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TWO NEW SPECIES IN THE GENUS *PSAMMODROMUS* (REPTILIA: LACERTIDAE) FROM THE IBERIAN PENINSULA

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ABSTRACT

The lacertid lizard *Psammodromus algirus* has been considered a uniform species across its distribution area in North Africa and southwestern Europe. Coloration data and discriminant function analysis of morphological data corroborate mitochondrial DNA and allozyme data to indicate northern and southern Iberian populations represent unknown species that are described here. Additional work is needed to fully understand biogeography and variation in this species complex.

RESUMEN

El lacértido *Psammodromus algirus* ha sido considerado hasta ahora una especie uniforme a lo largo del norte de Africa y de la península Ibérica. Datos de coloración así como un análisis mediante función discriminante de datos morfológicos confirman datos de ADN mitocondrial y de alozimas que muestran que poblaciones del norte y del sur de la península Ibérica pertenecen a especies no conocidas y que son descritas en este trabajo. Trabajo adicional es necesario para conocer con más detalle la biogeografía y variación en este complejo de especies.

KEY WORDS: Spain, Iberia, *Psammodromus algirus*

INTRODUCTION

Mitochondrial DNA variation in *Psammodromus algirus* (Linnaeus) 1758 indicates that European and African populations of this taxon represent different species. Subunit 4 of the NADH dehydrogenase gene (ND4) in sampled populations from Morocco differs from ND4 in populations from Iberia by an average *p*-distance of 4.6%. Examination of allozyme variation between continental populations also suggests differentiation; when comparing representatives from populations between continents, Nei's $\hat{D}$ values ranged from 0.04 to 0.13. In a sample of 35 presumptive gene loci, ten alleles from the 12 polymorphic loci were unique to Iberia and eight were unique to Morocco. Of these 20 unique alleles, four alleles (two from each continent) comprised the fixed difference identified in allozymes representing glucose-6-phosphate dehydrogenase (see Busack and Lawson in press for details).

While it is clear from these data that European and African populations present differing genetic histories, it is also clear from our investigations that there are representatives from at least two genetic stocks present within the Iberian Peninsula. ND4 in a population from Madrid Province differs from ND4 in a population from Cádiz Province by an average *p*-distance of 2.2 %, and fixed differences in allozymes representing acid phosphatase (Acp) and isocitrate dehydrogenase (Idh) from these two populations contribute to Nei's $\hat{D}$ values ranging from 0.10 to 0.11 (see Busack and Lawson in press for details).

Because the type locality for *Psammodromus algirus* is Mauritania (referring to all of north-western Africa in the eighteenth century; the species does not occur in the political unit currently known as Mauritania), we searched the species synonomy in Mertens and Wermuth (1960) and Alonso-Zarazaga (1998) for available names associated with European populations. Only *Lacerta* (*Algyra*) *cuvieri* Gray in Griffith 1831 and *Lacerta carinata* Schinz 1833 were found, and neither type specimen is extant nor associated with locality data more specific than "Spain." In addition, Gray's description ("Back and tail with keeled scales, belly with smooth imbricate scales, collar none, femoral pores numerous…tail long, round, brown, beneath yellowish, with two yellow streaks on each side; length four inches") is not sufficiently diagnostic and Schinz's description, that dorsals are small, lanceolate and keeled, with flanks covered by granular scales, describes neither *P. algirus* nor representatives of populations we examined. We considered both synonyms uninterpretable, dubious names (*nomina dubia*), and therefore unavailable.

