

A new genus and species for the amiiform fishes previously assigned to *Amiopsis* from the Early Cretaceous of Las Hoyas, Cuenca, Spain

HUGO MARTÍN-ABAD^{1,2,3*} and FRANCISCO JOSÉ POYATO-ARIZA¹

¹Unidad de Paleontología, Departamento de Biología, Universidad Autónoma de Madrid, Calle Darwin 2, 28049 Madrid, Spain

²JURASSICA Museum, Route de Fontenais 21, 2900 Porrentruy, Switzerland

³Department of Geosciences, University of Fribourg, Chemin du Musée 6, 1700 Fribourg, Switzerland

Received 1 April 2016; revised 13 January 2017; accepted for publication 1 February 2017

The Mesozoic actinopterygian fish *Amiopsis* has been reported from three different localities in the Iberian Peninsula. *Amiopsis woodwardi* was described from the Berriasian–Valanginian of El Montsec (Lérida, Spain). Isolated vertebral centra referred to *Amiopsis* were found in the Barremian of Buenache de la Sierra (Cuenca, Spain). Finally, amiiform material from the Barremian of Las Hoyas (Cuenca, Spain) were reported as *Amiopsis* cf. *A. woodwardi*, due to the overall similarity with the species from El Montsec. Here a detailed anatomical description of the material from Las Hoyas is provided for the first time. The unique combination of characters seen in this taxon, some of which are not shared with *Amiopsis* but with more derived amiids, indicates that it represents a new taxon, which is here named ***Hispanamia newbreyi* gen. nov., sp. nov.**

ADDITIONAL KEYWORDS: Amiidae – Amiopsinae – *Amiopsis woodwardi* – Barremian – El Montsec – *Hispanamia newbreyi* gen. nov., sp. nov. – Vidalamiinae.

INTRODUCTION

Amiopsis Kner, 1863 is a genus included in the family Amiidae, the only genus of the subfamily Amiopsinae (Grande & Bemis, 1998). There are several valid species currently referred to it, all from European localities (Martín-Abad & Poyato-Ariza, 2013a; Poyato-Ariza & Martín-Abad, 2013): *A. lepidota* (Agassiz, 1833) from the Late Jurassic of Solnhofen (Germany), *A. damoni* (Egerton, 1858) from the Late Jurassic of England, *A. woodwardi* (Sauvage, 1903) from the Early Cretaceous of El Montsec (Spain), *A. dolloi* Traquair, 1911 from the Early Cretaceous of Bernissart (Belgium) and *A. prisca* Kner, 1863, the type species, from the Late Cretaceous of Croatia. The monophyly of this genus is currently supported by only one multistate character state, the presence of three

or more lateral fossae on each side of most abdominal centra (Grande & Bemis, 1998).

Concerning the amiid record of the Iberian Peninsula, isolated remains reported as Amiidae indet. or Amiiformes indet. from Asturias (Ruiz-Omeñaca *et al.*, 2006), the Cameros Basin in La Rioja (Bermúdez-Rochas & Poyato-Ariza, 2007), Vega de Pas in Cantabria (Bermúdez-Rochas *et al.*, 2007) and Galve (e.g. Ruiz-Omeñaca *et al.*, 2004) might actually belong to *Amiopsis* but are in need of further analysis (Martín-Abad & Poyato-Ariza, 2013b). The genus *Amiopsis* has been recorded from three different localities in Spain. (1) *A. woodwardi* was described by Sauvage (1903) from the Berriasian–Valanginian laminated limestones of La Pedrera de Rúbies, in El Montsec (Lérida, north-east Spain). This species was later revised by Wenz (1968, 1988; see also Wenz & Poyato-Ariza, 1995), and more recently by Grande & Bemis (1998). (2) Vertebral centra referred to the subfamily Amiopsinae have been recovered from the Barremian of Buenache de la Sierra (Cuenca, Spain; Buscalioni *et al.*, 2008). Isolated amiiform teeth were also found at this site, but they were

*Corresponding author. E-mail: hugo.martin.abad@gmail.com
[Version of Record, published online 5 June 2017;
<http://zoobank.org/> urn:lsid:zoobank.org:pub:213A1503-1053-459E-8C7D-F83D4C9F47E1]

classified as Amiidae indet. (3) Finally, the Barremian laminated limestones of Las Hoyas (Cuenca, Spain) have also yielded specimens traditionally referred to *Amiopsis* (e.g. Sanz *et al.*, 1988; Poyato-Ariza & Wenz, 1995; Poyato-Ariza, 2005a). Several amiiform taxa from this locality are currently under study; initially, the fish fauna of Las Hoyas was considered to be similar to that of El Montsec, at least at the generic level (Sanz *et al.*, 1988), with three amiiform genera – *Caturus*, *Amiopsis* and *Vidalamia* – known from both. However, a more detailed comparison of both faunas has revealed that they differ more than initially thought with, for instance, the occurrence of several endemic taxa at Las Hoyas, such as the pycnodonts *Turbomesodon praeclarus* Poyato-Ariza & Wenz, 2004 and *Stenamaramia* Poyato-Ariza & Wenz, 2000, the goniorhynchiform *Gordichthys conguensis* Poyato-Ariza, 1994, and with different assemblages of primitive teleosts (Poyato-Ariza, 1997; see also Poyato-Ariza & Martín-Abad, 2016). The last-named study suggested that the three amiiform species from Las Hoyas belong to new taxa (Poyato-Ariza & Martín-Abad, 2016).

The objective of the present paper is to describe the taxon of amiiform fishes from Las Hoyas that was previously referred to *Amiopsis* and to test whether it represents the same taxon as that from El Montsec. A complete phylogenetic analysis will be carried out after other amiiform taxa from Las Hoyas are revised.

MATERIAL AND METHODS

MATERIAL EXAMINED

The material of this new taxon is deposited in the Las Hoyas collection at the Museo de las Ciencias de Castilla-La Mancha (MCCM LH) in Cuenca, Spain:

MCCM LH 023, small, complete and articulated skeleton with excellent preservation.

MCCM LH 076a/b, very small skeleton, nearly complete but not totally ossified, with very good preservation.

MCCM LH 085R, small, complete and articulated skeleton with excellent preservation.

MCCM LH 151Pa/b, small, almost complete and mostly articulated skeleton with good preservation.

MCCM LH 374Ra/b, medium-sized, anterior half of skeleton, articulated and excellently preserved. The skull was mechanically and chemically prepared.

MCCM LH 9576a/b, small, complete and articulated skeleton with excellent preservation. It was mechanically and chemically prepared locally.

MCCM LH 9645a/b, complete and articulated, lacking only the tips of fin rays and some teeth. Slab 'a' was acid-prepared locally, not transferred to resin. It is excellently preserved, with only some bones of the skull and a few neural arches damaged.

Slab 'b' shows only the imprint of some damaged skull bones.

MCCM LH 11286, small, complete and articulated skeleton with excellent preservation. It was mechanically and chemically prepared locally.

MCCM LH 15783a/b, very small skeleton, complete but not totally ossified, with very good preservation.

MCCM LH 16040a/b, complete and articulated, lacking only part of the opercular series, the pectoral girdle and some fin ray segments. Slab 'b' was mostly covered by matrix, with only part of the abdomen exposed, and was mechanically and acid-prepared locally, not transferred to resin. Preservation is very good, but the vertebrae of the exposed surface of the fish were already broken. Slab 'a' shows only the originally exposed surface.

MCCM LH 16257a, small, almost complete and articulated skeleton, with excellent preservation. It was acid-prepared locally.

MCCM LH 17274a/b, small, fairly complete and articulated skeleton, with excellent preservation. Both slabs have several cracks, which especially affect the skull and the axial skeleton.

MCCM LH 22600a, the smallest known specimen, complete and articulated skeleton not yet totally ossified, with excellent preservation.

MCCM LH 23062a/b, small, complete and articulated skeleton with good preservation. It was mechanically and chemically prepared locally.

MCCM LH 30878a/b, very small, complete and articulated skeleton not yet totally ossified, with good preservation.

MCCM LH 32022a/b, small, nearly complete and articulated skeleton, with good preservation.

MCCM LH 32244a/b, very small, nearly complete and articulated skeleton not yet totally ossified, with good preservation.

TYPE OF PRESERVATION AND PREPARATION METHODS

Fossil fishes from Las Hoyas usually appear complete and articulated and, even in the case of rare isolated elements, the preservation is exceptional. They are typically preserved as dark reddish to brown coloured bones in a light brown to light grey matrix. Nearly all the known specimens are preserved in lateral view, including their skulls, and are laterally compressed, rarely showing any three-dimensional preservation. Specimens are usually found as slab and counterslab after splitting the thin laminated limestones. Most of the specimens were prepared mechanically, chemically or a combination of both. For chemical preparation, a 2–4% solution of formic acid buffered with calcium phosphate was used; bones were coated with a highly diluted solution of B-72 paralyoid in acetone.

ANATOMICAL ABBREVIATIONS

ang, angular; **ao**, antorbital; **ar**, articular; **arp**, ascending ramus of parasphenoid; **bop**, branchiopercular; **br**, branchiostegals; **cl**, cleithrum; **co**, coronoid; **d**, dentary; **dplp**, posterior dermopalatine; **dpt**, dermopterotic; **dr**, distal radials; **dsp**, dermosphenotic; **ecp**, ectopterygoid; **ep**, epural; **epx**, epaxial fin rays; **es**, extrascapular; **fr**, frontal; **g**, gular; **h**, hyomandibula; **ha**, haemal arch; **hpx**, hypaxial fin rays; **hpxa**, anteroventralmost hypaxial caudal fin ray; **hpxd**, dorsalmost hypaxial caudal fin ray; **hs**, haemal spine; **hyp**, hypural; **ihm**, infrahaemal; **io**, infraorbital bones; **iop**, interopercular bone; **l**, lacrimal; **le**, lateral ethmoid; **lloc**, caudal extension of lateral line canal; **mpt**, metapterygoid; **mr**, middle radial; **mtg**, metapterygium; **mx**, maxilla; **n**, nasal; **op**, opercular bone; **pa**, parietal; **pas**, parasphenoid; **pastp**, parasphenoid tooth patch; **pb**, ossified portion of basipterygium; **pcl**, postcleithrum; **pfr**, principal fin rays; **phy**, parhypural; **pmx**, premaxilla; **pop**, preopercular bone; **pr**, proximal radials; **prfr**, precurrent fin rays; **pt**, posttemporal; **ptg**, propterygium; **q**, quadrate; **r**, rib; **ra**, elongate proximal radials; **ro**, rostral; **sag**, supraangular; **scl**, supracleithrum; **smx**, supramaxilla; **sn**, supraneural; **sop**, subopercular bone; **su**, supraorbital bones; **sym**, symplectic; **u**, ural centrum; **ud**, urodermal; **una**, ural neural arch; **vo**, vomer.

SYSTEMATIC PALAEOONTOLOGY

SUBCLASS ACTINOPTERYGII COPE, 1887
 INFRACLASS NEOPTERYGII REGAN, 1923,
SENSU ROSEN *ET AL.*, 1981
 DIVISION HOLOSTEI MÜLLER, 1844,
SENSU GRANDE, 2010
 SUBDIVISION HALECOMORPHI COPE, 1872,
SENSU GRANDE & BEMIS, 1998
 ORDER AMIIFORMES HAY, 1929,
SENSU GRANDE & BEMIS, 1998
 SUPERFAMILY AMIOIDEA BONAPARTE, 1838,
SENSU GRANDE & BEMIS, 1998
 FAMILY AMIIDAE BONAPARTE, 1838
 GENUS *HISPANAMIA* GEN. NOV.

urn:lsid:zoobank.org:act:AC531976-D36A-4089-8858-1C13D95DD668

? *Amiopsis* Kner, 1863: Sanz *et al.*, 1988: 619–620, table 1.

Urocles Jordan, 1919 (*Megalurus* Agassiz): Poyato-Ariza, 1989: 113, fig. 22B, table 1.

Amiopsis Kner, 1863: Poyato-Ariza, 1989: 113, fig. 22C, table 1.

? *Amiopsis* Kner, 1863: Gómez-Pallerola, 1990: 52.

Urocles Jordan, 1919 (*Megalurus* Agassiz) pro parte: Poyato-Ariza & Wenz, 1990: 303, fig. 5.

Amiopsis Kner, 1863 (*Megalurus* Agassiz) pro parte: Poyato-Ariza & Wenz, 1990: 304, figs 2B, 5.

Urocles Jordan, 1919 (*Megalurus* Agassiz): Sanz *et al.*, 1990: table 1.

Amiopsis Kner, 1863 (*Megalurus* Agassiz): Sanz *et al.*, 1990: table 1.

Amiopsis Kner, 1863: Poyato-Ariza, 1992: 117, fig. 31.

Amiopsis Kner, 1863: Sanz *et al.*, 1994: 186.

Amiopsis Kner, 1863 pro parte: Wenz & Poyato-Ariza, 1994: 204–210.

Urocles Jordan, 1919 (*Megalurus* Agassiz): Fregenal-Martínez, 1995: 150, table 1.

Amiopsis Kner, 1863 (*Megalurus* Agassiz): Fregenal-Martínez, 1995: 150, table 1.

Amiopsis Kner, 1863: Poyato-Ariza & Wenz, 1995, 47, fig. IV-11.

Amiopsis Kner, 1863: Ortega *et al.*, 1999, 206.

Amiopsis Kner, 1863: Sanz *et al.*, 1999: 158.

Amiopsis Kner, 1863: Sanz *et al.*, 2000: 158.

Amiopsis Kner, 1863: Sanz *et al.*, 2001: 359.

Amiopsis Kner, 1863: Ortega *et al.*, 2003: 434, 447.

Amiopsis Kner, 1863: Delclòs *et al.*, 2004: 40.

Amiopsis Kner, 1863: Poyato-Ariza, 2005b: 162, fig. 2C.

Amiopsis Kner, 1863: Buscalioni & Fregenal-Martínez, 2010: 311.

Amiopsis Kner, 1863 pro parte: Martín-Abad & Poyato-Ariza, 2013a: fig. 4.

Amiopsis Kner, 1863: Martín-Abad & Poyato-Ariza, 2013b: fig. 2.

Amiopsis Kner, 1863: Poyato-Ariza & Martín-Abad, 2016.

Type species: Hispanamia newbreyi sp. nov. by monotypy.

Generic diagnosis: Amiid fish differing from all other amiids by the following combination of derived and primitive characters: suborbital bones absent; jaw teeth labiolingually compressed, with sharply carinate caps; three lateral fossae on most of the vertebral centra; articular bone of the lower jaw formed by the fusion of an anterior and a posterior element; faint ornamentation on the dermal bones of the skull formed by small, irregularly disposed foramina and thin, shallow, parallel grooves; relatively short parietal (width-to-length ratio range well exceeding 0.90); ten or fewer ural centra; preopercular long and narrow, crescent-shaped; and posttemporal with lateral edge shorter than anterior edge.

Etymology: *Hispania*, ancient Latin name of Spain, and *Amia* (Ἀμια), ancient Greek name for a type of fish (probably the bonito), and name of the type genus of the family Amiidae.

HISPANAMIA NEWBREYI SP. NOV.

(FIGS 1–11)

urn:lsid:zoobank.org:act:E59B8E0F-B6C7-42D6-B8EF-FAC356648163

Urocles woodwardi (Sauvage, 1903): Sanz *et al.*, 1988: 619, table 1, pl. 2 fig.2.

Urocles woodwardi (Sauvage, 1903) pro parte: Gómez-Pallerola, 1990: 52, 70.

Amiopsis woodwardi (Sauvage, 1903) pro parte: Wenz & Poyato-Ariza, 1994: 204–210, tables 1, 2.

Amiopsis woodwardi (Sauvage, 1903) pro parte: Grande & Bemis, 1998: 516.

Amiopsis woodwardi (Sauvage, 1903) pro parte: Poyato-Ariza, Buscalioni & Cartanyà, 1999: 511.

Amiopsis woodwardi (Sauvage, 1903): Fregenal-Martínez & Meléndez, 2000: table 1.

Amiopsis woodwardi (Sauvage, 1903) pro parte: Wenz, 2003: 495.

Amiopsis woodwardi (Sauvage, 1903): Escaso, Sanz & Ortega, 2005: 228.

Amiopsis woodwardi (Sauvage, 1903): Poyato-Ariza, 2005a: 286.

Amiopsis woodwardi (Sauvage, 1903) pro parte: Martín-Abad & Poyato-Ariza, 2009: 265.

Amiopsis woodwardi (Sauvage, 1903) pro parte: Martín-Abad & Poyato-Ariza, 2013a: 78–82, figs 4, 6, table 1.

Amiopsis cf. *A. woodwardi* (Sauvage, 1903): Martín-Abad & Poyato-Ariza, 2013b: fig. 1.

Amiopsis cf. *A. woodwardi* (Sauvage, 1903): Poyato-Ariza & Martín-Abad, 2016 b: c.pl. 12.2.B.

New taxon #1: Martín-Abad, 2016.

Type locality: Las Hoyas, Cuenca, Spain.

Type stratum: Calizas de la Huérguina Formation (Vilas *et al.* 1982), Rambla de Las Cruces II Sequence at Las Hoyas (Fregenal-Martínez, 1998). Upper Barremian (Early Cretaceous).

Geographical distribution: The species is endemic to Las Hoyas.

Species diagnosis: As for the genus (monotypic genus).

Etymology: *newbreyi*, after Dr Michael G. Newbrey, palaeontologist and ichthyologist.

Holotype: MCCM LH 9645a/b, part and counterpart (Fig. 1).

Paratypes: MCCM LH 023, 076a/b, 085R, 151Pa/b, 374Ra/b, 9576a/b, 11286, 15783a/b, 16040a/b (Fig. 2), 16257a, 17274a/b, 22600a, 23062a/b, 30878a/b, 32022a/b, 32244a/b.

DESCRIPTION

Descriptive counts and measurements are provided in Tables 1–10. The known size of this species ranges from 12.3 mm standard length (SL) and 15.6 mm total length (TL) (specimen MCCM LH 22600a) to 254 mm SL and 308 mm TL (MCCM LH 9645a/b). A large proportion of the articulated specimens found so far are juveniles, some of them with a very low degree of ossification, and there are only a few subadult and even fewer large adult specimens. One specimen (MCCM LH 9645a/b) is much larger than the rest; it is almost 50% longer than the second largest specimen.

SKULL

Braincase and ethmoid region: All known specimens of *Hispanamia newbreyi* gen. nov., sp. nov. have the skull preserved in lateral view. This, together with the good preservation of the cheek bones of the specimens, always with a very complete dermocranium, does not allow any bone of the sphenotic, otic and occipital regions of the braincase to be viewed. Only part of the ethmoid region can be seen on some specimens.

