

A NEW SPECIES OF PELODYTID FROG FROM THE IBERIAN PENINSULA

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ABSTRACT: We describe a new species of the genus *Pelodytes* from the southern part of the Iberian Peninsula. The new species, the third known living species of Pelodytidae, is distinguished on the basis of external morphology, osteology, morphometrics, and allozymes

Key words: Anura; Pelodytidae; *Pelodytes ibericus* new species; Iberian Peninsula; Taxonomy; Morphology; Osteology; Allozymes

THE family Pelodytidae previously was thought to include only one genus with two living species. *Pelodytes punctatus* ("terra typica" near Beauvois, northern France) is widely distributed in western Europe, inhabiting large areas of the Iberian Peninsula and France, and some neighboring zones in northern Italy (Guyétant, 1997); reports of its presence in Belgium and Luxembourg have never been confirmed and are highly questionable (Sánchez-Herráiz and Barbadillo, 1997). *Pelodytes caucasicus* is a poorly known species endemic to the Caucasus Mountains (Bannikov et al., 1977; Golubev, 1980; Kuzmin, 1997).

The fossil record of pelodytids is not rich, but it shows that the family was present in the Tertiary of North America with at least two genera, both distinct from *Pelodytes*. One of them (*Tephrodytes*) has been found in the Arikareean of Montana (Henrici, 1994), and another (*Miopelodytes*) in the Miocene (Barstovian or Clarendonian) of Nevada (Taylor, 1941). Unstudied remains similar to *Pelodytes* have been reported from the Eocene (Bartonian and Priabonian) of Europe, and *Pelodytes* has been found in several deposits in western Europe from the Upper Miocene to the Pleistocene (Sanchiz, 1998). An extinct Neogene species (*Pelodytes arevacus*) has been described from Spain, and was

included in the lineage of *P. punctatus* (Sanchiz, 1978).

Iberian species of *Pelodytes* are small, secretive, nocturnal animals whose biology is poorly known (Paillette et al., 1992). Although widely distributed, their populations seem to be localized, showing an apparently fragmented distribution (Barbadillo, 1987; Sánchez-Herráiz and Barbadillo, 1997; Sindaco and Andreone, 1988). Paillette et al. (1992) found remarkable differences in the mating call between populations from Algarve (southern Portugal) and others from the Camargue (southern France) and Liguria (northwestern Italy) regions. This result led Paillette et al. (1992) to suggest the presence of a distinct dialect in the Portuguese population.

On the basis of these studies and our own observations, we decided to test the biological homogeneity of the Iberian populations of *Pelodytes*. Analysis of many different character sets, including external morphology, morphometrics, osteology, allozymes, DNA sequences, bioacoustics, and life history, revealed congruent results that show a clear differentiation of the southern Iberian populations. It is the purpose of this article to describe these populations as a new species on the basis of morphological and allozyme data.

MATERIALS AND METHODS

We selected a sample of populations of *Pelodytes* to cover the main biogeographic regions of its range in Spain (Appendix I). Field data were taken during the breeding

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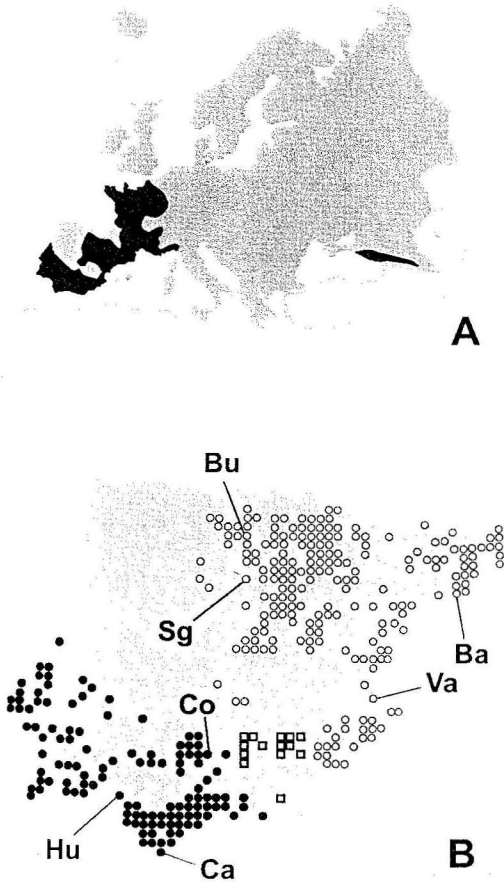


FIG. 1.—(A) General distribution of *Pelodytes*, modified from Guyétant (1997) and Kuzmin (1997); the eastern European range corresponds to *P. caucasicus*. (B) Proposed distribution of *Pelodytes* in the Iberian Peninsula, modified from Sánchez-Herráiz and Barbadillo (1997). Points are centered in the standard UTM grid of European atlases (20 × 20 km), but the grid is not shown. Black dots = *P. ibericus*. White dots = *P. punctatus*. No specific identification has been possible in the region indicated by squares (see text).

seasons of 1993 and 1994. Populations with less than five individuals sampled were not used in the primary morphometric analyses, but they were secondarily assigned to either of the larger groups according to their morphotypes. External morphological data were taken from live animals, and osteological data were collected from museum specimens; both types of data were collected from adult, reproductive males from six natural areas (Fig. 1, below). We used small samples of

the same populations, when available, for the electrophoretic analyses. We did not use the electrophoretic sample from Barcelona, which included mostly females, for morphometric comparisons. Museum abbreviations are EBD: Estación Biológica de Doñana, Seville (Spain); MBL: Museu Bocage, Lisbon (Portugal); MNCN: Museo Nacional de Ciencias Naturales, Madrid (Spain); MTKD: Museum für Tierkunde, Dresden (Germany).

External Morphology

Standard measurements were taken on living reproductive males (Table 1).

Osteological Analysis

We prepared adult male specimens from the MNCN as cleared and double stained skeletons using slight modifications of the techniques described by Dingerkus and Uhler (1977) and Wassersug (1976). Landmarks and measurements are defined in Appendix II and Fig. 2. Measurements were taken from camera lucida drawings. Osteological nomenclature follows Sanchez (1998).

Morphometric Analysis

We performed multivariate analyses on osteological measurements. Stepwise discriminant analyses were done using the SPSS package, with the option that maximizes the smallest *F*-ratio for pairs of groups. Only specimens for which complete data sets were available were included in the analyses. Measurement D(20–23) (see Appendix II and Fig. 2), which represents the length of the vertebral column, was used as an indicator of size. The standardized residuals obtained from the linear regressions of the variables (log-transformed) against D(20–23) were used as discriminant variables, to reduce the effects of size.

