

The first discovery of *in situ Pelophylax pueyoi* (Amphibia: Anura) from the late Miocene of Libros Konservat-Lagerstätte (Teruel, Spain)

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RH: Blain et al.—First *in situ Pelophylax pueyoi* from Spanish Miocene

ABSTRACT—For the first time, a specimen of *Pelophylax pueyoi* Navás, 1922a has been recovered *in situ*, about 600 meters from the main entrance inside the Libros II mine (Teruel, Spain). The fossil comes from the Libros Gypsum Unit (late Miocene), and represents a nearly complete articulated adult frog in ventral orientation, with partial preservation of soft tissues. The only apomorphic character diagnosing the family Ranidae is the presence of cylindrical sacral diapophyses. Other characteristics congruent with that of the family Ranidae can be observed: sphenethmoid fused medially, large and oval orbital fossa, well-developed pterygoids without alar expansion and the inner ramus clearly shorter than the posterolateral ramus, transverse processes of presacral vertebrae and sacral diapophyses of subequal length, sacrum unfused with the urostyle, probable bicondylar sacro-urostyler articulation, transverse processes of the urostyle lacking, absence of ribs, and elongated hind limb. An apomorphic combination of features of the genus *Pelophylax* can also be recognized, such as the more open sacral diapophysis, and less elongated and more robust femora than usually observed in the genus *Rana*. Finally, some discrete characteristics permit establishing a close relationship with *P. pueyoi*, such as the large size of the fossil, the wide proportion of the skull, and the somewhat trapezoidal distal contour of the V4 transverse processes. The carpus of *P. pueyoi* is described here for the first time, suggesting a similar condition of the adult carpal morphology found in most Neobatrachian species. Presence or absence of a praepollex in *P. pueyoi* still cannot be resolved.

INTRODUCTION

The village of Libros is located in the northeastern part of the Iberian Peninsula (Community of Aragon, Spain; Fig. 1), and is a world-famous locality, providing numerous fossils (see below), with exceptional preservation.

The Libros lacustrine sequence was deposited in the Teruel Basin in northeastern Spain during the early Miocene-late Pliocene (Ortí et al., 2003), and overlies Upper Triassic gypsum and Cretaceous carbonates (Anadón et al., 1992). The sequence comprises up to 500 m of alluvial terrigenous strata, lacustrine carbonates, and evaporites. The deepest water deposit in the sequence is the 120-m-thick Libros Gypsum Unit (Vallesian), which crops out in the Barrio de las Minas near Libros village. The unit is divided into, in ascending order, bituminous calcareous, gypsiferous, and gypsum-carbonate subunits (Ortí et al., 2003, 2010); native sulfur deposits occur in each of them. The 50-m-thick bituminous-calcareous subunit comprises intercalated charophytic limestones (wackestones and packstones) and laminated mudstones (including oil shales). Alternations of these lithologies indicate fluctuations between oxic (carbonate deposition) and anoxic (laminated mudstone deposition) conditions (Anadón et al., 1992).

The sedimentary deposits of the Libros Gypsum Unit from the Las Minas de Libros area have been exploited since the end of the 18th century, through 1956, in order to obtain sulfur. The bituminous shale from the mines, where fossil remains were sporadically found, was shredded by workers and used as fuel to melt the sulfur. Although these articulated fossils attracted the attention of many of the workers, particularly the women in charge of cutting up the material, for decades a large number of these fossils were lost in the furnace fire (Luque and Alcalá, 2002). Science did not become aware of the fossils of Libros until 1920, with the publication by Navás (1920) and the formal descriptions by Navás (1922a and 1922b) of two new species of water