The rostral (**ro**) is an unpaired V-shaped bone with relatively large paired lateral expansions (wings). Posteriorly, the rostral bone articulates with the nasals. The tip of each lateral arm of the rostral is continuous with the tip of the corresponding antorbital. The rostral bone overlies the premaxilla. On the medial anterior surface of each wing of the rostral there is a small opening to the rostral canal.

The paired lateral ethmoid (**le**) lies just ventral to the anterolateral corner of the frontal and the posterolateral corner of the nasal, and dorsal to the vomer and lacrimal. The lateral ethmoid is roughly hemispherical posteriorly and flatter anteriorly. It is partially overlapped by the antorbital. The lateral ethmoid articulated in life with the palatal complex (usually with the autopalatine), forming the anterior suspension of the palatal complex to the skull (Grande & Bemis, 1998).

Otoliths: As stated above, this region is not clearly visible in any of the known specimens and no otoliths have been observed.

Skull roof: The skull roof is formed by six paired bones: nasal, frontal, dermosphenotic, dermopterotic, parietal and extrascapular. As stated above, all the known specimens are preserved in lateral view, so the skull roof is never fully observable. The skull of the holotype (Fig. 3), nonetheless, is slightly compressed, and both the left and part of the right sides of the skull roof are visible. The skull roof is, however, not as well preserved as the rest of the specimen. Nevertheless, the shape and margins of most of the bones can be confidently traced. The skull of specimen MCCM LH 16040a/b (Fig. 4) is preserved in lateral view.

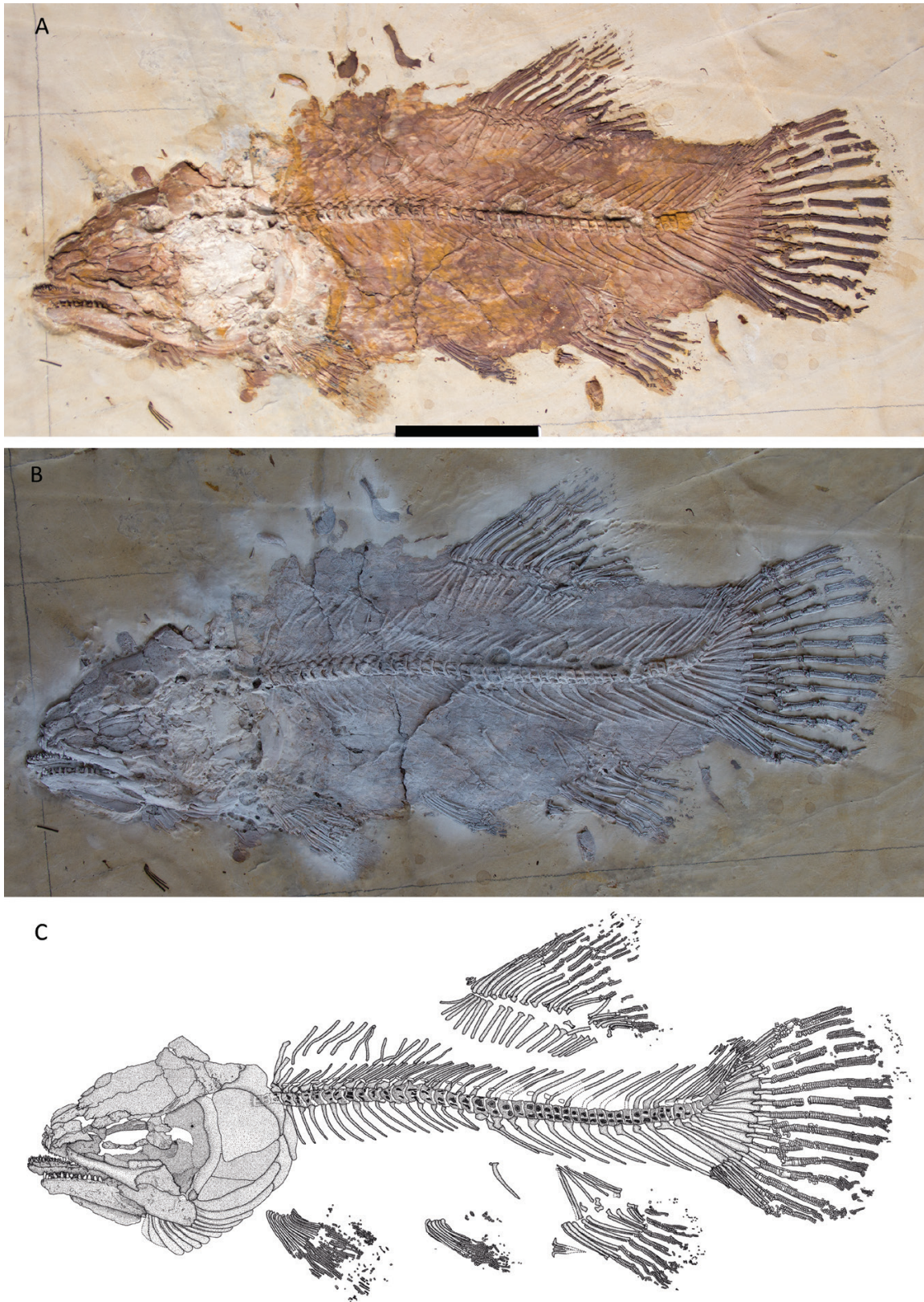


Figure 1. *Hispanamia newbreyi* gen. nov., sp. nov. (A) specimen MCCM LH 9645a (holotype). (B) specimen in A slightly coated with ammonium chloride. (C) digital drawing of the skeleton as preserved in specimen in A. Scale bar = 5 cm.



Figure 2. *Hispanamia newbreyi* gen. nov., sp. nov. (A) specimen MCCM LH 16040b. (B) specimen in A slightly coated with ammonium chloride. Scale bar = 5 cm.

The bones of the skull roof are very smooth, lacking a developed ornamentation. Even in the largest specimen the ornamentation consists only of very few, small irregularly disposed foramina and thin, shallow, parallel grooves. This contrasts with the taxa from other amiid subfamilies (Grande & Bemis, 1998), for which the ornamentation is usually moderately to highly developed. As found in *Amia calva*, there are no fenestrae, fontanelles or pineal openings on the skull roof. The bones are tightly sutured to each other in adult individuals.

Also as in *A. calva*, there are several pore clusters on the skull roof corresponding to the supraorbital sensory canal. These pores conform a linear pattern that runs from the nasal into the frontal, running near the lateral edge of the latter; whether this canal penetrates into the parietal is hard to confirm. The canal then continues into the dermosphenotic, where it branches towards the infraorbital series to connect with the infraorbital sensory canal. Finally, it continues through the dermopterotic, extrascapular and the lateral edge of the posttemporal.

At least one trough, running on the posterolateral part of the parietal and into the dermopterotic, is observable on the skull roof. This is termed middle pit-line trough (Grande & Bemis, 1998). In life, a row of closely spaced pit-line neuromasts would be situated along the floor of the trough, as found in *A. calva* (e.g. Jarvik, 1980).

The anteriormost bone of the skull roof is the nasal (**n**), which lies posterior to the rostral. The nasal is an elongated bone, slightly wider anteriorly than posteriorly. On the anterolateral margin of the nasal is a notch which forms, together with the antorbital, the posterior edge of the opening for the anterior narines. The nasal

is located anterior to the frontal, but does not actually articulate with it; in life, both bones are separated by connective tissue in *A. calva*, and probably in *H. newbreyi* as well. The left and right nasals are sutured to each other medially by means of an interdigitating suture. There are short, shallow, parallel grooves both on the anterior and on the posterior regions of the nasal.

Posterior to the nasal is the frontal (**fr**). As in *A. calva*, the frontal is the longest element of the skull roof, occupying almost 40% of the head length in the largest specimen. The frontal is approximately twice as long as wide, with a sub-rectangular general shape. It is wider posteriorly, and tapers abruptly at the level of the orbit. Anteriorly, the frontal has thin laminar projections that partially overlap the supramaxilla and, in turn, are overlapped by the nasal. The anterolateral margin is greatly excavated, and articulates with a series of supraorbital bones. The frontal has an irregular rather than straight contour, indicating interdigitating sutures with the parietal, dermopterotic and dermosphenotic. The frontal has very few relatively shallow, parallel grooves running from the centre of the bone towards the posterior and anterior margins.

Posterior to the frontal and medial to the dermopterotic is the parietal (**pa**). The shape of the parietal is highly variable, both among individuals and between the left and right sides of the same individual, depending on the curvature of the margins of articulation with other skull roof bones. In general, it is approximately as wide as long. The right and the left parietals are very similar in size. Medially (and probably anteriorly, but this cannot be confirmed because all the specimens show articulated skull



Figure 3. *Hispanamia newbreyi* gen. nov., sp. nov. (A) skull from specimen MCCM LH 9645a (holotype) slightly coated with ammonium chloride. (B) digital drawing of the skeleton as preserved in specimen in A. Scale bar = 2 cm.

roofs) the parietal has well-developed ventral laminar shelves that are overlain by the other-side parietal (and by the frontal anteriorly), forming a very tight articulation. The margins are irregularly curved, forming interdigitating sutures with the other-side parietal medially, with the frontal anteriorly and with the dermopterotic laterally. The posterior margin of the parietal is straight, and articulates with the extrascapular. The presence on

the posterior edge of a foramen to a canal, present on other amiid species including *A. calva* (Grande & Bemis, 1998: 42), cannot be confirmed.

Lateral to the frontal is the dermosphenotic (**dsp**). This bone, which is actually part of the infraorbital series, is tightly sutured into the skull roof, as is the common condition for amiid fishes, and is thus described in this section. The dermosphenotic is a small bone, slightly longer



Figure 4. *Hispanamia newbreyi* gen. nov., sp. nov. (A) skull from specimen MCCM LH 16040b. (B) specimen in A slightly coated with ammonium chloride. Scale bar = 2 cm.

than wide. It exhibits a more or less curved anterolateral edge, which forms part of the margin of the orbit, and an irregular posteromedial edge to articulate with the frontal. The posterior margin is irregular as well, and articulates with the dermopterotic. The margin of the orbit is more excavated anterior to the dermosphenotic, despite

the presence of supraorbital bones. Posterolaterally, the dermosphenotic articulates loosely with the last infraorbital. In lateral view, and just posterior to the orbital margin, the dermosphenotic has a pore that might correspond to an opening for the infraorbital canal, as in *A. calva* (Grande & Bemis, 1998: 48).

Posterior to the dermosphenotic and lateral to the posterior part of the frontal is the dermopterotic (**dpt**). The dermopterotic is longer than wide. It is wider posteriorly and tapers anteriorly, although there is individual variability in the width between the posterior and the anterior parts. It has straight posterior and lateral edges, and the posterolateral corner is very slightly expanded and curved. The medial and, especially, the anterior edge are more sinuous, conforming interdigitating sutures with the dermosphenotic, frontal and parietal. The dermopterotic is almost twice as long as the parietal and slightly narrower. It bears very few shallow, parallel grooves running along its longitudinal axis. The presence of a ventral laminar process and of an opening for the postotic sensory canal, which is the junction between the lateral line canal of the dermopterotic and the preopercular canal, typically observable in lateral view in amiid dermopterotics (e.g. *A. calva* in Grande & Bemis, 1998, figs 17, 24), cannot be confirmed.

The posteriormost bone of the skull roof is the extrascapular (**es**). The extrascapular is subtriangular in shape, and tapers medially. It is wider than long, with a straight anterior margin, and a posterior margin that tapers abruptly in the midline. The lateral margin is straight to slightly curved, and the medial margin is curved, not acute. The extrascapular has short, shallow, parallel grooves on its posterolateral region, difficult to see on some specimens.

Circumorbital bones: The infraorbital series is composed of eight bones. Only the second to the seventh are typically termed infraorbitals, because the first is the antorbital, and the eighth is the dermosphenotic, which is tightly sutured into the skull roof. All the bones of the infraorbital series enclose the infraorbital sensory canal; this canal branches anteriorly at the antorbital and posteriorly at the dermosphenotic, in both cases towards the supraorbital canal. For this reason, sensory canal pores can be seen on all the infraorbital bones if the preservation is good enough.

The anteriormost bone of the infraorbital series is usually referred to as the antorbital (**ao**). The antorbital is an elongate, slightly curved bone, wider in its middle. The antorbital articulates only loosely with the nasal of the skull roof; it does not contact the frontal posteriorly, but partially overlies the lateral ethmoid and the lacrimal. Anteriorly, the antorbital extends very close to the rostral bone, yet it does not articulate with it. The anterior region of the antorbital has openings for the anteriormost part of the lateral line sensory system, which continues through the lateral wing of the rostral bone. Posteriorly, the antorbital articulates only loosely with the next element of the infraorbital series, the lacrimal.

The lacrimal (**l**), usually termed infraorbital 1 as well, is the bone that forms the anterior margin of the orbit. The shape of the lacrimal is variable in amiids (Grande & Bemis, 1998); in *H. newbreyi* the lacrimal

is a flat bone, subtriangular in shape, located between the maxilla and the skull roof, and reaching the premaxilla anteriorly. It is longer than deep. The lacrimal articulates loosely with and is partly overlapped by the antorbital. Posteriorly, it has a notch for the articulation with the next infraorbital bone.

There are three infraorbitals (**io2–4**) forming the ventral margin of the orbit. These infraorbitals at the ventral margin of the orbit are termed subinfraorbitals by Grande & Bemis (1998). Only two of these three bones are visible in specimen MCCM LH16040b. These three infraorbitals are little more than ossified tubes. In adults, they are short bones, yet longer than deep, and subrectangular in shape. The first (**io2**) of them is slightly more expanded dorsoventrally than the other two. Their contour is irregular rather than straight.

There are two infraorbitals (**io5–6**) constituting the posterior margin of the orbit. These bones at the posterior margin of the orbit are termed postinfraorbitals by Grande & Bemis (1998). The shape and relative size of these infraorbitals are highly variable in amiid fishes (Grande & Bemis, 1998). For example, the infraorbitals 5–6 of *H. newbreyi* are much less developed than those of *A. calva* (e.g. Grande & Bemis, 1998). Infraorbital 5 is not complete in the holotype. It is roughly ovoid in shape, higher posteriorly than anteriorly. Its surface is not as smooth as that of other dermal bones; it has short, shallow grooves on its margins, and is slightly depressed on the centre. The infraorbital sensory canal runs through the anterior part of the bone and penetrates into the next infraorbital. Infraorbital 6 is not completely preserved on the holotype either, and thus it is difficult to confirm its relative size in comparison to infraorbital 5, which is considered to be of phylogenetic interest (Grande & Bemis, 1998). In specimen MCCM LH 16040a/b, only infraorbital 5 is preserved, but there is a very small displaced bone that might correspond to infraorbital 6, thus confirming a smaller size of the uppermost (**io6**) relative to the lowermost (**io5**) posterior infraorbitals. Nevertheless, this area is not very well preserved in this specimen, so nothing conclusive can be stated.

There are no suborbitals. These bones, located posterior to the last infraorbitals when present, do not exist in any known species of the subfamilies Amiinae and Vidalamiinae either. In contrast, *Solnhofenamia elongata* and several *Amiopsis* species have one or more suborbitals (Grande & Bemis, 1998).

There are two supraorbital bones (**su**). They are short, yet longer than high, with irregular rather than straight margins. The supraorbitals are attached loosely to the lateral margin of the anterior part of the frontal, where the latter shows a distinct facet forming the orbital margin. Both supraorbitals are arranged into a single row.

Neither the holotype nor specimen MCCM LH 16040a/b show clear remains of an ossified sclerotic ring. However, smaller specimens (e.g. MCCM LH 151Pa/b,

374Rb, 9576b, 11286) show a sclerotic ring that seems to be faintly ossified into two pieces (Fig. 5A, B).

Upper jaw: The upper jaw consists of a premaxilla, a maxilla and a supramaxilla. The anteriormost element is the premaxilla (**pmx**). The oral border of the premaxilla, where the teeth are implanted, is thick, robust and concave, articulating with its counterpart medially. Dorsally and posteriorly the premaxilla has a thin expansion, the nasal process of the premaxilla. This expansion seems to extend back to the anterior edge of the frontal. The premaxilla is overlapped by the nasal,

the antorbital and the rostral bone, with which it is not articulated. In turn, the premaxilla posteriorly covers the anterior part of the vomer, whose teeth are just posterior to, and in functional continuity with, those of the premaxilla. Posterolaterally, the premaxilla articulates with the maxilla. The premaxilla bears a single row of teeth that are large and slightly recurved towards the oral cavity. They are sharply pointed and have a carinate (keeled) acrodin cap. There are usually eight teeth on each premaxilla, all of them approximately of the same size.

