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Barremian anurans of the Iberian Peninsula: new insights into their taxonomic diversity

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Barremian anurans of the Iberian Peninsula: new insights into their taxonomic diversity

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ABSTRACT

The Barremian continental successions of the Iberian Peninsula have yielded numerous remains of anurans. Some of these finds consist of fragmentary bones whereas others furnish more complete evidence on the skeletal morphology and proportions of the represented taxa. Notwithstanding the foregoing, most of these records have been ascribed either to the relatively basal extant costatan clade or to the poorly known extinct genus *Eodiscoglossus* Villalta, 1954 based on insufficient data. Recent revisions of some of these materials have demonstrated the presence of traits presumably plesiomorphic and unknown in extant costatans, thereby casting doubts on their phylogenetic placements. Herein two specimens from the upper Barremian Las Hoyas *Konservat-lagerstätte* are thoroughly described and compared, providing evidence of additional anuran taxa in this site. One of these specimens, initially reported as cf. *Eodiscoglossus*, is referred to *Wealdenbatrachus* Fey, 1988, a genus already described in the coeval fossil site of Uña. Another specimen consisting of a partial postcranial skeleton is documented by a latex-rubber cast and a photograph; it represents a new taxon whose phylogenetic position remains uncertain due to the incompleteness of the available evidence. Comments on a third specimen that might belong to another taxon are included, although its detailed description awaits its full preparation. The overview of the Barremian taxa currently recognized from Iberia reveals the co-occurrence of taxa of different sizes, body proportions, and lifestyles, suggesting some ecological partitioning in consonance with the heterogeneous habitats represented in the yielding fossil sites.

KEY WORDS
Cretaceous,
Spain,
Anura,
Costata,
osteology,
phylogeny.

RÉSUMÉ

Anoures barrémiens de la péninsule Ibérique : nouvelles perspectives sur leur diversité taxonomique.
Les successions continentales du Barrémien de la péninsule Ibérique ont livré de nombreux restes d’anoures. Certaines de ces découvertes sont composées d’ossements fragmentaires désarticulés, tandis que d’autres documentent plus complètement la morphologie et les proportions squelettiques des taxons représentés. Néanmoins, de nombreux restes ont été attribués soit au clade Costata, soit au genre éteint peu connu *Eodiscoglossus* Villalta, 1954 sur la base de données insuffisantes. Des révisions récentes de ces fossiles ont mis en évidence la présence de traits vraisemblablement plésiomorphes et inconnus dans les membres actuels de ce clade, laissant ainsi planer un doute sur leurs positions phylogénétiques. Ici, deux spécimens de *Konservat-lagerstätte* de Las Hoyas du Barrémien supérieur ont été décrits et comparés de manière détaillée, fournissant des preuves de la présence de deux autres taxons dans ce site. L’un de ces spécimens, initialement rapporté comme cf. *Eodiscoglossus*, est attri-

bué à *Wealdenbatrachus* Fey, 1988, un genre déjà décrit dans le site contemporain d'Uña. L'autre, un squelette post-crânien incomplet, documenté uniquement par un moulage en latex-caoutchouc et une photographie, représente un taxon nouveau dont la position phylogénétique reste incertaine en raison de l'incomplétude des caractères disponibles. Des commentaires sur un troisième spécimen qui pourrait appartenir à un autre taxon sont inclus, bien que sa description détaillée requiert une préparation complète de ce spécimen. La vue d'ensemble des anoures barrémiens actuellement reconnus dans la Péninsule Ibérique met en évidence la présence de taxons de tailles, de proportions corporelles et de styles de vie différents, suggérant une certaine partition écologique en accord avec les habitats hétérogènes représentés dans les localités fossilifères.

MOTS CLÉS
Crétacé,
Espagne,
Anura,
Costata,
ostéologie,
phylogénie.

INTRODUCTION

The Lower Cretaceous continental successions of the Iberian Peninsula have yielded a significant number of well-preserved remains of plants, invertebrates, and vertebrates, particularly as a result of the intensive prospecting in recent years (e.g. Poyato-Ariza & Buscalioni 2016 and papers cited therein). Because of the complex geological history and singular paleogeographic position of Iberia in the Early Cretaceous, these finds have considerable interest as they document the biotic composition of subtropical ecosystems of that time and also shed light on the evolution of the individual lineages represented. Among the vertebrates, remains of anuran amphibians have been recovered in many Barremian fossil sites (Vergnaud-Grazzini & Wenz 1975; Fey 1988; Báez & Sanchíz 2007; Buscalioni *et al.* 2008; Báez 2013; Báez & Gomez 2016). Some of these fossil remains furnish evidence on the skeletal morphology and proportions of the represented taxa. This makes it possible not only to address their phylogenetic placements but also to gain some evidence on their body geometry that might correlate with different locomotor capabilities in extant taxa, thereby suggesting different lifestyles (e.g. Emerson 1978; Enriquez-Urzelai *et al.* 2015). Regarding the latter issue, it is interesting that in a preliminary study, Sanchíz (1991) recognized distinct statistically significant patterns of the relative proportions of the hindlimbs among a group of 12 specimens from the upper Barremian Las Hoyas *Konservat-lagerstätte*.

Many of these Early Cretaceous fossils have been referred to Discoglossidae (*sensu lato*) without an explicit discussion, usually owing to the presence of potentially plesiomorphic features retained in extant members of Costata, as discussed elsewhere (Báez & Gómez 2019).

Recent examination of available anuran materials from the upper Barremian Las Hoyas fossil site attested to the presence of articulated specimens with sets of characters that differ from those of the taxa previously described from the same beds (Báez 2013, 2016). The aim of the present study is to describe two of those specimens (MUPA-LH 00004 and 11392) thoroughly and discuss their features in the context of our present understanding of anuran phylogeny, as well as to compare them with pertinent available fossil finds. However, it should be noted that other specimens collected from the same beds but still undescribed might represent additional taxa. The diversity of the hitherto recorded anuran taxa from Las Hoyas is also reviewed, revealing different mophotypes in consonance with the paleoenvironmental complexity, and consequent habitat heterogeneity, inferred for some of the yielding sites (e.g. Buscalioni & Fregenal-Martínez 2010; Buscalioni & Poyato-Ariza 2016).

INSTITUTIONAL ABBREVIATIONS

MB. Am.	amphibian collection, Museum für Naturkunde, Berlin;
MGB	Museu de Geologia de Barcelona, Barcelona;
MNCN PV	Museo Nacional de Ciencias Naturales, Colección de Paleontología de Vertebrados, Madrid;
MUPA-LH	collection from Las Hoyas deposited in the Museo de Paleontología de Castilla-La Mancha, Cuenca (MUPA);
PIFUB	Institut für Palaontologie der Freien Universitat, Berlin.

PALEOGEOGRAPHIC AND GEOLOGICAL SETTING

The Cretaceous paleogeographic evolution of Iberia was strongly influenced by Pangea breakup with the relative plate motions of the large stable cratons of Africa and Eurasia, Central Atlantic and western Tethys openings, and North Atlantic rifting (Martín-Chivelet *et al.* 2002; Schettino & Turco 2011). During the Early Jurassic the Arctic-North Atlantic and the Tethys rift systems were tectonically active, and in the North and Central Atlantic domains marine environments started to develop (Ziegler 1988). By the Late Jurassic, the eastward propagation of the Central Atlantic Ocean was involved in the formation of an oceanic domain between the Iberian and African plates (Stampfli & Borel 2002; Schettino & Turco 2009, 2011; Vergés & Fernandez 2012), whereas in the northern margin of Iberia, Late Jurassic-Early Cretaceous extension produced the progressive opening of the Bay of Biscay. Throughout most of the Early Cretaceous time interval, the land of the Iberian microplate exposed above sea-level was part of an archipelago located at the western boundary of the Tethys Ocean between the African and European plates with a paleolatitude between 25°-30°N (Dercourt *et al.* 2000; Brikiatis 2016) within the