Electrophoretic Analysis

We analyzed a total of 49 specimens from six populations by horizontal starch gel electrophoresis, using the techniques described by Pasteur et al. (1987). Electrophoretic conditions and enzymatic systems are summarized in Table 2. Desig-

TABLE 1.—External standard measurements taken from living adult males of *P. ibericus* and *P. punctatus* (in mm): HW: maximal head width; LHL: hind limb length; LFL: forelimb length; SVL: snout-vent length. Indices are given as percentages. Sample size (n), mean (\bar{x}), standard deviation (SD), and standard error (SE). The samples do not differ from normality in Kolmogorov-Smirnov tests ($P > 0.15$), and two-tailed probability t -tests have shown significant differences ($P < 0.001$) for all comparisons.

Variable	Species	n	\bar{x}	SD	SE	Range
SVL	<i>P. punctatus</i>	124	37.019	3.278	0.294	30.0–46.5
	<i>P. ibericus</i>	41	33.470	2.053	0.321	29.6–39.0
LFL	<i>P. punctatus</i>	98	25.134	2.034	0.205	20.5–29.9
	<i>P. ibericus</i>	41	18.601	2.077	0.324	14.6–23.7
LHL	<i>P. punctatus</i>	124	62.531	5.192	0.466	49.6–73.0
	<i>P. ibericus</i>	41	52.751	4.409	0.689	46.5–67.0
HW	<i>P. punctatus</i>	98	14.242	1.123	0.113	12.0–17.1
	<i>P. ibericus</i>	41	13.414	0.878	0.137	11.5–15.5
LFL/SVL	<i>P. punctatus</i>	98	67.964	3.686	0.372	52.4–75.5
	<i>P. ibericus</i>	41	55.803	7.147	1.116	43.1–66.1
LHL/SVL	<i>P. punctatus</i>	124	169.175	7.881	0.708	149.0–187.7
	<i>P. ibericus</i>	41	157.533	7.004	1.094	144.8–173.1
HW/SVL	<i>P. punctatus</i>	98	38.505	1.830	0.185	34.5–42.3
	<i>P. ibericus</i>	41	40.131	2.207	0.345	34.3–43.3

... was numerical for loci according to increasing anodal migration, and also numerical for alleles according to their relative migration. The samples were obtained from the MNCN frozen tissue stock, for which amphibian specimens are normally anaesthetized with MS222 (Sandoz). Tissues (liver, muscle, and heart) were homogenized, centrifuged at 12,000 g, for 30 min, and stored at -70°C until processing. We calculated genetic variability parameters using the program BIOSYS (Swofford and Selander, 1989).

RESULTS

Qualitative Osteological Characters

The most important qualitative differences among the three species were found in cranial components. The frontoparietals are in contact medially in *Pelodytes caucasicus*, providing a complete cover for the skull roof, whereas in northern *P. punctatus* they remain close but mostly separated (only the Barcelona population presented some cases of medial contact, but only in a single point), being far apart in the Andalusian form (Fig. 3). Premaxillae contain 19–20 tooth positions in the two skeletons of *P. caucasicus* available, whereas the median is 15.5 in *P. punctatus* (range 13–18, $n = 10$) and 14 in the southern new species (range 12–18, $n = 32$). Processus palatinus of maxilla small, frequently free or

loosely fused to the rest of the bone in the Andalusian *Pelodytes*, present and larger in the other species of the genus. Number of maxillary teeth 46–50 in *P. caucasicus* ($n = 2$), 32–50 in *P. punctatus* (median 37, $n = 10$), 28–44 in the southern Iberian species (median 36, $n = 32$). Sphenethmoid proportionally shorter in the Andalusian form; sphenethmoid having a longer septum nasi in *P. punctatus*, and especially *P. caucasicus*. Sphenethmoid more dorsoventrally flattened in *P. caucasicus* than in the other two species. In the vertebral column, the neurapophyses of Vertebrae II–IV each have a long processus spinosus which overlaps the following vertebra in *P. caucasicus*, unlike the non-imbricating type observed in both Iberian species. Pectoral girdles are also distinct among *Pelodytes* (Fig. 4), in particular with respect to the scapular shape. *Pelodytes caucasicus* presents a wide, pelobatid-like scapula, lacking a crista anterior. In contrast, in Iberian *Pelodytes* the scapula is short mediolaterally, particularly in the southern new species. The scapular crista anterior is larger in the southern Iberian species than in the northern one, particularly in its distal part (see arrows in Fig. 5).

Several cartilaginous structures also show marked differences between the two Iberian species (no cleared and stained specimens of *P. caucasicus* were available).

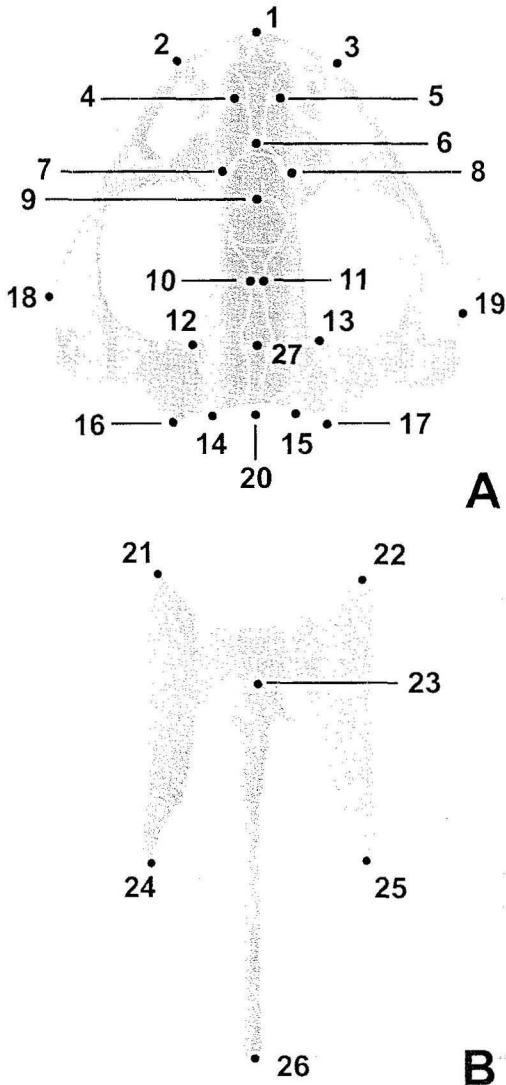


FIG. 2.—Osteological measurements taken on cleared and stained material. Numbers define landmark normal projections on the transverse plane. Landmarks and measurements are defined in Appendix II (A) Dorsal view of generalized skull of *P. punctatus*. (B) Dorsal view of generalized sacrum and urostyle of *P. ibericus*.

The shape of the tectum nasi is more elongated and narrower in the northern Iberian *P. punctatus* than in the southern new species (Fig. 3), and in the hyoid apparatus, the parahyoid bone of the Andalusian morphotype is shorter and has more divergent anterior rods than that of *P. punctatus* (Fig. 6).