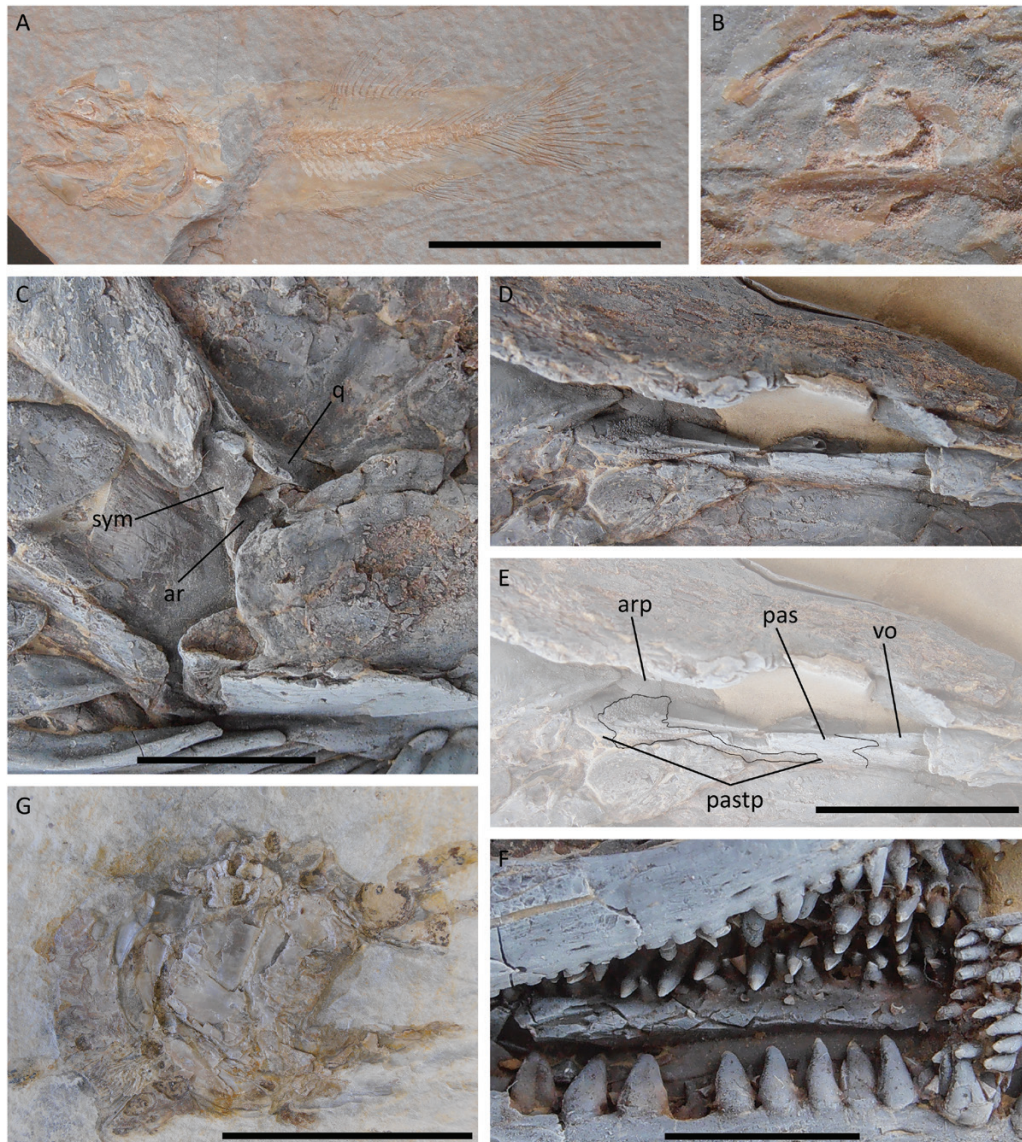


Figure 5. *Hispanamia newbreyi* gen. nov., sp. nov. (A) specimen MCCM LH 151Pa. Scale bar = 2 cm. (B) close-up of specimen from A showing sclerotic ring ossification. (C) close-up of jaw articulation from specimen MCCM LH 16040b slightly coated with ammonium chloride showing both the quadrate and the symplectic articulating with a single articular element. Scale bar = 5 mm. (D–E) close-up of orbit from specimen MCCM LH 16040b slightly coated with ammonium chloride showing the parasphenoid tooth patch. Scale bar = 1 cm. (F) close-up of mouth opening from specimen MCCM LH 16040b slightly coated with ammonium chloride showing keeled teeth. Scale bar = 5 mm. (G) specimen MCCM LH 9645b (holotype). Scale bar = 5 cm.

The maxilla (**mx**) seems to articulate only loosely with the rest of the skull, as in *A. calva*, where it rotates around the axis of a peg-like anterior process which fits into a socket formed by the vomer, premaxilla and preethmoid (Grande & Bemis, 1998). The premaxillary process of the maxilla is thin and ellipsoidal in section. The posterior expansion of the maxilla is much higher and flatter. The maxilla bears a single row of teeth, which extends back to over three-quarters of the length of the maxilla. These teeth are smaller than those of the premaxilla, and become much smaller posteriorly. The largest teeth are slightly curved towards the oral cavity. Each maxilla has around 25 teeth; according to Grande & Bemis (1998), the number of maxillary teeth increases throughout the life of the fish, at least in *A. calva*, a condition that, based on the specimens available, seems to occur also in *H. newbreyi*. The teeth are sharply pointed, and have keeled acrodin tips. The anterior dorsal margin of the maxilla is slightly excavated; when the mouth is closed, the lacrimal and, at least, the infraorbital 2 fit into this depression. Posteriorly, the dorsal edge of the maxilla is also excavated to hold the supramaxilla; this excavation, best observed in specimen MCCM LH 16040a/b, is termed the supramaxillary notch. The supramaxilla is tightly sutured to this excavation. The posterior edge of the maxilla is concave, forming the posterior maxillary notch, which seems not to be greatly developed; this notch is not clearly observed in the holotype specimen, because this region of the maxilla is not well preserved. The lateral surface of the maxilla is moderately smooth, with very shallow grooves on its posterior part.

The supramaxilla (**smx**) articulates with the maxilla immediately posterior to the supramaxillary notch. This bone is thin, elongate and relatively low. It is almost as long as half the length of the maxilla. Its lateral surface is smooth.

Lower jaw: To date, no specimen has been found showing a medial view of a complete lower jaw; only the anteriormost part of the right dentary and coronoids are visible on specimens preserved on their left side, and vice versa. As a consequence, only the presence of the following paired bones can be confirmed: dentary, at least three coronoids, angular, supraangular, articular (apparently formed by two fused elements, as commented later on) and a retroarticular.

On their lateral surface, both the dentary and the angular show relatively large pores corresponding to the mandibular sensory canal. This canal seems to turn upwards on the posterior part of the angular, approximately towards the ventral end of the preopercular, suggesting a possible connection through the skin with the sensory canal running through the latter, as is common in all neopterygians. In *A. calva* this connection exists and is termed the preopercular-mandibular canal (Grande & Bemis, 1998).

The anteriormost bone of the lower jaw is the dentary (**d**). The dentary is the largest element of the lower jaw. It bears a single row of approximately 15 teeth, which are the largest in the lower jaw. They are slightly recurved towards the oral cavity, and not completely round in cross-section but rather slightly compressed labiolingually. They have an acrodin cap that is strongly carinate or keeled. In lateral view, the dentary is deepest posteriorly and tapers anteriorly. The anterior part of the dentary is curved medially, to meet its counterpart forming a slightly rounded symphyseal region. The anterior part of the ventral margin of the bone is slightly concave. The dorsal margin is expanded posterior to the last tooth; this expansion, the coronoid process, is subtriangular in shape, and its posterior margin articulates with the supraangular bone. The posterior margin of the dentary is deeply notched in its articulation with the angular. In lateral view, the dentary is fairly smooth, with very shallow longitudinal grooves. The most pronounced structure on the surface of the dentary is the series of pores of the mandibular sensory canal, which runs ventrally on the anterior part of the dentary, then through the lower half of its lateral surface describing a soft curve, and then very close to the ventral surface of the bone posteriorly. In medial view, the dentary has a thin bony shelf where the coronoids are lodged. This bony shelf is actually the upper part of the meckelian groove, which harbours Meckel's cartilage.

Posterior to the dentary is the angular (**ang**). The angular is a thick bone, approximately half as long as the dentary, and as high as the middle part of the dentary. The ornamentation on the lateral surface of the angular is usually more pronounced than that of the dentary, with somewhat deeper grooves. A thin anterior projection of the angular sutures with the posterior notch of the dentary; another projection on the ventral surface of the angular also sutures with the dentary, so the articulation is V-shaped. The mandibular sensory canal continues from the dentary through the ventrolateral part of the angular. Posteriorly, the canal turns upwards and runs very close to the posterior margin of the angular. It exits the bone through its dorsal margin, where a large opening serves as the connection point with the sensory canal of the preopercular through the skin. The posterior margin of the angular is curved and ventrally notched. Its dorsal margin is fairly straight, and articulates with the supraangular.

The supraangular (**sag**) is smaller than the dentary and the angular. It articulates with the posterior edge of the dorsal expansion of the dentary and the dorsal margin of the angular. It constitutes the highest point of the lower jaw and of the coronoid process, providing the posterior part of the lower jaw with a roughly triangular shape. The supraangular has a smooth lateral surface, devoid of ornamentation.

There are, at least, three coronoid bones (**co**) on the inner side of the lower jaw. The coronoids are arranged in line and articulate with each other by means of interdigitating anterior and posterior margins. The posteriormost coronoid is the one articulating with the anterior margin of the prearticular, but this bone is not observable in any of the known specimens. The coronoids are short bones constituted by a bony base and numerous teeth; each coronoid bears 20–30 teeth. These teeth are irregularly arranged in three or four series. The teeth are conical and slightly recurved towards the oral cavity. They have a sharply pointed acrodin cap that is keeled. The teeth on the coronoids are smaller than those on the dentary, but are located nearly at the same level on the lower jaw.

Among the bones that usually ossify from Meckel's cartilage, only the retroarticular and the articular are observable on the known specimens.

The articular (**ar**) is only observable in specimen MCCM LH 16040a/b, and is slightly broken, so it is difficult to confirm whether it is a single bone or two different elements fused together. The presence of a very thin line that could be a suture, and the different directions of the anterior and posterior parts suggest the latter option as more probable. So, it is interpreted that the articular is apparently formed by the fusion of an anterior plus a posterior element. The articular forms the so-called double jaw articulation with the quadrate and the symplectic, which is a traditional diagnostic character for halecomorph fishes; the anterior part of the articular bone articulates with the condyle of the quadrate, whereas the posterior part of the articular bone articulates with the socket-like ventral end of the symplectic (Fig. 5C). Overall, the articular is small and convex; its anterior part is located between the angular and the prearticular (which is actually not visible in any specimen), and is anterolaterally directed. The posterior part of the articular bone articulates with the medial surface of the posterodorsal corner of the angular. The articular is visible in lateral view through the posterior corner of the articulation between the angular and supraangular. An articular formed by two elements tightly sutured to each other constitutes an important phylogenetic character according to Grande & Bemis (1998).

The retroarticular is the posteriormost bone of the lower jaw. The retroarticular articulates with the posteroventral corner of the medial surface of the angular. In lateral view, it is visible through the posteroventral notch of the angular. The retroarticular is a small rounded bone that is dorsally concave and has a small dorsal expansion on its medial surface, creating a sort of hemispheric fossa. In *A. calva*, this fossa serves as the surface of attachment for the large hyomandibula and interoperculomandibular ligaments (Grande & Bemis, 1998).

Palate: The palatal complex of amiid fishes includes one unpaired bone, the parasphenoid, and numerous paired bones. Among them, the autopalatine cannot

be seen in any known specimen, probably because it is placed in a deep plane and laterally overlapped by the large lacrimal. The presence of parasphenoid, vomer, two dermopalatines, ectopterygoid, endopterygoid and metapterygoid can be confirmed. None of these bones can be described in detail, because they are only partially visible; they are never observable in ventral or medial view, where most of their important characteristics are, nor are they usually completely visible in lateral view.

The parasphenoid (**pas**) is observable in lateral view crossing the orbit of most of the specimens, but this view does not provide much morphological information. It extends, at least, from almost the anterior margin of the orbit to the hyomandibula. The tooth patch of the parasphenoid extends a long way anteriorly, almost to the suture with the vomers (Fig. 5D, E). Posteriorly, the tooth patch extends into the ascending rami of the parasphenoid. This patch is formed by hundreds of small and pointed teeth.

The vomer (**vo**) is relatively long. It extends from the premaxilla and exceeds the anterior margin of the orbit. The suture between the parasphenoid and the vomers is interdigitated.

The anterior dermopalatine is a short, low bone located medial to the anterior part of the maxilla. It probably articulates with the vomer, as in other amiids, but this cannot be confirmed. It articulates posteriorly with the posterior dermopalatine by means of an interdigitating suture. It bears a row of very few, large, curved teeth (at least three or four are observable). These teeth are larger than those of the maxilla and coronoids, but smaller than those of the premaxilla and dentary. They have a small acrodin cap that is keeled, but not as strongly as those of the dentary, coronoids and premaxilla. The presence on this bone of more teeth medial to the row of large teeth cannot be confirmed, although in specimen MCCM LH 16040a/b there seems to be at least one smaller tooth medial to the large teeth.

The posterior dermopalatine (**dplp**) is approximately as long as the anterior one. It is also a low bone, and is located between the anterior dermopalatine and the ectopterygoid, with which it also articulates by means of an interdigitating suture; the large teeth of these three bones form a medial row continuous to that of the maxilla. The teeth of the posterior dermopalatine are as large as, or even slightly larger than, those of the anterior dermopalatine, and very similar in shape. They are very few in number (two to three are distinguishable).

The ectopterygoid (**ecp**) is a long bone, reaching the level of the posterior end of the maxilla. In lateral view, it is a thin, tube-like bone, slightly higher anteriorly, and with a long, low, triangular posterodorsal expansion. It bears, at least, a row of teeth (at least four or five are visible) whose size decreases from anterior to posterior, smaller than those of the dermopalatines. As in the anterior dermopalatine, the occurrence of

additional, smaller, medial teeth, present in other amiids, cannot be confirmed.

The endopterygoid is a flat, relatively large bone. Its anterior margin, supposedly articulating with the autopalatine and dermopalatine, is largely covered laterally by the lacrimal and infraorbitals 2–4. Laterally it articulates with the dorsomedial margin of the ectopterygoid, and extends inwards to the parasphenoid. Its posterior margin is sutured to the anterior margin of the metapterygoid.

The metapterygoid (**mpt**) is the posteriormost element of the palatal complex. The metapterygoid is a chondral bone that ossifies within the palatoquadrate cartilage (in addition to the quadrate and the autopalatine; Jollie, 1984). This region of the skull, which usually is partially overlaid by the infraorbital series, is best seen on specimen MCCM LH 16040a/b. The metapterygoid is a relatively large, flat bone. Its dorsal margin is deeply notched, bearing a laterally pointed middle process. In life, this notch is crossed by the trigeminal nerve in *A. calva* (Grande & Bemis, 1998). The anterior, ventral and posterior margins of the bone form a more or less continuous curve; the anterodorsal and posterodorsal expansions that form the notch are subtriangular in shape. The metapterygoid is tightly articulated to the endopterygoid and ectopterygoid anteriorly. Posteriorly, it partially overlaps the hyomandibula, and ventrally it is tightly articulated to the quadrate.

Teeth: The large teeth of the jaws and palatal bones are not completely conical, but rather labiolingually compressed, especially those of the dentary. The teeth are sharply pointed, with an acrodin cap usually preserved. This cap is keeled in most of the teeth, especially in those of the dentary, coronoids and premaxilla (Fig. 5F). The largest teeth are on the dentary and premaxilla. The large teeth have long, hollow shafts as in all other amiids (Grande & Bemis, 1998). There are patches of very numerous little teeth (shagreen) on several palatal bones; these tiny teeth are conical and pointed.

Hyoid arch: In addition to the palatal bones discussed above, the hyomandibula, the quadrate and the symplectic also contribute to the suspensorium. As for the metapterygoid, these bones are best seen in specimen MCCM LH 16040a/b, but also on the counterslab of the holotype, especially the hyomandibula (Fig. 5G). The hyomandibula and the symplectic are part of the hyoid arch, which also includes the anterior and posterior ceratohyal, the hypohyal and the basihyal; the last two are not visible in any known specimen.

The hyomandibula (**h**) is a large bone located posterior and dorsal to the metapterygoid. The hyomandibula is not tightly sutured to the metapterygoid, but rather is overlapped by its posterodorsal margin, as found in relatively small specimens of *A. calva* (Grande & Bemis, 1998). Dorsally, it reaches the level of the ventrolateral surface of the dermopterotic; in the extant *A. calva*, the

hyomandibula articulates with the autopterotic cartilage into a groove under the dermopterotic (Grande & Bemis, 1998). The dorsal margin is the longest part of the hyomandibula; the bone tapers in the middle, and then becomes slightly longer again ventrally, giving it the shape of a hatchet. Posteriorly, the hyomandibula has a little expansion near the dorsal margin that extends backwards to the opercular, with which it articulates. Ventrally, the hyomandibula reaches the quadrate. Close to the centre of the bone there is a large foramen plus a groove for passage of the hyomandibular trunk nerves (Grande & Bemis, 1998) that are visible both on the lateral and on the medial surfaces of the bone. Around this foramen plus groove, the hyomandibula has a Y-shaped prominent ridge on its lateral surface. In lateral view, the hyomandibula is partly covered by the preopercular.

The quadrate (**q**) is part of the double jaw articulation by contacting ventrally the anterior part of the articular bone of the lower jaw. The quadrate is a laterally flat bone with a ventral, convex, laterally directed process, which is the articular surface for the jaw articulation. Overall, the quadrate has a subtriangular shape with rounded corners. Anteriorly, the quadrate is sutured with the metapterygoid; whether it articulates with the ectopterygoid as well, as found in *A. calva* (Grande & Bemis, 1998), cannot be confirmed, because the anteroventral margin of the quadrate is overlapped by the supraangular. The posteroventral margin of the quadrate has a slightly convex edge, which continues the ventral articular process, and which is in contact with the anteroventral margin of the preopercular. The quadrate does not contact the symplectic, at least as far as can be seen in the available specimens.

The symplectic (**sym**) cannot be described in much detail. In lateral view it is almost completely overlaid by the preopercular, except for its ventralmost part. This ventral part is rounded and has several thin lobe-like expansions, which form a slightly concave surface for articulation with the posterior part of the articular bone of the lower jaw.

The anterior ceratohyal is visible in specimen MCCM LH 16040a/b, whereas the presence of the posterior ceratohyal is more difficult to confirm. The anterior ceratohyal can be observed in several smaller individuals (e.g. MCCM LH 023, 085R, 374Rb, 9576, 16257a, 17274a) as well. The anterior ceratohyal is a long bone with a slightly expanded anterior end and that gets gradually wider posteriorly. Its posterior margin is straight. The branchiostegal rays articulate with its lateral surface.

Opercular series, branchiostegal rays, and gular: The opercular series is composed of the opercular, subopercular and interopercular bones plus the long preopercular, which lies anterior to them. The branchiostegal rays are located ventral to the opercular series, and the large gular plate, which is an unpaired bone, is located anterior to the branchiostegals. The opercular,

subopercular and interopercular bones are not well preserved in lateral view in any of the large specimens, but they are preserved in medial view in the counterslab of the holotype, and their medial imprint is also visible on specimen MCCM LH 16040a/b. For this reason, the ornamentation of these bones, which is usually fairly developed in other amiids, cannot be confirmed. However, the smooth branchiostegals, together with a comparatively faint ornamentation on the rest of the dermal skull bones, suggest that the bones of the opercular series were probably faintly ornamented as well.

The preopercular (**pop**) is a long, narrow, crescent-shaped bone. It is relatively constant in width, with only the ventral and especially the dorsal ends being slightly narrower. Anteriorly it overlies the symplectic and the posterior part of the hyomandibula, and is in contact with the posterior margin of the quadrate. Its dorsal end contacts the dermopterotic; through this point, the supratemporal sensory canal and the preopercular canal are connected. The preopercular sensory canal runs along the entire length of this bone, and several lateral line pores can be seen on its posterior edge. Ventrally the preopercular reaches the level of the angular bone of the lower jaw, and the preopercular canal is continuous with the mandibular canal. In medial view (observable in the counterslab of the holotype specimen) the preopercular has a long ridge that serves for the insertion of the anterior edges of the opercular, subopercular and interopercular, which lie posterior to it. The preopercular is smooth, except on its dorsalmost part, where it bears several short but relatively deep, parallel grooves, and a long groove running on the anterior part of its lateral surface.

