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MORPHOLOGICAL VARIATION IN THE IPANEMA BAT, *PYGODERMA BILABIATUM*, WITH DESCRIPTION OF A NEW SUBSPECIES

Pygoderma bilabiatum is known from Surinam, southeastern Brazil, Paraguay, northern Argentina (Jones and Carter, 1976), and Bolivia (Ojeda and Bárquez, 1978) but is poorly represented in museum collections. Significant secondary sexual variation (females being larger) was found in a recent study of 48 Paraguayan specimens (Myers, 1981). No review of intraspecific variation is available (see Swanepoel and Genoways, 1979). We here report on variation in the dental formula in this phyllostomid species and briefly review sexual and geographic variation.

We examined 78 individuals of *P. bilabiatum* from Surinam, Brazil, Paraguay, Bolivia, and Argentina. Cranial measurements were taken with dial calipers to the nearest 0.1 mm. All specimens measured were adults with fused phalangeal epiphyses and cranial sutures. All statistical analyses were performed on the IBM 370/158 computer at the University of Oklahoma, using the Statistical Analysis System programs (Helwig and Council, 1979).

Previous authors (Wagner, 1843; Peters, 1864; Miller, 1907; Husson, 1962, 1978) have reported the dental formula of *P. bilabiatum* as 2/2, 1/1, 2/2, 2/2, total 28. We found no deviation from the reported molar number in 26 males, but 15 of 52 females from Argentina, Bolivia, Brazil, and Paraguay had small, peglike third molars on one or both mandibles as follows: 4, right only; 2, left only; 9, both sides. One of these females (UMMZ 125807) also had three upper molars on both sides. Third lower molars apparently occur only in females (Fisher's exact test, $P < 0.01$ for the 2-tailed case; Sokal and Rohlf, 1981). Presence of third molars is known to be variable in both sexes in a number of stenodermatine bats, including *Vampyressa bidens* (Davis, 1975), several species of *Artibeus* (Davis, 1969, 1970*a*, 1970*b*), *Stenoderma rufum* (Jones et al., 1971), and *Ardops nichollsi* (Jones and Schwartz, 1967; Jones and Baker, 1979).

Secondary sexual and geographic variation was examined in 33 cranial characters for 76 specimens (51 females, 25 males) of *P. bilabiatum* by analysis of variance (two-way ANOVA; Sokal and Rohlf, 1981). For analysis of geographic variation, preliminary clustering and ordination analysis indicated that Brazilian and Paraguayan specimens were not distinct, and that the specimen from northwestern Argentina was quite similar to those from Bolivia. Therefore, 65 specimens from Paraguay and Brazil were pooled and compared with the 11 specimens from Bolivia and Argentina. Character variances were tested for heterogeneity using the F-max test (Sokal and Rohlf, 1981). Two characters (upper M2 length and masseter moment arm length) were found to be heteroscedastic. In both cases this was due to the invariance of the values for the Bolivian males. When this group was ignored both characters were found to be homoscedastic; thus they were retained in the analysis.

Of the 33 characters examined, 31 exhibited statistically significant secondary sexual variation with the females being larger in all 31 (ANOVA, $P < 0.05$; Table 1). Myers (1981) found each of the 13 characters (11 cranial) he studied to be significantly dimorphic, with the females larger in all. Of the seven characters common to both studies, we found all to be dimorphic. Our results support Myers' (1981) conclusion that *P. bilabiatum* is sexually dimorphic in size, and further suggest that the phenomenon occurs throughout the range of the species. The ANOVA showed 23 of the 33 characters to be geographically variable ($P < 0.05$; Table 1), with the Bolivian specimens being larger in all 23. This geographic variation in size may result from reduced gene flow across the Gran Chaco of northern Argentina and western Paraguay, a natural barrier from which *Pygoderma* is not known. Only one of the 33 characters showed an interaction effect between sexes and localities (ANOVA, $P < 0.05$; Table 1). This indicates that, in general, sexual and geographical variation in size are independent, and that the specimens from Bolivia and northwestern Argentina constitute an unrecognized subspecies for which we propose the name:

Pygoderma bilabiatum magna, *new subspecies*

Holotype.—Adult female, skin and skull, no. 246399, American Museum of Natural History; from Ichilo, 7 km N Santa Rosa, 800 m, Santa Cruz, Bolivia; obtained 10 July 1975 by R. A. Ojeda and R. M. Bárquez, original no. 59.