Discriminant Analyses

Absolute ages were inferred in some instances by skeletochronology of fingers, to determine if size differences between the two Iberian species could be merely due to age, which was not the case (Sánchez-Herráiz et al., 1997). In a discriminant analysis of the osteological data (Table 3), each of the samples of *Pelodytes* was considered a predefined group. In this analysis, the first, second, and third canonical axes accounted, respectively, for 83.19%, 8.40%, and 5.15% of the among-sample variability. A large overlap on the first and second canonical axes was observed among the samples from Burgos, Segovia, and Valencia. Also samples from Cádiz, Huelva, and Córdoba overlapped on the first and second canonical axes. Nevertheless, each of the samples from Burgos, Segovia, and Valencia was completely separated from those of the Andalusian region (Cádiz, Huelva, and Córdoba) on the first canonical axis (Fig. 7). The absolute magnitudes of the standardized canonical coefficients (Table 4) indicate that D(4–7) (nasal medial length), D(10–11) (minimum separation of frontoparietals) and D(18–19) (maximum skull width) were the greatest contributors to the separation on the first axis.

According to the results of the preliminary multivariate analysis, a second discriminant analysis was performed using two predefined groups obtained from the amalgamation of the Andalusian populations (Cádiz, Córdoba, and Huelva; $n = 20$) and the northern ones (Burgos, Segovia, and Valencia; $n = 25$) respectively. No overlap between groups was detected, each of them being widely separated from the other (Fig. 8). Variables D(18–19), maximum skull width (maximal in the southern species), and D(10–11), minimum separation of the frontoparietals (maximal in the northern species), were the greatest contributors to the separation of the groups, which was 100% for all cases (Table 4).

Allozyme Analysis

A total of 18 enzymatic systems (Table 2) were consistently scored. These 18 systems

TABLE 2.—List of proteins analyzed, number of the Enzyme Commission (EC), loci detected, tissues in which they were found active and buffers used for electrophoresis (L = liver, M = muscle, S = stomach). Buffers: 1 = Tris-Citrate pH 7.0 (TC-7); 2 = Tris-Citrate pH 8.0 (TC-8); 3 = Lithium hydroxide pH 8.3 (LiOH); 4 = Aminopropil-morpholine pH 7 (AC-7)

Enzyme	EC	Loci	Tissue	Buffer
Asenylate kinase	2.7.4.3	AK-1°, AK-2°	M, S	1
Alcohol dehydrogenase	1.1.1.1	ADH-1°, ADH-2°, ADH-3°	L	2
Aspartate aminotransferase	2.6.1.1	sAAT-1°	M, L	2
Esterase	3.1.1.1	EST-1°, EST-2°	M	3
Fumarate hydratase	4.2.1.2	FUM°	M	1
Glutamate dehydrogenase	1.4.1.2	GDH°	L	2
Glucose-6-phosphate isomerase	5.3.1.9	GPI°	L, M, S	4, 1, 2
Hexokinase	2.7.1.1	HK-1° HK-2°	M S	1 1
Isocitrate dehydrogenase	1.1.1.42	IDPH-1°, IDPH-2°, IDPH-3°	M	2
L-Lactate dehydrogenase	1.1.1.27	LDH-1°, LDH-2°	M	4
Malate dehydrogenase	1.1.1.37	mMDH°, sMDH	M	1, 4
Malic enzyme-NADP	1.1.1.40	ME-1°, ME-2°, ME-3°, ME-4°	L, M	2, 4
Mannose-6-phosphate isomerase	5.3.1.8	MPI-1°, MPI-2°	L, M	2
Peptidase leucyl-glycyl-glycine	3.4.11.4	PEPLGG-1°, PEPLGG-2°	M	3
Peptidase leucyl-proline	3.4.11.-	PEPLP°	M	3
Phosphoglucomutase	5.4.2.2	PGM°	M	3
6-Phosphogluconate dehydrogenase	1.1.1.44	PGDH°	L, M	2, 4
Superoxide dismutase	1.15.1.1	SOD°	L	2

represented 32 presumptive loci, 19 of which were monomorphic: *ADH-1°*, *ADH-3°*, *AK-1°*, *AK-2°*, *EST-1°*, *FUM-1°*, *IDPH-2°*, *IDPH-3°*, *mMDH°*, *sMDH°*, *ME-1°*, *ME-2°*, *ME-4°*, *MPI-1°*, *PEP(LGG)-1°*, *PEP(LGG)-2°*, *PEP(LP)°*, *PGM°* and *SOD°*. Thirteen loci were polymorphic; their allele frequencies and sample sizes are given in Table 5. Inferred variability parameters are shown in Table 6. The population with least polymorphism is that of Huelva (6.3%), which nevertheless exceeds the mean heterozygosity values observed in Córdoba or Burgos (Table 6). Table 7 shows the matrix of genetic distances among the populations, using the unbiased Nei (1978) and modified Rogers (1972) dis-

tances. Two groups (Andalusian and northern populations) are clearly defined, having low Nei genetic distances within each group (0.002–0.062 within the northern group, and 0–0.002 in the southern one), and values of 0.15–0.19 between them. Figure 9 presents a Wagner tree using Rogers' distances (cophenetic correlation = 0.99).

The northern and southern groups can be separated by three diagnostic loci: *IDPH-1°*, *ME-3°*, and *MPI-2°*. The northern group also exhibited a unique allele shared by the three populations (*6PGD°98*, frequency > 27% in all three populations), and another one was found in the southern group (*EST-2°92*, frequency > 10% in all three populations) (Table 5).

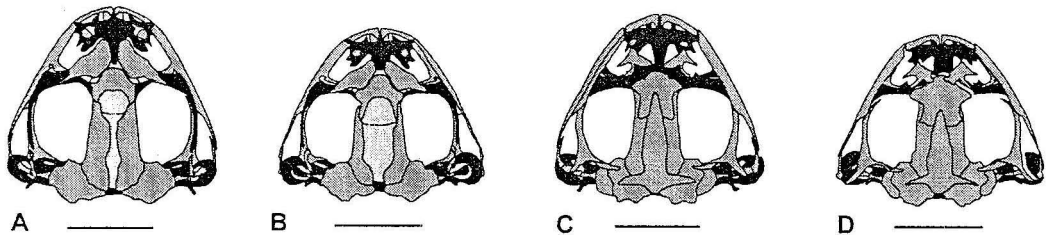


FIG. 3.—(A, C) Male skulls of *Pelodytes punctatus* based on MNCN 20161 (SVL = 36.0 mm) and (B, D) *P. ibericus*, based on MNCN 20117 (SVL = 35.5 mm) drawn at the same width (A, B) dorsal view (C, D) ventral view. Cartilage in dark grey. Scale = 5 mm.