The opercular (**op**) is approximately as wide as it is high, the widest part being at the ventral margin of the bone. The dorsal and posterior edges of the opercular bone form a continuous curve, whereas the anterior and ventral margins are straight, forming a slightly acute angle. The articular facet of the opercular, which articulates with the posterior opercular process of the hyomandibula, is small, and is located close to the anterodorsal corner of the bone. Ventral to the opercular is the subopercular.

The subopercular (**sop**) is as long as the opercular, but much shallower. The anterodorsal process of the subopercular lies anterior to the opercular, because, in contrast to the usual condition in amiids, the opercular does not have an anteroventral notch for it to fit into. The dorsal and ventral edges of the subopercular, which articulate with the opercular and interopercular, respectively, are straight and nearly parallel to each other. The anterior edge, which articulates with the preopercular, is only slightly curved, and forms a rounded anteroventral corner. The posterior edge is curved, and articulates with the lateral surface of the last branchiostegal ray.

Ventral to the subopercular is the interopercular (**iop**). The interopercular is a smaller bone,

subtriangular in shape. Its anterior edge, which also articulates with the preopercular, is straight. Its posterior edge, longer than the anterior, is slightly convex, and makes an acute, rounded ventral corner. Its dorsal edge, which articulates with the ventral margin of the subopercular, is rather straight. It articulates ventrally with the last branchiostegal ray.

There are usually 11–12 branchiostegal rays (**br**), including the last or dorsalmost one, termed branchiopercular (**bop**) by Grande & Bemis (1998). In general, the branchiostegal rays are elongated, slightly curved bones that form a series that extends from the ventral part of the skull, between the lower jaws, into its posterolateral side, the last one articulating with the subopercular and interopercular bones. The anterior-most branchiostegal rays are smaller, and they become progressively longer and larger towards the end of the series. The last branchiostegal ray is, thus, the longest and largest one; it is greatly expanded. Anteriorly, the branchiostegal rays are thin, almost tube-like in shape, and they get flatter and more expanded posteriorly, except the last and largest branchiostegals, which are subtriangular anteriorly. The anterior ends of the branchiostegal rays are not visible in the holotype; in specimen MCCM LH 16040a/b, they seem to articulate with a flat, relatively broad bone which is the anterior and/or posterior ceratohyal. Anterior to the first, ventralmost branchiostegal rays is the gular plate.

The gular (**g**), or gular plate, is a median bone that covers the bucco-pharyngeal cavity of the skull ventrally between the two rami of the lower jaw. It is a very flat and broad bone. The gular plate is not entirely observable in any of the large specimens. However, as far as can be seen, it is ovoid in shape, with curved posterior and lateral margins, and tapers anteriorly. Annular concentric marks can be seen on its ventral and/or dorsal surface. In smaller specimens (e.g. MCCM LH 151Pa, 374Rb, 17274a) the gular plate is entirely visible; in the smallest ones, it has a straighter posterior margin (Fig. 6A, B) that becomes more curved as the fish grows.

Branchial arches: The branchial arches complex of amiids, as for all other actinopterygians, is constituted by numerous bones, several of which have attached patches of pointed teeth. Unfortunately, this complex is never accurately preserved in fossils. It is almost completely unknown in *H. newbreyi*, either because it is missing (not preserved) or, most probably, because it is covered by other skull bones. In specimen MCCM LH 16040a/b there are a few tooth patches that would be attached to bones of the branchial arches. Each patch comprises around three to ten very thin and pointed teeth, approximately the same size as those of the tooth patch of the parasphenoid.

Sensory canals: The main sensory canals are illustrated in Figure 7. The dermal bones comprising

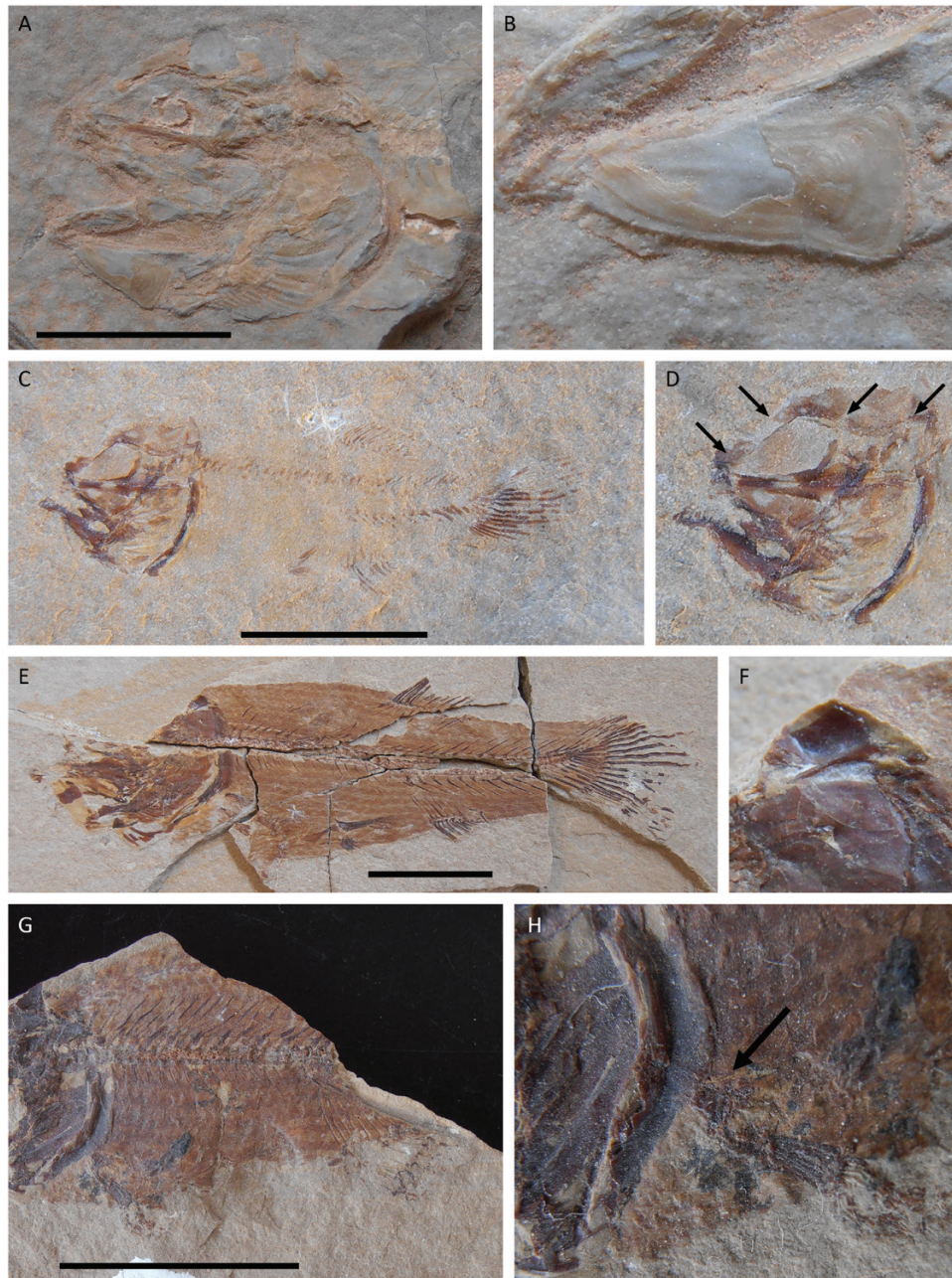


Figure 6. *Hispanamia newbreyi* gen. nov., sp. nov. (A) skull from specimen MCCM LH 151Pa. Scale bar = 1 cm. (B) close-up of specimen from A showing the gular plate. Note the annular concentric marks. (C) specimen MCCM LH 15783a. Scale bar = 5 mm. (D) close-up of specimen from C showing early ossification of dermal bones comprising sensory canals, as indicated by arrows. (E) specimen MCCM LH 17274a. Scale bar = 1 cm. (F) close-up of specimen from E showing ventral rod-like process, possibly for articulation with the intercalar bone of the braincase. (G) specimen MCCM LH 374Ra. Scale bar = 2 cm. (H) close-up of specimen from G showing a probable scapulocoracoid ossification.

the sensory canals of the head are among the first to ossify, and they do so as delicate, thin tubes around the canals (Fig. 6C, D). This is clearly visible in some of the smallest specimens, such as MCCM LH 15783a/b (13 mm SL) or MCCM LH 32244a/b (15.5 mm SL).

AXIAL SKELETON

Figure 8 shows the division of the axial skeleton in different regions. The numbers of vertebral elements are given in Tables 6 and 7.

Vertebrae: The autocentra are solid, perichordally ossified and amphicoelous. A small opening for the

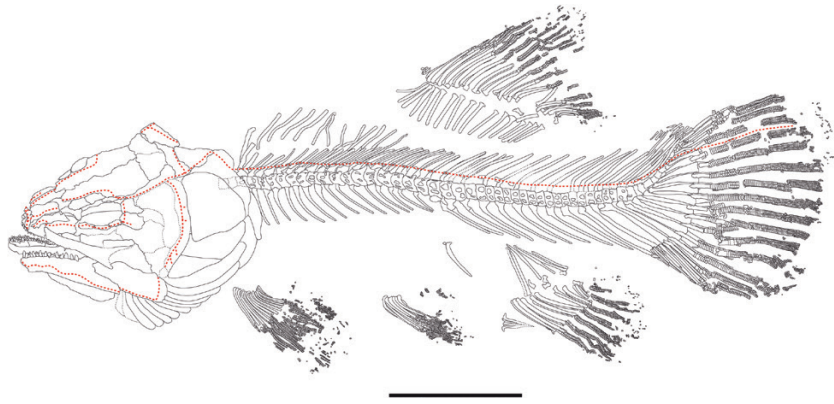


Figure 7. *Hispanamia newbreyi* gen. nov., sp. nov. Skeletal reconstruction of specimen MCCM LH 9645a (holotype) showing the main sensory canals. Scale bar = 5 cm.

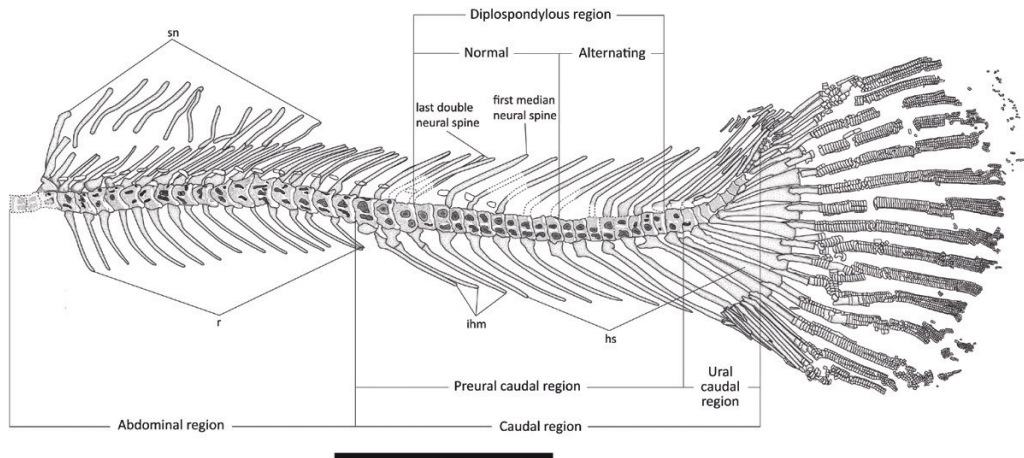


Figure 8. *Hispanamia newbreyi* gen. nov., sp. nov. Axial skeleton of specimen MCCM LH 9645a (holotype). Scale bar = 5 cm.

notochordal canal remains in each autocentrum even in the largest specimens. The autocentra are approximately rounded in contour in anterior/posterior view and higher than long. All the autocentra have two or three deep excavations, termed lateral oval fossae, on each side of their lateral surface. Additionally, they can have smaller fossae, either circular or elongated in shape. There are several diplospondylous vertebrae, both the normal and the alternating type. There are no epineurals or epi-pleurals, as found in all other known amiid species. The vertebrae of all large specimens are only observable in lateral view, or slightly tilted, which allows us to confirm their rounded contour, but does not allow the dorsal and ventral views to be described in great detail.

Abdominal region: There are usually 18–21 abdominal autocentra. The anterior few (two or three) abdominal autocentra are lower than the rest. The first one or two vertebrae are covered by the skull bones. In addition to them, the abdominal vertebrae bear well-developed ribs (**r**), which are curved, broader on their

proximal end than they are on their distal end. The distal tips of the ribs are pointed. The abdominal vertebrae lack ossified parapophyses. The ribs seem to articulate more laterally and anteriorly on the anteriormost autocentra, and gradually move to a more ventral and posterior position on the more posterior abdominal autocentra. The last ribs also become gradually slightly smaller, the last pair being the smallest, although they are not extremely smaller, and have the same narrow shape as the rest. The last abdominal autocentrum lacks ribs. All the abdominal vertebrae have neural arches. There are no median spines on the abdominal autocentra, since the right and left half neural arches do not fuse to each other distally, but develop into paired spine-like structures, as found in *A. calva* (Grande & Bemis, 1998). The neural arches have pointed distal tips and proximal ends or bases that are expanded and lie dorsal to the posterior half of the autocentrum, even overlying part of the next autocentrum, especially the posteriormost ones. The neural

arches of the first abdominal vertebrae are shorter and slightly flattened in the sagittal plane. Associated with the first neural arches is a series of supraneurals (**sn**). Supraneurals are long, thin bones flattened in the sagittal plane located slightly dorsal to the first neural arches, sometimes inserting between two consecutive neural arches, except the first one, which is shorter and articulates with its corresponding neural arch. Some variability in the number of supraneurals is observable, with 13–15, usually 14, supraneurals present, the first one just posterior to the skull and the last ones lying ventral to the anteriormost axonosts of the dorsal fin.

Preural caudal region: The preural caudal region begins with a vertebra bearing haemal arches. There are usually 23–25 preural caudal autocentra. This region contains all of the diplospondylous vertebrae. In summary, diplospondyly is the duplication of the number of autocentra for each body segment or myoseptum, presumably to increase flexibility in the posterior part of the body (Schaeffer, 1967; see also Wenz, 1977; and Schultze & Arratia, 1986).

The preural caudal region is usually composed of three monospondylous vertebrae anteriorly and becomes diplospondylous only more posteriorly. The first diplospondylous vertebrae are of the normal type; posteriorly, there is a shift to alternating diplospondyly, which affects only three or four vertebrae (vertebrae 28–31 in the holotype specimen). Finally, the last vertebra or pair of vertebrae of the preural caudal region are of the normal diplospondyly type again. Ventrally, the anteriormost vertebrae of the preural caudal region (the three first in the case of the holotype, and at least two in specimen MCCM LH 16040a/b) bear short haemal arches (**ha**) that do not fuse distally to form median haemal spines. Instead, these short anterior haemal arches articulate with long, spine-like median bones termed infrahaemals (**ihm**), which are also present in the extant *A. calva*. The next preural caudal vertebrae bear haemal arches that do fuse distally to form median haemal spines. The infrahaemals and the haemal spines are approximately the same length, much longer than the abdominal ribs, and both are thin bones with pointed distal tips. The last few haemal spines are involved in the support of the caudal fin forming the caudal endoskeleton. These last haemal spines gradually become flatter distally, acquiring a hypural-like shape. The last one is called the parhypural (**phy**). Dorsally, the vertebrae of the preural caudal region bear a pair of neural arches that form neural spines distally. The neural arches of the first three or four vertebrae do not fuse distally, and thus they form paired neural spines, like those of the abdominal region. The neural arches of the rest of the preural caudal vertebrae do fuse to each other distally,

forming median neural spines. The paired and the median neural spines of the preural caudal region are approximately the same length; they are also the same length as those of the abdominal region and, as with the latter, they have pointed distal tips.

Ural region: The ural caudal region of the vertebral column comprises the vertebrae that bear hypurals. They support fin rays, forming the caudal endoskeleton (see description below).

APPENDICULAR SKELETON

Pectoral girdle and fin: The pectoral girdle of amiids is composed of numerous paired bones. As Grande & Bemis (1998) show, not all the elements of the pectoral girdle ossify in all amiid species. The dorsalmost element of the pectoral girdle is the posttemporal (**pt**). The anterior edge of the posttemporal is overlaid by the posterior part of the extrascapular, the posteriormost bone of the skull roof. The posttemporal is triangular in shape, with straight margins forming rounded corners (Fig. 3). The anterior margin of the bone, which is disposed perpendicular to the longitudinal axis of the body, is as long as, or slightly longer than, its lateral margin, which is parallel to the longitudinal axis of the body. Its medial surface is covered by the anteriormost dorsal scales, which are inserted between the posteromedial margin of the extrascapular and the anteromedial margin of the posttemporal. The dorsal surface of the posttemporal is irregularly ornamented with shallow grooves. There are also pores of the lateral line sensorial system that enters from the extrascapular and runs diagonally through the posttemporal towards its posterolateral corner, where the bone connects with the supracleithrum. The posttemporal is not observable in ventral view in any of the large specimens; however, one of the juvenile specimens (MCCM LH 17274a) has a posttemporal with a ventral rod-like process possibly for articulation with the intercalary bone of the braincase (Fig. 6E, F), as found in *A. calva* (Grande & Bemis, 1998: fig. 36).

The supracleithrum (**scl**) is placed ventral to the posttemporal (Fig. 3). The supracleithrum is a relatively large, flat bone mostly covered by the operculum in lateral view. Its posterior margin is convex, with a more or less developed posterodorsal expansion. It is smooth, but it has a couple of large pores for the lateral line sensory system on its dorsal margin. The canal exits the bone posteriorly, connecting with the lateral line body system. Ventrally, the supracleithrum articulates with the cleithrum anteriorly, and with the postcleithrum posteriorly, overlying them.

The postcleithrum (**pcl**) is much smaller than the supracleithrum and the cleithrum (Fig. 3). It is partially covered by the supracleithrum dorsally and by

the cleithrum ventrally. The visible lateral surface of this bone is smooth; it is higher than long, and its posterior margin is convexly rounded.