Selected measurements of the type specimen (in mm) are: total length, 84; length of hind foot, 12; length of ear, 22.1; length of radius, 43.1; greatest length of skull (not including incisors), 22.2; condylobasal length, 19.6; postorbital width, 7.9; zygomatic width, 14.7; length of maxillary toothrow, 6.5; length of mandibular toothrow, 6.9; weight, 27.5 g.

Distribution.—Known presently from the vicinity of the type locality in central Bolivia and from north-

TABLE 1.—*Two-way ANOVA for 33 cranial characters in* Pygoderma bilabiatum. *Data are* $\bar{X}$, *SE, (range), and CV for Bolivian-Argentine and Paraguayan-Brazilian specimens.*

Character	Bolivia-Argentina		Paraguay-Brazil		*F* values[a]	
	Males (N = 3)	Females (N = 8)	Males (N = 22)	Females (N = 43)	Sex	Country
Skull length (not incl. incisors)	20.8 ± 0.35 (20.1–21.2) 2.92	21.6 ± 0.20 (20.6–22.2) 2.57	19.9 ± 0.07 (19.2–20.4) 1.64	20.7 ± 0.05 (20.1–21.3) 1.54	89.09***	60.09***
Condylobasal length	18.3 ± 0.26 (17.8–18.7) 2.50	19.1 ± 0.17 (18.1–19.6) 2.57	17.4 ± 0.06 (16.7–18.0) 1.68	18.3 ± 0.04 (17.7–18.7) 1.38	142.00***	80.91***
Rostral length	9.7 ± 0.13 (9.4–9.8) 2.39	10.2 ± 0.13 (9.6–10.7) 3.61	9.3 ± 0.07 (8.8–9.9) 3.51	9.9 ± 0.06 (9.1–10.6) 3.88	49.63***	6.94*
Lacrimal width	8.5 ± 0.12 (8.3–8.7) 2.44	8.8 ± 0.08 (8.3–9.0) 2.61	8.5 ± 0.04 (8.2–8.9) 2.28	9.0 ± 0.05 (8.4–9.8) 3.40	47.70***	1.28
Postorbital width	7.6 ± 0.07 (7.5–7.7) 1.53	7.7 ± 0.08 (7.4–8.0) 3.01	7.6 ± 0.04 (7.2–7.8) 2.30	7.7 ± 0.05 (7.2–8.8) 3.85	4.22*	0.40
Zygomatic width[b]	13.5 ± 0.10 (13.4–13.6) 1.05	14.5 ± 0.10 (14.2–15.0) 1.81	13.7 ± 0.05 (13.2–14.1) 1.66	14.3 ± 0.05 (13.6–15.3) 2.12	83.18***	4.78*
Mastoid width[c]	12.0 ± 0.12 (11.8–12.2) 1.73	12.8 ± 0.09 (12.3–13.1) 1.96	12.2 ± 0.04 (11.8–12.5) 1.53	12.4 ± 0.04 (11.7–13.0) 1.96	39.81***	10.60**
Braincase width[d]	10.5 ± 0.24 (10.2–11.0) 3.95	10.6 ± 0.07 (10.3–10.9) 1.85	10.3 ± 0.04 (10.1–10.6) 1.60	10.5 ± 0.04 (9.8–11.0) 2.38	4.98*	5.07*
Braincase height	9.4 ± 0.21 (9.1–9.8) 3.84	9.3 ± 0.08 (9.0–9.7) 2.53	9.1 ± 0.04 (8.7–9.6) 2.29	9.1 ± 0.03 (8.6–9.6) 2.28	0.12	8.08**
Braincase length	11.1 ± 0.41 (10.4–11.8) 6.31	11.4 ± 0.13 (10.7–11.7) 3.33	11.0 ± 0.05 (10.5–11.5) 2.19	11.0 ± 0.05 (10.4–11.7) 2.76	0.34	9.12**