frogs he named “*Rana pueyoi*” and “*Rana quelledbergi*” (now both included inside the genus *Pelophylax*). After that, other paleontologists, like Hernández Pacheco and Royo Gómez, as well as many fossil amateurs visited the mines, and they certainly bought some specimens from workers and local collectors (Luque and Alcalá, 2002). Reverend Emilio Castro, who for many years was in charge of teaching Natural Sciences at the “La Salle” School in Teruel, explained in a letter how he was propositioned by Villalta and Crusafont to prepare about 45 frogs to give one to each of the conference attendants, on the occasion of the III Paleontology Course in Sabadell in 1956, and how it was possible to buy fossils directly from the miners in the village (Castro, 2002). What put an end to the Libros mines were the oil refineries, which yielded sulfur more easily, and the desire to get rid of the tax they had to pay to the State for military uses, from 30% to 50% of the production (Castro, 2002). From the moment the mining company stopped the exploitation of sulfur, regular collecting of fossil specimens ceased, since it was necessary to process a large amount of material to find any (Luque and Alcalá, 2002). To date, this exceptional biota includes a beaver, birds, snakes, amphibians, insects, arachnids, and leaves (Navás, 1922a, 1922b; Sanchíz y Gil de Avalué, 1977; Olson, 1995; Peñalver, 1996; McNamara et al., 2006, 2009, 2012; Cuenca-Bescós, 2020), but surprisingly, no fish. Consequently, almost all the fossils from Libros that have been subsequently traded come from the exchange and sale between private collections, mismanagement of museum collections, or were kept by former mine workers and have been sold following closure of the mines (Luque and Alcalá, 2002).

From the following, it can be deduced that no fossil has ever been found *in situ* inside the mines. During the 2010s, CEET (“Centro de Estudios espeleológicos turolenses”) speleologists mapped the interior of the Libros mines. One of them has

been called Libros II (CEET, 2020). Its main entrance is blocked, so access is through secondary galleries. In the main gallery, about 600 meters from the main entrance, a singular object was found by chance by the mapping crew on the roof of the gallery, about 2.5 meters high. On a later visit, one of us (JIC) verified that it was a skeleton of a fossil frog in a very fine laminate clay. The stratigraphic position is not easy to determine inside the mine. Tentatively we consider that it could be located in the Lower or Upper Laminite of the bituminous calcareous subunit of Orti et al. (2010). For the first time, a specimen of the famous fossil frogs of Libros has been found *in situ*, not mined by the inhabitants of village. The present study aims to describe this fossil frog in detail to update knowledge of this taxon.

MATERIAL AND METHODS

The articulated fossil frog described herein is deposited in the ‘Museo de Ciencias Naturales de la Universidad de Zaragoza’ (MPZ; Canudo, 2018) with the collection number MPZ 2022/579. A “cleavage plane” (resulting from the erosion and/or the excavation work of the miners) goes through the specimen, splitting for example the vertebral column down the middle, and also causing that some bones missing in the specimen may have been present on the respective (and lost) counterpart.

One of us (JIC) on May 21st, 2017, together with speleologists from CEET, was in charge of extracting the fossil from the mine roof. It was necessary to transport a scaffold to the interior of the mine, which was mounted under the fossil. Because of the fractures in the rock where the fossil was located, it was consolidated with 3% paraloid, and a layer of Japanese paper was placed on it. The rock fragment that the frog was

preserved in was extracted with using a chisel and a hammer, which allowed the entire block to be removed with the fossil.

In 2022, the fossil was loaned to the Conservation and Restoration Area of IPHES-CERCA to remove the Japanese paper and adhesive initially used to wrap the fossil during its extraction. This tissue was located at specific zones of the fossil matrix, also covering parts of the specimen.

General pictures were taken using a Nikon D800 camera with a 40 mm Nikon Macro lens. Additional detailed pictures were processed with the DinoCapture 2.0 software, using photographs from the AM4115TL Dino-Lite Edge digital microscope.

Zoological nomenclature basically follows Speybroeck et al. (2020), and the osteological nomenclature of Sanchiz (1998), based on Bolkay (1919), was used. Carpal nomenclature follows Roček et al. (2022). Finger numbering follows Alberch and Gale (1985) who assume that the first digit was lost in anurans.