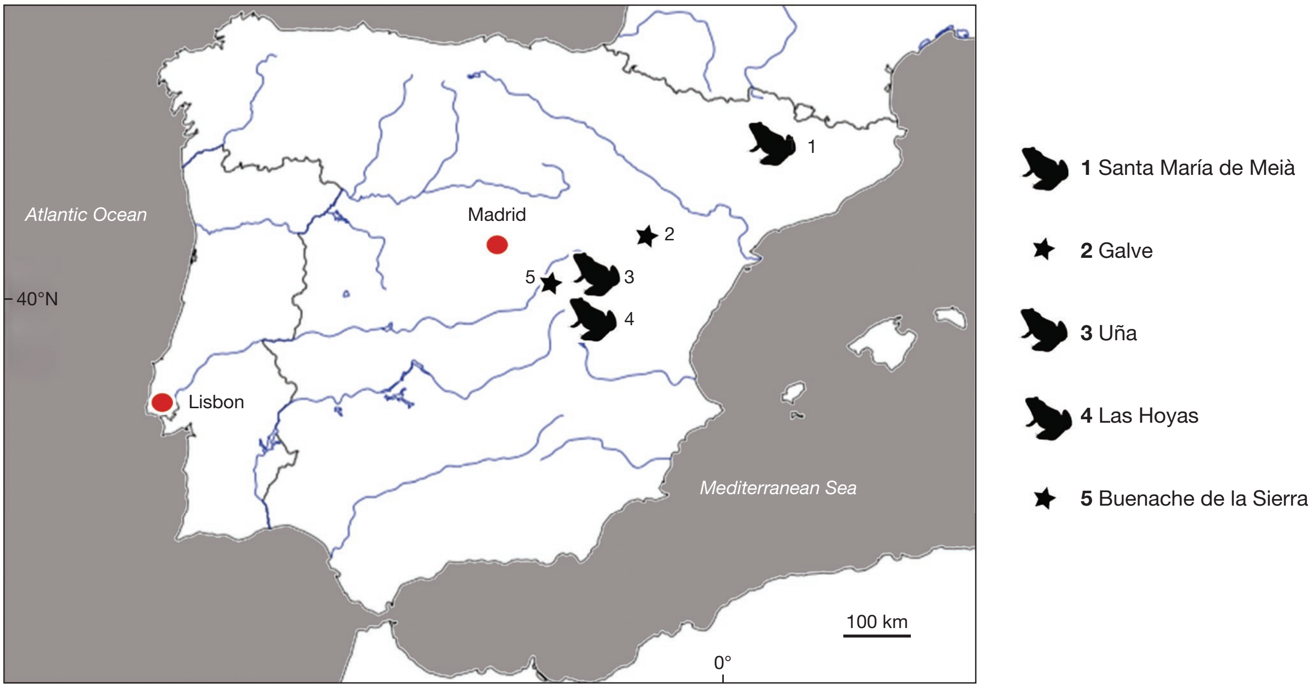

FIG. 1. — Map of the Iberian Peninsula showing the geographical location of Barremian sites from which anuran remains have been collected. Stars denote scarce, fragmentary, disarticulated bones; frog silhouettes denote more complete or articulated remains.

subtropical belt (Buscalioni *et al.* 2018 and papers cited therein). The paleoclimate has been inferred as warm with highly seasonal rainfall (Barale *et al.* 1984; Buscalioni & Fregenal-Martínez 2010; Blanco *et al.* 2018). This insular paleogeographical position has attracted the attention on the abundant and taxonomically diverse fossil remains recorded in the continental Lower Cretaceous of the Iberian Peninsula (e.g. Canudo *et al.* 2009; Buscalioni & Poyato-Ariza 2016).

The Iberian Basin (Iberian Ranges or Iberian Chain, northeastern Iberia) is one of several extensional, rift intracratonic basins formed in the Iberian Plate as a response to continental break-up. There, rifting and subsidence resulted in the formation of different depocenters that accumulated thick successions of Upper Jurassic-Lower Cretaceous continental to shallow marine sediments (Meléndez *et al.* 1994; Meléndez 1995; Martín-Chivelet *et al.* 2002). Oxfordian non-marine facies are well represented whereas those of Tithonian age occur extensively throughout the Iberian Plate (Martin-Closas *et al.* 2016).

MATERIAL AND METHODS

PROVENANCE AND PRESERVATIONAL DATA

Several of the Lower Cretaceous continental beds of Iberia have yielded anuran remains but because preservation varies among sites, comparisons and inferences about the relationships and lifestyles of the taxa represented are limited and/or not always possible. Disarticulated, fragmentary, and three-dimensionally preserved anuran bones have been recorded in several fossil sites of the Teruel province within the extensive Maestrazgo paleogeographic domain of eastern Spain, such as the material discovered in the Hauterivian-lower Barremian lacustrine deposits of the Blesa Formation (La Cantalera site, Canudo *et al.* 2010). Likewise, disarticulated anuran bones have been described from outcrops of the coeval El Castellar Formation in a marginal depocenter, Galve (Fig. 1), within the same domain (Yacimiento Herrero and Colladico Blanco sites, Estes & Sanchíz 1982). In the Southwestern paleogeographic domain, isolated, partial anuran bones occur in outcrops of the upper Barremian Tragacete Formation in the Buenache de la Sierra small depocenter (Fig. 1) within the Serranía de Cuenca Basin (El Inglés Quarry, Buscalioni *et al.* 2008, 2018).

By contrast, other Lower Cretaceous sites have yielded anuran specimens that, although two-dimensionally preserved, are articulated or partially articulated, thus generally providing evidence on their general skeletal morphology and proportions. Such is the type of preservation for *Neusibatrachus wilferti* Seiffert, 1972 (Seiffert 1972; Báez & Sanchíz 2007) and *Eodiscoglossus santonjae* Villalta, 1954 (Villalta 1954; Hecht 1970; Báez & Gómez 2016) recorded in the lower Barremian lacustrine limestones of the La Pedrera de Rúbies Formation, in a complex basin that developed in the northern fringe of the Iberian Plate (Santa Maria de Meià, El Montsec, Lleida province; Fig. 1). Several partially articulated specimens, including adult and metamorphosing individuals, have been discovered in this locality but their taxonomic assignment by Vergnaud-Grazzini & Wenz (1975) to *Eodiscoglossus santonjae* requires careful re-assessment (Báez & Gómez 2016). Farther south, in the Serranía de Cuenca Basin, outcrops of the upper Barremian La Huérguina Formation in a small depocenter near the city of Cuenca, Cuenca province, contain the world-wide famous Konservat-lagerstätte of Las Hoyas (Fig. 1) that has yielded

Table 1. — Barremian anuran taxa from the Iberian Peninsula represented by articulated specimens.

Taxon	Holotype	Type locality	Horizon and age	SVL (mm)
Eodiscoglossus santonjae Villalta, 1954	MNCN PV-4723	La Pedrera de Rúbies, Santa Maria de Meià (El Montsec), Lleida province, Spain	La Pedrera de Rúbies Lithographic Limestones Fm, early Barremian	27.5
Neusibatrachus wilferti Seiffert, 1972	MB.Am.1469 a, b (formerly PIFUB 33 a, b)	La Pedrera de Rúbies, Santa Maria de Meià (El Montsec), Lleida province, Spain	La Pedrera de Rúbies Lithographic Limestones Fm, early Barremian	21.0
Gracilibatrachus avallei Báez, 2013	MUPA-LH 21171 a, b	Las Hoyas fossil site, Cuenca province, Spain	La Huérguina Formation, late Barremian	20.5
Iberobatrachus angelae Báez, 2013	MUPA-LH 11393 a, b	Las Hoyas fossil site, Cuenca province, Spain	La Huérguina Formation, late Barremian	40.0
Wealdenbatrachus jucarensis Fey, 1988	PIFUB 101/U70V	Jucar River valley, near the village of Uña, Cuenca province, Spain	La Huérguina Formation, late Barremian	50.0
New taxon	MUPA-LH 11392	Las Hoyas fossil site, Cuenca province, Spain	La Huérguina Formation, late Barremian	*c.* 42.0

exceptionally well-preserved ichno-fossils and body fossils (Buscalioni & Poyato-Ariza 2016 and papers cited therein). Anurans recovered from the rithmically laminated limestones are mostly preserved two-dimensionally, as articulated, partial or complete skeletons of adults and tadpoles (e.g. MUPA-LH 29669, a tadpole, pers. obs.). Many specimens include impressions of some soft-tissue structures (e.g. Báez 2013). Although rare, articulated three-dimensionally preserved anuran skeletons have also been recovered from these beds (e.g. MUPA-LH 5429, Báez 2016: pl. 1E-F). The anuran taxa *Gracilibatrachus avallei* Báez, 2013 and *Iberobatrachus angelae* Báez, 2013 (Báez 2013) are based on specimens from Las Hoyas as are the three specimens that document additional taxa described herein. Coal-rich limestones of the same stratigraphic unit near the village of Uña, Cuenca province (Fig. 1), contain partially articulated or associated remains of single adult individuals that are three-dimensionally preserved and belong to *Wealdenbatrachus jucarensis* Fey, 1988 (Fey 1988; Báez & Gómez 2019).

Data on the holotypes of all the currently recognized Barremian species from Iberia represented by articulated specimens are presented in Table 1. Not included in that table is *Monsechobatrachus gaudry* (Vidal, 1902) Fejérváry, 1921. That species is based on a poorly preserved natural cast from the lower Barremian locality Santa Maria de Meià (El Montsec), Lleida province, and was considered a *nomina vana* by Sanchíz (1998). The type specimen (MGB 541) belongs to a froglet whose snout-vent length is about 24 mm; the presence of paired frontoparietals (Roček 2000; pers. obs.) forming the boundaries of an anterior fontanelle makes its identification as a palaeobatrachid, a taxonomic placement that was considered possible by Estes & Reig (1973), unlikely.