We next initiated an analysis of morphological differenti-

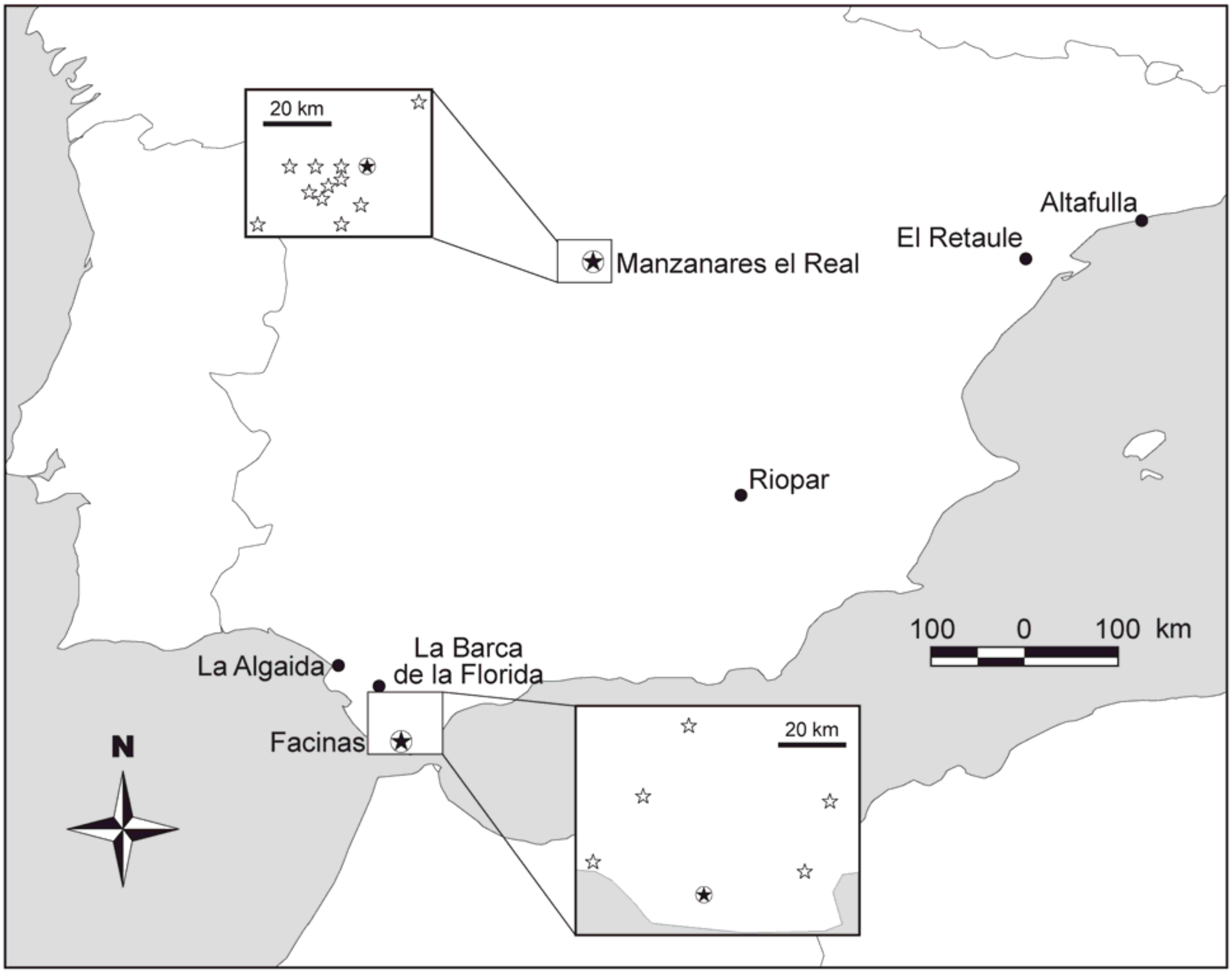

Fig. 1.—Study areas in Iberia. Closed stars in circles indicate holotype and paratype localities, open stars indicate localities of additional material utilized for species descriptions. See appendix for precise locality information.

ation involving both populations we knew to be genetically differentiated, and compared data from those populations to data from four additional populations in Iberia as a means by which to understand morphological differentiation in representatives of these lizards in the Iberian Peninsula. Allozyme (Acp and Idh) and mtDNA (ND4) data (Busack and Lawson in press), in concert with morphological data indicate that populations inhabiting the north and the south of the Iberian Peninsula are not conspecific. The morphological data supporting this conclusion, together with a description of two new species from Iberia, are presented herein.

MATERIALS AND METHODS

To reduce the possibility of error introduced when several investigators take measurements and record data, all specimens were processed by Salvador in Madrid. Continuously distributed characters (snout-vent length [SVL]; snout length [anterior margin of eye to anterior edge of rostral]; head length [posterior margin of occipital to anterior edge of rostral]; head width [measured at level of anterior margin of tympanum]; forearm length; fourth toe length (front foot); hind leg length; and body length [posterior margin of front limb to anterior margin of rear limb] were measured to 0.1 mm with dial calipers. Number of chin shields (in medial contact behind the mental); infralabial scales; supralabial scales (anterior to subocular); dorsal scale rows (mid-body); transverse ventral scale rows (axilla to groin); longitudinal ventral scale rows (mid-body); enlarged (=broader than long) forearm scales (axilla to wrist); subdigital lamellae (fourth digit, front foot) and femoral pores were also recorded.

Ocellus area was determined by producing a camera lucida image of the ocellus with a 1 mm scale included, scanning (425 pixels/mm) this image into a computer equipped with Adobe Photoshop©, and counting the number of pixels included within the ocellus. The 1 mm scale included in the drawing was then used to calculate the number of pixels included in 1 mm^2 and, hence, the area of the ocellus. The number of scales involved in the ocellus is the number of scales with blue pigmentation that contribute directly to the appearance of the ocellus. Summaries of raw data and vouchers and localities for the six populations (males and females) are provided in Tables 1 and 2 and in the appendix, respectively.

We used SYSTAT 11.00.0l (Systat Software, Inc. 2004) for calculating statistical values and performing classical discriminant function analysis (DFA). Population of origin (Fig. 1) was considered the grouping variable, morphological variables were considered predictors, prior probabilities were computed from group sizes, and a covariance matrix was used to calculate Mahalanobis distance to group centroids. The Mahalanobis approach standardizes the data by scaling in terms of standard deviations, and sums pooled within-group variance-covariance, thereby adjusting for intercorrelations among our highly-correlated variables (Hair et al. 1992).

Sexually mature (SVL ≥ 62 mm for Madrid Province, SVL ≥ 55 mm for Cádiz Province; unpublished data) males and females were analyzed separately, and we used an iterative process for data reduction. Number of chin shields (females 2–4, males 2–3; $\bar{x} = 3$ in each sex), infralabial scales (females and males 5–7; $\bar{x} = 6$ in each), supralabial scales (females 3–5, males 4–5; $\bar{x} = 4$ in each) and longitudinal ventral scale rows (six in all) did not contribute to discriminatory power and were eliminated from further consideration. Next, using meristic and continuous variables separately, we performed DFA with the goal of achieving the highest possible percentage of correct classification into groups. Number of transverse ventral scale rows and forearm length did not enhance discriminatory power within the dataset for females, and number of transverse ventral scale rows, number of enlarged forearm scales, number of dorsal scale rows and snout length did not enhance discriminatory power within the dataset for males and were not considered in the iterative analyses.

We utilized data representing head length, head width, fourth toe length, hind leg length, body length, number of subdigital lamellae and number of femoral pores as the basic dataset for our analysis of both sexes. In addition, forearm length, ocellus area and number of scales involved in the ocellus enhanced discriminatory power for males while snout length, the number of dorsal scale rows, and the number of enlarged forearm scales enhanced discriminatory power for females; these characters were then added to the basic dataset for each sex, as appropriate, in the iterative DFA analyses.