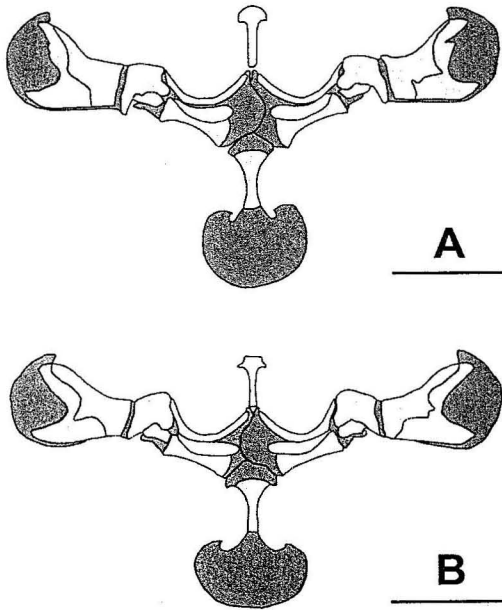


FIG. 4.—Pectoral girdle of (A) *Pelodytes ibericus* based on MNCN 20117 (SVL = 35.5 mm, male) and (B) *P. punctatus* based on MNCN 20161 (SVL = 36.0 mm, male). All elements drawn in the same plane. Cartilage in dark grey. Suprascapular cartilage drawn in the bottom to make possible the observation of the complete cleithral shape. Scale = 5 mm.

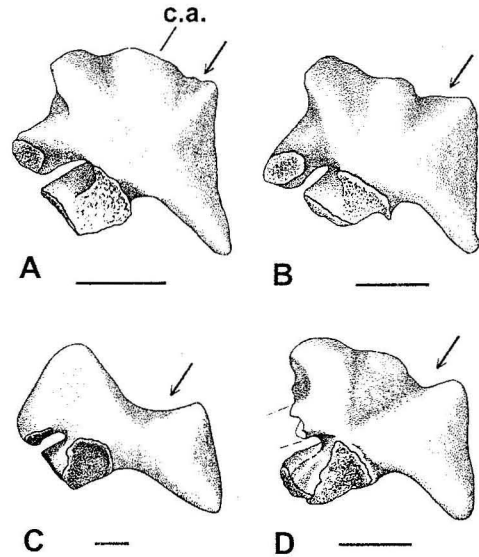


FIG. 5.—External views of left scapulae of *Pelodytes*. (A) *P. ibericus* (MNCN 18151, male SVL = 31.0 mm). (B) *P. punctatus* (MNCN 18496, male SVL = 35.7 mm), selected to show the largest crista anterior found in the sample. (C) *P. caucasicus* (MNCN 18133, male SVL = 48 mm), and (D) extinct *P. arcuatus* (MNCN PV35126), pars acromialis slightly broken in recent times, see photograph of the complete bone in Sanchiz (1978). c.a. = crista anterior. Scales = 1 mm.

Allelic frequencies within each population were in agreement with the expected values under a Hardy-Weinberg equilibrium model, and none of the 26 Chi-square tests were found to be statistically significant. This genetic structure was also reflected by the Wright F -statistics (Wright, 1965, 1978), with global values of $F_{is} = 0.006$, $F_{it} = 0.664$, and $F_{st} = 0.662$. These parameters indicate equilibrium, or lack of substructure, within each population, as well as an important global differentiation as a consequence of the differences present between the northern and southern groups. Within each group, the values of F_{st} are 0.056 (for the southern group) and 0.339 for the northern one. The northern

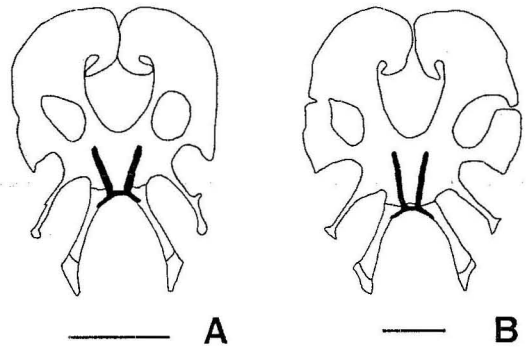


FIG. 6.—(A) Hyoid elements of *P. ibericus* based on MNCN 20143 (male, SVL = 33.3 mm) and (B) *P. punctatus* based on MNCN 20161 (male, SVL = 36.0 mm). Parahyoid bone in black, other bones in white. Cartilage in grey. Scale = 5 mm.

TABLE 3.—Discriminant analysis of osteological measurements. Classification results and predicted group membership (%) among the populations analyzed; n = number of specimens.

Population	n	Burgos	Segovia	Valencia	Cádiz	Huelva	Córdoba
Burgos	7	57.1	14.3	28.6	0	0	0
Segovia	10	20.0	80.0	0	0	0	0
Valencia	8	12.5	12.5	75.0	0	0	0
Cádiz	7	0	0	0	71.4	14.3	14.3
Huelva	5	0	0	0	0	100	0
Córdoba	8	0	0	0	0	25.0	75.0

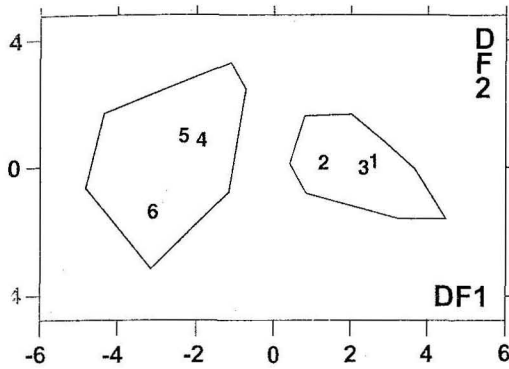


FIG 7.—Discriminant analysis of the six analyzed populations. Numbers refer to the population means 1 = Burgos 2 = Segovia 3 = Valencia 4 = Córdoba 5 = Cádiz. 6 = Huelva DF1-2 = discriminat functions 1 and 2.

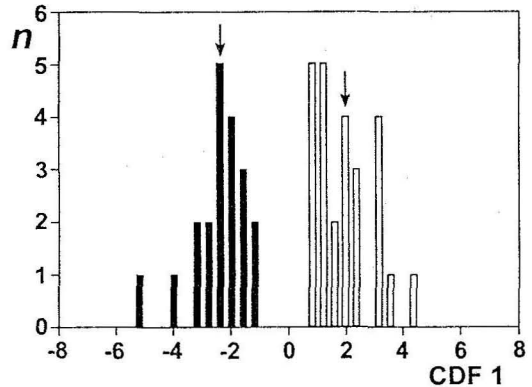


FIG 8.—Discriminant analysis of the two groups of populations analyzed. n = number of cases White histogram = *Pelodytes punctatus* Black histogram = *P. ibericus* Group means indicated by an arrow.

group showed a higher differentiation than the southern one due to the characteristics of the Catalonian population (Barcelona): three alleles not found in the two other populations, with frequencies > 0.250. The genetic distances (Table 7) and the phenetic tree (Fig. 9) also demonstrated the slight separation of the Barcelona sample within the northern group.