Anatomical nomenclature and phylogenetic framework

I follow Bolkay (1919), Trueb (1973), and Roček (1994, 2003) in using general anatomical terminology. Terminology concerning the pelvic girdle follows Gómez & Turazzini (2015) and that for manus and pes follows Fabrezi & Alberch (1996), unless stated otherwise. The taxonomy of extant forms at family, genus, and species levels is that of Frost (2019). Names of larger anuran clades such as Costata and Lalagobatrachia are those of Frost *et al.* (2006), whereas Pipanura is applied *sensu* Ford & Cannatella (1993) as a node-based name to include the most recent ancestor of xenoanurans (i.e., pipoids: Rhinophrynidae + Pipidae) and acosmanurans (anomocoelans + neobatrachians) and all its descendants. The stem-based name Pipimorpha is applied to those xenoanuran taxa that are closer to extant Pipidae than to extant Rhinophrynidae including crown-group Pipidae, as defined by Ford & Cannatella (1993) and used subsequently by other authors (e.g. Jones *et al.* 2003; Báez 2013; Gardner & Rage 2016). The phylogenetic framework is provided by recent hypotheses of relationships based on molecular data for extant lineages (e.g. Blackburn *et al.* 2010; Pyron & Wiens 2011; Biton *et al.* 2013) or on morphology for extant and extinct taxa (e.g. Báez 2013; Dong *et al.* 2013; Gómez 2016; Gao & Chen 2017). Descriptions and illustrations were made with the aid of a Nikon binocular SMZ 10 with an attached camera lucida.

SYSTEMATIC PALEONTOLOGY

Order ANURA Fischer von Waldheim, 1813

Genus **Wealdenbatrachus** Fey, 1988

Type species. — *Wealdenbatrachus jucarensis* Fey, 1988.

Type locality, stratigraphic horizon, and age. — Uña, Cuenca province, Spain; La Huérguina Formation; late Barremian.

Wealdenbatrachus sp.

Material. — MUPA-LH 00004. This incomplete specimen consists mainly of an impression of an adult individual in ventral aspect with an estimated 42 mm snout-vent length (SVL: direct line distance from tip of snout to posterior limit of ischia) and preserved two-dimensionally (Fig. 2A, B). Photographs of this specimen under incandescent light (Fig. 2A) and with exposure to UV radiation (Fig. 2B) were also available for study.

Locality, horizon, and age. — Las Hoyas fossil site, 30 km from the city of Cuenca, Cuenca province, Spain; La Huérguina Formation; late Barremian.

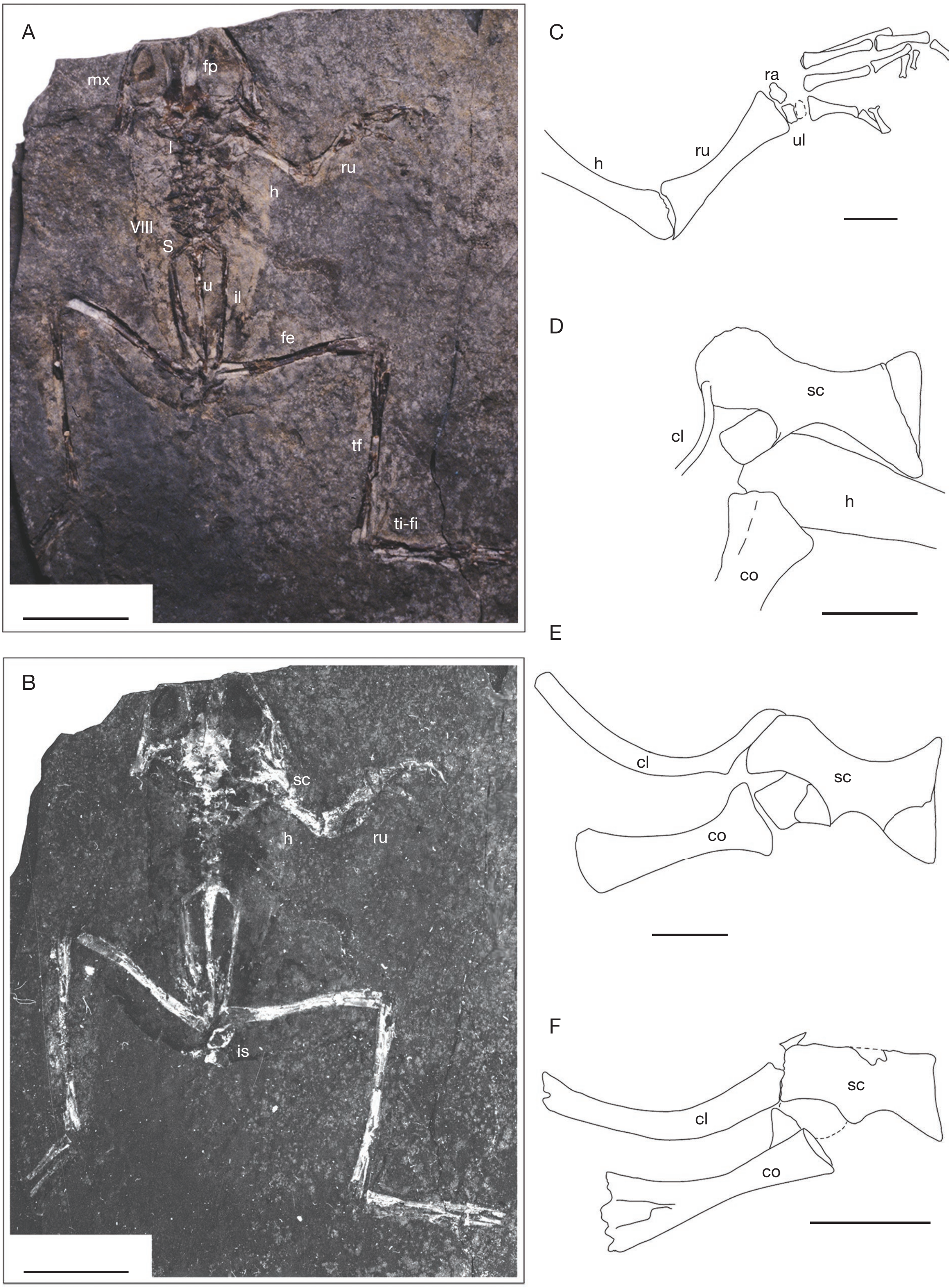

Fig. 2. — *Wealdenbatrachus* Fey, 1988 sp. (MUPA-LH 00004, individual exposed in ventral view): **A**, general view (photograph under incandescent light); **B**, general view (photograph under UV light); **C**, interpretive drawing of left anterior limb; **D**, interpretive drawing of part of left pectoral girdle in ventral view; **E**, *Wealdenbatrachus jucarensis* Fey, 1988 from Uña, restoration of part of the pectoral girdle in ventral view (redrawn from Báez & Gómez 2019); **F**, MUPA-LH 05429, interpretive drawing of part of the right side of pectoral girdle in ventral view, reversed for comparison. Abbreviations: **cl**, clavicle; **co**, coracoid; **fe**, femur; **fp**, frontoparietal; **h**, humerus; **il**, ilium; **is**, ischion; **mc**, metacarpal; **mx**, maxilla; **ra**, radiale; **ru**, radioulna; **s**, sacrum; **sc**, scapula; **tf**, tibiofibular; **ti-fi**, tibiale-fibulare; **u**, urostyle; **ul**, ulnare; **I-VIII**, presacral vertebrae I-VIII. Scale bars: A, B, 10 mm; C-F, 2 mm.

REMARKS

The skeleton is almost wholly articulated but the anterior portion of the skull, the left forelimb and corresponding half of the pectoral girdle, and the distal portions of the autopodium of both hindlimbs are missing. A photograph of this specimen was included in a brief note on the amphibians from the Las Hoyas fossil site (Evans *et al.* 1995: fig. IV-18, labelled as LH 79900). Previously the specimen was considered referable to the genus *Eodiscoglossus* (Evans *et al.* 1995) but assigned to the genus *Eodiscoglossus* with doubts and depicted as a line drawing by Roček (2000: fig. 9, labelled as LH 004-R and erroneously scaled). It was also commented on as cf. *Eodiscoglossus* sp. indicating uncertainty with regard to its generic allocation and depicted partially by Báez (2016: fig. 5, labelled as MUPA-LH 00004). However, herein some of its features are reinterpreted, differing from previous opinions. Examination of the actual specimen and the photographs led to the description below, in which left and right refer to the actual skeletal orientation.