RESULTS

When the dataset for males was analysed by DFA, the classification process correctly assigned 81% of all specimens to the populations from which they were collected. During data collection, however, we noted that specimens from La Algaida more closely resembled specimens from Manzanares el Real than specimens from geographically closer La Barca de la Florida or Facinas (Fig. 1). When we considered only these four populations, the classification function correctly assigned 96% of specimens to their respective populations (Fig. 2A). When we combined samples from La Algaida with those from Manzanares el Real and samples from La Barca de la Florida with those from Facinas to reduce the dataset to two groups, the DFA again correctly assigned all but two of 49 specimens (96%; one specimen from each combined locality was misclassified into the alternate grouping; Fig. 2B). During our final iteration, we used datasets for Albacete (=Riopar), Facinas plus La Barca de la Florida, Manzanares el Real plus La Algaida, and Tarragona (El Retaule plus Altafulla). While the overall classification percentage was high (82%), with Facinas plus La Barca de la Florida at 100%, and Manzanares el Real plus La Algaida at 89%, samples representing Albacete and Tarragona were correctly assigned less frequently (46% and 60%, respectively). Of incorrectly assigned Albacete material, three specimens were considered more similar to those from Manzanares el Real plus La Algaida, one was considered more similar to those from Facinas plus La Barca de la Florida, and three were misclassified as having originated from Tarragona (data not shown).

Examination of the dataset for females by DFA correctly assigned 93% of all specimens to the populations from which they were collected. When we considered only specimens from Facinas, La Algaida, La Barca de la Florida, and Manzanares el Real as we had for males, the classification function also correctly assigned 93% of specimens to their respective populations (Fig. 2A). Combining samples from La Algaida with those from Manzanares el Real and samples from La Barca de la Florida with those from Facinas resulted in correct assignment of all but six of 61 specimens (90%; with three specimens from each combined locality misclassified into the alternate grouping; Fig. 2B). During our final iteration, we again used datasets for Albacete, Facinas plus La Barca de la Florida, Manzanares el Real plus La Algaida, and Tarragona. Overall classification percentage was again high (84%), with Facinas plus La Barca de la Florida at 85%, and Manzanares el Real plus La Algaida at 88%, and with samples representing Albacete and Tarragona again correctly assigned less frequently (71%, with two specimens being placed with Manzanares el Real plus La Algaida and 67%, with one specimen placed with Facinas plus La Barca de la Florida and one with Albacete, respectively [data not shown]).

These results, coupled with previously published results from an analysis of mitochondrial DNA and allozymes (Busack and Lawson in press), convince us that *Psammodromus algirus* actually represents a species complex in which there are at least two separate, undescribed, species inhabiting the Iberian peninsula. We take this opportunity to describe these previously unrecognized species with the expectation that our work on the *Psammodromus algirus* species complex will provide the impetus for more detailed study of phylogeography in this lizard.

SYSTEMATIC ZOOLOGY

(Indented phylogenetic taxonomy without ranks following Estes et al. 1988:255)

Reptilia Laurenti 1768
  Squamata Merrem 1820
    Scleroglossa Estes, de Querioz, and Gauthier 1988
      Autarchoglossa Wagler 1830
        Scincomorpha Camp 1923
          Lacertoidea Camp 1923
            Lacertiformes Estes, de Queiroz, and Gauthier 1988
              Psammodromus Fitzinger 1826

Psammodromus manuelae, new species
(Fig. 3A)

Holotype.—MNCN 36792, an adult male, collected by J. Ibáñez, 24 June 1973.

Type locality.—Manzanares el Real, Madrid Province, Spain, 40°44' N, 3° 52' W.

Paratypes.—CM 60946 and 60950; MNCN 7830, 36791 and 36797; USNM 199211 and 199212.

Etymology.—This new species is dedicated to Manuela González, wife of Alfredo Salvador.

Diagnosis.—One of two members in the *Psammodromus algirus* complex known to inhabit Europe. In addition to mtDNA and allozyme differences published earlier (Busack and Lawson in press), *P. manuelae* can be distinguished from the other known European member of the complex (see below) by, in males, having an average of eight (vs four) blue scales in the ocellus, and an ocellus area of approximately 4 mm^2 (vs 2 mm^2). In addition, males tend to have a higher number of femoral pores ($\bar{x}$ = 18 vs $\bar{x}$ = 16) and dorsal scale rows ($\bar{x}$ = 25 vs $\bar{x}$ = 24) and, generally, a wider head ($\bar{x}$ = 11.7 mm vs 10.7 mm). Coloration in males differs from the other known European member of the complex in that the blue ocelli are bordered in black, as opposed to not being bordered in black, the dorsal surfaces of the head, body, limbs and tail are uniform brown as opposed to being uniform pale olive brown, the lateral band is dark brown with black scales and yellow spots tending to form vertical, and parallel, series that alternate along each side of the body, as opposed to being pale olive brown with very few black scales.

Females tend to have a lower number of subdigital lamellae ($\bar{x}$ = 14 vs $\bar{x}$ = 15) and higher number of femoral pores ($\bar{x}$ = 16 vs $\bar{x}$ = 14) and dorsal scale rows ($\bar{x}$ = 25 vs $\bar{x}$ = 24), and, generally, a wider head ($\bar{x}$ = 10.2 mm vs 9.6 mm) than the other known European member of the complex. General coloration in female *P. manuelae* is lighter, but similar to that of males; females, however, have neither black scales nor yellow spots on the sides, and the small blue ocellus is bordered by brown instead of black.

Description (holotype, MNCN 36792).—Snout-vent length 71.0 mm, snout length 6.0 mm, head length 16.4 mm, head width 11.4 mm, forearm length 23.3 mm, fourth toe length 6.6 mm, hind leg length 38.4 mm, body length 32.0 mm, tail length 159.0 mm; dorsal scale rows 26, transverse ventral scale rows 25, longitudinal ventral scale rows 6 , supralabial scales 4, infralabial scales 6, three pairs of chin shields, enlarged forearm scales 17, subdigital lamellae 15, femoral pores 16. In preservative, dorsal surfaces of head, body, limbs and tail are uniform brown; lower surfaces of head, body, limbs and tail are whitish. There are two longitudinal yellowish stripes present on each side of the body; dark scales border above the anterior portion of the upper stripe and the lateral band between the stripes is dark brown with black scales and yellow spots. These spots tend to form vertical, and parallel, series along each side of the body. There are two black-bordered blue ocelli present in the anterior portion of the lateral band. The area of the most anterior ocellus on the right side is 2.08 mm^2 and there are 6 scales involved (inset, Fig. 3A)