TAXONOMY

Pelodytes ibericus sp. nov

Holotype.—MNCN 23662, adult male collected on 26 november 1997 by Carmen Díaz-Paniagua and Miguel Tejado at the Doñana Biological Reserve (36° 59' N, 6° 27' W, elevation 10 m), Province of Huelva (Spain).

Paratypes.—All from the same locality,

date and collectors as the holotype. MNCN 23663 fluid preserved adult female. MNCN 23664–23665, EBD 29822, and MBL Amphibia-391, fluid preserved adult males. MNCN 20115–20119, cleared and double stained skeletons of adult males.

Diagnosis.—In addition to the morphometric differences already indicated, *Pelodytes ibericus* can be distinguished from other members of the genus by the following combinations of features: External morphology—male size smaller than *P. punctatus* (Table 1), much smaller than *P. caucasicus* (SVL about 55 mm, Bannikov et al., 1977). Proximal subarticular tubercles conical in *P. ibericus*, rounded in *P. punctatus* (Fig. 12); subarticular tubercles in *P. caucasicus* much larger and promi-

TABLE 4.—Discriminant analysis of osteological measurements. Standardized canonical coefficients of the discriminant function among the populations or species analyzed. Numbers in the variable column refer to distances between landmarks, indicated in Fig. 2 and described in Appendix II.

Variables	FUNC 1	FUNC 2	FUNC 3	FUNC 1
Analysis	Populations	Populations	Populations	Species
D(10–11)	–0.52454	0.36662	0.53156	–0.48361
D(1–6)	0.32685	–0.17137	0.63980	0.41484
D(4–7)	0.53303	0.37760	0.40898	0.35842
D(2–3)	0.36787	–0.38476	–0.84014	0.47369
D(20–27)	0.34443	–0.59827	0.16330	0.44914
18–19)	–0.47350	–0.12940	0.66701	–0.48818
{[21–24 + 22–25]/2}	0.27682	0.70588	–0.21302	0.23094
D(16–17)				0.30419
Eigenvalue	5.78200	0.58770	0.35810	4.89140
% variance	83.19	8.46	5.15	100

TABLE 5.—Allele frequencies for polymorphic loci and contingency tests CT1: contingency test among Barcelona (BA), Burgos (BU), and Valencia (VA) populations. CT2: contingency test among Cádiz (CA), Córdoba (CO), and Huelva (HU) populations

Locus		BU	VA	BA	CO	HU	CA	χ^2	df	P
AAT°	n	11	10	6	7	5	10			
	100	1.000	1.000	1.000	1.000	1.000	0.950			
	108	0.000	0.000	0.000	0.000	0.000	0.050			
	Global							3.940	5	0.558
	CT2							1.228	2	0.541
ADH-2°	n	10	9	6	7	5	8			
	100	0.900	1.000	0.750	1.000	1.000	1.000			
	95	0.000	0.000	0.250	0.000	0.000	0.000			
	105	0.100	0.000	0.000	0.000	0.000	0.000			
	Global							27.212	10	0.002
	CT1							13.000	4	0.011
EST-2°	n	11	8	6	5	4	6			
	100	1.000	0.938	1.000	0.900	0.750	0.750			
	92	0.000	0.000	0.000	0.100	0.250	0.250			
	106	0.000	0.063	0.000	0.000	0.000	0.000			
	Global							16.877	10	0.077
	CT1							2.168	2	0.338
	CT2							0.937	2	0.626
GDH°	n	11	10	6	6	5	10			
	100	0.955	0.955	1.000	1.000	1.000	0.950			
	90	0.045	0.000	0.000	0.000	0.000	0.000			
	98	0.000	0.000	0.000	0.000	0.000	0.050			
	Global							11.017	15	0.751
	CT1							3.177	4	0.529
	CT2							1.127	2	0.569
HK-1°	n	11	10	6	3	5	10			
	100	1.000	1.000	0.750	0.000	0.000	0.000			
	83	0.000	0.000	0.250	1.000	1.000	1.000			
	Global							80.837	5	0.000
	CT1							11.118	2	0.004
HK-2°	n	9	10	6	7	5	9			
	100	0.833	0.600	1.000	0.286	0.400	0.444			
	103	0.167	0.350	0.000	0.000	0.000	0.000			
	105	0.000	0.050	0.000	0.714	0.600	0.556			
	Global							54.407	10	0.000
	CT1							7.891	4	0.096
	CT2							0.862	2	0.650
IDPH-1°	n	8	10	6	6	5	10			
	100	1.000	1.000	1.000	0.000	0.000	0.000			
	98	0.000	0.000	0.000	1.000	1.000	1.000			
	Global							78.000	4	0.000
LDH-1°	n	10	10	6	7	5	10			
	100	1.000	1.000	0.833	1.000	1.000	1.000			
	4	0.000	0.000	0.917	0.000	0.000	0.000			
	Global							86.965	5	0.000
	CT1							46.504	2	0.000
LDH-2°	n	11	10	6	7	5	10			
	100	1.000	1.000	1.000	0.929	1.000	1.000			
	120	0.000	0.000	0.000	0.071	0.000	0.000			
	Global							6.062	5	0.300
	CT2							2.193	2	0.334
ME-3°	n	11	9	6	5	5	10			
	100	1.000	1.000	1.000	0.000	0.000	0.000			
	107	0.000	0.000	0.000	1.000	1.000	1.000			
	Global							92.000	5	0.000

TABLE 5.—Continued

Locus		BU	VA	BA	CO	HU	CA	χ^2	df	P
MPI-2°	n	11	10	6	7	5	10			
	100	1.000	0.900	0.417	0.000	0.000	0.000			
	110	0.000	0.100	0.583	0.000	0.000	0.000			
	120	0.000	0.000	0.000	1.000	1.000	1.000			
	Global							134.369	10	0.000
	CT1							20.040	2	0.000
6PGD°	n	10	9	6	7	4	10			
	100	0.600	0.722	0.583	1.000	1.000	1.000			
	98	0.400	0.278	0.417	0.000	0.000	0.000			
	Global							20.019	5	0.001
	CT1							0.834	2	0.659
PGI°	n	9	10	5	7	5	10			
	100	1.000	0.750	0.200	0.714	1.000	1.000			
	121	0.000	0.250	0.800	0.286	0.000	0.000			
	Global							37.517	5	0.000
	CT1							20.909	2	0.000
	CT2							9.429	2	0.009

than in the other two species. Head proportionally wider, with snout less prominent and shorter than in *P. punctatus* (Table 1). Relative length of fore and hind limbs and fingers shorter than in *P. punctatus*. (Table 1). In males of *P. ibericus*, when hindlimbs are properly addressed, the tibiotarsal articulation at most reaches anterior corner of eye, and quite often it does not reach the eye or only its posterior corner, whereas tibiotarsal articulation may reach from the anterior corner of eye to snout tip in *P. punctatus*, and beyond the snout in *P. caucasicus*. Osteology—in comparison with *P. punctatus*, the frontoparietals of *P. ibericus* are narrower and the minimum distance between them is larger (Table 8), whereas in *P. caucasicus* the frontoparietals are in contact medially with each other along their entire length. Sep-

tum nasi proportionally wider and much shorter in *P. ibericus* than in *P. punctatus* (Fig. 3). Sphenethmoids shorter in *P. ibericus* than in the other species (Fig. 10). In comparison with *P. punctatus*, the hyobranchial skeleton of *P. ibericus* shows a parathyoid shape (in black: Fig. 6) with a wider angle between its anterior rods. The cranium is shorter, wider, and less compact in *P. ibericus* than in *P. punctatus*, as indicated by significant differences in all the related osteological measurements (Table 8). Furthermore, *Pelodytes ibericus* shares no alleles with *P. punctatus* at three allozyme loci: *IDH-1°*, *ME-3°*, and *MPI-2°* (Table 5).