DESCRIPTION

The paired frontoparietals form the boundaries of an anterior pear-shaped fontanelle; posterior to this fontanelle, these bones are medially in contact to one another. The laterally expanded anterior portions of the frontoparietals make the skull roof wider anteriorly than posteriorly. At the level of the posterior margin of the orbits each frontoparietal widens laterally, so it slightly overlapped the medial part of the corresponding otic capsule. A low *pars contacta* that in life was in contact with the lateral walls of the sphenethmoid is clearly discernable. In the parietal region a rounded scar together with a poorly preserved, similar contralateral scar form a structure with an overall oval outline; this structure is identified as the posterior part of the *incrassatio frontoparietalis*. The photograph under UV light (Fig. 2B) reveals a portion of a laminar bone slightly shifted to the left that extends anteriorly as well as laterally to invest the ventral surface of the braincase and the medial region of the otic capsules. This is identified as part of the cultriform process and corpus of the parasphenoid slightly shifted to the left side.

The maxillary arches were complete; they included the missing premaxillae, dentate maxillae, and quadratojugals; on the right side, the last bone is discernable showing that it was relatively long. The three-radiated pterygoids are preserved on both sides of the skull; the anterior ramus articulates with the maxilla at mid-orbit length, whereas the long ventral ramus contacts the *pars articularis* of the quadrate. On the right side, the ossified *pars media plectri* of the middle ear is preserved close to the corresponding otic capsule (Fig. 2B). It has a slender style, distally, and an expanded footplate that was applied to the oval foramen.

The vertebral column is composed of eight presacral vertebrae, the sacrum, and the urostyle (Fig. 2A, B). The anteroventral margin of the atlas is moderately convex and projects laterally on both sides suggesting the presence of elongated cotyles located ventral to the neural canal; this vertebra lacks transverse processes. The vertebral bodies are poorly preserved although they appear to be longer than wide and slightly waisted at midlength. The type of articulation between successive vertebrae is not discernable. Vertebrae II, III, and IV have well-developed transverse processes associated with stout ribs. The shortest of these ribs are those associated with vertebra II, which are flared posteriorly. Distinct swellings mark the contact between the expanded distal end of the transverse processes and proximal epiphysis of the ribs. The distal epiphyses of the ribs are also expanded. In contrast, the posterior four presacrals have more delicate, shorter transverse processes; these processes are nearly laterally oriented on vertebrae V and VI and moderately anteriorly directed on the last two vertebrae (VII and VIII). The sacrum bears narrow and posterolaterally directed sacral diapophyses that are only slightly expanded distally. The articulation between sacrum and urostyle is seemingly bicondylar. The urostyle is proportionally long, being longer than the length of the presacral column (Fig. 2A, B). At the anterior end of the urostyle there are indications of a relatively wide coccygeal portion, although transverse processes are not clearly discernable.

Elements of the left anterior limb and pectoral girdle are evident (Fig. 2C, D). The scapula is medium-sized, waisted at its midlength, and thus probably devoid of a well-developed anterior crest (Fig. 2D). The partial impression of the clavicle indicates that it was an arched bone, suggesting an arciferal type of girdle; it is not preserved in its natural position probably owing to its partial disarticulation from the scapula. The coracoid of the same side is also disarticulated; its proximal head is expanded, whereas the rest of the bone is directed posteromedially and its impression disappears near the vertebral column. The left humerus and radioulna are clearly discernable (Fig. 2C). The carpus is incompletely preserved but some carpal elements can be discerned distal to the radioulna; in the proximal row two trapezoidal elements, radiale and ulnare, are evident. Impressions of the four metacarpals are clear although metacarpal V is partially hidden behind metacarpal IV; the longest is metacarpal IV and the shortest is metacarpal II which has a distinctly wide proximal end. The phalangeal formula is 223?. The discernible distal phalanges are distinctly long and narrow; their tips have a bilobed shape owing to the presence of a median groove (Báez 2016: fig. 5B) (Fig. 2C).

The pelvic girdle includes long ilia, the shafts of which bear well-developed dorsal crests along their lengths. The acetabular regions of these bones are not exposed. The displaced right ischium is exposed laterally near their proximal ends; this displacement indicates that ilium and ischium were not fused to one another. The femur, preserved on both sides, is distinctly sigmoid and its length is greater than that of the tibiofibula (tibiofibula to femur ratio about 1.24). The tibiale and fibulare are in contact with each other at both ends, leaving a long and narrow intertarsal space; the length of this segment of the limb is about 60% that of the zeugopodium. Only the proximal portions of four metatarsals in the left hindlimb are clearly preserved.

Assignment of MUPA-LH 00004 to Wealdenbatrachus

Restudy of the original material of the late Barremian *Wealdenbatrachus jucarensis* Fey (Báez & Gómez 2019) led to the careful assessment of several features, some of them probably derived, in MUPA-LH 00004 that might be shared with that species and, hence, justify assignment to the same genus. This comparison strongly suggests that the genus *Wealdenbatrachus* Fey, 1988 previously known from Uña (Fey 1988) is represented in the coeval site of Las Hoyas, geographically near but with different depositional and taphonomic conditions (Gomez *et al.* 2001), confirming the previous opinion of Sanchíz (1998). In particular, the paired frontoparietals of MUPA-LH 00004 form the boundaries of a distinctly long, pear-shaped fontanelle as in *W. jucarensis* and not a short, V-shaped dorsal opening as it was depicted previously by Báez (2016). As in the species from Uña, the dorsal skull table is wider anteriorly than posteriorly (Fig. 2A, B) and each frontoparietal bears a distinct narrow pars contacta, whereas these bones are not fused to the sphenethmoid. Also, each frontoparietal extends posterolaterally to overlap a narrow strip of the medial region of the corresponding otic capsule. Most other known features of this specimen from Las Hoyas match those of the original material of *W. jucarensis*, redescribed and depicted in the revision of Báez & Gómez (2019). As in the latter species, vertebrae II to IV bear transverse processes that are associated with robust ribs, particularly those associated with presacral III. The posterior vertebrae have transverse processes whose degree of development and orientation resemble those of *W. jucarensis*; thus, vertebrae V, VI bear transverse processes that are nearly perpendicular to the vertebral column axis whereas the last two presacrals (VII,VIII) have distally blunt, anterolaterally directed transverse processes, although somewhat more anteriorly directed than in *W. jucarensis*. Transverse processes on the last two presacrals are curved anteriorly in the holotype of *Eodiscoglossus santonjae* (Báez & Gómez 2016). In all these taxa the sacral vertebra has relatively narrow diapophyses that are posterolaterally directed (Fig. 2A, B). As in *W. jucarensis*, the scapula is of moderate size and has a distinctly concave anterior margin that suggests that the well-developed anterior lamina that occurs in the short and wide scapula of crown costatans is absent (Fig. 2D, E). By contrast, in *E. santonjae* the scapulae appear to have straight anterior margins (Báez & Gómez 2016). A distinct dorsal crest on the iliac shafts occurs in MUPA-LH 00004 and also in *W. jucarensis*, whereas in *E. santonjae* this crest appears to have been less developed. The relative proportions of the hindlimb segments show some resemblance to those of *W. jucarensis* in having the femur shorter than the tibiofibula, unlike the hindlimbs of *E. santonjae*, in which these bones are nearly of the same length (Estes & Reig 1973; Báez & Gómez 2016). Also, the tibiale and fibulare are rather elongate and slender. Although forelimb autopodial bones of *W. jucarensis* are hitherto unknown, it is interesting to mention that the metacarpals and digits in MUPA-LH 00004 are thin (Fig. 1C) unlike the more robust elements of most extant costatans and the Barremian basal crown anuran *Liaobatrachus* from the Jehol Group of China (Dong *et al.* 2013). Although the tips of the distal phalanges of the manual digits in “archaeobatrachians” (i.e., non-neobatrachians) have been described as “simple” (Cannatella 1985), examination of several specimens of extant costatans revealed bilobate or grooved ends in *Discoglossus jeanneae* (MNCN 41059, male, pers. obs.). A similar morphology was noted in *Discoglossus sardus* by Pugener & Maglia (1997) and described as lacking a groove but bifurcated by Kamermans & Vences (2009). The variation and insufficient knowledge on the condition of the tips of the distal phalanges in “archaeobatrachian” anurans prevent me to consider it for justifying taxonomic separation.