Variation (paratypes, all from Manzanares el Real).—Mean ± SE, and ranges for values of the three males are: snout-vent length 71.0 ± 0.0 (no variation) mm, snout length 6.9 ± 0.3 (6.4–7.4) mm, head length 17.8 ± 0.7 (16.7–19.1) mm, head width 12.3 ± 0.6 (11.7–13.4) mm, forearm length 22.3 ± 0.2 (22.0–22.8) mm, fourth toe length 6.6 ± 0.3 (6.2–7.2) mm, hind leg length 39.9 ± 0.2 (39.5–40.1) mm, body length 35.2 ± 1.4 (32.5–36.7) mm; dorsal scale rows 25.3 ± 0.7 (24–26), transverse ventral scale rows 23.7 ± 0.3 (23–24), enlarged forearm scales 20.7 ± 1.2 (19–23), subdigital lamellae 14.3 ± 0.9 (13–16), femoral pores 17.7 ± 0.9 (16–19). Ocellus area varied between 3.75 mm^2 (USNM 199212) and 3.76 mm^2 (CM 60946), and there were six (CM 60946) and eight (USNM 199212) scales involved in these ocelli. Coloration is similar to that of the holotype but the number of blue ocelli on the right side varies between one (MNCN 36797), two (CM 60946) and three (USNM 199212).

Mean ± SE, ranges and sample sizes for values of the females are: snout-vent length 69.4 ± 3.1 (62.5–76.0) mm (n=4), snout length 6.1 ± 0.2 (5.7–6.4) mm (n=3), head length 15.4 ± 0.5 (14.4–16.2) mm (n=3), head width 10.1 ± 0.5 (9.2–10.9) mm (n=3), forearm length 21.2 ± 0.6 (20.0–22.7) mm (n=4), fourth toe length 6.1 ± 0.1 (5.8–6.3) mm (n=4), hind leg length 34.2 ± 0.6 (32.7–35.5) mm (n=4), body length 37.4 ± 2.0 (33.2–42.8) mm (n=4), dorsal scale rows 25.5 ± 0.7 (24–27, n=4), transverse ventral scale rows 24 ± 0.4 (23–25, n=4), enlarged forearm scales 18.5 ± 0.7 (17–20, n=4); subdigital lamellae 13.8 ± 0.6 (12–15, n=4), femoral pores 15.8 ± 0.3 (15–16, n=4). General coloration in females is similar, but lighter, than that of males. Lateral aspect is dark brown in MNCN 7830, 36791 and 60950, and light brown in USNM 199211. All females have neither black scales nor yellow spots on the sides, and the small blue ocellus is bordered by brown.

Distribution.—Presently known only from the immediate vicinity of the type locality (see discussion for details).

Psammodromus jeanneae, new species
(Fig. 3B)

Holotype.—MNCN 11941 (S. D. Busack field series [SDB] 1526; GenBank DQ 150373 [NADH subunit 4] and DQ 150387 [NADH subunit 2]; MVZ 232055 [tissue sample]), an adult male, collected by S.D. Busack and J.A. Visnaw, 12 June 1982.

Type locality.—25.6 km NE of Facinas (36° 08 N, 5° 42 W) along CA-221, Cádiz Province, Spain, elevation ca. 200 m.

Paratypes.—CM 53198–53199 and 54566; MNCN 11937–11938,

TABLE 1. Comparison of male continuous and meristic characters in named and referred (La Algaida and La Barca de la Florida, respectively) populations of *Psammodromus manuelae* and *P. jeanneae*, and in populations for which determination was inconclusive (Albacete and Tarragona). Data presented as mean (range) sample size.

	P. manuelae (n=25)	La Algaida (n=26)	*P. jeanneae* (n=13)	La Barca de la Florida (n=15)	Albacete (n=14)	Tarragona (n=5)
Snout-vent length	70.7(65.0–77.0)25	64.9(59.0–71.0)26	69.2(60.0–75.0)13	60.6(54.5–71.0)15	70.3(64.0–78.0)14	70(60.0–77.0)5
Snout length	6.4(5.7–7.4)25	6.4(5.2–7.3)25	6.5(5.6–7.6)13	5.8(5.2–6.9)15	6.2(5.6–7.1)14	6.3(5.4–6.9)5
Head length	16.9(14.9–19.1)25	16.6(14.1–18.1)25	16.7(14.2–17.9)13	15.3(14.0–17.5)15	16.5(15.0–18.1)14	16.1(13.8–16.9)5
Head width	11.7(9.5–13.4)25	10.6(9.4–11.8)26	10.7(9.7–11.6)11	9.4(8.5–11.8)15	11.2(9.7–12.4)13	10.7(9.1–12.2)5
Forearm length	22.5(20.8–25.0)25	20.8(18.5–23.0)26	22.0(20.2–25.4)13	18.8(16.6–22.0)15	21.4(17.8–22.9)14	21.2(18.6–22.8)5
Fourth Toe length	6.4(5.7–7.4)25	5.9(5.0–6.7)25	6.4(5.0–7.8)13	5.7(5.0–7.2)14	6.3(5.2–7.1)14	6.0(5.4–6.3)5
Hind Leg length	39.1(35.1–44.4)25	36.1(32.6–39.6)26	36.3(31.5–39.7)13	33.3(28.8–40.1)15	34.4(22.1–38.4)14	34.6(30.2–36.3)5
Body length	34.4(27.8–37.7)25	32.5(27.8–43.2)26	34.2(29.2–37.5)13	28.7(24.4–32.5)15	34.2(28.2–41.2)14	34.6(29.2–38.1)5
Dorsal scale rows	25.4(23–27)25	25.2(23–27)24	24.2(22–26)13	24.2(22–27)15	24.9(23–28)14	24.2(23–25)5
Transverse ventral scale rows	22.5(20–25)25	22.9(21–26)26	22.8(21–24)13	22.5(20–25)15	22.6(21–24)14	23(23)5
Enlarged forearm scales	18.8(17–23)25	18.0(16–21)25	17.9(15–19)13	18.1(16–20)15	17.9(16–19)14	16.8(15–19)5
Subdigital lamellae	15.0(13–16)25	14.7(13–16)26	15.0(14–15)13	14.4(13–16)14	13.6(12–15)14	12.8(11–14)5
Femoral pores	17.8(15–20)25	17.8(15–20)26	15.5(14–17)11	16.1(15–18)14	16.9(15–19)14	15.4(14–16)5
Ocellus area	3.7(1.9–8.9)15	2.2(1.2–3.6)14	1.9(1.1–3.5)12	1.2(0.5–3.8)15	2.2(1.0–3.4)14	1.9(0.9–2.9)5
Ocellus scales	7.7(6–13)15	6.0(4–10)14	4.3(2–9)12	4.1(2–8)15	6.9(3–15)14	5(2–7)5