Few skeletal elements of the extinct Miocene species *P. arevacus* are known, but it differs from *P. ibericus* in having a scapula in which the crista anterior does

TABLE 6.—Genetic variability measures in the populations surveyed. A locus is considered polymorphic if more than one allele was detected. Columns: (A) Mean sample size analyzed per locus. (B) Mean number of alleles per locus. (C) Percentage of loci polymorphic. (D) Mean heterozygosity (direct count). (E) Mean heterozygosity expected (Hardy-Weinberg unbiased estimate, Nei, 1978). Standard error of estimates in parentheses.

Population	A	B	C	D	E
Barcelona	5.8 (0.2)	1.2 (0.1)	18.8	0.057 (0.030)	0.075 (0.030)
	10.6 (0.2)	1.1 (0.1)	12.5	0.032 (0.017)	0.034 (0.019)
Vall de Navia	9.3 (0.3)	1.2 (0.1)	18.8	0.046 (0.022)	0.056 (0.024)
Córdoba	6.1 (0.2)	1.1 (0.1)	12.5	0.029 (0.019)	0.038 (0.020)
Huelva	4.7 (0.1)	1.1 (0.0)	6.3	0.041 (0.029)	0.030 (0.021)
Cádiz	8.9 (0.3)	1.1 (0.1)	12.5	0.043 (0.026)	0.035 (0.021)

TABLE 7—Genetic distances among the populations surveyed. Below diagonal, Modified Rogers distance (Wright, 1978). Above diagonal, Nei (1978) unbiased genetic distance.

Population	Burgos	Valencia	Barcelona	Córdoba	Huelva	Cádiz
Burgos	—	0.002	0.062	0.162	0.155	0.154
Valencia	0.068	—	0.052	0.150	0.149	0.149
Barcelona	0.248	0.228	—	0.182	0.192	0.191
Córdoba	0.383	0.368	0.403	—	0.001	0.002
Huelva	0.376	0.368	0.413	0.062	—	0.000
Cádiz	0.374	0.367	0.411	0.066	0.015	—

not reach the suprascapular margin (Fig. 10 and illustrations in Sanchiz, 1978, 1998).

Description of the holotype.—Head dorsally flattened, wider than long; snout subacuminate in dorsal view, rounded in profile; nostrils barely prominent dorsally, located at anterior terminus of snout; eye large, notably protuberant dorsally; interocular distance slightly smaller than eye diameter, larger than internarial and eye-nostril distances; pupil vertical; tympanum externally visible, smaller than eye diameter and positioned near corner of mouth; supratympanic fold distinct, extending from posterior corner of eye to level of forelimb. Vomerine teeth in two patches between the choanae; premaxillary and maxillary teeth present. Forelimb moderately slender; relative lengths of fingers: $I < II < IV < III$; fingers with dermal fringes; webbing absent; one large, conical subarticular tubercle present proximally on each finger; three flattened metacarpal tubercles; inner and outer tubercles subequal in size, and larger than central tubercle; dark nuptial pads on pollex, inner side of second finger, ventral sides of arm and forearm, and in axilla. Hind limbs slender, when adpressed, tibiotarsal articulation reaching the anterior corner of eye; inner metatarsal tubercle large, rounded and prominent anteriorly; outer metatarsal tu-

bercle absent; proximal subarticular tubercles indistinct, remaining subarticular tubercles absent; relative lengths of toes: $I < II < V < IV$ (digit III clipped in both legs); webbing absent; toes with conspicuous dermal fringe to tip. Skin of dorsum and flanks granular, with distinct warts; skin of throat and venter smooth; ventral surfaces of thighs granular.

Measurements of the holotype (in mm).—SVL 29.7, head length 10.05, head width 11.7, shank length 14.1, foot length 14.9, eye diameter 3.3, interocular distance 2.9, eye-nostril distance 2.45, internarial distance 2.4.

Etymology.—*ibericus*, Latin adjective in allusion to the endemic status of the species on the Iberian peninsula.

Color in ethanol.—Dorsum grey, with numerous dark warts. Dorsal surfaces of forelimbs and hind limbs pale grey with irregular rounded spots. Throat pale grey, darker on the lateral margins. Venter and ventral surfaces of limbs pale cream.

Remarks.—The larval ontogenetic de-

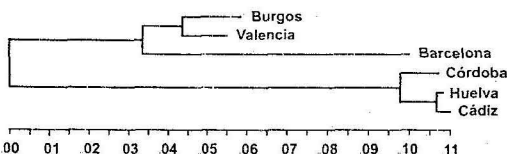


FIG. 9—Wagner dendrogram calculated with Rogers genetic distances (Wright, 1978) among populations. The cophenetic correlation is 0.99

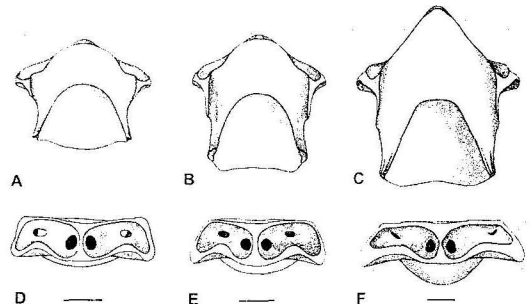


FIG. 10—(A, D) Male sphenethmoid of *Pelodytes ibericus* based on MNCN 18152 (SVL = 33.0 mm), (B, E) *P. punctatus* based on MNCN 18496 (SVL = 35.7 mm), and (C, F) *P. caucasicus* based on MNCN 18133 (SVL = 48 mm). (A-C) Dorsal view; (D-F) anterior view. Scale = 1 mm.