Comparison between MUPA-LH 00004 and LH 05429 from Las Hoyas

The specimen MUPA-LH 00004 was previously compared with the specimen MUPA-LH 05429 also from Las Hoyas by Báez (2016). The latter specimen consists of the partial, articulated, three-dimensionally preserved skeleton of an adult individual exposed in ventral view and it has been only partially prepared (Báez 2016; pls 1E, F). It should be noted that several parts of this skeleton are still hidden beneath sediment and remain unknown (e.g. anterior palatal region, posterior portions of pelvic girdle and urostyle, femurs, tibiofibulae); therefore, a detailed description, comparisons, and discussion on its taxonomic placement will be presented elsewhere when fully exposed. Despite the evident presence of some features widespread in basal anurans (e.g. eight presacral vertebrae, adults with free ribs associated with vertebrae II-IV), MUPA-LH 00004 and LH 05429 differ from each other in many discernable characters indicating that they represent different taxa, probably different genera. The pterygoid of the latter specimen bears a broad, anteromedially directed flange between the anterior and medial rami of the pterygoid, unlike the same bone in *Wealdenbatrachus jucarensis* and MUPA-LH 00004. The flange in MUPA-LH 05429 recalls the well-developed orbital flange that extends from the anterior to the medial ramus of the pterygoid described in the extant Asian bombinatorid costatan *Bombina microdeladigitora* Liu, Hu & Yang, 1960 and apparently is unknown in other anuran species (Clarke 1988, 2007). In MUPA-LH 00004 the scapula is relatively dorsoventrally long and its shaft is distinctly waisted, indicating the lack of a well-developed anterior crest as in the scapula of *W. jucarensis* (Fig. 2D, E). The scapular morphology clearly differs from that in MUPA-LH 05429, in which this bone is relatively shorter and has a straight leading margin despite being slightly broken off (Fig. 2F). It is also worth mentioning that the mesopodium is partially preserved in LH 05429 (Fig. 3) with some of the bones hidden beneath sediment; this skeletal part is unknown in *W. jucarensis* and poorly preserved in MUPA-LH 00004. In MUPA- LH 05429, three nodular proximal mesopodial elements (including a separate small bone between articular facets of a large radiale and a somewhat smaller ulnare) are clearly present (Fig. 3). Distal to these elements it is possible to identify a large distal carpal 5 on the postaxial side and close to Element Y. The distal carpal 4 is preserved distally between the bases of metacarpals IV and III. The preserved mesopodium also includes a prepollex carpal in contact with

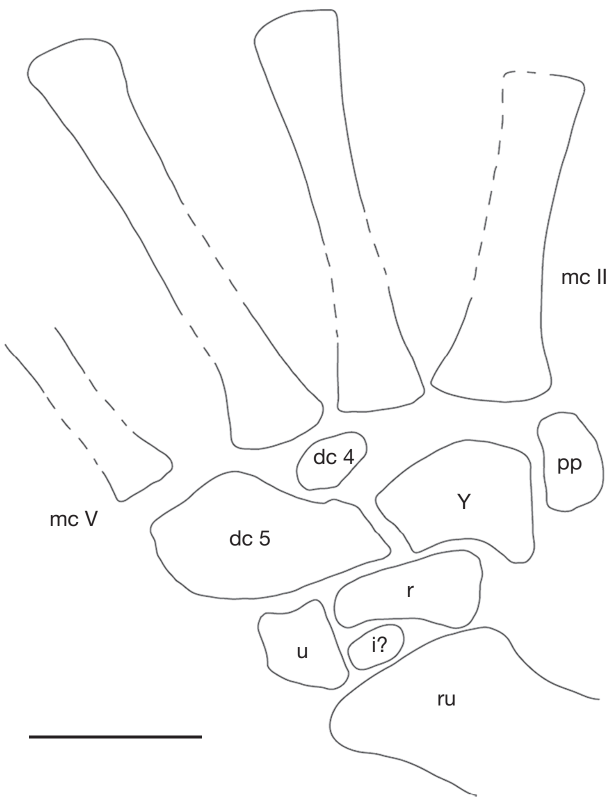

Fig. 3. — Anura indet. MUPA-LH 05429. Line-drawing of right hand. Abbreviations: **dc**, distal carpal; **i?**, intermedium?; **mc**, metacarpal; **pp**, prepollex; **r**, radiale; **ru**, radioulna; **u**, ulnare ; **Y**, element Y. Scale bar: 1 mm.

and lateral to Element Y (Fig. 3). Although the metacarpals are partially discernable it is possible to ascertain that they are not relatively long. The presence of a separate small bone in the proximal row of the autopodium was described and identified as the intermedium in the Middle Jurassic *Notobatrachus* Reig, 1956 "1955" (Estes & Reig 1973) and in the early salientian *Triadobatrachus* Kuhn, 1962 (Ascarrunz *et al.* 2016). Because developmental data is lacking in these extinct salientians, it is not possible to determine whether this additional bone originates from the ulna or from the ulnare and hence to compare its development with the intermedium of other tetrapods, including salamanders. The impression of this median proximal carpal element is not present in the holotype of *Eodiscoglossus santonjae* (Báez & Gómez 2016) nor it occurs in the well-preserved but isolated forelimb from the type locality of *E. santonjae* (Vergnaud-Grazzini & Wenz 1975: fig. 5). Even if it has a different origin from that of the intermedium of salamanders, its presence as a distinct free proximal carpal has not been recorded in extant anurans (Fabrezi *et al.* 2017).

NEW GENUS AND SPECIES?

Material

MUPA-LH 11392. This specimen is represented by the latex-rubber cast of a partial skeleton exposed in dorsal view preserved in one slab (Fig. 4A-C), lacking the skull and probably the anterior two vertebrae, as well as by a photograph of possible counterpart which was obtained by the scanning of a slide (Fig. 5C).

Locality, horizon, and age

Las Hoyas fossil site, 30 km from the city of Cuenca, Cuenca province, Spain. La Huérguina Formation, late Barremian.

Remarks

The latex cast (deposited in the Museo de Paleontología de Castilla- La Mancha) and photograph (Repositorio fotográfico de Las Hoyas LHSa-001, MUPA-LH 11392,

Museo de Paleontología de Castilla-La Mancha) document the existence of an actual single specimen probably preserved as part and counterpart because of their incongruent positive and negative reliefs, but whose whereabouts are unknown at present. According to the *International Code of Zoological Nomenclature*, recommendation 73.1.4 designation of the illustration of a single specimen as a holotype is to be treated as designation of the specimen illustrated; the fact that the specimen no longer exist or cannot be traced does not of itself invalidate the designation. However, because of the insufficient anatomical data coupling with the impossibility of examining the actual specimen, I refrain from formally recognizing a new taxon herein. This specimen possesses a distinctive set of features that set it aside from other recognized taxa, as discussed below, and probably represents a new taxon.

The specimen MUPA-LH 11392, now seemingly lost but from which a latex cast was prepared in the early 1990s (Fig. 4A-C), consisted of the impressions and scraps of bone of one adult individual preserving the six most posterior presacral vertebrae, sacrum, urostyle, pelvis, most of the right forelimb and scapula, and right hindlimb lacking the distal portion. Photograph and interpretive drawing of this cast, labelled as H-5 of the private Diaz-Romeral collection, appeared in a brief preliminary summary on the first fossil anurans discovered from Las Hoyas fossil site presented during a conference in Cuenca (Sanchíz 1991). A photograph of a slide showing the same individual H-5, but that it seems to belong to a counterpart (also lost) is available for study (Fig. 5C). Subsequently, this specimen was mentioned as LH 11392 (Evans *et al.* 1995). It is evident that the lost fossil has a distinctive combination of features that differs from those of other known specimens not only from the same beds but also from other Barremian sites, indicating that it likely pertains to an additional taxon among the anurans of Las Hoyas as suggested previously (Evans *et al.* 1995). However, the specimen(s) remained undescribed to date.

Description

Examination of both the photograph (Fig. 5C) and the latex cast of the putative counterpart (MUPA-LH 11392; Fig. 4A-C) revealed the features described below.

The neural arch laminae of the four most anterior preserved vertebrae are longer than wide, distinctly dorsally protuberant at the level of the postzygapophyses, and fully imbricated so that the spinal cord was completely concealed between