SYSTEMATIC DESCRIPTION

Class AMPHIBIA Linnaeus, 1758

Suborder NEOBATRACHIA Reig, 1958

Family RANIDAE Batsch, 1796

Genus *PELOPHYLAX* Fitzinger, 1843

PELOPHYLAX PUEYOI Navás, 1922a

Holotype—MPZ94-1052. A complete articulated frog in ventral view. The fossil corresponds to one of the two parts (the counterpart is missing) and is only constituted by bone fragments that remain adherent to the slab. Only outer morphology of bones can be documented: premaxillae, maxillae, sphenethmoid, angulosplenials,

exoccipital, scapulae, humeri, radioulnae, metacarpals, vertebrae, sacrum, urostyle, ilia, ischium, femora, tibiofibulae, tibiale, fibulare, and partially tarsals and metatarsals.

Diagnosis—The diagnosis by Navás (1922a) refers mainly on the external shape of the frog rather than on its osteology. Sanchíz y Gil de Avalle (1977) provides the first osteological (composite) diagnosis of the species based on 33 fossil specimens from Libros housed in the Museo Nacional de Ciencias Naturales de Madrid. Among *Pelophylax* representatives, *P. pueyoi* is characterized by its larger body (snout-vent) length, wider skull proportions, the trapezoidal distal contour of the fourth vertebra transverse processes, the relative length of the metacarpals, and the poorly developed posterior process of the parasphenoid.

Locality, Horizon, and Age—Libros (Spain), Libros Gypsum Unit, late Miocene.

Comments—Another specimen of *P. pueyoi* has been figured in the original publication by Navás (1922a) that may serve as paratype, but we still did not identified it in any museum collection. Although historically in use, Sanchíz y Gil de Avalle (1977) clearly stated that *P. pueyoi* may be a junior synonym of *Pelophylax meriani* from the lower Miocene of Germany. Revision of the phylogeny of the whole genus *Pelophylax* (25 extant species, most of them with still unclear taxonomical affinities and/or without any osteological description) encompasses this work. We thus follow here provisionally the historical name given by Navás (1922a) of *P. pueyoi*.

Referred specimens: 1 articulated specimen (MPZ 2022/579; Fig. 2).

Description: The recovered block shows an articulated adult frog (snout-vent length estimated around 104 mm). The area of the junction of the skull with the vertebral

column is badly preserved, and bones of the pectoral girdle are not clearly preserved. The cranium is only documented by the impression of the bones on the sediment. The frog is presented in ventral view (posterior end of the urostyle under the pelvic girdle), with the left and right forearms in dorsal view (laterality is based on the respective position of the fingers and carpals). Neither of the two humeri is sufficiently preserved to be sexed (in several anuran families a medial crest is only present in males). The first phalanx of the second digit is not preserved preventing the specimen to be sexed, as this phalanx usually bears a tuberosity in males (*tuberos pro musculus abductor indicis longus sensu* Ecker, 1864, 1889). Finally, the hindlimbs seem to be preserved in ventral view (based on the toes numbering). The adult status of MPZ 2022/579 is justified by the large body size of the specimen, the ossification of the carpals, and the fusion of the epiphyses with the diaphysis on the femora and tibiofibulae.

Cranium

The skull shape is mainly recognizable by the impressions of the pterygoid, angulosphenial, probable maxilla, and the remnants of the sphenethmoid. The left side of the skull is better preserved than the right, and shows an impression of the posterior part of the angular. The orbital margins (composed hypothetically by the outer outlines of the palatine, frontoparietal, exoccipital, and pterygoid) are observable on both sides of the skull. Anterior to the level of the posterior margin of the palatines, some crushed bone is present that seems to represent the anterior part of the snout, but no element is clearly identifiable. The skull seems to be wider than long (estimated width/length ratio around 1.4). The sphenethmoid is clearly unpaired, and possibly slightly longer than wide. Anterior lateral processes are well demarcated, somewhat robust, and laterally projected. The triradiate morphology of the left pterygoid can be inferred from the

preserved outlines. The impression of the left pterygoid suggests a slender element. The longest maxillary ramus is well curved distally and is much longer than the inner ramus. The angulosplenial is paired and curved. The articulation at its posterior end seems to be enlarged. Additionally, anterior to the mandible, a deep impression may represent the lateral surface of the left maxilla.