TABLE 8—Mean and standard deviation (in parentheses) of the osteological measurements (in mm) taken from cleared and stained museum specimens (all adult males) Numbers in the variable column refer to distances between landmarks, indicated in Fig. 2 and described in Appendix II; *n* = sample size. BU = Burgos. CA = Cádiz CO = Córdoba HU = Huelva. SE = Segovia. VA = Valencia

Variable	BU	CA	CO	HU	SE	VA
<i>n</i>	7	7	8	5	10	8
D(20–23)	13 719 (1 054)	14 042 (1 124)	12 672 (1 080)	13 129 (0 508)	14 608 (0 858)	12 879 (0 427)
D(1–27)	12 764 (0 745)	11 480 (0 609)	10 583 (0 648)	10 736 (0 288)	13 421 (0 810)	12 205 (0 513)
D(1–20)	12 145 (0 780)	11 083 (0 632)	10 153 (0 612)	10 155 (0 349)	12 891 (0 758)	11 550 (0 312)
D(20–27)	0 619 (0 108)	0 397 (0 189)	0 430 (0 124)	0 581 (0 073)	0 530 (0 121)	0 655 (0 243)
D(23–26)	8 369 (0 611)	8 119 (0 516)	7 488 (0 761)	7 741 (0 297)	8 696 (0 650)	7 780 (0 397)
D(18–19)	13 796 (1 098)	13 603 (0 675)	12 485 (0 966)	13 047 (0 378)	14 352 (0 930)	13 527 (0 423)
D(16–17)	5 121 (0 243)	4 989 (0 181)	4 522 (0 425)	4 567 (0 249)	5 414 (0 299)	4 772 (0 310)
D(21–22)	3 873 (0 266)	3 874 (0 324)	3 857 (0 554)	3 358 (0 339)	4 314 (0 296)	3 833 (0 283)
D(24–25)	4 002 (0 397)	4 358 (0 248)	4 143 (0 301)	3 594 (0 316)	4 376 (0 378)	4 150 (0 216)
D(2–3)	5 319 (0 413)	4 834 (0 249)	4 411 (0 445)	4 534 (0 210)	5 787 (0 389)	5 103 (0 423)
D(4–7)	2 687 (0 190)	2 409 (0 263)	2 161 (0 239)	2 041 (0 189)	2 728 (0 193)	2 638 (0 179)
D(10–11)	0 312 (0 139)	1 064 (0 131)	0 984 (0 256)	1 230 (0 450)	0 416 (0 183)	0 490 (0 251)
D(1–6)	3 314 (0 375)	2 844 (0 188)	2 481 (0 286)	2 687 (0 177)	3 467 (0 335)	3 405 (0 353)
D(6–9)	1 924 (0 189)	1 795 (0 160)	1 576 (0 154)	1 553 (0 183)	2 120 (0 216)	1 628 (0 232)
D(9–20)	6 172 (0 421)	5 891 (0 478)	5 694 (0 404)	5 529 (0 148)	6 706 (0 388)	6 087 (0 235)
D([21–24 + 22–25]/2)	7 080 (0 655)	6 571 (0 268)	5 933 (0 710)	5 576 (0 287)	7 606 (0 509)	6 781 (0 167)

velopment of Andalusian *Pelodytes ibericus* has been fully described (under the name *P punctatus*) by Talavera (1990).

Color in life and variation—Sexual dimorphism in *P. ibericus* appears to be less marked than in *P. punctatus*, but quantitative data are not available. Male variation

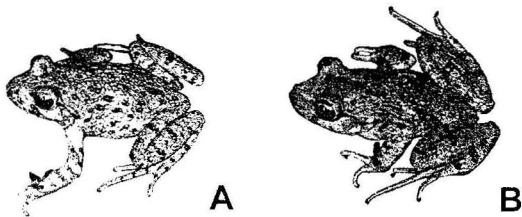


FIG. 11—Photographs of living specimens of *P. punctatus* (right) and *P. ibericus* (left). These specimens were not collected.

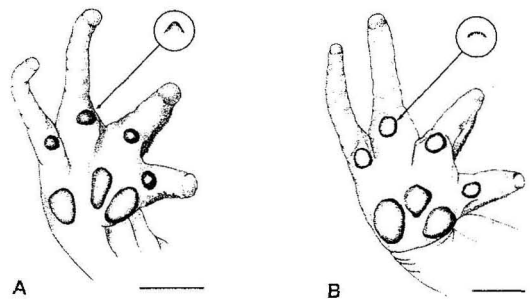


FIG. 12.—(A) Palmar view of hands of *P. ibericus*, based on MNCN 23691 (male, SVL = 29.9 mm) and (B) *P. punctatus*, based on MNCN UZA1825 (male, SVL = 34.2 mm) Scale = 2 mm.

in some external measurements are indicated in Table 1. Skin of dorsum smooth to granular, with prominent round to ovoid warts (Fig. 11). Notable intrapopulation differences in coloration were observed among individuals. The dorsum background color varies from brownish grey, olive-brown to plain green, or dark brown with green spots. In some specimens there are two pale bands on the dorsum making an "X"-shaped design. In most cases, the warts are darker than dorsum background color, varying from plain green to dark brown. Venter white to pale cream. Throat white to pale cream in females, white to violet or dark grey in males. Ventral surface of limbs highly variable, from pale cream to violet. Nuptial pads in breeding males brown to black. Iris has the lower $\frac{2}{3}$ brown and the upper third gold. Pupil vertical in bright light, rounded at night.

Distribution.—The known geographic range of *Pelodytes ibericus*, modified from Sánchez-Herráiz and Barbadillo (1997), includes southern Portugal and the Spanish Andalusian and Badajoz provinces (Fig. 1). If the presence of this species is confirmed in northern Portugal, it is possible that *P. ibericus* represents the only species of *Pelodytes* living in this country. Its altitudinal distribution ranges from lowlands, including areas close to the sea, to the medium altitude (<900 m) mountain regions of Sierra Morena (Córdoba and Jaén provinces). It seems possible that *P. punctatus* and *P. ibericus* are presently not sympatric, the only possible exception could be the arid Jaén-Murcia mountain region, a border zone with historical records of *Pelodytes* (surveyed time ago by voluntary herpetologists for the National Atlas), specimens of which we have been unable to find in museums, nor have we been able to locate these populations in the field.

Habitat and habits.—We have observed *Pelodytes ibericus* in association with ponds shallow to medium in depth (<1.5 m), and also in seasonal streams and flooded areas. It seems to show a preference for open areas with high insulation. Breeding activity occurs from October–March at different times each year, depending on local conditions associated with periods of

rain. Precipitation occurs unpredictably in the southern Iberian regions, therefore breeding season records for localities have low predictive value.

Some differences in calls have been found between *P. punctatus* and *P. ibericus*. Paillete et al. (1989) found that mating calls from Camargue (southern France) were composed of two different notes "a" and "b" repeated sequentially (e.g., ab, ab), whereas males of southern Portugal (*P. ibericus*) had more complex calls, with a single "a" followed by a repeated series of "b" (e.g., abb, abb). Our recordings ($n > 35$ for each species) corroborate this result and are concordant with the morphological and genetic differentiation found between *P. ibericus* and *P. punctatus*. The northern Spanish populations studied emit a mating call with only two notes, while the Andalusian ones are composed of series of two notes in which the second is repeated from 2–5 times (Sánchez-Herráiz et al., 1997, unpublished data). In addition, we have observed that *P. punctatus* frequently emits underwater mating calls, never recorded in *P. ibericus*.