TABLE 2. Comparison of female continuous and meristic characters in named and referred (La Algaida and La Barca de la Florida, respectively) populations of *Psammodromus manuelae* and *P. jeanneae*, and in populations for which determination was inconclusive (Albacete and Tarragona). Data presented as mean (range) sample size.

	P. manuelae (n=25)	La Algaida (n=17)	*P. jeanneae* (n=10)	La Barca de la Florida (n=13)	Albacete (n=7)	Tarragona (n=8)
Snout-vent length	72.5(62.5–79.0)25	62.3(56.0–66.0)17	68.7(60.0–76.0)10	61.0(57.0–66.0)13	69.1(60.0–75.0)7	69.0(64.0–75.5)8
Snout length	6.0(5.3–6.6)24	5.8(5.2–6.4)17	6.1(5.4–6.6)10	5.2(4.3–6.0)13	5.4(5.0–6.1)7	5.8(5.6–6.3)6
Head length	15.3(13.7–16.7)24	14.7(13.7–15.5)17	15.3(13.5–16.7)10	13.8(12.5–14.8)13	14.6(12.8–15.8)7	14.6(13.5–15.6)6
Head width	10.2(8.8–11.6)24	9.1(8.1–10.3)17	9.6(7.9–10.3)10	8.3(7.5–9.0)11	9.8(9.0–10.6)7	9.5(8.1–10.6)6
Forearm length	21.5(20.0–27.1)25	18.9(16.2–20.4)17	21.2(18.6–23.7)10	18.0(15.8–19.1)13	19.5(17.4–21.6)7	20.1(19.2–21.5)8
Fourth Toe length	6.0(5.3–7.2)25	5.4(4.8–6.0)17	6.6(5.9–7.3)10	5.5(5.0–5.9)13	5.4(4.4–5.8)7	5.9(5.6–6.3)8
Hind Leg length	35.3(32.1–39.6)25	31.3(28.3–34.6)17	34.1(31.8–37.6)10	30.4(27.1–32.7)13	31.8(28.9–34.6)7	31.4(30.2–32.8)8
Body length	39.1(33.2–44.3)25	33.1(30.0–35.3)17	36.4(29.1–43.7)10	32.8(28.3–37.2)13	35.9(32.6–41.2)7	35.8(31.4–40.5)8
Dorsal scale rows	25.4(22–27)25	25.5(23–28)17	23.8(22–27)10	23.9(22–27)13	24.6(23–27)7	23.3(21–25)8
Transverse ventral scale rows	23.8(22–27)25	24.0(23–26)17	23.9(22–26)10	23.9(22–26)13	24.6(23–26)7	23.4(21–26)8
Enlarged forearm scales	18.4(17–20)25	18.3(17–20)17	18.1(17–19)10	17.7(17–19)12	17.0(15–18)7	17.0(15–18)8
Subdigital lamellae	13.9(12–16)25	15.4(14–16)17	15.1(13–16)10	14.6(14–16)13	12.9(11–15)7	12.6(11–14)8
Femoral pores	16.0(14–19)25	16.4(13–20)17	14.4(13–16)10	14.5(13–18)13	15.6(15–17)7	14.4(13–17)8