Vertebral Column

The vertebral column is well visible on MPZ 2022/579 from the third (if we presume the presence of the typical eight presacral vertebrae) vertebra to the sacrum. Due to fragmentary preservation, it is not possible to judge if the presacral vertebrae are procoelous or have non-imbricated neural arches, as is typical in ranids. Transverse processes permit individual identification of each vertebra. There are no free ribs. The third vertebra (V3) has the longest transverse processes, which are oriented perpendicular to the column axis. The fourth vertebra (V4) has transverse processes oriented slightly posteriorly and with distal contour somewhat trapezoidal. V5 has long, cylindrical transverse processes, oriented very slightly posteriorly. V6-V8 have long, cylindrical, perpendicular transverse processes. The sacrum seems not to be fused to the urostyle, and its diapophyses are strong and cylindrical, projecting posteriorly and above the dorsal plane. The angle between the sacral diapophyses is quite open (around 135°). The urostyle is slender, probably bicotyler, and apparently without transverse processes. It is not possible to judge if the urostyle bears a relatively high neural crest that gradually decreases in height posteriorly.

Forelimb

The forelimb is short and relatively gracile. The humerus is long and gracile, although its proximal end is not preserved. The radius and ulna are fused. The radioulna is not very widened distally, whereas the proximal extremity (= olecranon) is concave for the articulation with the humeral condyle. Adult carpal morphology of both hands is visible (Fig. 3). The best preserved carpus (on the right hand, at the left of the body) shows the presence of the ulnare (i.e., *os pyramidale* in Ecker, 1864), radiale (i.e., *os lunatum* in Ecker, 1864), distal radial (i.e., *os naviculare* in Ecker, 1864; and element Y in Fabrezi and Barg, 2001), the distal carpal element (i.e., *os capitato-hamatum* in Ecker, 1864; and distal carpal 3-4-5 in Fabrezi and Barg, 2001), and distal carpal 2 (i.e. *os trapezoides* in Ecker, 1864; and carpal 2 in Fabrezi and Barg, 2001). This corresponds to type B of Fabrezi and Barg (2001), with no fusion of the distal radial and the distal carpal 2 in the adult stage.

On MPZ 2022/579 (Fig. 3), the ulnare is relocated between the radiale and the distal carpal element, probably due to a relocation during preservation. Originally, carpals were certainly arranged in two rows, proximal and distal. The proximal row has three bones: the radiale, ulnare, and distal radial. The radiale originally articulated with the radial part of the articular surface of the radioulna, the distal carpal element, and the distal radial and the ulnare. No clear articulation surfaces are delimited on the radiale. The ulnare originally articulated with the ulnar part of the posterior articular extremity of the radioulna and the with the distal carpal element. The distal radial, medial-most third bone of the proximal row, do not articulate with the radioulna. It is articulated with the radiale by a somewhat saddle-shaped surface. The distal row also consists of three bones, of which only two are preserved here: the distal carpal element and the distal carpal 2. The distal carpal element is the largest bone. In both wrists, it is the largest bone, and articulates with all three bones of the first row. It is crescentic, at least on the

left hand, with the concavity directed posteriorly, and on the convex surface has three facets for the three outer metacarpals III, IV and V. Finally, distal carpal 2 is a smaller bone, in comparison with all remaining carpals, lying medial to the distal carpal element; it articulates with the second metacarpal, and anteriorly with the distal radial. Presence or absence of a praepollex cannot be determined. Digits (metacarpals and phalanges) are represented by their impressions, which makes it impossible to determine the phalangeal formula. Each hand is composed of four digits (as in most anurans). The fourth (i.e. third one in Sanchíz y Gil de Avalle, 1977) digit seems to be the longest.

Pelvic Girdle

The pelvic girdle is present in ventral view, and is composed of two ilia and fused ischium. The presence of a well-developed dorsal crest on the ilial shaft cannot be ascertained. The ischium seems to form the posterior half of the acetabulum. The pubis is usually present in ranids (as in most anurans) as a cartilaginous element ventral to the acetabulum, and is located between the anteroventral margin of the ischium and the posteroventral margin of the ilium. In MPZ 2022/579, it is not clearly identifiable, nor is its degree of ossification.