RESUMEN

Se describe una nueva especie del género *Pelodytes* procedente del sur de la Península ibérica. La nueva especie es la tercera especie viviente conocida de la familia Pelodytidae, y su descripción se basa en rasgos de morfología externa, osteología, morfometría y análisis genético fundamentado en electroforesis de aloenzimas.

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APPENDIX I

Specimens Examined

Unless otherwise indicated, the museological specimens are complete adults preserved in fluid. Museum abbreviations indicated in Material and Methods. C&S = cleared and stained specimen. DS = dry skeleton.

Pelodytes caucasicus: REPUBLIC OF GEORGIA: *Borzhomi*: Akhaldaba MNCN 19197. No locality data. MNCN 18133 DS, MTKD D9740 DS.

Pelodytes ibericus: PORTUGAL: *Baixo Alentejo*: Porto Covo MNCN 18153-18158 DS. SPAIN: *Cádiz*: Alcalá de los Gazules MNCN 18145-18148 DS, 18150-18152 DS. Algodonales EBD 586, 590, 595. Medina Sidonia MNCN 18487-18493 DS. Sanlúcar de Barrameda MNCN 2718. Tarifa, Facinas MNCN 18159 DS, 20141 C&S, 20142-20147, 20206-20220 C&S. *Córdoba*: Córdoba MNCN 20183-20188 C&S, MNCN 20189 DS, MNCN 20191-20198 C&S. Nava de Cabra EBD 29825. *Granada*: Huetor-Santillán, Monte Carbonal EBD 580-581, 583-584. *Huelva*: Aljaraque MNCN 18145 DS. Almonte, Reserva Biológica de Doñana EBD 29822, NBL Amphibia-391, MNCN 20115-20119 C&S, 23662-23665. Los Corrales MNCN 18134-18144 DS. Niebla MNCN 340-344. *Sevilla*: Alcalá de Guadaira MNCN 391. Coripe EBD 596. El Pedroso EBD 2946-2953. Sevilla EBD 5314. El Viso del Alcor EBD 8521. In addition, living specimens (not collected) were measured from: *Alicante*: Sella and Polop. *Cádiz*: Tarifa and Alcalá de los Gazules. *Córdoba*: Córdoba, Sierra Morena and Cabra. *Huelva*: Neighborhood of the Parque Nacional de Doñana.

Pelodytes punctatus: SPAIN: *Albacete*: No locality data EBD 29835. *Alicante*: Santa Pola MNCN 674–680. *Barcelona*: El Bruli EBD 29833. Garraf MNCN 20176–20182 C&S. *Burgos*: Comejo MNCN 2715. Merindad del Rio Ubierna MNCN 18495–18500 DS, MNCN 20148–20165 C&S, MNCN 20201–20205 C&S. *Castellón*: Sierra Engarcerán MNCN 20783. *Ciudad Real*: Caracollera MNCN 377. *Cuenca*: Embalse de La Toba MNCN 19776 C&S. *Huesca*: Otín EBD 20440. *Madrid*: Ciempozuelos, Salinas de Espartinas MNCN 689. Rivas del Jarama MNCN 18494 DS. Tielmes MNCN 21624. *Palencia*: Barruelo de Santullán MNCN UZA1879. *Rioja*: El Rasillo de Cameros MNCN UZA1814, UZA1824–1826, UZA1827–1831, UZA1832–1834, UZA1875, UZA2476. Valgañón MNCN 19775 C&S. *Segovia*: Montejo de la Vega de la Serrezuela MNCN 20120–20140 C&S, MNCN 23692 DS. *Soria*: Layna MNCN 19402–19403. Torralba EBD 29839. Teruel: Mora de Rubielos MNCN UZA1877. *Valencia*: Llombay MNCN UZA1803–1813, MNCN UZA1815–1823. Plá dels Coralls MNCN 20166–20175 C&S. Torrente MNCN 688. No locality data MNCN 666–668, 670–673, 681–686, 2720–2725. *Zaragoza*: No locality data MNCN UZA1835. Tarazona MNCN UZA1914. Questionably, one badly preserved specimen from an unknown locality in the Almería province (EBD 26828) could be the most meridional record of the species. In addition, living specimens (not collected) were measured from: *Burgos*: Cernégula, Fuencaliente de Lucio, Huérmeces, Humada, Masa, Moradillo de Sedano, Mundilla, Quintanilla, Quintaniloma, Renedo de la Escalera, San Martín de Ubierna, Sasamón, Sotopalacios, Tubilla-Masa, and Villadiego. *Cuenca*: Serranía de Cuenca and Uña. *Madrid*: Tielmes. *Palencia*: Aguilar de Campoo and Valoria. *Segovia*: Montejo de la Vega de la Serrezuela. *Soria*: Aguilar-Barruelo. *Toledo*: Los Yébenes. *Valencia*: Plá dels Coralls and Simat de Valldigna.

APPENDIX II

Definitions of Landmarks and Measurements

Landmarks are defined anatomically below. Their normal (orthogonal) projections on the transverse plane are represented in Fig. 2, and all measurements (Tables 4, 8) are distances between projected landmarks, indicated by their numbers. For example, D(2–3) indicates the straight length between the normal projected landmarks 2 and 3, i.e., between the projections on the transverse plane of the left and right midpoints of the articulation between premaxilla and maxilla. Definitions of landmarks: 1: most anterior point of the premaxillary articulation. 2, 3: midpoints of the left (2) or right (3) articulation between premaxilla and maxilla. 4, 5: most anterior point of left (4) or right (5) nasal. 6: in the sagittal axis, the most posterior point of the tectum nasi, in contact with the most anterior point of sphenethmoid. 7, 8: most posterior points of left (7) or right (8) nasals in their medial margin. 9: in the sagittal axis, the most posterior point of the dorsal tectum of the sphenethmoid. 10, 11: points in the left (10) or right (11) frontoparietal medial margin at the level in which the distance between both bones is minimal. 12, 13: posterior-medial corner of the left (12) or right (13) orbit, as indicated by the most lateral frontoparietal point. 14, 15: lateral points of the left (14) or right (15) occipital condyles. 16, 17: most posterior points of the left (16) or right (17) prootic-exoccipital complex. 18, 19: most posterior points of left (18) or right (19) maxilla. 20: midpoint between the normal projections on the sagittal plane of landmarks 14 and 15. 21, 22: most anterior points of the sacral left (21) or right (22) transverse processes. 23: in the sagittal axis, point of articulation between sacrum and urostyle. 24, 25: most posterior points of the sacral left (24) or right (25) transverse processes. 26: most posterior point of urostyle. 27: midpoint between the normal projections on the sagittal plane of landmarks 12 and 13.

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