez-Fuentes, E. 1995. Turtles. In: M.N. Meléndez (ed.), *Las Hoyas, a lacustrine Konservat-Lagerstätte, Field trip guide book, II International Symposium on Lithographic Limestones, Lleida-Cuenca*, 55–56. Universidad Complutense de Madrid, Madrid.
- Joyce, W.G. 2000. The first complete skeleton of *Solnhofia parsoni* (Cryptodira, Eurysternidae) from the Upper Jurassic of Germany and its taxonomic implications. *Journal of Paleontology* 74: 684–700.
- Joyce, W.G. 2003. A new Late Jurassic turtle specimen and the taxonomy of *Palaeomedusa testa* and *Eurysternum wagleri*. *PaleoBios* 23 (3): 1–8.
- Joyce, W.G. 2007. Phylogenetic relationships of Mesozoic turtles. *Bulletin of the Peabody Museum of Natural History* 48: 3–102.
- Joyce, W.G. and Gauthier, J.A. 2004. Palaeoecology of Triassic stem turtles sheds new light on turtle origins. *Proceedings of the Royal Society B* 271: 1–5.
- Joyce, W.G., Chapman, S.D., Moody, R.T.J., and Walker, C.A. 2011. The skull of the solemydid turtle *Helochelydra nopscai* from the Early Cretaceous (Barremian) Sussex Formation of the Isle of Wight, England. *Special Papers in Paleontology* 86: 75–97.
- Krebs, B. 1995. The Barremian vertebrate locality Uña (Province of Cuenca).

- Materials for a comparison with Las Hoyas. In: *Extended Abstract, II International Symposium on Lithographic Limestones, Lleida-Cuenca*, 95–97. Ediciones de la Universidad Autónoma de Madrid, Madrid.
- Lapparent de Broin, F. de 2001. The European turtle fauna from the Triassic to the present. *Dumerilia* 4: 155–216.
- Lapparent de Broin, F. de, Lange-Badré, B., and Dutrieux, M. 1996. Nouvelles découvertes de tortues dans le Jurassique supérieur du Lot (France) et examen du taxon Plesiochelyidae. *Revue de Paléobiologie* 15: 533–570.
- Lee, Y.-N., Hutchison, J.H., and Chang, K.-H. 2009. The first Mesozoic turtle from South Korea. *Cretaceous Research* 30: 1287–1292.
- Lydekker, R.A. 1889. On remains of Eocene and Mesozoic Chelonia and a tooth of (?) *Ornithopsis*. *Quarterly Journal of the Geological Society* 45: 227–246.
- Lyson, T.R. and Joyce, W.G. 2011. Cranial anatomy and phylogenetic placement of the enigmatic turtle *Compsemys victa*. *Journal of Paleontology* 85: 789–801.
- Maisch, M.W., Matzke, A.T., and Sun, G. 2003. A new sinemydid turtle (Reptilia: Testudines) from the Lower Cretaceous of the Junggar Basin (NW-China). *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* 12: 705–722.
- Matzke, A.T., Maisch, M.W., Pfretzschner, H.-U., Sun, G., and Stöhr, H. 2004a. A new basal sinemydid turtle (Reptilia: Testudines) from the Lower Cretaceous Tugulu Group of Junggar Basin (northwest China). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 2004 (3): 151–167.
- Matzke, A., Maisch, M.W., Sun, G., Pfretzschner, H.-U., and Stöhr, H. 2004b. A new xinjiangchelyid turtle (Testudines; Eucryptodira) from the Jurassic Qigu formation of the southern Junggar Basin, Xinjiang, North-West China. *Palaentology* 47: 1267–1299.
- Matzke, A.T., Maisch, M.W., Sun G.E., Pfretzschner, H.-U., and Stöhr, H. 2005. A new Middle Jurassic xinjiangchelyid turtle (Testudines; Eucryptodira) from China (Xinjiang, Junggar Basin). *Journal of Vertebrate Paleontology* 25: 63–70
- Meylan, P. 1988. *Peltochelys* Dollo and the relationships among the genera of the Carettochelyidae (Testudines: Reptilia). *Herpetologica* 44: 440–450.