Hindlimb

The hind limb is elongated. Both the femur and tibiofibula are relatively straight. The femur is elongated, rather robust and has a sigmoid curvature. No femoral crest is visible. The tibiofibula is somewhat longer than the femur. It is rather elongated and slender, and as far as we can judge, its extremities do not seem to be particularly expanded. Preservation does not permit observation of the longitudinal sulci, usually

visible at each end of the bone. The tibiale and fibulare are not medially fused, and are also slender and elongate. According to Ecker (1864, 1889), the robustness (i.e. wide of diaphysis) of the tibiale and fibulare differs in *Pelophylax* kl. *P. esculentus*: the tibiale being slightly more robust than the fibulare. As far as we can judge based on impressions, the dissymmetry concerning robustness between tibiale and fibulare is not evident on MPZ 2022/579. The *spatium intertarsale* is rather long and elliptic. The left foot preserves some impression of the digits, but individual metatarsals are not distinguishable. The fourth digit seems to be the longest, but only very slightly in comparison to the third and fifth ones. Due to the preservation, again no phalangeal formula can be proposed here.

Soft Tissues

A relatively high percentage of adult frogs from the Miocene Libros Konservat-Lagerstätte are characterized by the preservation of their soft tissues, some in histological detail (McNamara et al., 2006, 2009; Rossi et al., 2019). Several soft-tissue features have been described in fossil frogs (i.e., McNamara et al., 2009): these differ in their color, texture, or location, and invariably correspond to, or are associated with, specific anatomical features. The soft-tissue visible on MPZ 2022/579 is located mainly around the trunk area and also, although less evident, around the right femur. They probably correspond to the dark brown, carbonaceous, bacterial biofilm described in McNamara et al. (2006, 2009), and match the body outline of a frog. According to these authors, the bacterial biofilm is thicker in the thorax and abdomen, and does not define any anatomical feature in most of the specimens (77%), and represents the degraded remains of the internal body contents.

DISCUSSION AND DIAGNOSIS

Taxonomic assignment of MPZ 2022/579 is rather difficult to establish, due to the poor preservation of the skeleton. The only apomorphic character diagnosing the family Ranidae is the presence of cylindrical sacral diapophyses. Other characteristics congruent with that of the family Ranidae can be observed: sphenethmoid fused medially, large and oval orbital fossa, well-developed pterygoids without alar expansion and the inner ramus clearly shorter than the posterolateral ramus, transverse processes of presacral vertebrae and sacral diapophyses of subequal length, sacrum unfused with the urostyle, probable bicondylar sacro-urostyler articulation, transverse processes of the urostyle lacking, absence of ribs, and elongated hind limb (i.e., Sanchiz, 1998). An apomorphic combination of features of the genus *Pelophylax* can also be recognized on MPZ 2022/579, such as the more open sacral diapophysis (approximately 135°) than in genus *Rana* (mix/max = 95-125°; Böhme, 2001; Blain and Arribas, 2017), and less elongated and more robust femora than usually observed in the genus *Rana*. Finally, some discrete characteristics permit establishing a close relationship between MPZ 2022/579 and the extinct species *Pelophylax pueyoi* Navás, 1922a, such as the relatively large size of the fossil, the wide proportion of the skull, and the somewhat trapezoidal distal contour of the V4 transverse processes (Navás, 1922a; Sanchíz y Gil de Avalle, 1977). In agreement with the description of *P. pueyoi* by Sanchíz y Gil de Avalle (1977), MPZ 2022/579 shows a very elongated hind limb, with a similar ratio between the different elements. Both the femur and tibiofibula are relatively straight. The tibiofibula is somewhat longer than the femur. The estimated length ratios of the femur/tibiofibula = 0.93 (right) and 0.91 (left) of MPZ 2022/579 fall within the minimum/maximum values (0.87/0.97) given by Sanchíz y Gil de Avalle (1977) for *P.*

pueyoi. The tibiale and fibulare are similarly slender and elongated. The estimated length ratio of the tibiofibula/tibiale-fibulare = 1.97 (right) and 2.05 (left) of MPZ 2022/579, which fall inside the minimum/maximum (1.86/2.07) of *P. pueyoi*.