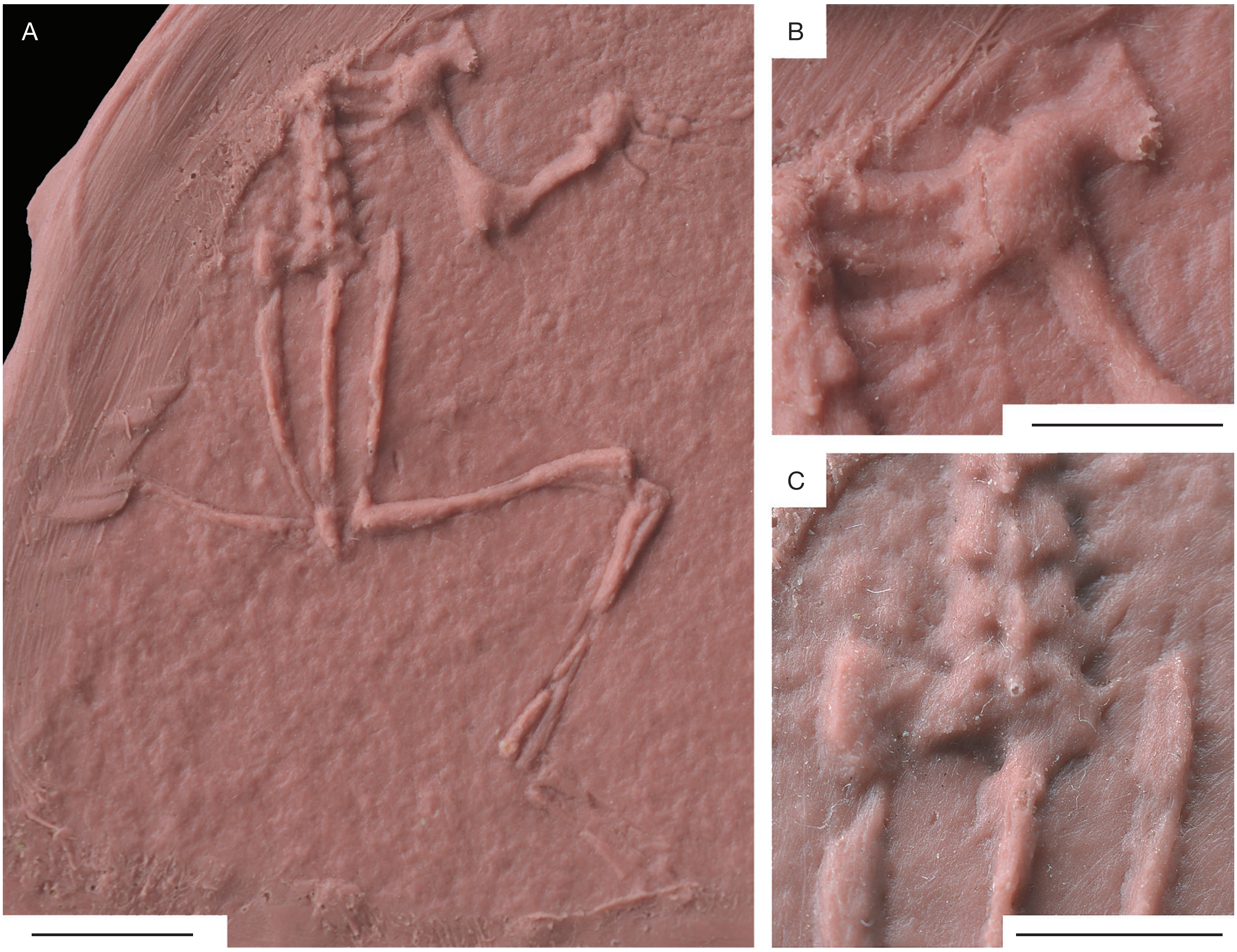

Fig. 4. — Anura indet.? New genus and species from Las Hoyas, Spain (MUPA-LH 11392): **A**, latex-rubber cast showing a general view of the specimen in dorsal view; **B**, close-up of partial pectoral girdle in dorsal view (cast); **C**, close-up of sacral region in dorsal view (cast). Note acuminate, fine transverse process on anterior part of urostyle. Scale bars: A, 10 mm; B, C, 5 mm.

successive vertebrae. On these vertebrae large neural spines project from the neural arches, each overlapping the posteriorly adjacent vertebra; the tips of these spines are missing or remained cartilaginous and thus are not preserved (Fig. 5A). By contrast, the neural arches of the last two presacral vertebrae are slightly wider than long and somewhat flatter than those of the more anterior vertebrae. These vertebrae are less imbricate, with posterior margins excavated to the left and right of the small spinous processes where the neural canal might have been slightly exposed dorsally. The two most anteriorly preserved vertebrae are associated with long processes indicating that these are probably vertebrae III and IV; these processes are delicate, sigmoid, slightly posteriorly directed, and distally expanded according to the photograph (Fig. 5B, C). The presence of a distinct swelling in the process borne by vertebra III might be an indication that this element consists of a relatively long rib articulated to a proximal short transverse process; this is not so clearly obvious in the processes of vertebra IV suggesting a more complete ankylosis of these parts, if present. Both pairs of processes are of nearly the same length and reach as far laterally as the sacral diapophyses. The transverse processes of the four following vertebrae (presumably vertebrae V-VIII) are short and nearly of the same length. Those of vertebra V are laterally oriented; instead, the fine, distally acuminating processes of the last three presacral vertebrae (VI-VIII) are oriented at an acute angle with respect to the longitudinal axis of the column, especially those of the two most posterior vertebrae (Figs 4A; 5B, C). Mid-dorsal ridges on the neural arches of the vertebrae V-VII are clearly discernable in the latex cast (Fig. 4A, C).

The sacral vertebra (presumably vertebra IX) bears moderately distally expanded, dorsoventrally flat sacral diapophyses with slightly convex lateral margins. These diapophyses are represented by their impressions and fragments (Fig. 5C). These diapophyses are anteriorly and posteriorly symmetrically developed with respect to the line of maximum width perpendicular to the sagittal plane of the column. Although fusion of the sacral vertebra with the urostyle can be ruled out based on the slightly more dorsal portion of the sacral laminae with respect to the coccygeal region of the urostyle, poor preservation of this area prevents unambiguous determination of the nature of the sacrourostylar articulation. The urostyle is slightly rotated to the right; examination of the cast shows a broad portion resembling a neural arch with a fine, acuminate, lateroposteriorly directed transverse process on the anterior part of the urostyle (Fig. 4C). A low ridge extends on the dorsal surface of the urostyle along its anterior half. According to the length of the preserved portion of the vertebral column, the urostyle was somewhat longer than the presacral column.

Elements of the right half of the pectoral girdle in dorsal view are discernible (Figs 4A, B; 5A, D). The scapula is medium-sized; the leading edge of the bone is concave, thus lacking a well-developed anterior crest, and the shaft is markedly waisted (Fig. 4B). Proximally (ventrally) a notch between the *partes acromialis* and *glenoidalis* is not clearly discernable whereas the anteromedial corner of the bone is damaged. The clavicle is not well exposed owing to the overlapping transverse process of vertebra III; a poorly preserved, acuminate piece of bone lying anterior to the scapula is barely discernable in the photograph (Fig. 5C); this piece of bone might be the proximal portion of the clavicle. The coracoid is partially obscured by the transverse process of vertebra V. The photograph clearly shows a triangular laminar element lying on the articulation of the right humerus and radioulna (Fig. 5C); this element might be the displaced cleithrum of this side. The leading margin of this element is straight, forming a right angle with the margin that probably extended along the entire scapula-suprascapular cartilage articulation. The proximal and distal ends of the humerus are hidden by the overlying scapula and cleithrum respectively. Likewise, the proximal end of the radioulna is obscured by the putative isolated cleithrum but a clear distinction between the radial and ulnar components appears evident along most of the bone length. In the cast, the silhouettes of at least three metacarpals are discernable distal to unidentifiable carpal elements hidden beneath a rounded mass. Their proximal ends are partially overlapped by the latter mass, but it is evident that they are not particularly long and have slightly expanded distal ends (Fig. 4A). The proximal two phalanges of digits V, IV, and III are also discernable in the cast; they are robust and expanded at both ends. Other phalanges are barely evident.

The ilia have distinctly long shafts (Fig. 5C, D). The presence of dorsal crests is difficult to assess; these structures appear to be present along the posterior half of the shafts although they were partially scraped off as shown in the latex cast. These bones are not well exposed in lateral aspect and, consequently, it is not possible to describe the acetabular region. Impressions of the ischia in situ are barely discernable.

The femur is sigmoid (Fig. 4A), whereas a proximal femoral crest is not clearly evident. The tibiofibula is also entirely preserved; its length is slightly greater than that of the femur (tibiofibula to femur ratio of about 1.109); deep grooves occur along its anterior and posterior portions revealing its dual nature. The tibiale and fibulare are in contact with one another at both ends, leaving an oval intertarsal space; the length of this hindlimb segment represents about 50% of that of the tibiofibula. The compound structure is slightly wider distally than it is proximally.

Impression of the body outline is evident in the photograph (Fig. 5C), suggesting that MUPA-LH 11392 was an individual with highly muscular hindlimbs. Whitish masses surrounding yellowish corpuscles fill most of the body cavity; they might be interpreted as eggs, if so, the specimen belongs to an adult female.

Comparative osteology

Firstly, it is evident that this specimen belongs to a different taxon than the one represented by the specimen MUPA-LH 00004 described above or LH 05429. In particular, the sacral diapophyses are expanded distally and are anteriorly and posteriorly symmetrically developed, thus being strikingly different from the posteriorly directed, narrow diapophyses of these other specimens. Also, the three most posterior presacrals bear transverse processes that are long, acuminate, and markedly anteriorly directed in contrast to the blunt processes of vertebrae VII and VIII of MUPA-LH 00004 and the nearly laterally directed processes borne by vertebrae VI-VIII of MUPA-LH 05429. In MUPA-LH 11392 and LH 00004 the femur is shorter than the tibiofibula, although their respective lengths are more similar to one another in the former specimen.