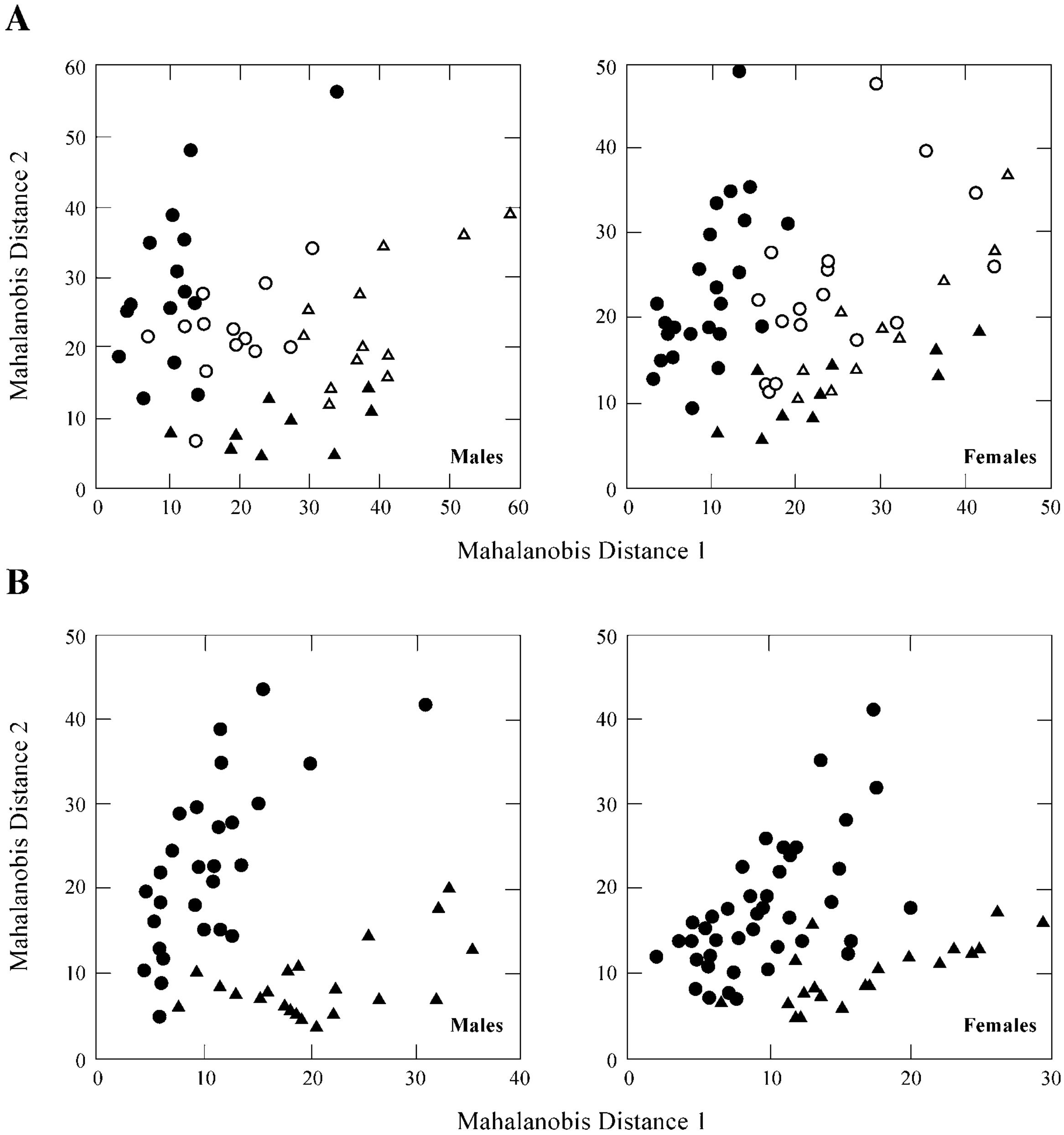

Fig. 2.—Results from Discriminant Function Analysis. **A**, Manzanares el Real represented by closed circles; La Algaida, open circles; Facinas, closed triangles; and La Barca de la Florida, open triangles. **B**, Manzanares el Real plus La Algaida represented by closed circles; Facinas plus La Barca de la Florida, closed triangles.

11940 (SDB 1525, GenBank DQ 150372 [NADH subunit 4] and DQ 150386 [NADH subunit 2]), 11942 (SDB 1527, GenBank DQ 150374 [NADH subunit 4]; MVZ 232056 [tissue sample]), 11944, and 36727.

Etymology.—Named in honor of Jeanne A. Visnaw, wife of Stephen D. Busack, who succumbed to ovarian cancer on 9 September 2005. Jeanne was an integral part of Busack's life, including all field and laboratory work, from 1977 to 2005. She located and captured the first example of this species during 1982, and prepared both the voucher and its tissue for later examination.

Diagnosis.—One of two members in the *Psammodromus algirus* complex known to inhabit Europe. In addition to mtDNA and allozyme differences published earlier (Busack and Lawson in press), *P. jeanneae* can be distinguished from *P. manuelae* by, in males, having an average of four (vs eight) blue scales in the ocellus, and an ocellus area of approximately 2 mm^2 (vs 4 mm^2). In addition, males tend to have a lower number of femoral pores ($\bar{x} = 16$ vs $\bar{x} = 18$) and dorsal scale rows ($\bar{x} = 24$ vs $\bar{x} = 25$), and, generally, a narrower head ($\bar{x}$ = 10.7 mm vs 11.7 mm). Coloration differs from *P. manuelae* in having dorsal sur-