The cleithrum (**cl**) is, as usual, the largest bone of the pectoral girdle (partially covered by the branchiostegal rays in Fig. 3). This bone is composed of an anterior pointing arm and a dorsal pointing arm. The dorsal arm is shorter than the anterior arm; it overlies the anterior part of the postcleithrum and articulates with the ventral part of the supracleithrum. It is partially covered by the operculum laterally. The end of this arm is a thick, tube-like expansion. The posterior margin of the bone, where both the anterior and the dorsal arms are joined, is convexly rounded, depicting a continuous curve. This posterior expansion of the bone is very thin, and it is smooth in lateral view, in contrast to the condition in amiines. The anterior arm is not clearly visible in any of the large specimens. Smaller specimens have a very thick dorsal margin on the anterior arm. The anterior end of this arm is slightly expanded and forms an acute angle. The clavicle elements are not visible in any of the known specimens. According to Grande & Bemis (1998), these elements are not normally visible in well-articulated skulls, because they lie between the anterior arm of the cleithrum and bones of the opercular series. They do not articulate tightly with the cleithrum either, and thus they disarticulate easily.

There are also several chondral elements in the pectoral girdle of amiids. The scapulocoracoid complex is not visible in any of the known specimens, so it seems not to be ossified, as is often the case in other amiid species. The only exception is a juvenile individual (MCCM LH 374Ra/b), which has a small ossification apparently articulating with both the cleithrum and the radial elements of the pectoral fin that might be the scapulocoracoid (Fig. 6G, H); this part of the specimen is, however, not very well preserved, so nothing conclusive can be really said. Nonetheless, the scapulocoracoid complex might be covered by the cleithrum in most specimens, since it articulates on the medial surface of the latter. According to Grande & Bemis (1998), the scapulocoracoid complex does not ossify in *A. calva* until very late in ontogeny.

In most specimens, the radial elements are preserved only as imprints, suggesting a faint ossification. There are seven to nine radial elements in the pectoral fins (Fig. 9A). The first of them is thicker and shorter, and probably corresponds to the propterygium (**ptg**). The radials (**ra**) are thin, short, cylindrical bones. The last element is also shorter and thicker, and is not completely parallel to the others, but somehow diagonally disposed, suggesting it might be the posterior end of a metapterygium (**mtgo**). According to Grande & Bemis (1998), only the posterior part of the metapterygium

ossifies in adult individuals of *A. calva*. Posteriorly, the ensemble of the radial elements form a convex surface, where the fin rays articulate. The pectoral rays, 13–16 in number, are not in a one-to-one ratio with the radials; instead, several rays articulate with each radial. The pectoral fin rays are long, the more posterior ones gradually decreasing in length, so that the pectoral fin has a slightly convexly rounded posterior margin. The pectoral fin rays become branched as the fish grows; the longest rays are branched twice in the largest specimen, the holotype.

Pelvic girdle and fin: The only elements of the pelvic girdle and fin that apparently ossify are the basipterygium and the fin rays (Fig. 9B). A small ossification, slightly wider anteriorly than posteriorly, occurring in a small specimen (MCCM LH16257a) might represent the metapterygium (**mtg**). The basipterygium (**pb**), whose ossification is also termed pelvic bone, is relatively large, flat and hourglass-shaped. The narrower point of the bone is much closer to the posterior end than to the anterior end, both of which get gradually wider. In adults, the anterior margin is twice as wide as the posterior margin. There are six or seven principal rays in the pelvic fin, which are segmented and branched in large individuals. There is also a much smaller, neither segmented nor branched ray anterior to the rest. The pelvic fin has a slightly convex posterior margin. The prepelvic length represents approximately 50% of the standard length of the fish in large individuals. The pelvic fin is smaller and shorter than the pectoral fin.

UNPAIRED FINS

Dorsal and anal fins: The dorsal fin (Fig. 9C, D) is short and triangular in shape, with a straight to slightly convexly rounded posterior margin. The dorsal fin is located only slightly closer to the caudal fin than to the head; the predorsal length represents approximately 60% of the standard length of the fish in large individuals, and the dorsal fin base 16%. It has 14–16 principal rays supported by 15–17 pterygiophores. The pterygiophores are median structures comprising a proximal radial (**pr**), a middle radial (**mr**) and a distal radial (**dr**). The proximal radials are the longest elements, and they are spine-like, round in cross-section, with a broadened distal end. All of the proximal radials are approximately the same length. Apparently, the proximal radial of the first pterygiophore is slightly curved anteriorly and closer to the next one than are any of the others. The proximal ends of the proximal radials are not in contact with the neural spines of the vertebral column but notably separated from them. The proximal radials are disposed diagonally to the longitudinal axis of the body, in anteroventral to posterodorsal sense. The distal end

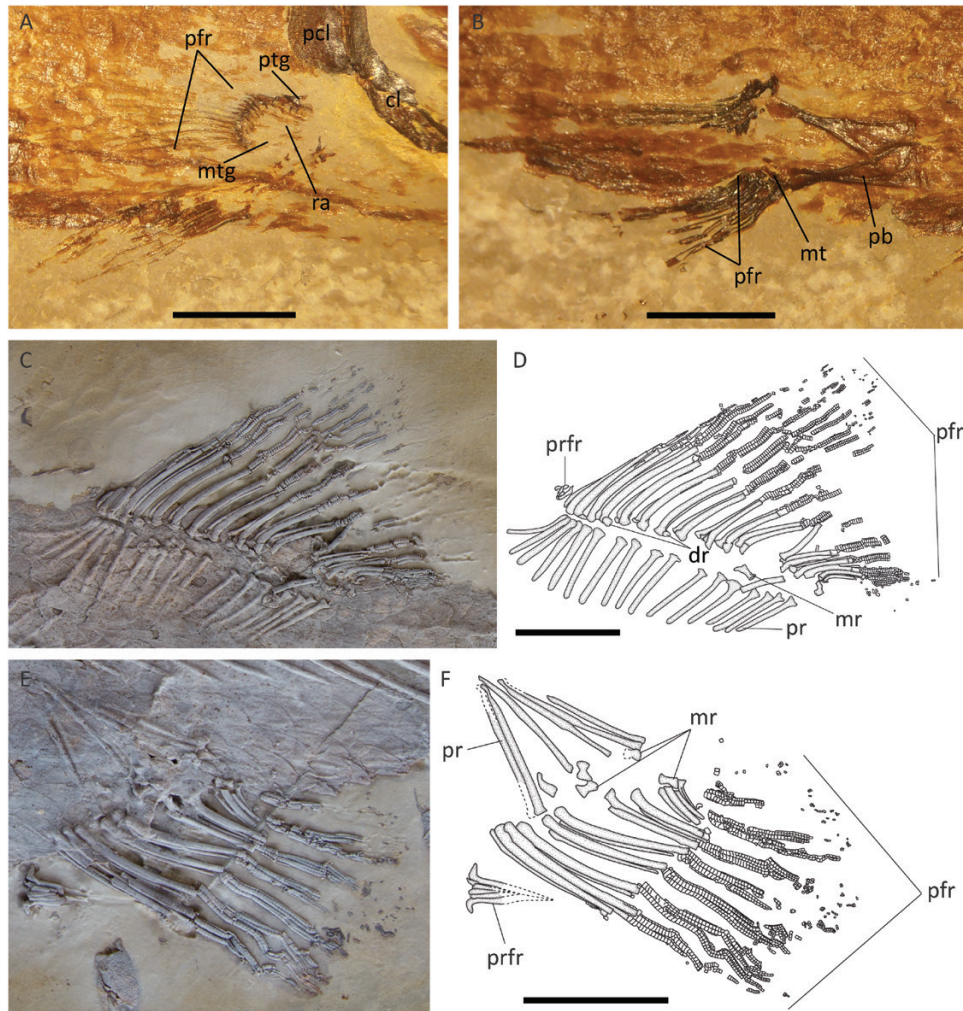


Figure 9. *Hispanamia newbreyi* gen. nov., sp. nov. (A) pectoral fin from specimen MCCM LH 16257a. Scale bar = 2 mm. (B) pelvic fin from specimen MCCM LH 16257a. Scale bar = 2 mm. (C) dorsal fin from specimen MCCM LH 9645a (holotype) slightly coated with ammonium chloride. (D) interpretative drawing of specimen in C. Scale bar = 5 cm. (E) anal fin from specimen MCCM LH 9645a (holotype) slightly coated with ammonium chloride. (F) interpretative drawing of specimen in E. Scale bar = 5 cm.

of each proximal radial articulates with the proximal end of a middle radial. Middle radials are small, tube-like bones with broad tips. As seen in *A. calva* (Grande & Bemis, 1998), the posterodistal end of each middle radial seems to articulate with the anterodistal end of the next proximal radial. Thus, each proximal radial, except the first one, makes contact with two middle radials. The distal radials are very small bones that articulate with the distal ends of the middle radials and lie between the two halves of their corresponding lepidotrichia. Each pterygiophore supports one fin ray, except the first one or two, which can support more than one due to the existence of a few, usually two or three, precurrent rays at the beginning of the dorsal

fin. These precurrent rays (**prfr**) are very small, and neither segmented nor branched. The principal rays are both segmented and branched. Except for the first one or two principal fin rays, which are shorter, the principal dorsal fin rays are longer anteriorly and gradually shorter posteriorly.

The anal fin (Fig. 9E, F) is also short, with a slightly convexly rounded margin. Its anterior insertion is located anterior to the posterior end of the dorsal fin; the preanal length represents 72–74% of the standard length of the fish in the largest specimens. The anal fin is slightly closer to the caudal fin than to the pelvic fins. The anal fin base represents approximately 10% of the standard length.

Its internal structure is very similar to that of the dorsal fin, and is composed of two or three precurrent fin rays, seven to eight principal fin rays and eight pterygiophores. All the proximal radials are approximately the same length. The principal rays are longer anteriorly, and gradually shorten posteriorly. As with the dorsal fin, the proximal ends of the proximal radials are not in contact with the haemal spines of the vertebral column, but separated from them. They are also diagonally disposed in anterodorsal to posteroventral sense.

Caudal fin: The caudal fin (Fig. 10) is convexly rounded in outline. As is characteristic of amiid fishes, it is a large fin, not extremely long and as high as the highest part of the body contour.

Endoskeleton: There are usually seven to nine auto-centra in the ural caudal region. The ural autocentra decrease in size from anterior to posterior. The ural region turns upwards towards the anterodorsal corner of the caudal fin. Distinguishing the parhypural from the first hypural in fossils is not easy (see Nybelin, 1963). According to Taverne (1997), the first hypural in

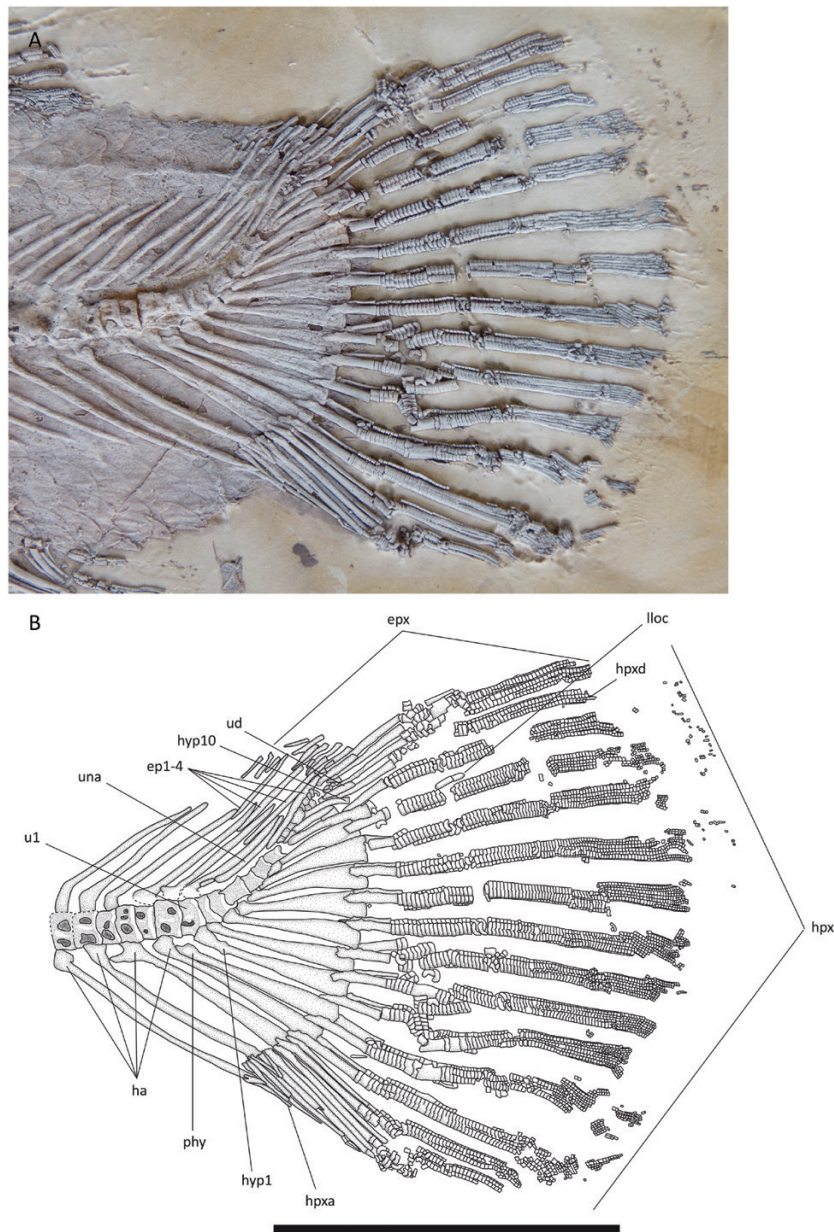


Figure 10. *Hispanamia newbreyi* gen. nov., sp. nov. (A) caudal fin from specimen MCCM LH 9645a (holotype) slightly coated with ammonium chloride. (B) interpretative drawing of specimen in A. Scale bar = 5 cm.

amiids can sometimes be identified by being slightly separated from the rest of the hypurals by a more or less marked diastema and by bearing a larger articular head, almost similar to a haemal arch. According to our own experience, the presence of a marked diastema is a more reliable criterion to identify the first hypural than the size of its articular head. Dorsally, the first ural vertebra usually bears a median neural spine, as with those of the preural region. The following ural vertebrae do not have neural arches articulating with them; instead, there are one or two long spine-like structures that probably represent fused ural neural arches (Grande & Bemis, 1998).

The hypurals and the epurals of the ural region serve as support for the caudal fin rays, thus forming the caudal fin endoskeleton. The hypurals (**hyp**) are flattened distally, their posterior corners almost contacting each other, and their distal tips form a slightly concave curve. The anteriormost hypurals are as long as the posteriormost preural haemal spines, but they become much shorter towards the posterior part of the ural region. The posteriormost hypurals are also narrower. The proximal ends of the epurals are located between the distal tips of the last preural and the ural neural spines. The epurals (**ep**) are thin, long, spine-like bones, similar to the supraneurals of the anterior abdominal. Small variability in the number of epurals is present: for instance, the holotype has four epurals, whereas specimen MCCM LH 16040a/b has only three. There are no uroneurals, as in all other amiids.

Exoskeleton: Most of the caudal fin rays are hypaxial rays (**hpx**); that is, they extend below the upturned notochord and vertebral column. There are also several epaxial rays (**epx**), which extend above and anterior to the upturned part of the notochord.

The anteriormost hypaxial rays are very short, and they become longer posteriorly. These precurrent rays are not branched, and only the largest among them present segmentation on their distal ends. The principal caudal rays are hypaxial, all segmented and branched; they provide the caudal fin with its characteristic rounded outline. The proximal segment of these rays is long, and articulates with the elements of the caudal endoskeleton. Their proximal ends are acute, and then they become slightly expanded. The segments that form these rays become smaller distally, as the rays get branched. The longer the rays are, the higher the number of branches they develop. In the largest specimen known, the holotype, the distal ends of the largest rays usually have six to eight small branches. The principal hypaxial rays articulate with the last preural haemal spines, the parhypural and the hypurals; each of these structures usually articulates with a single hypaxial fin ray. As for the precurrent hypaxial rays, several of them articulate with the same preural haemal spine. Several epaxial rays articulate with each epural. Only the two to four longest epaxial rays are segmented and branched. *Hispanamia newbreyi* lacks fringing fulcra in its caudal fin.

There is at least one urodermal, located just dorsal to the last hypural. Urodermals (**ud**) are small ossifications interpreted as homologous to rhombic scales present in the caudal region of most halecomorphs (Arratia & Schultze, 1992).

SCALES

Scales are organized in approximately 16 horizontal rows and 35 vertical rows (Fig. 11). They extend from

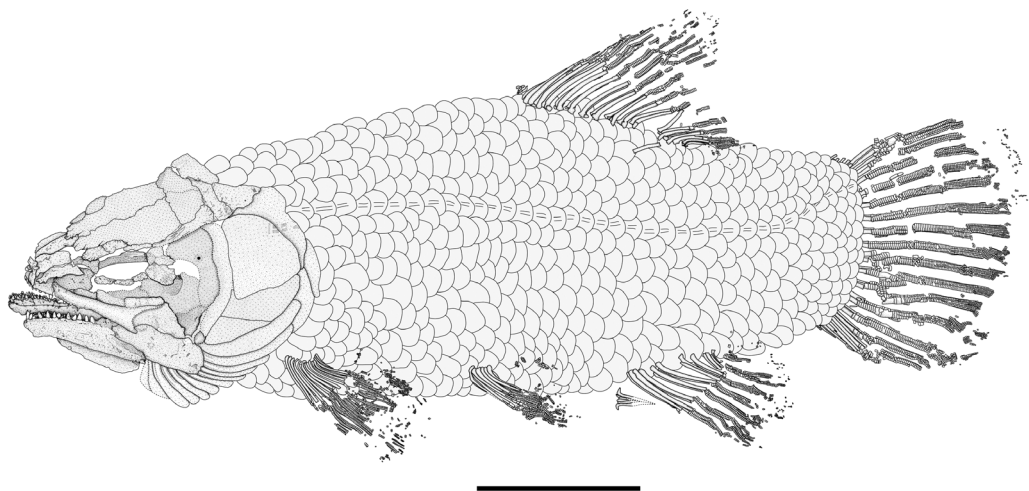


Figure 11. *Hispanamia newbreyi* gen. nov., sp. nov. Interpretative drawing of scale organization in specimen MCCM LH 9645a (holotype). Scale bar = 5 cm.