- Meylan, P.A. and Gaffney, E.S. 1989. The skeletal morphology of the Cretaceous turtle, *Adocus*, and the relationships among the Trionychoidea. *American Museum Novitates* 2941: 1–60.
- Meylan, P.A., Moody, R.T.J., Walker, C.A., and Chapman, S.D. 2000. *Sandownia harrisi*, a highly derived trionychoid turtle (Testudines: Cryptodira) from the Early Cretaceous of the Isle of Wight, England. *Journal of Vertebrate Paleontology* 20: 522–532.
- Milner, A.R. 2004. The turtles of the Purbeck Limestone Group of Dorset, Southern England. *Palaentology* 47: 1441–1467.
- Nopcsa, F. 1928. Palaeontological notes on the reptiles. IV. *Helochelydra* and *Hylaeochelys*, two little known tortoises from the Wealden and Purbeck Formations. *Geologica Hungarica, Seria Palaentologica* 1 (1): 44–84.
- Ortega, F., Sanz, J.L., Barbadillo, L.J., Buscalioni, A.D., Diéguez, C., Evans, S.E., Fregenal-Martínez, M.A., Fuente, M. de la, Madero, J., Martín-Closas, C., Martínez-Delclós, X., Meléndez, N., Moratalla, J.J., Pérez-Moreno, B.P., Pinardo-Moya, E., Poyato-Ariza, F.J., Rodríguez-Lazaro, J., Sanchiz, B., and Wenz, S. 1999. El yacimiento de Las Hoyas (La Cierva, Cuenca), un Konservat-Lagerstätte del Cretácico inferior. In: E. Aguirre (ed.), *Patrimonio Paleontológico de Castilla-La Mancha*, 195–216. Junta de Comunidades de Castilla-La Mancha, Toledo.
- Pace, C.M., Blob, R.W., and Westneat, M.W. 2001. Comparative kinematics of the forelimb during swimming in red-eared slider (*Trachemys scripta*) and spiny softshell (*Apalone spinifera*) turtles. *Journal of Experimental Biology* 204: 3261–3271.
- Parham, J.F. and Hutchinson, J.H. 2003. A new eucryptodiran turtle from the Late Cretaceous of North America (Dinosaur Provincial Park, Alberta, Canada). *Journal of Vertebrate Paleontology* 23: 783–798.
- Peng, J.-H. and Brinkman, D.B. 1993. New material of *Xinjiangchelys* (Reptilia: Testudines) from the Late Jurassic Qigu Formation (Shishugou Group) of the Pingfengshan locality, Junggar Basin, Xinjiang. *Canadian Journal of Earth Sciences* 30: 2013–2026.
- Pérez-García, A. 2011. Revisión de la serie tipo de *Peltochelys duchastelii* (Chelonii, Trionychoidea) del Cretácico Inferior de Bernissart (Bélgica). In: A. Pérez-García, F. Gascó, J.M. Gasulla, and F. Escaso (eds.), *Viajando a Mundos Pretéritos. Ayuntamiento de Morella*, 249–260. Morella, Castellón.
- Pérez-García, A. and Ortega, F. 2009. Juan Vilanova y Piera (1821–1893) y la primera tortuga hallada en el Mesozoico español. *Geogaceta* 47: 17–20.
- Pérez-García, A., Murelaga, X., and Gasulla, J.M. 2008a. Una nueva tortuga (Chelonii, Eucryptodira) del Cretácico Inferior (Aptiense) de Morella (Castellón). In: J.I. Ruiz-Omeñaca, L. Piñuela, J.C. García-Ramos (eds.), *Libro de Resúmenes de las XXIV Jornadas de la Sociedad Española de Paleontología*, 175–176. Asturias.