The relatively short length of the metacarpals and the relatively long and anteriorly concave scapular blade clearly indicate that MUPA-LH 11392 is not a pipimorph xenoanuran; in particular, the proportions of the neural arches and the distally expanded sacral diapophyses are unlike those of *Gracilisuchus* Báez, 2013, a member of this lineage described from Las Hoyas (Báez 2013). Also, MUPA-LH 11392 clearly differs from the lalagobatrachian *Iberobatrachus* Báez, 2013 from the same beds (Báez 2013) in having more widely expanded sacral diapophyses, longer ribs/transverse processes, anteriorly directed transverse processes on the last three presacrals instead of only the last two, longer anteriorly concave scapular blade, and, probably, triangular, not distally bifurcated, cleithrum. Additionally, it has delicate posterolaterally directed transverse processes on the urostyle (or borne by a postsacral neural arch) instead of the prominent, posteriorly directed postsacral transverse processes that occur in *Iberobatrachus*.

Difference in preservation precludes detailed comparisons of MUPA-LH 11392 with the type species of *Wealdenbatrachus* from Uña; however, it is clear that *W. jucarensis* has posteriorly deflected, narrow sacral diapophyses thus differing from the distally expanded, transversally oriented sacral diapophyses of MUPA-LH 11392. Also, in *W. jucarensis* the ribs borne by vertebrae III and IV are only moderately longer than the transverse processes to which they are articulated and are robust and not sigmoid in shape, unlike those of MUPA-LH 11392. In addition, the posterior presacral vertebrae of *W. jucarensis* bear transverse processes that are slightly anteriorly directed and, thus, differ from the more markedly anteriorly directed, acuminate processes of MUPA-LH 11392. The scapula of MUPA-LH 11392 resembles that of *W. jucarensis* in having

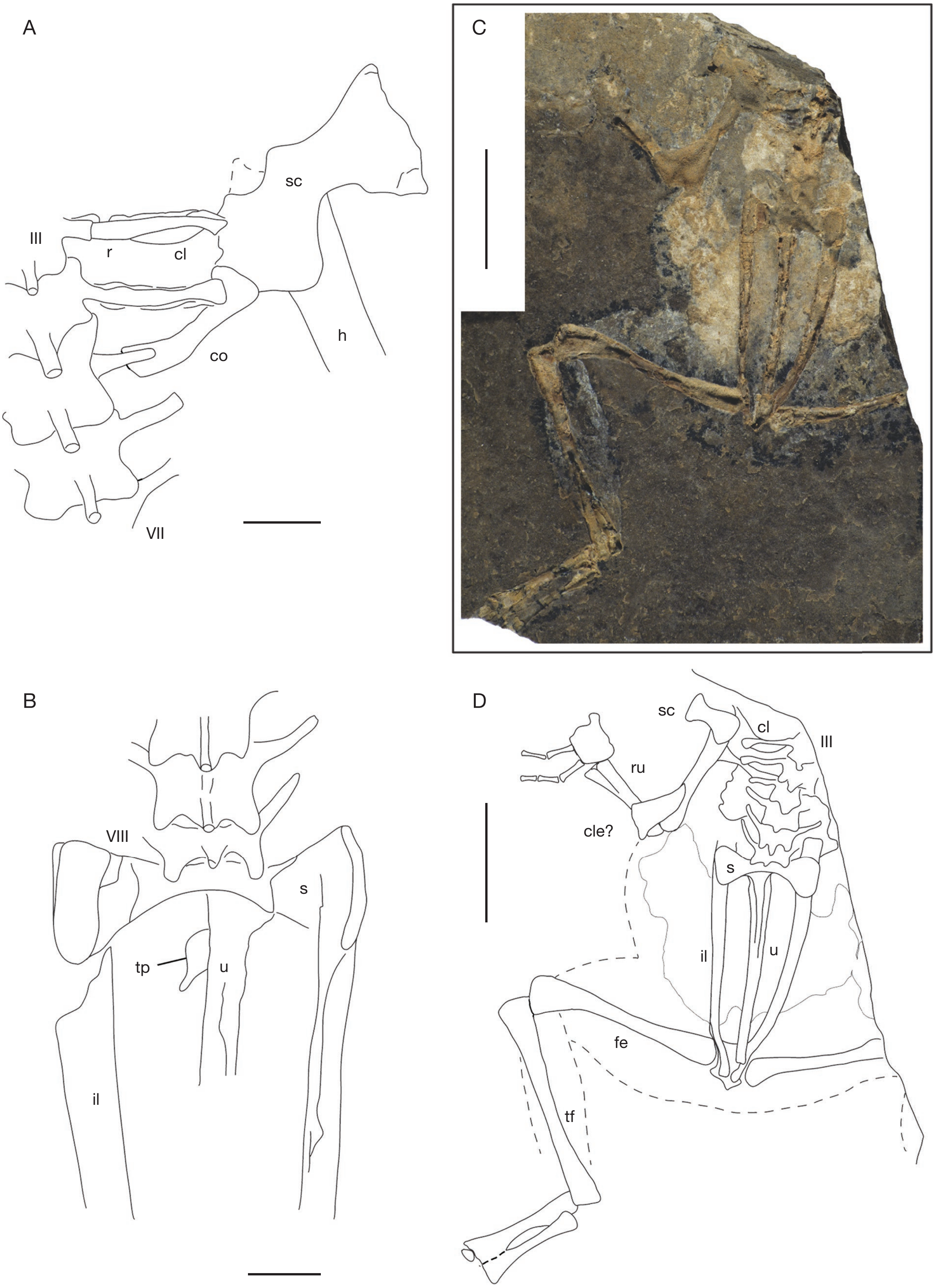

FIG. 5. — Anura indet.? New genus and species from Las Hoyas, Spain (MUPA-LH 11392): **A**, partial pectoral girdle in dorsal view drawn from the latex cast; **B**, sacral region in dorsal view drawn from the latex cast; **C**, photograph of specimen (now presumed lost) in dorsal view; **D**, interpretive line-drawing of C. Abbreviations: **cl**, clavicle; **cle**, cleithrum; **co**, coracoid; **fe**, femur; **h**, humerus; **il**, ilium; **r**, rib; **ru**, radioulna; **s**, sacrum; **sc**, scapula; **tf**, tibiofibula; **ti-fi**, tibiale-fibulare; **tp**, transverse process; **u**, urostyle; **III-VIII**, presacral vertebrae III-VIII. Scale bars: A, B, 2 mm; C, D, 10 mm.

a distinctly waisted shaft but differs in lacking a widely expanded *pars acromialis*; also, the cleithrum of *W. jucarensis* appears more extensive (Báez & Gómez 2019) than the putative same bone of MUPA-LH 11392. As in *W. jucarensis*, the femur is shorter than the tibiofibula, although less markedly so. In the early Barremian *Eodiscoglossus santonjae* from northeastern Spain (Table 1) these hindlimb bones are of nearly similar length (Báez & Gómez 2019: fig. 6). The neural arch laminae of the anterior presacrals are thick and contrast further from those of *E. santonjae* in being longer than wide, instead of wider than long and fully imbricated. The sacral diapophyses are distally expanded in MUPA-LH 11392, thus clearly differing from the narrow, posterolaterally directed processes on the sacrum of *Eodiscoglossus* (Báez & Gómez 2016).

When compared with extant leiopelmatids, this specimen differs in having probably eight presacrals (not nine), fully imbricate neural arches of presacrals II-VI, widely expanded sacral diapophyses, long ribs on vertebrae III and IV seemingly ankylosed to the short transverse processes, and a ridge along the anterior half of the urostyle. Imbricate neural arches occur also in the Jurassic putative stem anurans *Prosalirus* Shubin & Jenkins, 1995 (Jenkins & Shubin 1998), *Vieraella* Reig, 1961, and *Notobatrachus* (Estes & Reig 1973; Báez & Basso 1996; Báez & Nicoli 2004), the latter two taxa having a higher number of presacrals than the specimen from Las Hoyas described herein, whereas the total number in the former is unknown. Sacral diapophyses are only occasionally expanded in *Notobatrachus* but are not expanded in the other two Jurassic taxa. In those three extinct taxa a dorsal ridge on the urostyle is lacking and iliac shafts are crestless or bear low ridges. Additionally, in *Vieraella* and *Notobatrachus* the proportions of the pelvis and hindlimbs shown by the known specimens are also markedly different from those of MUPA-LH 11392. The basal anuran genus *Liaobatrachus* from the Lower Cretaceous of China (Dong *et al.* 2013) also has imbricate presacrals, although nine in number, and free ribs (on vertebrae II-IV and occasionally one additional pair on vertebra V). However, the posterior five presacrals (V-IX) bear transverse processes that are laterally directed or slightly inclined anteriorly, unlike the anteriorly directed processes on the three posterior presacrals of MUPA-LH 11392. The sacral diapophyses of *Liaobatrachus* are expanded and have distinctly convex lateral margins and the articulation of sacrum and urostyle is monocondylar whereas the condition of this articulation in MUPA-LH 11392 is not clear. In addition, the scapular shaft of *Liaobatrachus* bears an anterior crest, which is absent in MUPA-LH 11392. The recently described *Genibatrachus* Gao & Chen, 2017 from the Barremian-Aptian of China (Gao & Chen 2017) differs strikingly from MUPA-LH 11392 in having narrow, posterolaterally directed sacral diapophyses, distinctly arched iliac shafts, and laterally directed transverse processes on the last three presacrals.