Table 1. Measurements for a growth series of *Hispanamia newbreyi* gen. nov., sp. nov.: head bones. SL, standard length; HL, head length

Specimen no. (SL)	Head length (as % of SL)	Mandibular length (as % of HL)	Gular length (as % of HL)	Frontal length (as % of HL)	Snout length (as % of HL)	Postorbital length (as % of HL)
MCCM LH 22600a (12.3 mm est.)*	4.0 mm est.* (32%)	?	?	?	?	?
MCCM LH 15783a/b (13.3 mm)	4.4 mm (33%)	2.3 mm (52%)	?	2.1 mm (48%)	0.8 mm (18%)	0.5 mm (11%)
MCCM LH 32244a/b (15.9 mm)	5.6 mm (35%)	3.1 mm (55%)	2.4 mm (43%)	2.7 mm (48%)	0.8 mm (14%)	0.6 mm (11%)
MCCM LH 076a/b (16.2 mm est.)*	5.2 mm est.* (32%)	?	?	?	?	?
MCCM LH 30878a/b (19.4 mm)	7.0 mm (36%)	3.6 mm (51%)	2.6 mm (37%)	2.9 mm (41%)	1.6 mm (23%)	1.0 mm (14%)
MCCM LH 32022a/b (24.0 mm)	8.3 mm (35%)	4.7 mm (57%)	3.2 mm (39%)	3.8 mm (46%)	1.3 mm (16%)	1.1 mm (13%)
MCCM LH 023 (26.0 mm)	8.3 mm (32%)	4.5 mm (54%)	3.3 mm (40%)	3.6 mm (43%)	1.4 mm (17%)	0.9 mm (11%)
MCCM LH 11286 (31.7 mm)	10.2 mm (32%)	4.9 mm (48%)	+2.2 mm	4.6 mm (45%)	2.2 mm (22%)	1.2 mm (12%)
MCCM LH 085R (32.0 mm)	10.6 mm (33%)	5.3 mm (50%)	4.1 mm (39%)	5.0 mm (47%)	?	1.4 mm (13%)
MCCM LH 9576a/b (39.1 mm)	12.2 mm (31%)	6.3 mm (52%)	4.5 mm (37%)	5.5 mm (45%)	2.2 mm (18%)	1.8 mm (15%)
MCCM LH 16257a (41.0 mm)	13.0 mm (32%)	6.6 mm (51%)	4.8 mm (37%)	5.4 mm (42%)	2.7 mm (21%)	1.8 mm (14%)
MCCM LH 151Pa/b (46.9 mm)	14.8 mm (32%)	8.4 mm (57%)	5.5 mm (37%)	6.5 mm (44%)	2.9 mm (20%)	1.9 mm (13%)
MCCM LH 17274a/b (47.6 mm)	15.1 mm (32%)	8.8 mm (58%)	5.0 mm (33%)	6.3 mm (42%)	3.1 mm (21%)	?
MCCM LH 23062a/b (50.4 mm)	15.6 mm (31%)	8.8 mm (56%)	5.4 mm (35%)	6.6 mm (42%)	2.6 mm (17%)	2.2 mm (14%)
MCCM LH 374Ra/b (62.2 mm est.)*	19.9 mm (32%)	9.9 mm (50%)	6.9 mm (35%)	7.8 mm (39%)	3.6 mm (18%)	3.0 mm (15%)
MCCM LH 16040b (181 mm)	57 mm (31%)	35 mm (61%)	21 mm (37%)	25 mm (44%)	16 mm (28%)	9 mm (16%)
MCCM LH 9645a/b (254 mm)	81 mm (32%)	55 mm (68%)	26+ mm (32%)	31 mm (38%)	22 mm (27%)	11+ mm (14%)

*Estimated by % of SL represented by HL in other specimens, which is the most constant % of SL. When only the head is lacking, SL is estimated by the % of SL represented by the rest of the body (100% - % of SL represented by HL).

right posterior to the bones of the pectoral girdle anteriorly to the caudal fin posteriorly, even covering the proximal, long segments of the caudal fin rays. The surface overlapped by each adjacent scale exceeds half the length of the scale. The scales of contiguous rows slightly overlap each other laterally as well. The shape of the scales is approximately constant throughout the body, basically ovoid in contour and longer than high, except for those scales covering the caudal fin rays, which are shorter and more circular. The size of the scales is also constant in most of them, but those of the ventral region, especially between the pectoral fins, are smaller.

The scales are very similar to those of other amiiforms in that they are thin, lack several characteristics common in other neopterygian groups (e.g. ctenii, radii, enamel tissue, vascular canals, thick bony base, peg-and-socket articulation), and especially in that they have ridges that are parallel to each other and radiate from the focus to end in the anterior, posterior and lateral margins of the scale instead of forming concentric circles (circuli) following the contour of the scale around the focus. The scales of *H. newbreyi* are described in more detail in [Martin-Abad \(2016\)](#).

Table 2. Measurements for a growth series of *Hispanamia newbreyi* gen. nov., sp. nov.: head bones. SL, standard length

Specimen no. (SL)	Gular width to length ratio	Frontal width to length ratio	Parietal width to length ratio	Parietal length to frontal length ratio	Snout length to postorbital length ratio	Opercle width to height ratio
MCCM LH 22600a (12.3 mm est.)	?	?	?	?	?	?
MCCM LH 15783a/b (13.3 mm)	?	0.29	1.14	0.33	1.6	?
MCCM LH 32244a/b (15.9 mm)	0.42	0.37	1.22	0.33	1.33	0.89
MCCM LH 076a/b (16.2 mm est.)	?	?	?	?	?	?
MCCM LH 30878a/b (19.4 mm)	0.35	0.38	1.20	0.34	1.6	0.87
MCCM LH 32022a/b (24.0 mm)	?	0.42	1.13	0.42	1.2	?
MCCM LH 023 (26.0 mm)	?	0.41	1.21	0.43	1.55	0.95
MCCM LH 11286 (31.7 mm)	?	0.30	1.25	0.28	1.83	0.85
MCCM LH 085R (32.0 mm)	0.44	0.30	?	?	?	0.81
MCCM LH 9576a/b (39.1 mm)	?	0.29	1.08	0.31	1.22	0.94
MCCM LH 16257a (41.0 mm)	?	0.31	1.04	0.30	1.5	0.97
MCCM LH 151Pa/b (46.9 mm)	0.38	0.32	1.18	0.26	1.53	1.03
MCCM LH 17274a/b (47.6 mm)	0.38	0.32	1.05	0.33	?	0.9
MCCM LH 23062a/b (50.4 mm)	?	0.40	1.23	0.26	1.18	?
MCCM LH 374Ra/b (62.2 mm est.)	0.46	0.37	1.14	0.33	1.2	?
MCCM LH 16040b (181 mm)	?	0.32	1.0	0.28	1.8	0.95
MCCM LH 9645a/b (254 mm)	?	0.32	1.1	0.32	2	0.87

LATERAL LINE TRUNK SYSTEM

The sensory canals of the skull connect with the lateral line along the trunk (Fig. 7). Posterior to the extrascapular, the sensory canals run through the posttemporal and the upper part of the supraclithrum, as in *A. calva* (Grande & Bemis, 1998: 53). In the holotype, the lateral line runs just above the level of the neural arches of the vertebrae; in this specimen, approximately equally spaced marks have been preserved, which can be tracked backwards at least to the ninth preural caudal autocentrum (as defined in Grande & Bemis, 1998). In *A. calva*, there is a very thin ossification, located between two of the

largest caudal fin rays, which corresponds to a caudal extension of the lateral line canal (lloc; e.g. Grande & Bemis, 1998: figs 81, 82). In the holotype of *H. newbreyi* there is a thin, tube-like ossification located between the fourth and fifth hypaxial caudal fin rays that might also correspond to the caudal extension of the lateral line canal.

DISCUSSION

The detailed anatomical description of the new taxon from Las Hoyas previously referred to *Amiopsis* has

Table 3. Measurements for a growth series of *Hispanamia newbreyi* gen. nov., sp. nov.: body proportions. SL, standard length; TL, total length

Specimen no. (SL)	Total length (SL as % of TL)	Body depth (as % of SL)	Prepectoral length (as % of SL)	Prepelvic length (as % of SL)	Predorsal length (as % of SL)	Preanal length (as % of SL)
MCCM LH 22600a (12.3 mm est.)	15.6 mm est. (79%)	1.5 mm (12%)	?	6.3 mm est. (51%)	7.1 mm est. (58%)	8.0 mm est. (65%)
MCCM LH 15783a/b (13.3 mm)	15.7 mm (85%)	3.8 mm (29%)	?	7.3 mm (55%)	8.4 mm (63%)	8.9 mm (67%)
MCCM LH 32244a/b (15.9 mm)	19.3 mm (82%)	4.5 mm (28%)	?	8.9 mm (56%)	9.8 mm (61%)	10.8 mm (68%)
MCCM LH 076a/b (16.2 mm est.)	19.8 mm est. (82%)	4.2 mm (26%)	?	8.0 mm est. (49%)	9.1 mm est. (56%)	11.2 mm est. (69%)
MCCM LH 30878a/b (19.4 mm)	24.6 mm (79%)	5.3 mm (27%)	?	11.9 mm (61%)	12.5 mm (64%)	14.6 mm (75%)
MCCM LH 32022a/b (24.0 mm)	27.9 mm (86%)	6.7 mm (28%)	?	15.1 mm (63%)	14.2 mm (59%)	18.3 mm (76%)
MCCM LH 023 (26.0 mm)	32.0 mm (81%)	8.5 mm (33%)	9.7 mm (37%)	14.1 mm (54%)	15.3 mm (59%)	17.5 mm (67%)
MCCM LH 11286 (31.7 mm)	38.7 mm (82%)	9.2 mm (29%)	9.8 mm (31%)	15.8 mm (50%)	18.4 mm (58%)	20.9 mm (66%)
MCCM LH 085R (32.0 mm)	38.6 mm (83%)	11.3 mm (35%)	10.8 mm (34%)	15.3 mm (48%)	18.9 mm (59%)	20.6 mm (64%)
MCCM LH 9576a/b (39.1 mm)	47.4 mm (82%)	11.0 mm (28%)	13.0 mm (33%)	19.7 mm (50%)	22.9 mm (59%)	27.1 mm (69%)
MCCM LH 16257a (41.0 mm)	47.4 mm (86%)	10.8 mm (26%)	13.9 mm (34%)	21.4 mm (52%)	24.9 mm (61%)	28.0 mm (69%)
MCCM LH 151Pa/b (46.9 mm)	56.9 mm (82%)	12.0 mm (26%)	16.5 mm (35%)	27.3 mm (58%)	28.7 mm (61%)	35.8 mm (76%)
MCCM LH 17274a/b (47.6 mm)	58.1 mm (82%)	14.2 mm (30%)	16.2 mm (34%)	25.1 mm (53%)	28.5 mm (60%)	33.6 mm (71%)
MCCM LH 23062a/b (50.4 mm)	62.4 mm (81%)	13.9 mm (28%)	15.8 mm (31%)	24.7 mm (49%)	29.4 mm (58%)	34.0 mm (67%)
MCCM LH 374Ra/b (62.2 mm est.)	75.9 mm est.* (82%)	20.4 mm (33%)	19.6 mm (32%)	29.0 mm (47%)	?	39.2 mm (63%)
MCCM LH 16040b (181 mm)	222 mm (82%)	51 mm (28%)	51 mm (28%)	95 mm (52%)	114 mm (63%)	134 mm (74%)
MCCM LH 9645a/b (254 mm)	308 mm (82%)	94 mm (37%)	79 mm (31%)	133 mm (52%)	151 mm (59%)	183 mm (72%)

*Estimated by % of TL represented by SL in the other specimens.

revealed a unique combination of characters, thus representing a new taxon.

The order Amiiformes is supported by three synapomorphies: two or fewer ossified ural neural arches, the absence of opisthotic bone and the absence of pterotic bone (Grande & Bemis, 1998). *Hispanamia* complies with the first, usually having one or two ural neural arches. The other two characters, however, cannot be verified, as with most amiiform fossils, because the endocranium is not observable.

The superfamily Amioidea is also supported by three synapomorphies: a caudal fin with a convexly rounded posterior margin, the absence of fringing fulcra on median fins, and a one-to-one arrangement of hypurals and caudal fin rays (Grande & Bemis, 1998). As described above, *Hispanamia* complies with these three character states.

The family Amiidae is supported by four synapomorphies: presence of solid, perichordally ossified, drum-shaped diplospondylous autocentra; an occiput extending posterior to the proximal end of the

Table 4. Measurements for a growth series of *Hispanamia newbreyi* gen. nov., sp. nov.: fin measurements and ratios. SL, standard length

Specimen no. (SL)	Dorsal fin base (as % of SL)	Anal fin base (as % of SL)	Dorsal to anal fin base ratio	Caudal fin length (as % of SL)	Caudal peduncle length (as % of SL)	Caudal peduncle depth (as % of SL)	Dorsal margin* (as % of SL)
MCCM LH 22600a (12.3 mm est.)	2.1 mm (17%)	1.2 mm (10%)	1.75	3.3 mm (27%)	2.7 mm (22%)	1.7 mm (14%)	2.3 mm (19%)
MCCM LH 15783a/b (13.3 mm)	2.0 mm (15%)	1.4 mm (10%)	1.43	2.6 mm (20%)	3.8 mm (29%)	1.9 mm (14%)	2.6 mm (20%)
MCCM LH 32244a/b (15.9 mm)	2.3 mm (14%)	1.4 mm (9%)	1.64	3.7 mm (23%)	4.0 mm (25%)	2.6 mm (16%)	2.7 mm (17%)
MCCM LH 076a/b (16.2 mm est.)	2.5 mm (15%)	1.5 mm (9%)	1.67	3.4 mm (21%)	4.2 mm (26%)	2.9 mm (18%)	3.8 mm (23%)
MCCM LH 30878a/b (19.4 mm)	3.2 mm (16%)	2.2 mm (11%)	1.45	4.2 mm (22%)	4.7 mm (24%)	3.7 mm (19%)	3.8 mm (20%)
MCCM LH 32022a/b (24.0 mm)	3.3 mm (14%)	2.2 mm (9%)	1.5	4.6 mm (19%)	5.2 mm (22%)	4.3 mm (18%)	4.9 mm (20%)
MCCM LH 023 (26.0 mm)	4.0 mm (15%)	2.0 mm (8%)	2.0	5.0 mm (19%)	8.2 mm (32%)	5.3 mm (20%)	5.5 mm (21%)
MCCM LH 11286 (31.7 mm)	5.0 mm (16%)	2.8 mm (9%)	1.79	6.3 mm (20%)	10.5 mm (33%)	5.4 mm (17%)	6.2 mm (20%)
MCCM LH 085R (32.0 mm)	4.4 mm (14%)	2.6 mm (8%)	1.69	6.8 mm (21%)	10.4 mm (32%)	6.6 mm (20%)	7.0 mm (22%)
MCCM LH 9576a/b (39.1 mm)	5.5 mm (14%)	3.4 mm (9%)	1.62	8.2 mm (21%)	10.7 mm (27%)	6.3 mm (16%)	7.6 mm (19%)
MCCM LH 16257a (41.0 mm)	6.0 mm (15%)	3.6 mm (9%)	1.67	+7.1 mm (+17%)	10.6 mm (26%)	7.0 mm (17%)	7.7 mm (19%)
MCCM LH 151Pa/b (46.9 mm)	8.4 mm (18%)	4.0 mm (9%)	2.1	10.2 mm (22%)	10.6 mm (23%)	7.8 mm (17%)	8.2 mm (17%)
MCCM LH 17274a/b (47.6 mm)	6.5 mm (14%)	3.9 mm (8%)	1.67	9.6 mm (20%)	12.3 mm (26%)	7.1 mm (15%)	8.8 mm (18%)
MCCM LH 23062a/b (50.4 mm)	8.0 mm (16%)	4.7 mm (9%)	1.70	11.4 mm (23%)	14.4 mm (29%)	8.1 mm (16%)	10.2 mm (20%)
MCCM LH 374Ra/b (62.2 mm est.)	?	6.5 mm (10%)	?	?	?	?	?
MCCM LH 16040b (181 mm)	29 mm (16%)	17 mm (9%)	1.71	37 mm (20%)	44 mm (24%)	32 mm (18%)	32 mm (18%)
MCCM LH 9645a/b (254 mm)	48 mm (19%)	25 mm (10%)	1.92	55 mm (22%)	57 mm (22%)	53 mm (21%)	50 mm (20%)

*Length between dorsal and caudal fins.

exoccipital; the presence of anteriorly projecting spine-like processes on neural and/or haemal arches; and the presence of three or more lateral fossae on each side of most centra (Grande & Bemis, 1998). *Hispanamia* complies with the first of these characters, as described above. The exoccipital is not observable in any of the known specimens, so the second of these characters cannot be confirmed. *Hispanamia* has anteriorly projecting spine-like processes on the neural and haemal arches of some of the last preural caudal vertebrae,

very similar to those of *A. calva* (e.g. Grande & Bemis, 1998: fig. 82), but not as developed as in other amiid species (e.g. *A. lepidota*, see Grande & Bemis, 1998: figs 362, 363). Finally, *Hispanamia* has three lateral fossae on most autocentra; more precisely, it has three fossae in the abdominal autocentra and in the monospondylous caudal autocentra, whereas there are usually two lateral fossae on most diplospondylous preural caudal autocentra. This character is the only synapomorphy supporting the subfamily Amiopsinae and the genus

Table 5. Meristic characters for a growth series of *Hispanamia newbreyi* gen. nov., sp. nov.: head region. SL, standard length; L, left; R, right

Specimen no. (SL)	L and R premaxillary teeth	L and R maxillary teeth	L and R dentary teeth	L and R coronoids	L and R branchiostegals
MCCM LH 22600a (12.3 mm est.)	?	?	?	?	?
MCCM LH 15783a/b (13.3 mm)	?	?	10+; ?	?	11; ?
MCCM LH 32244a/b (15.9 mm)	?; +4	+10; ?	11+; ?	?	12; ?
MCCM LH 076a/b (16.2 mm est.)	?	?	?	?	?
MCCM LH 30878a/b (19.4 mm)	+4; ?	?	13+; ?	?	12; ?
MCCM LH 32022a/b (24.0 mm)	8; ?	+14; ?	+10; ?	?	12; ?
MCCM LH 023 (26.0 mm)	?	?	?	?	?; 13
MCCM LH 11286 (31.7 mm)	?; 5+	?; 20+	?; 14+	?	?; 11
MCCM LH 085R (32.0 mm)	?	?	?	?	?; 11
MCCM LH 9576a/b (39.1 mm)	7+; +3	?	+8; ?	?	11; ?
MCCM LH 16257a (41.0 mm)	?	?; +6	?; +7	?	11; +7
MCCM LH 151Pa/b (46.9 mm)	8; ?	+7; ?	+6; ?	?	11; 11
MCCM LH 17274a/b (47.6 mm)	?; +5	?	14+; +8	?	+7; 10
MCCM LH 23062a/b (50.4 mm)	?; +5	?; +6	?; +12	?	?; 10
MCCM LH 374Ra/b (62.2 mm est.)	?; 7	?	?; +11	?	12; 10+
MCCM LH 16040b (181 mm)	+4; 7+	?; 26	?; 14	3; ?	?; 10+
MCCM LH 9645a/b (254 mm)	8; ?	+19; ?	13; ?	?; 3+	12; ?