As stressed by Sanchíz y Gil de Avalu (1977), *P. pueyoi* is morphologically very close to the present *Pelophylax ridibundus*, but seems to differ by the existence of a larger body (snout-vent) length, wider skull proportions, the trapezoidal shape of the transverse processes of V4, and the relative lengths of the metacarpals (not observable on MPZ 2022/579). The other extinct species described from the late Miocene of Libros *Pelophylax quellebergi* Navás, 1922a is much smaller (Navás, 1922a; Sanchíz y Gil de Avalu, 1977), and according to Navás (1922a), its skull is narrower than in *P. pueyoi*. Concerning this last character, Sanchíz y Gil de Avalu (1977) expresses some doubt, or at least calls for caution. According to him, although it is perfectly possible that the skull of *P. pueyoi* was much wider than long in life (and much wider than in *P. quellebergi*, *Pelophylax* kl. *P. esculentus* and *Pelophylax ridibundus*), crushing during fossilization could affect the proportions of the skull, and especially the width. Concerning relative body size (expressed as snout-vent length in herpetology), most of *P. pueyoi* are around 9 cm (with the largest ones reaching around 10.5 cm; McNamara et al., 2009). Such a body size is well out the maximum observed in the extant *P. lessonae* (reaching 4 to 7 cm in adults; i.e., Vukov et al., 2018) and *P. quellebergi* (reaching 7.5 cm), but inside the maximum body size observed for most of extant European *Pelophylax*, as *Pelophylax perezi* and *P. ridibundus* (around 8 cm for adults, but reaching up to 11 cm for females; i.e., Egea-Serrano, 2014). In herpetology, approximation to head width is given by the relation between head width and snout-vent length (HW/SVL). This ratio is 0.341 ± 0.012 (n: 13; min/max: 0.322/0.359; Crochet et al., 1995) for *P. perezi*, 0.376 ± 0.015 (n: 5; min/max: 0.353/0.393; Crochet et al., 1995)

for *P. ridibundus*, and 0.341 (n: 36; Vukov et al., 2018) for *P. lessonae*. The same ratio for MPZ 2022/579 can be estimated around 0.384, thus entering inside the modern upper range of *P. ridibundus* and the lower one of *P. pueyoi* (0.399 ± 0.039 ; n = 20; min/max = 0.348/0.493), but well out the ones of *P. quellebergi* (0.330 ± 0.030 , n = 3; min/max: 0.300/0.357), *P. perezi* and *P. lessonae*. Again these comparisons must be taken carefully, due to the crushing during fossilization, and the fact that SVL cannot be directly measure on the fossil specimens. The trapezoidal shape of the transverse processes of V4 has been described in both *P. pueyoi* and *P. quellebergi* (Navás, 1922a; Sanchíz y Gil de Avalle, 1977). As already raised by Sanchíz y Gil de Avalle (1977) the morphology of *P. quellebergi* is very similar to the one of *P. pueyoi* and it is possible that *P. quellebergi* corresponds to the juvenile of *P. pueyoi*, but these hypotheses are not testable on the fossil record available up to the date. We therefore diagnose MPZ 2022/579 as pertaining to the group *P. pueyoi-quellebergi* based on the morphology of the transverse processes of V4, and to *P. pueyoi* by its larger body size and head width. The carpus (wrist) of *P. pueyoi* is described here for the first time, and is similar to type B of Fabrezi and Barg (2001), i.e., similar to the adult carpal morphology found in most Neobatrachian species, and similar to what is actually observed in the genus *Pelophylax* (i.e. Ecker, 1864, 1889). Finally, the last point to be raised is the absence of a detailed comparison between *P. pueyoi* and *Pelophylax meriani* from the lower Miocene of Germany (Meyer, 1860) in order to establish an eventual synonymy. Both forms seem to be morphologically concordant according to Sanchíz y Gil de Avalle (1977). The closest form to *P. meriani* is also the extant *Pelophylax ridibundus*, as suggested by Boulenger (1891) on the basis of the vomerian dentition.