Members of the crown-group Costata have eight presacral vertebrae, the most anterior three of which usually bear free ribs in adults. Ankylosis of ribs and transverse processes, however, has been reported in some extant representatives (e.g. *Bombina orientalis* (Boulenger, 1890): Blanco & Sanchíz 2000; *Alytes cisternasii* Boscá, 1879: Clarke 1988). In most costatan taxa the ribs are not much longer than the bearing transverse processes. One exception is the extant bombinatorid *Barbourula* Taylor & Noble, 1924, which has relatively long ribs that include the ankylosed ossified distal cartilages (Clarke 1987). The shapes of the neural arches also recall those of *Barbourula*, but this latter taxon has much more broadly expanded sacral diapophyses than MUPA-LH 11392. The scapula of the Las Hoyas specimen is medium-sized, unlike the short, wide, anteriorly straight scapula, and, probably, the distally V- shaped cleithrum, of all members of crown-group Costata, suggesting a position outside the basal node of this clade.

THE BARREMIAN ANURANS OF IBERIA AND THEIR SIGNIFICANCE

Diverse lines of evidence have stressed the increase of paleoenvironmental complexity, and consequent habitat heterogeneity in Barremian continental environments in Iberia (e.g. Buscalioni & Fregenal-Martínez 2010; Buscalioni & Poyato-Ariza 2016). Given the biphasic life-cycle of most anurans, the availability of suitable aquatic habitats, in particular breeding sites being either ephemeral, temporary, or permanent, strongly affects their local distribution. As mentioned above, continental successions in three areas of the Iberian plate have yielded articulated or partially articulated anuran remains, along with plants, including early angiosperms, invertebrate, and other vertebrates. The lower Barremian lithographic limestones that crop out in the eastern part of the Serra del Montsec were deposited in a coastal lake system that experienced marked water-level oscillations (Barale *et al.* 1984). The slightly younger sequence that includes the fossiliferous laminated limestones of Las Hoyas represents a wetland with a complex mosaic of terrestrial and aquatic environments, encompassing alluvial plains, marshes, swamps, as well as temporary ponds and permanent lakes (Buscalioni & Fregenal-Martínez 2010; Blanco *et al.* 2018). In particular, the laminated limestones that contain the anuran remains were deposited in a perennial shallow lake with an anoxic bottom that had no marine influence (Buscalioni & Poyato-Ariza 2016). These latter lacustrine beds and those of El Montsec share the presence of pipimorph xenoanurans of small size (SVL 16-23 mm) with markedly long digits owing to the great length of the metacarpals. These basal pipimorphs lack several features that have been related to a fully aquatic lifestyle present in more derived members of this lineage (Báez 2013) and they might have had a less fully aquatic behavior. Their remains are scarce in the anuran-yielding site of El Montsec, which represents the most distal part of the ancient lake (Gibert *et al.* 2000). There, the only pipimorph specimen described as yet is an articulated postmetamorphic, but juvenile, individual (Báez & Sanchíz 2007) and the group is not represented among the other specimens from the same site reported subsequently

(Vergnaud-Grazzini & Wenz 1975; pers. obs.). Likely, fully grown as well as immature individuals inhabited better oxygenated marginal areas of the lake or nearby ponds. In the highly prospected fossiliferous laminated limestones of Las Hoyas, the presence of pipimorphs is documented by a few specimens of slightly different developmental stages, belonging to a morphologically rather similar and slightly more derived taxon than the one recorded in El Montsec (Báez 2013). These occurrences, although few in number, are significant from both the evolutionary and paleogeographical viewpoints. These basal pipimorphs from Iberia possess several features expected in the ancestral morphotype of the Laurasian water-dwelling palaeobatrachids, whose earliest known occurrences are from the Upper Cretaceous of Europe (Wuttke *et al.* 2012) but which are extinct today. Isolated bones from the Berriasian of Morocco were attributed to a basal pipimorph (Jones *et al.* 2003). It is also noteworthy that more derived, crownward pipimorphs represented by numerous adults as well as immature specimens are recorded in beds of Early Cretaceous age along the northern fringe of the West Gondwana landmass (Nevo 1968; Trueb 1999; Trueb & Báez 2006), where many fossil discoveries document their persistence in the continental blocks resulting after its split (e.g. Báez & Rage 1998; Rage & Dutheil 2008; Gardner & Rage 2016; Gómez 2016).

All other Barremian anurans represented by articulated or partially articulated specimens from Iberia are non-pipimorph frogs that share more recent common ancestors with other crown-group frogs than leiopelmatids. Most of these remains have been ascribed to Discoglossidae either in a broad or a strict sense based on phenetic resemblance, probably because of the presence of features that might be plesiomorphic but are retained in extant members of the Costata clade (e.g. free ribs in adults, transverse processes on the urostyle, clavicles overlapping the anteromedial portion of the scapular *pars acromialis*) and might have been widespread in extinct early diverging lineages. Moreover, as discussed elsewhere (Báez & Gómez 2016, 2019), morphological adult features of extant costatans traditionally considered diagnostic (e.g. opisthocoelous epichordal presacral vertebrae, wide and short scapulae with a straight anterior margin owing to the presence of an anterior crest) are not present in many of these fossils and, by contrast, they possess conditions (e.g. amphicoelous vertebrae, moderately long, distinctly waisted scapular shafts) that might be ancestral, thus casting doubts on their placement in relation to other anurans. Also, some level of homoplasy might be expected because of incongruent character distribution.

The articulated skeleton of generalized proportions of a sexually mature male, preserved as part and counterpart, from the lower Barremian laminated limestones at Santa Maria de Meià (El Montsec) formed the basis of the taxon *Eodiscoglossus santonjae*. Originally estimated to be a “primitive discoglossid”, it might be a stem-group Costata as, according to our present understanding of anuran relationships, the record of xenoanurans mentioned above implies that the lineage represented by costatans today had already diverged, although a position as a stem lalagobatrachian has also been proposed (Báez & Gómez 2016). Poor preservation of the holotype makes it difficult to compare with the remains of about ten individuals, including metamorphs, subsequently collected in the same beds and referred to the same species (Vergnaud-Grazzini & Wenz 1975; Báez & Gómez 2016). Different features in adult individuals of about the same SVL (Báez & Gómez 2016) suggest that these additional specimens represent more taxa than just *Eodiscoglossus*.

The late Barremian lacustrine limestones of Las Hoyas have yielded the peculiar *Iberobatrachus* with a distinctly narrow neurocranium, short and anteriorly straight scapula, and extensive cleithrum, which was retrieved as a crown-group costatan (Báez 2013). As discussed herein, the Las Hoyas anurofauna includes *Wealdenbatrachus*, well represented by the species *W. jucarensis* in the coeval coal rich clays belonging to the La Huérguina Formation of the nearby Uña depocenter. These latter beds record the water-table oscillations in the marginal zone of an alkaline lake, as well as fan-deltaic sedimentation. Connections between these two upper Barremian depocenters were periodic (Gomez *et al.* 2001), the anuran assemblage recovered from Las Hoyas being more diverse than the monospecific anuran sample so far described from Uña. Interestingly, the proportions of the hindlimb segments of *Wealdenbatrachus jucarensis*, with a high tibiofibula to femur ratio value, suggest that it was a strong terrestrial jumper (Báez & Gómez 2019) unlike *Eodiscoglossus santonjae* or, possibly, the taxon represented by MUPA-LH 11392 which had less specialized proportions similar to those present in walkers/ hoppers with a wider repertoire of locomotor modes.

CONCLUSIONS

The Barremian lacustrine beds of the Iberian Peninsula have yielded numerous articulated or partially articulated remains of anurans, representing several taxa that furnish significant information on the early diversification of lalagobatrachians. As discussed elsewhere, some of them pertain to the pipimorph lineage, providing support to their proposed Jurassic divergence based on palaeontological grounds. However, the most abundant remains are those of the diverse non-pipimorphs crown-group frogs, among which three additional taxa are recognized herein in the anuran assemblage from the late Barremian Las Hoyas *Konservat-lagersätte* based on their sets of traits. Cranial as well as postcranial features support the presence of the genus *Wealdenbatrachus*, also present in the coeval lacustrine limestones of Uña. A distinctive combination of postcranial features of another specimen indicates that it belongs to an additional taxon, still not formally named. The evolutionary placements of these taxa and others previously reported, however, remain contentious highlighting the need for additional data on ontogenetic and individual variation amongst “archaeobatrachians” as well as a phylogenetic analysis with a broad taxonomic sampling and a data-set including osteological features to investigate rigorously their distribution and history.

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