Amiopsis as monophyletic clades, and is shared by *Hispanamia*. However, it can also be interpreted as a plesiomorphy within the family Amiidae, since non-amiid halecomorphs with ossified autocentra, such as sinamiids or ionoscopiforms, present lateral fossae. These groups usually have two lateral fossae instead of three, leading Grande & Bemis (1998) to regard the number of lateral fossae present as a multistate character.

The subfamily Vidalamiinae is strongly supported by numerous derived characters, most of which are not shared by *Hispanamia*: (1) vidalamiines have two different articular elements not in contact with each other in the lower jaw, whereas *Hispanamia* has one

articular bone, possibly by fusion of two elements; (2) vidalamiines have a strong ornamentation on the dermal bones of their skulls, in contrast to the relatively smooth bones on *Hispanamia*; (3) vidalamiines have a relatively long parietal (width-to-length ratio range not exceeding 0.90), whereas *Hispanamia* has a comparatively shorter parietal (width-to-length ratio between 1.00 and 1.25); (4) vidalamiines have a high number of ural autocentra (11–22), whereas *Hispanamia* has nine or fewer; (5) vidalamiines have a preopercular that is wide in the middle, tapering dorsally and ventrally, whereas the preopercular of *Hispanamia* is crescent-shaped, long and narrow; (6) vidalamiines have a posttemporal bone with the

Table 6. Meristic characters for a growth series of *Hispanamia newbreyi* gen. nov., sp. nov.: vertebrae and autocentra. SL, standard length

Specimen no. (SL)	Total vertebrae (total autocentra)	Total preural vertebrae (total preural autocentra)	Preural caudal autocentra (ural caudal autocentra)	Abdominal autocentra (vertebrae involved in supporting caudal fin)	Total diplospondyloous vertebrae	Vertebrae with normal diplospondyly (alternating diplospondyly)
MCCM LH 22600a (12.3 mm est.)	?	?	?	?	?	?
MCCM LH 15783a/b (13.3 mm)	?	?	?	?	?	?
MCCM LH 32244a/b (15.9 mm)	?	?	?	?	?	?
MCCM LH 076a/b (16.2 mm est.)	?	?	?	?	?	?
MCCM LH 30878a/b (19.4 mm)	?	?	?	?	?	?
MCCM LH 32022a/b (24.0 mm)	+33 (+42)	+26 (+35)	20 (7)	+15 (10)	9	4 (5)
MCCM LH 023 (26.0 mm)	37 (49)	30 (41)	22 (8)	19 (10)	12	8 (4)
MCCM LH 11286 (31.7 mm)	38 (49)	31 (41)	23 (8)	18 (11)	11	7 (3)
MCCM LH 085R (32.0 mm)	35 (45)	31 (41)	23 (4)	18 (9)	11	5 (6)
MCCM LH 9576a/b (39.1 mm)	38 (48)	31 (41)	23 (7)	18 (12)	10	7 (3)
MCCM LH 16257a (41.0 mm)	+36 (+42)	+27 (+33)	+12 (9)	17 (14)	+6	3+ (3+)
MCCM LH 151Pa/b (46.9 mm)	42 (53)	35 (46)	25 (7)	21 (12)	11	8 (3)
MCCM LH 17274a/b (47.6 mm)	40 (51)	33 (44)	25 (7)	19 (11)	11	8 (3)
MCCM LH 23062a/b (50.4 mm)	41 (52)	34 (45)	22 (7)	20 (11)	11	7 (4)
MCCM LH 374Ra/b (62.2 mm est.)	?	?	?	18 (?)	?	?
MCCM LH 16040b (181 mm)	41 (50)	35 (44)	19 (6)	21 (12)	9	6 (3)
MCCM LH 9645a/b (254 mm)	39 (48)	32 (41)	22 (7)	19 (11)	9	5 (4)

lateral edge longer than the anterior edge, whereas the posttemporal in *Hispanamia* has a lateral edge shorter than the anterior edge. However, *Hispanamia* shares two of the other diagnostic characters of the Vidalamiinae: the absence of suborbital bones and the presence of labiolingually compressed, sharply carinate caps of the jaw teeth.

In summary, *Hispanamia* has a combination of characters including the only synapomorphy of Amiopsinae and two of the diagnostic characters of Vidalamiinae

while differing from the latter in six diagnostic characters. As a consequence, its assignation to one subfamily or the other is uncertain at present.

This new taxon is clearly distinguishable from *A. woodwardi*, the species to which this material from Las Hoyas was previously referred, in several characters: (1) *Hispanamia* seems to lack a substantial scapulocoracoid ossification, which is present in *A. woodwardi*; (2) the jaw teeth of *Hispanamia* are labiolingually compressed and have sharply carinate

Table 7. Meristic characters for a growth series of *Hispanamia newbreyi* gen. nov., sp. nov.: vertebral elements associated with autocentra. SL, standard length

Specimen no. (SL)	Ossified supraneurals	Ossified median neural spines in caudal region	Ossified paired neural spines in caudal region	Total ossified neural arches	Ossified infrahaemals	Ossified median preural haemal spines
MCCM LH 22600a (12.3 mm est.)	?	11+	3	?	?	+8
MCCM LH 15783a/b (13.3 mm)	?	12	3	34	3	12
MCCM LH 32244a/b (15.9 mm)	+9	11	4	+33	4	13
MCCM LH 076a/b (16.2 mm est.)	13	12	3	34+	3	12
MCCM LH 30878a/b (19.4 mm)	13	12	3	35	3	14
MCCM LH 32022a/b (24.0 mm)	+10	13	2	+29	3	12
MCCM LH 023 (26.0 mm)	14	14	3	35	4	14
MCCM LH 11286 (31.7 mm)	15	12	3	34	3	12
MCCM LH 085R (32.0 mm)	13	13	2	33	2	14
MCCM LH 9576a/b (39.1 mm)	14	12	3	33	2	13
MCCM LH 16257a (41.0 mm)	15	13	2	34	4	14
MCCM LH 151Pa/b (46.9 mm)	14	13	2	34	3	13
MCCM LH 17274a/b (47.6 mm)	14	13	3	35	3	14
MCCM LH 23062a/b (50.4 mm)	12+	12	4	34	4	14
MCCM LH 374Ra/b (62.2 mm est.)	14	?	2	+21	3	?
MCCM LH 16040b (181 mm)	14	13	2	35	2	14
MCCM LH 9645a/b (254 mm)	13	12	3	35	3	11

caps, which are absent in the uncompressed *A. woodwardi*. Numerous meristic characters are also different between both species, namely the number of: (3) premaxillary teeth: up to eight in *Hispanamia*, and five in *A. woodwardi*; (4) maxillary teeth: 26 vs. 30, respectively; (5) branchiostegal rays: 11–12 vs. 14–15; (6) total vertebrae: 38–41 vs. 45–48; (7) total centra: 48–53 vs. 58–61; total diplospondylous vertebrae: 9–12, usually 9–11, vs. 12–14; (8) ossified supraneurals: 13–15, usually 13–14, vs. 15–16; (9) ossified median neural spines in the caudal region: 11–14, usually 12–13, vs. 13–18; (10) ossified neural arches: 33–35 vs. 37–42;

(11) ossified median preural haemal spines: 11–14 vs. 16–18; (12) ossified epurals: 3–5, usually 4, vs. 4–6, usually 5; (13) ossified hypochordal elements supporting the caudal fin rays: usually 14–16 vs. 17–18; and (14) principal caudal fin rays: 18–20 vs. 22–23. In contrast to the meristic features, the measurement ratios and percentages of the two species are very similar to each other; compare tables 140–143 in Grande & Bemis (1998) with Tables 1–4 in the present paper. This would indicate that the overall similar shape of both taxa is the reason why they have traditionally been related since the discovery of the material from Las Hoyas.

Table 8. Meristic characters for a growth series of *Hispanamia newbreyi* gen. nov., sp. nov.: paired fins and radials, and scales. SL, standard length; L, left; R, right

Specimen no. (SL)	L and R pectoral fin rays	L and R branched pectoral fin rays	L and R pelvic fin rays (no. branched)	Scales along lateral line (along dorsal fin base)	Scale rows above lateral line (below lateral line)
MCCM LH 22600a (12.3 mm est.)	?	?	+5; +4 (0; 0)	?	?
MCCM LH 15783a/b (13.3 mm)	?	?	+4; 6+ (0; 0)	?	?
MCCM LH 32244a/b (15.9 mm)	?	?	7; +4 (0; 0)	?	?
MCCM LH 076a/b (16.2 mm est.)	?	?	7; 7 (0; 0)	?	?
MCCM LH 30878a/b (19.4 mm)	?	?	7; +2 (0; 0)	?	?
MCCM LH 32022a/b (24.0 mm)	+6; +4	?	6; 7 (0; 0)	?	?
MCCM LH 023 (26.0 mm)	14; ?	0; ?	7; +4 (0; 0)	37 (12)	8 (10)
MCCM LH 11286 (31.7 mm)	?; 14	?; 0	+5; 7 (0; 0)	33 (11)	7 (9)
MCCM LH 085R (32.0 mm)	?; 14	?; 0	7; 7 (0; 0)	32 (11)	7 (9)
MCCM LH 9576a/b (39.1 mm)	14; ?	0; ?	+4; 7 (0; 4)	34 (11)	7 (9)
MCCM LH 16257a (41.0 mm)	+10; 14	0; 0	7; 7 (?; ?)	33 (10)	7 (9)
MCCM LH 151Pa/b (46.9 mm)	+11; +10	?	7; 7 (?; ?)	?	?
MCCM LH 17274a/b (47.6 mm)	+8; 13	?; 0	7; 7 (4+; ?)	32 (9)	6 (10)
MCCM LH 23062a/b (50.4 mm)	13+; +8	?	+5; 6 (?; ?)	31 (10)	6 (9)
MCCM LH 374Ra/b (62.2 mm est.)	11+; 13	7; ?	7; ? (?; ?)	? (?)	6 (10)
MCCM LH 16040b (181 mm)	15; 16	?	7; 6 (?; 6)	33 (10)	7 (10)
MCCM LH 9645a/b (254 mm)	13; ?	12; ?	7; ? (6; ?)	35 (13)	7 (9)

Amiopsiines and vidalamiines are known from both marine (e.g. *A. lepidota* Agassiz, 1833; *Pachyamia latimaxillaris*, Chalifa & Tchernov, 1982) and freshwater deposits (e.g. *A. dolloi* Traquair, 1911; *Calamopleurus mawsoni* Woodward, 1902; *Calamopleurus africanus* Forey & Bemis, 1998, [Cavin et al., 2015](#)). All known *Amiopsis* species come from the Late Jurassic to early Late Cretaceous of Europe. The subfamily Vidalamiinae is more cosmopolitan, with representatives from Europe, North America, South America and Africa; its record extends from the Early Cretaceous to the Eocene ([Grande & Bemis,](#)

[1998](#); [Martín-Abad & Poyato-Ariza, 2013a](#)). Thus, *H. newbreyi* would fit into the known fossil record of either of the two subfamilies, in terms of palaeobiogeography, chronostratigraphy and continental/marine origin of the deposits.

CONCLUSIONS

The fish material from the Early Cretaceous of Las Hoyas previously assessed as *Amiopsis* cf. *A. woodwardi* is transferred to *Hispanamia newbreyi* gen. nov., sp. nov. This new taxon exhibits a unique combination

Table 9. Meristic characters for a growth series of *Hispanamia newbreyi* gen. nov., sp. nov.: dorsal and anal fins and supports. SL, standard length

Specimen no. (SL)	Dorsal fin rays	Branched dorsal rays	Ossified dorsal proximal radials	Anal fin rays	Branched anal rays	Ossified anal proximal radials
MCCM LH 22600a (12.3 mm est.)	i, 14	0	0	+4	0	+3
MCCM LH 15783a/b (13.3 mm)	ii, 15	0	0	7	0	7
MCCM LH 32244a/b (15.9 mm)	i, 15	0	14	i, 8	0	8
MCCM LH 076a/b (16.2 mm est.)	i, 14+	0	14+	i, 8	0	+5
MCCM LH 30878a/b (19.4 mm)	i, 15	0	16	i, 8	0	8
MCCM LH 32022a/b (24.0 mm)	i, 14	0	13+	i, 8	0	8
MCCM LH 023 (26.0 mm)	i, 15	0	15	i, 9	0	8
MCCM LH 11286 (31.7 mm)	ii, 14	0	14	i, 9	0	8
MCCM LH 085R (32.0 mm)	i, 14	0	14	i, 9	2	8
MCCM LH 9576a/b (39.1 mm)	i, 14	0	14	ii, 9	5	9
MCCM LH 16257a (41.0 mm)	i, 15	?	14	ii, 9	?	8
MCCM LH 151Pa/b (46.9 mm)	ii, 15	0	16	i, 9	?	9
MCCM LH 17274a/b (47.6 mm)	i, 15	?	14	ii, 9	?	9
MCCM LH 23062a/b (50.4 mm)	i, 15	5	15	i, 9	?	9
MCCM LH 374Ra/b (62.2 mm est.)	?	?	?	i, 9	7	8
MCCM LH 16040b (181 mm)	ii, 15	12	16	ii, 9	9	8
MCCM LH 9645a/b (254 mm)	ii, 16	14	17	I, 7	7	6+

of characters that allows us to diagnose and differentiate it from all known amiids.

It shares the only synapomorphy that supports the monophyly of the subfamily Amiopsinae and, therefore, of the genus *Amiopsis*: presence of three lateral fossae on each side of most vertebral autocentra. It also shares the derived state of two characters of the subfamily Vidalamiinae: absence of suborbital bones and labiolingually compressed jaw teeth with sharply carinate caps, considered to be more derived in the phylogeny of the order Amiiformes. However, in turn, the new taxon differs from Vidalamiinae in six other characters diagnostic for this subfamily. Therefore,

taxonomic assessment of *H. newbreyi* is not possible at present due to this apparently contradictory evidence.

The occurrence of this new taxon in the Early Cretaceous continental deposits of Las Hoyas in Spain is congruent with the record of both amiopsines and vidalamiines; primitive amiiforms are interpreted as marine forms, but both Amiopsinae and Vidalamiinae remains have been retrieved from continental deposits, and in both cases their fossil record includes Early Cretaceous European localities.

The exact phylogenetic position of *H. newbreyi* will be discussed after the other amiiform taxa from

Table 10. Meristic characters for a growth series of *Hispanamia newbreyi* gen. nov., sp. nov.: caudal fin and skeleton. SL, standard length

Specimen no. (SL)	Ossified hypurals	Ossified hypochordal elements supporting caudal rays	Ossified epurals	Total caudal rays	Epaxial caudal rays (hypaxial rays)	Branched caudal rays
MCCM LH 22600a (12.3 mm est.)	7	10	0	16, i	0 (16, i)	0
MCCM LH 15783a/b (13.3 mm)	9	12	0	16, i	0 (16, i)	0
MCCM LH 32244a/b (15.9 mm)	9	13	4	16, ii	0 (16, ii)	0
MCCM LH 076a/b (16.2 mm est.)	9	12	3	15, iii	0 (15, iii)	0
MCCM LH 30878a/b (19.4 mm)	10	14	4	16, iii	0 (16, iii)	0
MCCM LH 32022a/b (24.0 mm)	10	13	5	v, 19, iii	v, 3 (16, iii)	0
MCCM LH 023 (26.0 mm)	10	15	4	vi, 18, v	vi, 3 (15, v)	0
MCCM LH 11286 (31.7 mm)	11	14	5	v, 19, v	v, 3 (16, v)	0
MCCM LH 085R (32.0 mm)	10	15	4	vi, 18, i+	vi, 3 (15, i+)	7
MCCM LH 9576a/b (39.1 mm)	10	15	4	vi, 20, iii	vi, 4 (16, iii)	9
MCCM LH 16257a (41.0 mm)	11	16	4	v, 19, iii	v, 3 (16, iii)	10
MCCM LH 151Pa/b (46.9 mm)	11	15	4	vi, 20, iv	vi, 4 (16, iv)	10
MCCM LH 17274a/b (47.6 mm)	10	14	4	v, 20, iv	v, 3 (17, iv)	10+
MCCM LH 23062a/b (50.4 mm)	10	14	4	v, 19, ii	v, 4 (15, ii)	14
MCCM LH 374Ra/b (62.2 mm est.)	?	?	?	?	?	?
MCCM LH 16040b (181 mm)	10	16	4	v, 20, iii	v, 4 (16, iii)	16
MCCM LH 9645a/b (254 mm)	10	15	4	v, 19, ii	v, 2 (17, ii)	15

Las Hoyas (one of them is traditionally referred to *Vidalamia*) are described, so that the relationships and composition of the Amiposinae and Vidalamiinae will be revised.

ACKNOWLEDGEMENTS

Ángela Delgado Buscalioni is acknowledged for the scientific direction of several consecutive Research Projects on Las Hoyas, Jesús Madero Jarabo (Museo de las Ciencias de Castilla-La Mancha, Cuenca, Spain) for the loan of the material and

Mercedes Llandres for the preparation of the holotype specimen. A special acknowledgement goes to the students, researchers and amateur palaeontologists who have participated in Las Hoyas fieldwork and helped collect the fossil material, including the late José Luis Ortiz (our very dear Chikuto). Comments by Lionel Cavin and an anonymous reviewer greatly improved the manuscript. Funding for this project comes from an FPU grant provided to H.M.-A. (AP2007-00894, MICINN, Spain). This paper is a contribution to projects CGL-2009-11838 (MICINN, Spain) and CGL-2013-42643 P (MINECO, Spain).