As explained in the introduction, the discovery of fossils at the Libros mines were purportedly only done during the shredding of the bituminous shale by workers. Density of fossils inside the sediments also indicates a low possibility of finding fossils in situ in the mines. All these arguments let us to suggest here that the recovery of the described fossil frog MPZ 2022/579 certainly constitutes the only in situ find for this site.

The finely laminated shale of MPZ 2022/579 is lithologically similar to that of other Libros frog specimens. The visual inspection inside the mine did not uncover any other example of fossil vertebrates, which seems to indicate that these fossils were scarce and there was no accumulation. In our opinion, only the massive exploitation of a mine with a large removal of land allowed the recovery of dozens of specimens of fossil frogs in the past, giving the erroneous impression of an accumulation of specimens in the same stratigraphic level.

The last point concerns the original position of the frog, which is exposed in ventral view on the slab, and thus would have been probably fossilized originally lying on its belly on the lake bottom.

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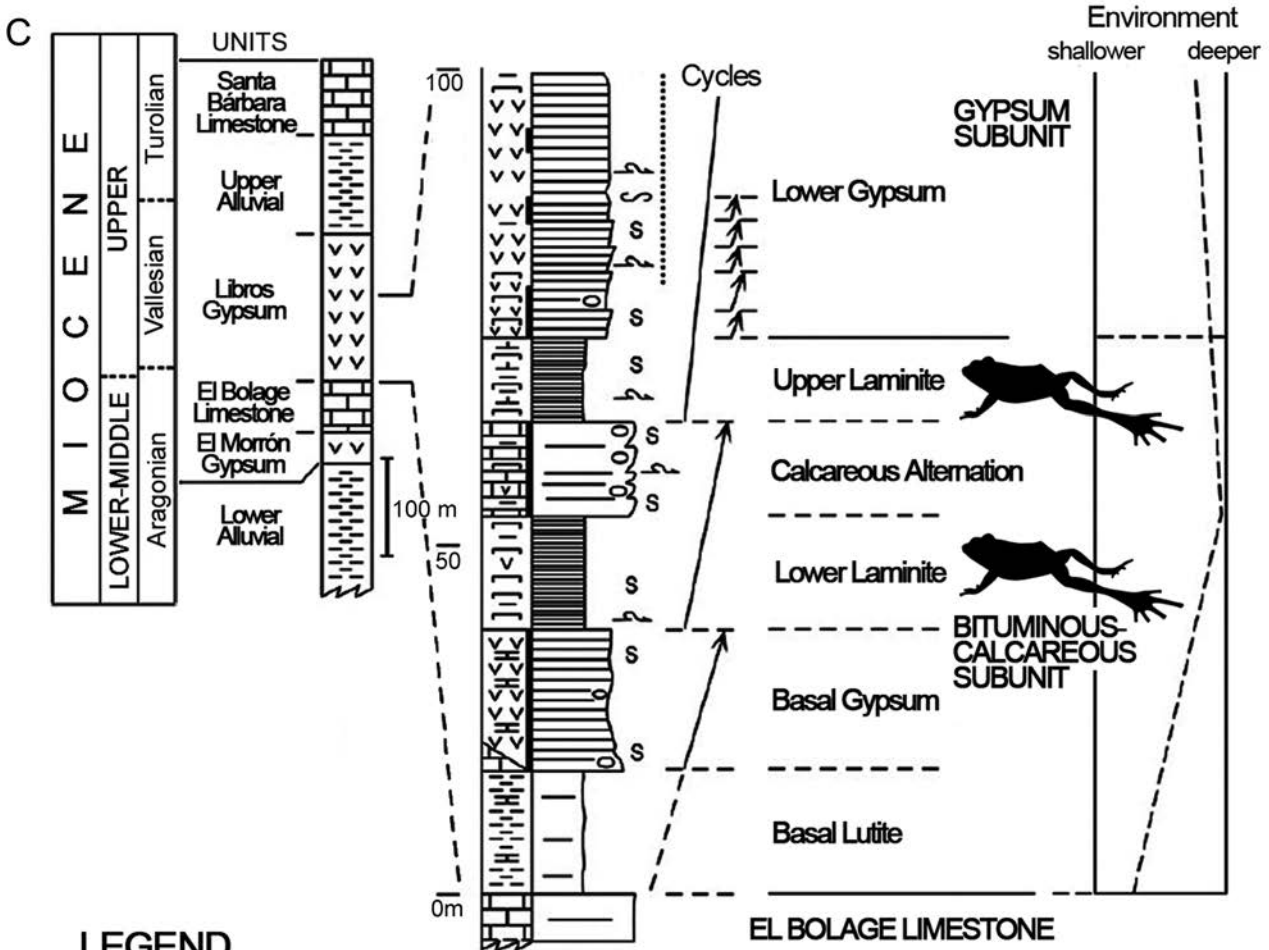
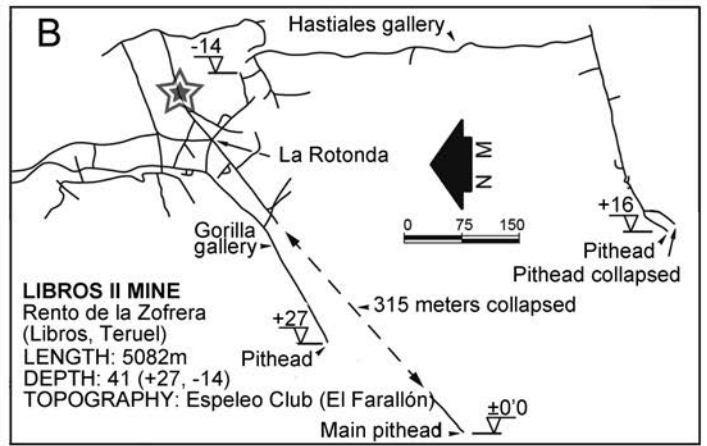
Captions