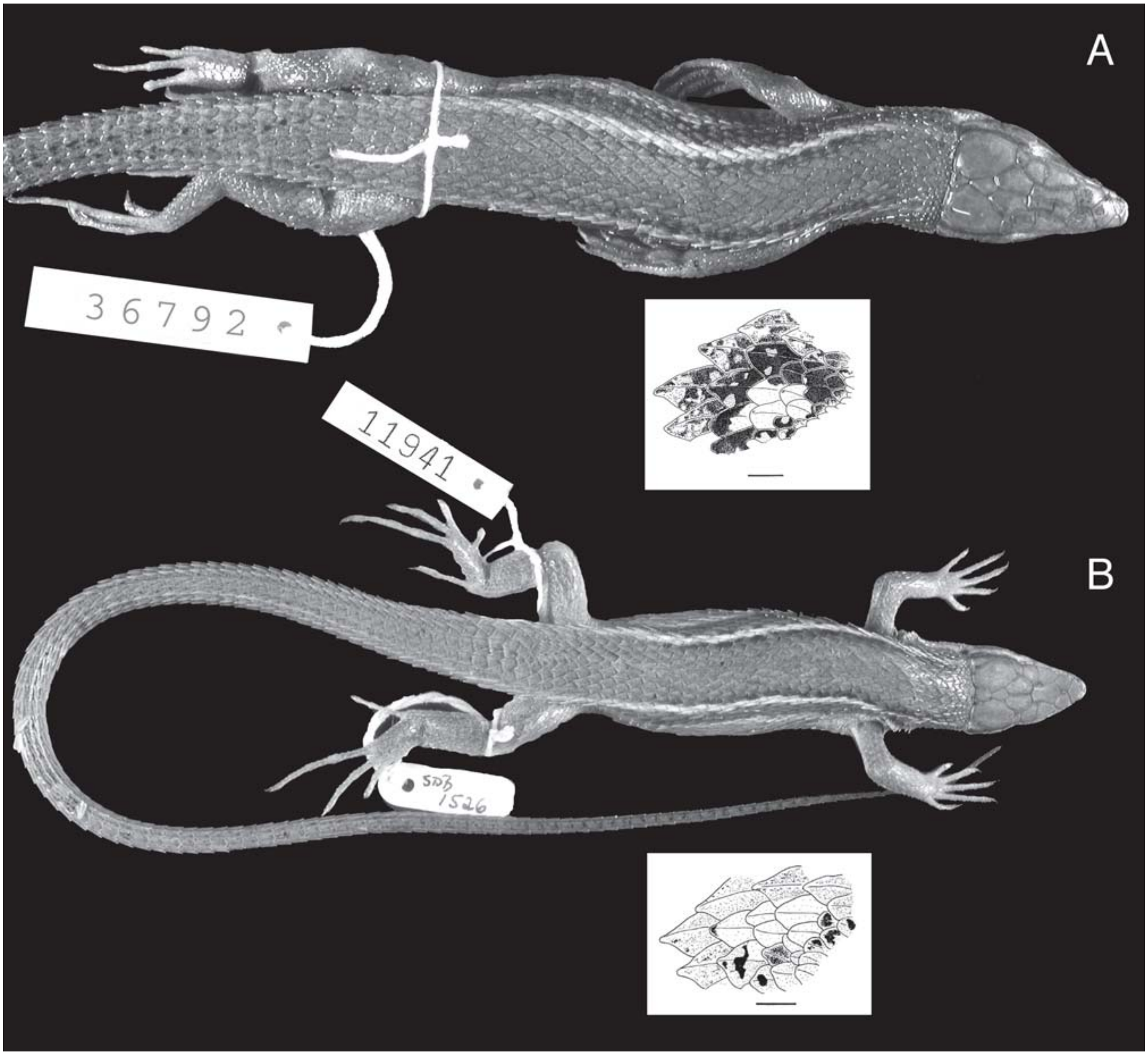

Fig. 3.—Holotypes of *Psammodromus manuelae* (A) and *P. jeanneae* (B). Insert is a camera lucida representation of the anterior right ocellus; scale bar represents 1 mm.

faces of the head, body, limbs and tail uniform pale olive brown as opposed to uniform brown, the two longitudinal stripes on each side of the body white as opposed to yellowish, and the lateral band between these stripes pale olive brown with very few black scales as opposed to dark brown with black scales and yellow spots.

Females tend to have a higher number of subdigital lamellae ($\bar{x}$ = 15 vs $\bar{x}$ = 14) and lower number of femoral pores ($\bar{x}$ = 14 vs $\bar{x}$ = 16) and dorsal scale rows ($\bar{x}$ = 24 vs $\bar{x}$ = 25), and, generally, a narrower head ($\bar{x}$ = 9.6 mm vs 10.2 mm) than *P. manuelae*. Coloration in females is similar to that of males.

Description (holotype, MNCN 11941).—Snout-vent length 71.0 mm, snout length 6.4 mm, head length 17.1mm, head width 11.0 mm, forearm length 23.2 mm, fourth toe length 6.8 mm, hind leg length 37.0 mm, body length 37.5 mm, tail length 209.0 mm, mass (in life) 11.8 g; dorsal scale rows 24, transverse ventral scale rows 23, longitudinal ventral scale rows 6, supralabial scales 4, infralabials 6, three pairs of chin shields, enlarged forearm scales 18, subdigital lamellae 14, femoral pores 15. In preservative, dorsal surfaces of head, body, limbs and tail are uniform pale olive brown; lower surfaces of head, body, limbs and tail are whitish. There are two longitudinal white stripes present on each side of the body; the anterior portion of the upper stripe is bordered above by dark scales and the lateral band between the stripes is pale olive brown with very few black scales. There are two blue ocelli that are not bordered in black present in the anterior portion of the lateral band (inset, Fig. 3B).

Variation (paratypes, all from the vicinity of Facinas).—Mean ± SE, and ranges for values of the six males are: snout-vent length 72.7 ± 1.2 (68.0–75.0) mm, snout length 6.8 ± 0.2 (6.2–7.6) mm, head length 17.2 ± 0.3 (16.4–17.9) mm, head width 11.1 ± 0.2 (10.4–11.6) mm, forearm length 22.7 ± 0.6 (21.2–25.4) mm, fourth toe length 6.9 ± 0.3 (5.9–7.8) mm, hind leg length 37.7 ± 1.2 (32.5–39.7), body length 35.5 ± 0.4 (34.0–36.9) mm; dorsal scale rows 24.2 ± 0.5 (22–25), transverse ventral scale rows 22.5 ± 0.4 (21–24), enlarged forearm scales 18.3 ± 0.3 (17–19), subdigital lamellae 15.3 ± 0.3 (14–16), femoral pores 15.5 ± 0.4 (14–17), ocellus area 1.8 ± 0.3 (1.1–2.8) mm^2, scales involved in ocelli 3.3 ± 0.6 (2–6). General coloration similar to holotype, anterior portion of upper stripe bordered above by dark scales except in CM 53198–53199 where the upper stripe is bordered above by brown scales. Two blue ocelli on the right side in MNCN 11940 and one blue ocellus in the others.

Mean ± SE, and ranges for values of the three females are: snout-vent length 70.8 ± 2.2 (66.5–73.0) mm, snout length 6.1 ± 0.2 (5.9–6.4) mm, head length 15.2 ± 0.2 (14.9–15.5) mm, head width 9.9 ± 0.1 (9.8–10.0) mm, forearm length 22.6 ± 0.6 (21.7–23.7) mm, fourth toe length 6.8 ± 0.3 (6.2–7.3) mm, hind leg length 34.6 ± 0.7 (33.5–35.9), body length 38.2 ± 2.0 (34.3–40.6) mm; dorsal scale rows 24.0 ± 1.0 (22–25), transverse ventral scale rows 24.7 ± 0.3 (24–25), enlarged forearm scales 18.7 ± 0.3 (18–19), subdigital lamellae 15.3 ± 0.3 (15–16), femoral pores 13.3 ± 0.3 (13–14). General coloration similar to holotype, anterior portion of upper stripe bordered above by dark scales in MNCN 11937–11938, and by light scales in CM 54566. MNCN 11938 has a small whitish spot on the anterior portion of the right side.

Distribution.—Presently known only from the immediate vicinity of the type locality (see discussion for details).