REFERENCES

- Agassiz L.** 1833–1843. *Recherches sur les Poissons Fossiles*. Neuchâtel: Petitpierre.
- Arratia G, Schultze H-P.** 1992. Reevaluation of the caudal skeleton of certain actinopterygian fishes. III. Salmonidae. Homologization of caudal skeletal structures. *Journal of Morphology* **214**: 187–249.
- Bermúdez-Rochas DD, Delvene G, Moratalla J, Hernán J, de la Fuente M.** 2007. Primeros datos paleontológicos del yacimiento del Cretácico Inferior Vega de Pas 1 (Cuenca Vasco-Cantábrica, Cantabria, España). In: Bermúdez-Rochas DD, Najarro M, Quesada C, eds. *II Semana de Jóvenes Investigadores del IGME*. Publicaciones del Instituto Geológico y Minero de España, 23–28.
- Bermúdez-Rochas DD, Poyato-Ariza FJ.** 2007. New fossiliferous sites with fish fauna from the Basque-Cantabrian and Cameros basins, Early Cretaceous of Spain. *Journal of Vertebrate Paleontology* **27**, Abstracts: 47–48.
- Bonaparte CL.** 1838. *Selachorum tabula analytica*. *Nouveaux Annales des Sciences Naturelles*, **2**.
- Buscalioni AD, Fregenal-Martínez MA.** 2010. A holistic approach to the palaeoecology of Las Hoyas Konservat-Lagerstätte (La Huérguina Formation, Lower Cretaceous, Iberian Ranges, Spain). *Journal of Iberian Geology* **36**: 297–326.
- Buscalioni AD, Fregenal MA, Bravo A, Poyato-Ariza FJ, Sanchíz B, Báez AM, Cambra-Moo O, Martín-Closas C, Evans SE, 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.
- Cavin L, Boudad L, Tong H, Lång E, Tabouelle J, Vullo R.** 2015. Taxonomic composition and trophic structure of the continental bony fish assemblage from the early Late Cretaceous of southeastern Morocco. *PLoS ONE* **10**: e0125786.
- Chalifa Y, Tchernov E.** 1982. *Pachyamia latimaxillaris*, new genus and species (Actinopterygii: Amiidae), from the Cenomanian of Jerusalem. *Journal of Vertebrate Paleontology* **2**: 269–285.
- Cope ED.** 1872. Observations on the systematic relations of the fishes. *Proceedings of the American Association for the Advancement of Science* **20**: 317–343.
- Cope ED.** 1887. Zittel's Manual of Palaeontology. *American Naturalist* **21**: 1014–1019.
- Delclòs X, Martín-Closas C, Buscalioni AD, Fregenal-Martínez MA, de la Fuente M, Gomez B, Poyato-Ariza FJ, Soriano C.** 2004. Tafonomía y paleoecología del ecosistema acuático de Las Hoyas (Barremiense superior, Serranía de Cuenca). *Geo-Temas* **6**: 39–42.
- Egerton PMG.** 1858. *Megalurus damoni*. *Memoires of the Geological Survey of the United Kingdom*, Figures and descriptions illustrative of British organic remains, Decade IX **9**: 1–3.
- Escaso F, Sanz JL, Ortega F.** 2005. Un Konservat-Lagerstätte del Cretácico Inferior de Europa: Las Hoyas. *Boletín de la Real Sociedad Española de Historia Natural, Sección Geología* **100**: 221–233.
- Forey PL, Grande L.** 1998. An African twin to the Brazilian *Calamopleurus* (Actinopterygii: Amiidae). *Zoological Journal of the Linnean Society* **123**: 179–195.
- Fregenal-Martínez MA.** 1995. *El sistema lacustre de las Hoyas (Cretácico Inferior, Serranía de Cuenca); Estratigrafía y Sedimentología*. Tarancón: Publicaciones de la Excm. Diputación Provincial de Cuenca.
- Fregenal-Martínez MA.** 1998. *Análisis de la cubeta sedimentaria de Las Hoyas y su entorno paleogeográfico (Cretácico Inferior, Serranía de Cuenca). Sedimentología y aspectos tafonómicos del yacimiento de Las Hoyas*. Unpublished D. Phil. Thesis, Universidad Complutense de Madrid, Dept. Estratigrafía.
- Fregenal-Martínez MA, Meléndez N.** 2000. The lacustrine fossiliferous deposits of the Las Hoyas Subbasin (Lower Cretaceous, Serranía de Cuenca, Iberian Ranges, Spain). In: Gierlowski-Kordesch, EH, Kelts KR, eds. *Lake basins through space and time*. *AAPG Studies on Geology* **46**: 303–314.
- Gómez-Pallerola JE.** 1990. Nota sobre los peces Osteictios de las calizas litográficas del Cretácico Inferior del Montsec (Lérida). *Boletín Geológico y Minero* **101**: 28–72.
- Grande L.** 2010. An empirical synthetic pattern of gars (Lepisosteiformes) and closely related species, based mostly on skeletal anatomy. The resurrection of *Holostei*. *Copeia* **10**: i–x, 1–871.
- Grande L, Bemis WE.** 1998. A comprehensive phylogenetic study of amiid fishes (Amiidae) based on comparative skeletal anatomy. An empirical search for interconnected patterns of Natural History. *Journal of Vertebrate Paleontology*, Memoir 4 suppl. to vol. **18**: i–x, 1–690.
- Hay OP.** 1929. Second bibliography and catalogue of the fossil Vertebrata of North America. *Publications of the Carnegie Institute of Washington* **390**: 1–2003.
- Jarvik E.** 1980. *Basic structure and evolution of vertebrates*. Vol. I. New York: Academic Press.
- Jollie M.** 1984. Development of the head and pectoral skeleton of *Amia* with a note on the scales. *Gegenbaurs Morphologisches Jahrbuch, Leipzig* **130**: 315–351.
- Kner R.** 1863. Über einige fossile Fische aus den Kreide- und Tertiärschichten von Comen und Podused. *Sitz Akademie für Wissenschaften Wien, Math- Naturwissenschaften* **48**: 126–148.
- Martín-Abad H.** 2016. Anatomical differentiation of isolated scales of amiiform fishes (Amiiformes: Actinopterygii) from the Early Cretaceous of Las Hoyas (Cuenca, Spain). *Comptes Rendus Palevol*. <http://dx.doi.org/10.1016/j.crpv.2016.08.006>.
- Martín-Abad H, Poyato-Ariza FJ.** 2009. El registro de los peces amiiformes de la Península Ibérica. *Paleolusitana* **1**: 261–267.
- Martín-Abad H, Poyato-Ariza FJ.** 2013a. Historical patterns of distribution in Pycnodontiform and Amiiform fishes in the context of moving plates. *Geologica Belgica* **16**: 217–226.
- Martín-Abad H, Poyato-Ariza FJ.** 2013b. Amiiforms from the Iberian Peninsula: historic review and research prospects. In: Arratia G, Schultze H-P, Wilson MVH, eds. *Mesozoic fishes 5 – Global diversity and evolution*. München: Verlag Dr. Friedrich Pfeil, 73–86.

- Müller J. 1844. Ueber den Bau und die Grenzen der Ganoiden und über das natürliche System der Fische. *Bericht über die zur Bekanntmachung geeigneten Verhandlungen der Akademie der Wissenschaften Berlin* 1846: 117–216.
- Nybelin O. 1963. Zur Morphologie und Terminologie des Schwanzskelettes der Actinopterygier. *Arkiv för Zoologi Uppsala* 2: 485–516.
- Ortega F, Buscalioni AD, Delclòs X, Fregenal-Martínez MA, Martín-Closas C, Poyato-Ariza FJ, Sanz JL, Soriano C. 2003. Los fósiles del Cretácico de Las Hoyas: un yacimiento excepcional. In: Nucho del Rivero R, ed. *Patrimonio Geológico de Castilla-La Mancha*. Madrid: Enresa Ediciones, 422–447.
- Ortega F, Sanz JL, Barbadillo L, Buscalioni AC, Diéguez C, Evans SE, Fregenal-Martínez MA, de la Fuente M, Madero J, Martín-Closas C, Martínez-Delclòs X, Meléndez N, Moratalla JJ, Pérez-Moreno BP, Pinardo-Moya E, Poyato-Ariza FJ, Rodríguez-Lázaro J, Sanchiz B, Wenz S. 1999. El yacimiento de Las Hoyas (La Cierva, Cuenca): un Konservat-Lagerstätte del Cretácico Inferior. In: Aguirre E, Rábano I, eds. *La Huella del pasado. Fósiles de Castilla-La Mancha*. Toledo: Gobierno de Castilla-La Mancha, 195–215.
- Poyato-Ariza FJ. 1989. Ictiofauna del yacimiento de Las Hoyas. In: Sanz JL, coord. *La fauna del pasado en Cuenca*. Cuenca: Instituto Juan de Valdés, 83–124.
- Poyato-Ariza FJ. 1992. Introducción al estudio de los peces fósiles: problemas recientes en taxonomía. In: Astibia H, ed. *Paleontología de Vertebrados. Faunas y Fiogenia, Aplicación y Sociedad*. País Vasco: Servicio Editorial de la Universidad del País Vasco, 75–152.
- Poyato-Ariza FJ. 1994. A new Early Cretaceous gonorynchiform fish (Teleostei: Ostariophysii) from Las Hoyas (Cuenca, Spain). *Occasional papers of the Museum of Natural History of the University of Kansas* 164: 1–37.
- Poyato-Ariza FJ. 1997. A new assemblage of Spanish Early Cretaceous teleostean fishes, formerly considered 'leptolepids': phylogenetic relevance. *Comptes rendus de l'Académie des sciences de Paris, Série IIA (Sciences de la Terre et des planètes)* 325: 373–379.
- Poyato-Ariza FJ. 2005a. Palaeoecology of the fishes from the Early Cretaceous lake of Las Hoyas, Cuenca, Spain, with a hypothesis of sexual dimorphism for the Chanidae *Rubiesichthys*. *Bulletin of the Kitakyushu Museum of Natural History and Human History, Serie A* 3: 153–168.
- Poyato-Ariza FJ. 2005b. About Las Hoyas. In: Poyato-Ariza FJ, ed. *Fourth International Meeting on Mesozoic Fishes. Systematics, homology, and nomenclature*. Madrid: Ediciones de la Universidad Autónoma de Madrid, 281–294.
- Poyato-Ariza FJ, Buscalioni AD, Cartanyà J. 1999. The Mesozoic record of osteichthyan fishes from Spain. In: Arratia G, Schultze H-P, eds. *Mesozoic fishes 2. Systematics and fossil record*. München: Verlag Dr. Friedrich Pfeil, 505–533.
- Poyato-Ariza FJ, Martín-Abad H. 2013. History of two lineages: comparative analysis of the fossil record in Amiiiformes and Pycnodontiformes (Osteichthyes, Actinopterygii). *Spanish Journal of Palaeontology* 28: 79–90.
- Poyato-Ariza FJ, Martín-Abad H. 2016. Osteichthyans. In: Poyato-Ariza FJ, Buscalioni AD, eds. *Las Hoyas: a Cretaceous wetland. A multidisciplinary synthesis after 25 years of research on an exceptional fossil Lagerstätte from Spain*. München: Verlag Dr. Friedrich Pfeil, 114–132.
- Poyato-Ariza FJ, Wenz S. 1990. La ictiofauna española del Cretácico inferior. In: Civis-Llovera J, Flores JA, eds. *Actas Paleontológicas (Actas IV Jornadas paleontología)*. Acta Salmanticensis, Biblioteca de las Ciencias 68: 299–311.
- Poyato-Ariza FJ, Wenz S. 1995. Ichthyofauna. In: Meléndez N, ed. *Las Hoyas, a lacustrine Konservat-Lagerstätte*. Cuenca, Spain. II International Symposium on Lithographic Limestones. Lérida: Universidad Complutense de Madrid, 43–49.
- Poyato-Ariza FJ, Wenz S. 2000. A new pycnodontiform fish from the Early Cretaceous of Las Hoyas (Cuenca, Spain). *Bulletin de la Société Géologique de France* 171: 251–258.
- Poyato-Ariza FJ, Wenz S. 2004. The new pycnodontid fish genus *Turbomesodon*, and a revision of *Macromesodon* based on Lower Cretaceous new material from Las Hoyas, Cuenca, Spain. In: Arratia G, Tintori A, eds. *Mesozoic fishes 3. Systematics, palaeoenvironment and biodiversity*. München: Verlag Dr. Friedrich Pfeil, 341–378.
- Regan CT. 1923. The skeleton of *Lepidosteus*, with remarks on the origin and evolution of the lower neopterygian fishes. *Proceedings of the Zoological Society of London* 1923: 445–461.
- Rosen DE, Forey PL, Gardiner BG, Patterson C. 1981. Lungfishes, tetrapods, paleontology and plesiomorphy. *Bulletin of the American Museum of Natural History* 167: 159–276.
- Ruiz-Omeñaca JI, Canudo JI, Aurell M, Bádenas B, Barco JL, Cuenca-Bescós G, Ipas J. 2004. Estado de las investigaciones sobre los vertebrados del Jurásico superior y Cretácico Inferior de Galve (Teruel). *Estudios Geológicos* 60: 179–202.
- Ruiz-Omeñaca JL, García-Ramos JC, Piñuela L, Bardet N, Bermúdez-Rochas DD, Canudo JL, Pereda-Suberbiola X. 2006. Restos directos de vertebrados del Jurásico de Asturias. In: Fernández-Martínez E, ed. *XXII Jornadas de la Sociedad Española de Paleontología. Libro de Resúmenes*. Universidad de León, 171–173.
- Sanz JL, Barahona F, Barbadillo LJ, Buscalioni AD, Diéguez C, Evans SE, Fregenal-Martínez MA, Díaz-Romeral A, Jiménez E, López-Moron N, Madero J, Martín-Closas C, Martínez-Delclòs X, McGowan G, Meléndez N, Milner AR, Moratalla JJ, Ortega F, Pérez-Moreno BP, Poyato-Ariza FJ, Rabada D, Rasskin-Gutman D, Rodríguez-Lázaro J, Sanchiz B, Trincao P, Wenz S. 1994. Diez años de investigación en el yacimiento de Las Hoyas (Cretácico Inferior, Cuenca). In: Fernández-López S, coord. *Comunicaciones de las X Jornadas de Paleontología*. UCM/CSIC/SEP, 185–186.
- Sanz JL, Diéguez C, Fregenal-Martínez MA, Martínez-Delclòs X, Meléndez N, Poyato-Ariza FJ. 1990. El yacimiento de fósiles del Cretácico Inferior de Las Hoyas, provincia de Cuenca (España). *Comunicaciones de la Reunión de Tafonomía y Fosilización* 337–355.
- Sanz JL, Diéguez C, Fregenal-Martínez MA, Martínez-Delclòs X, Meléndez N, Poyato-Ariza FJ. 1990. El

- yacimiento de fósiles del Cretácico Inferior de Las Hoyas, provincia de Cuenca (España). In: Fernández-López S, coord. *Comunicaciones de la Reunión de Tafonomía y Fossilización*. Universidad Complutense de Madrid, 337–355.
- Sanz JL, Diéguez C, Poyato-Ariza FJ. 1999.** Il Cretacico inferiore di Las Hoyas (Spagna). In: Pinna G, ed. *Alle radici della Storia Naturale d'Europa*. Milano: European Paleontological Association/Jaca Book, 155–160 and 249–250, pl. 73–77.
- Sanz JL, Diéguez C, Poyato-Ariza FJ. 2000.** Die Unterkreide von Las Hoyas, Cuenca, Spanien. In: Pinna G, ed. *Europäische Fossilagerstätten*. Berlin: European Paleontological Association/Springer Verlag, 155–160 and 249–250, pl. 73–77.
- Sanz JL, Fregenal-Martínez MA, Meléndez N, Ortega F. 2001.** Las Hoyas. In: Briggs DEG, Crowther PR, eds. *Palaeobiology II*. Oxford: Blackwell Science, 356–359.
- Sanz JL, Wenz S, Yébenes A, Estes R, Martínez-Delclòs X, Jiménez-Fuentes E, Diéguez C, Buscalioni AD, Barbadillo LJ, Vía L. 1988.** An Early Cretaceous faunal and floral continental assemblage: Las Hoyas fossil site (Cuenca, Spain). *Geobios* **21**: 611–635.
- Sauvage HE. 1903.** Noticia sobre los peces de la caliza litográfica de la provincia de Lérida (Cataluña). *Memorias de la Real Academia de Ciencias y Artes de Barcelona*, 3ª época **4**: 467–481.
- Schaeffer B. 1967.** Osteichthyan vertebrae. *Journal of the Linnean Society, Zoology* **47**: 185–195.
- Schultze H-P, Arratia G. 1986.** Reevaluation of the caudal skeleton of actinopterygian fishes: 1. *Lepisosteus* and *Amia*. *Journal of Morphology* **190**: 215–241.
- Taverne L. 1997.** Sur la presence du genre *Calamopleurus* (= *Enneles*) (Pisces, Actinopterygii, Amiidae) dans l'ichthyofaune marine éocretacée de Guinée Équatoriale (Afrique). *Musée Royal de l'Afrique Centrale, Tervuren, Belgique, Département de Géologie et Minéralogie, Rapport Annuel 1995 & 1996*: 215–220.
- Traquair R. 1911.** Les poissons wealdiens de Bernissart. *Mémoires du Musée Royal d'Histoire naturelle de Belgique* **6**: 1–65.
- Vilas L, Mas R, García A, Arias C, Alonso A, Meléndez N, Rincón R, with the collaboration of Elizaga E, Fernández Calvo C, Gutiérrez C, Meléndez F. 1982.** Ibérica Suroccidental. In: *El Cretácico de España*. Madrid: Editorial de la Universidad Complutense, 457–513.
- Wenz S. 1968.** Note préliminaire sur la faune ichthyologique du Jurassique supérieur du Montsec (Espagne). *Bulletin de la Société Géologique de France* **7**: 116–119.
- Wenz S. 1977.** Le squelette axial et l'endosquelette caudal d'*Enneles audax*, poisson amiidé du Crétacé de Ceará (Brésil). *Bulletin du Muséum national d'Histoire naturelle Paris* **490**: 341–348.
- Wenz S. 1988.** Les Amiïdés (Pisces, Halecomorphi) du Crétacé inférieur du Montsec (province de Lérida, Espagne): *Amiopsis woodwardi* (Sauvage, 1903). *Quaderns Institut d'Estudis Ilerdencs* **1**: 1–50.
- Wenz S. 2003.** Les *Lepidotes* (Actinopterygii, Semionotiformes) du Crétacé inférieur (Barrémien) de Las Hoyas (Province de Cuenca, Espagne). *Geodiversitas* **25**: 481–499.
- Wenz S, Poyato-Ariza FJ. 1994.** Les Actinopterygiens juveniles du Crétacé inférieur du Montsec et de Las Hoyas (Espagne). *Geobios M. S.* **16**: 203–212.
- Wenz S, Poyato-Ariza FJ. 1995.** Fishes. In: Martínez-Delclòs X, ed. *Montsec and Montral-Alcover, two Konservat-Lagerstätten. Catalonia, Spain. II International Symposium Lithographic Limestones*. Lérida: Institut d'Estudis Ilerdencs, 47–53.
- Woodward AS. 1902.** On an amioid fish (*Megalurus mawsoni*, sp. n.) from the Cretaceous of Bahia, Brazil. *Annals and magazine of Natural History (ser. 7)* **9**: 87–89.