- Pérez-García, A., Ortega, F., Murelaga, X., and Dantas, P. 2008b. *Plesiochelys* sp. (Testudines; Eucryptodira) de la Fm. Freixial (Jurásico Superior) en Ulsa (Torres Vedras, Portugal). *Publicaciones del Seminario de Paleontología de Zaragoza* 8: 331–344.
- Rieppel, O. 1980. The skull of the Upper Jurassic cryptodire turtle *Thalassmys*, with a reconsideration of the chelonian braincase. *Palaentographica, Abteilung A* 171: 105–140.
- Renous, S., Lapparent de Broin, F. de, Depecker, M., Davenport, J., and Bels, V.L. 2008. Evolution of locomotion in aquatic turtles. In: J. Wyneken, V.L. Bels, and M.H. Godfrey (eds.), *The Biology of Turtles*, 97–138. CRC Press, Boca Raton.
- Sanz, J.L., Wenz, S., Yébenes, A., Estes, R., Martínez-Delclós, X., Jiménez-Fuentes, E., Diéguez, C., Buscalioni, A.D., Barbadillo, L.J., and Vía, L. 1988. An Early Cretaceous faunal and floral continental assemblage: Las Hoyas fossil site (Cuenca, Spain). *Geobios* 21: 611–635.
- Sauvage, H.E. 1898. Vertébrés fossiles du Portugal. Contribution à l'étude des poissons et des reptiles du Jurassique et du Crétacique. *Memorias Comissão do Serviço Geológico de Portugal, Lisboa* 1897–1898: 1–46.
- Sukhanov, V.B. 2000. Mesozoic turtles of Central Asia. In: M.J. Benton, M.A. Shishkin, D.M. Unwin, and E.N. Kurochkin (eds.), *The Age of Dinosaurs in Russia and Mongolia*, 309–367. Cambridge University Press, Cambridge.
- Sukhanov, V.B. and Narmandakh, P. 2006. New taxa of Mesozoic turtles from Mongolia. *Fossil Turtle Research* 1: 119–127.
- Tong, H., Buffetaut, E., and Suteethorn, V. 2006. *Isanemys*, a new adocid turtle from the Sao Khua Formation (Early Cretaceous) of the Khorat Plateau, northeastern Thailand. *Fossil Turtle Research* 1: 128–137.
- Tong, H., Ji, S.-A., and Ji, Q. 2004. *Ordosemys* (Testudines: Cryptodira) from the Yixian Formation of Liaoning Province, northeastern China: new specimens and systematic revision. *American Museum Novitates* 3438: 1–20.
- Zangerl, R. 1969. The turtle shell. In: A. d'A. Bellairs and T.S. Parsons (eds.), *The Biology of the Reptilia* 1, 311–339. Academic Press, London.

Appendix 1

Scored characters for *Hoyasemys jimenezi* into the data matrix of Joyce (2007): quadratojugal A, 0; premaxilla B, 0; premaxilla E, 0; pterygoid A, 1; pterygoid C, 1; pterygoid D, 1; pterygoid G, 0; basisphenoid A, 0; basisphenoid B, 1; jugular foramina A, 1; dentary A, 0; splenial A, 1; carapace A, 0; carapace B, 0; nuchal B, 0; neural A, 0; peripheral A, 1; costal A, 0; costal B, 0; costal C, 0; supramarginal A, 2; vertebral A, 1; entoplastron A, 1; entoplastron C, 1; entoplastron D, 0; entoplastron E,

0; hyoplastron A, 0; mesoplastron A, 2; hypoplastron A, 0; xiphoplastron A, 0; xiphoplastron B, 0; plastral scutes A, 0; extragular C, 1; abdominal A, 0; cervical rib A, 1; cervical vertebra A, 1; cervical articulation A, 1; cervical articulation B, 0; cervical articulation C, 0; cervical articulation D, 0; chevron A, 1; caudal B, 0; scapula B, 1; scapula C, 1; ilium D, 0; ischium A, 1; hypoischium A, 1; manus A, 0; manus B, 0; manus C, 0; pes B, 1.