FIGURE 1. Geographic and geological context. **A**, Geographic map of Iberian Peninsula with location of Libros II Mine; **B**, Topographic plan of Libros II Mine (CEET, 2020) with location of fossil frog marked by a star; **C**, General stratigraphic succession of lower part of Libros Gypsum unit in Las Minas area (modified from Ortí et al., 2010). Various stratigraphic intervals composing the Las Minas succession (macrocycle), cycles (medium-scale cycles and some minor cycles; arrows), and environmental interpretation are indicated. Frog silhouettes indicate two probable stratigraphic locations for *Pelophylax pueyoi* Navás, 1922a (MPZ 2022/579).
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FIGURE 2. *Pelophylax pueyoi* Navás, 1922a (MPZ 2022/579). Nearly complete skeleton preserved in bituminous calcareous rocks (Natural History Museum of the University of Zaragoza). Photograph (**left**) and explanatory drawing (**right**).
Abbreviations: **ang**, angulosplenial; **carp**, carpus; **fe**, femur; **fibl**, fibulare; **fp**, frontoparietal; **hu**, humerus; **il**, ilium; **isc**, ischiopubis; **max**, maxilla; **pal**, palatine; **pmax**, premaxilla; **pte**, pterygoid; **ru**, radioulna; **sacr**, sacrum; **sphe**, sphenethmoid; **tf**, tibiofibula; **tibl**, tibiale; **V3-V8**, presacral vertebrae; **II-V**, numeration of metacarpals and metatarsals according to Alberch and Gale (1985). Grey area represents preserved bone. White arrows show preserved soft tissues. Scale bar equals 3 cm.
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FIGURE 3. *Pelophylax pueyoi* Navás, 1922a (MPZ 2022/579). Adult carpal morphology of right hand (on left side of body). Abbreviations: **II-IV**, numeration of digits according to Alberch and Gale (1985). Scale bar equals 5 mm.

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LEGEND

Lithology

- limestone
- marl
- lutite
- oil-shale
- gypsum (primary)
- gypsum (diagenetic)

Bedding

- massive to bedded
- thin bedded
- laminated

Fossils

- fossil frog

Structures & Textures

- dotted gypsum
- slumps
- sulfur (nodules or lenses)
- sulfur (irregular occurrences)
- macroscopic gypsum pellets