DISCUSSION

Busack and Lawson (in press) estimated that clades representing *Psammodromus algirus* inhabiting northern and southern shores of the Strait of Gibraltar likely ceased reproductive contact between 3.23 and 2.98 million years ago (Pliocene), and cessation of complete reproductive contact between northern and southern Spanish populations began approximately 1.54 to 1.40 million years ago (early to mid-Pleistocene). If *Psammodromus* inhabited the Guadalquivir Basin as events associated with the formation of the Strait of Gibraltar unfolded, ancestral *P. jeanneae* would have become dissociated from the Moroccan *P. algirus*. As geologic change progressed, and the region became less fragmented, *P. jeanneae* likely was temporally limited in its northward expansion by the Río Guadalquivir, and later variously affected by Pliocene-early Pleistocene climate changes in eastern Iberia (de Jong 1998; García and Arsuaga 2003). Our limited distributional data suggest an evolutionary scenario for *P. jeanneae* and *P. manuelae* similar to that proposed by García-Paris and Jockusch (1999) and Martínez-Solano (2004) for the anuran genus *Discoglossus* in this same region.

Our data suggest a very close morphological similarity between *Psammodromus manuelae* and the population currently inhabiting La Algaida (Fig. 2, Tables 1 and 2). Because of this similarity, we refer the La Algaida population to *P. manuelae* with the realization that this placement assumes a secondary invasion by *P. manuelae* into areas east of the Río Guadalquivir. The population east of the Río Guadalete (7.8 km east of La Barca de la Florida), however, is morphologically similar to *P. jeanneae*, and we feel confident referring this population to *P. jeanneae* and thereby further delimiting its distribution as east and south of the shores of the Río Guadalete within Cádiz Province, Spain.

As sample sizes from Albacete and Tarragona were limited (21 and 13, respectively), and discriminant function misclassifications were high (43% and 31%, respectively), we are reluctant to assign either population to species. Our data and those of Busack and Lawson (in press) suggest that further study is necessary before we fully understand evolution and biogeography of the *Psammodromus algirus* species complex in Europe.

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APPENDIX. Material examined.

Geographic coordinates from Official Standard Names Gazetteer for Spain (1961), United States Board on Geographic Names, Department of the Interior, Washington, D.C., and Mapa Topográfico Nacional de España (2003), Instituto Geográfico Nacional, Madrid (MTN50, Sheet 521) for El Retaule. Museum acronyms follow Leviton et al. (1985).

Psammodromus jeanneae. SPAIN (Cádiz Province): Alcalá de los Gazules (36° 28' N, 5° 44' W), CM 51084; Barbate de Franco (36°12' N, 5° 55' W), CM 55453–55454 and 55487–55488; Benalup de Sidonia (36° 20' N, 5° 49' W), CM 53389, 53410 and 53412, MNCN 11945–11947; Castellar de la Frontera (36° 19' N, 5° 27' W), MNCN 11954 (tissue sample: MVZ 232053); Facinas (36°08' N, 5°42' W), CM 53198–53199 and 54566 (paratypes), MNCN 11937–11938 (paratypes), 11940, 11941 (holotype), 11942 (paratype), 11944 and 36727 (paratypes); and Los Barrios (36° 11' N, 5° 30' W), MNCN 11953 (tissue sample: MVZ 232051).

Referred to *Psammodromus jeanneae*. SPAIN (Cádiz Province): La Barca de la Florida (36°40' N, 5° 55' W), CM 51088–51089, 51095–51097, 51106, 51330–51331, 51333, 51923, 51930–51931, 51933, 51935, 51948, 51951–51952, 51977, 52179, 53091–53092, 53108, 53304–53306, 53045c and 53045d.

Psammodromus manuelae. SPAIN (Madrid Province): Alpedrete (40° 40' N, 4° 01' W), MNCN 6263, 36994–36996; Cerceda (40° 42' N, 3° 56' W), MNCN 37003; Cercedilla (40° 44' N, 4° 04' W), MNCN 37004–37005; Collado-Villalba (40° 39' N, 3° 59' W), MNCN 37009, 37011–37013; Hoyo de Manzanares (40° 38' N, 3°53' W), MNCN 37021–37024; Manzanares el Real (40°44' N, 3°52'W), CM 60946 and 60950 (paratypes), USNM 199211–199212 (paratypes), MNCN 7830 and 36791 (paratypes), 36792 (holotype) and 36797; Mataelpino (40° 44' N, 3° 56' W), MNCN 37015 and 37096; Moralzarzal (40° 41' N, 3° 58' W), MNCN 37099–37100; Navacerrada (40° 44' N, 4° 00' W), MNCN 6363, 6365–6367, and 6415; Puerto de Canencia (40° 54' W, 3° 44' W), MNCN 37000–37002; San Lorenzo de El Escorial (40° 35' N, 4° 09' W), MNCN 7786 and 7787; and Torrelodones (40° 35' N, 3° 56' W), MNCN 37036–37037, 37110–37111, 37113–37117, 37119–37120, 37122 and 37129.

Referred to *Psammodromus manuelae*. SPAIN (Cádiz Province): La Algaida (36° 52' N, 6° 18' W), CM 53250, 53331,53352–53353, 53375–53377, 53379, 53382, 53398, 53401–53402, 53439–53440, 53442–53443, 53468–53469, 53891, 54589–54591, 54593, 54677, 54677 (b, d, f, and h), 54790–54792, 54795 (b and c), 54874, 54874 (b and f), 55304, 55329, 55334–55335, 55472, 55660 and 55662.

Psammodromus species indeterminate. SPAIN (Albacete Province): Riopar (38° 30' N, 2° 27' W), MNCN 7832–7834, 36839–36844, 36851–36852, 36854–36855, 36857–36858 and 36861–36866. (Tarragona Province): Altafulla (41° 08' N, 1° 23' E), MNCN 36755–36756, 36790, 36799–36800, 36802–36805, 36821, 36823; and El Retaule, Serra de Caro (40° 45' N, 0° 16' E), MNCN 36786–36787.