Palatal length	7.2 ± 0.19 (6.8–7.4) 4.48	7.5 ± 0.12 (7.0–7.9) 4.58	6.8 ± 0.06 (6.6–7.6) 3.87	7.3 ± 0.03 (6.9–7.6) 2.52	63.26***	13.35***
Maxillary toothrow length	5.9 ± 0.18 (5.6–6.2) 5.21	6.3 ± 0.12 (5.7–6.8) 5.34	5.4 ± 0.03 (5.2–5.7) 2.45	6.0 ± 0.02 (5.7–6.3) 2.22	180.80***	39.75***
Post-canine toothrow length	4.7 ± 0.09 (4.6–4.9) 3.23	5.2 ± 0.09 (4.9–5.7) 5.09	4.5 ± 0.04 (4.2–5.0) 4.59	5.0 ± 0.02 (4.7–5.3) 2.61	137.14***	16.61***
Palatal width at canines	2.8 ± 0.09 (2.7–3.0) 5.39	3.0 ± 0.05 (2.7–3.2) 4.96	2.8 ± 0.02 (2.6–3.0) 3.96	2.9 ± 0.03 (2.1–3.3) 6.87	11.48**	5.77*
Palatal width at M2	3.8 ± 0.12 (3.6–4.0) 5.43	3.9 ± 0.08 (3.6–4.2) 5.57	3.6 ± 0.02 (3.4–3.9) 3.14	4.0 ± 0.03 (3.4–4.3) 4.58	55.42***	0.25
Mandibular fossa length	1.1 ± 0.03 (1.1–1.2) 5.09	1.3 ± 0.02 (1.2–1.4) 4.88	1.2 ± 0.02 (1.0–1.4) 9.90	1.3 ± 0.02 (1.1–1.6) 8.43	22.29***	1.11
Mandibular fossa width	2.1 ± 0.07 (2.0–2.2) 5.59	2.2 ± 0.10 (1.6–2.5) 12.59	2.1 ± 0.04 (1.7–2.4) 8.56	2.2 ± 0.03 (1.9–2.7) 8.12	9.30**	0.11
Upper M2 length[d]	0.6 ± 0.00 (0.6–0.6) 0.00	0.7 ± 0.06 (0.5–1.0) 24.17	0.6 ± 0.02 (0.4–0.8) 17.78	0.7 ± 0.02 (0.4–0.9) 18.97	24.02***	0.28
Upper M2 width[d]	0.8 ± 0.03 (0.8–0.9) 6.93	1.2 ± 0.09 (0.8–1.5) 21.54	0.8 ± 0.03 (0.5–1.0) 19.19	1.1 ± 0.02 (0.8–1.3) 9.12	81.40***	3.32
Upper canine height[e]	2.9 ± 0.12 (2.7–3.1) 6.90	3.0 ± 0.04 (2.9–3.2) 3.55	2.7 ± 0.02 (2.4–2.8) 3.21	2.9 ± 0.02 (2.5–3.2) 5.40	37.40***	15.50***
Dentary length	12.5 ± 0.22 (12.2–12.9) 3.04	13.1 ± 0.10 (12.8–13.6) 2.07	11.9 ± 0.04 (11.5–12.3) 1.66	12.7 ± 0.03 (12.0–13.2) 1.80	164.81***	44.62***
Condylocanine length	12.2 ± 0.15 (12.0–12.5) 2.17	12.7 ± 0.10 (12.3–13.1) 2.25	11.6 ± 0.03 (11.3–11.8) 1.38	12.3 ± 0.03 (11.8–13.0) 1.65	204.57***	63.30***

TABLE 1.—*Continued*

Character	Bolivia-Argentina		Paraguay-Brazil		*F* values[a]	
	Males (N = 3)	Females (N = 8)	Males (N = 22)	Females (N = 43)	Sex	Country
Condyle to M1 length	8.1 ± 0.21 (7.8–8.5) 4.45	8.4 ± 0.11 (7.9–8.8) 3.58	7.6 ± 0.04 (7.2–7.9) 2.33	8.2 ± 0.03 (7.7–8.6) 2.58	117.41***	29.73***
Mandibular toothrow length	6.1 ± 0.15 (5.9–6.4) 4.34	6.5 ± 0.09 (6.1–6.9) 3.74	5.7 ± 0.04 (5.3–6.0) 3.45	6.2 ± 0.03 (5.8–6.7) 3.25	116.45***	28.33***
Mandibular foramen to anterior edge of dentary	9.2 ± 0.30 (8.8–9.8) 5.56	9.7 ± 0.15 (9.0–10.2) 4.49	8.6 ± 0.06 (8.0–9.0) 3.02	9.3 ± 0.04 (8.7–9.9) 2.81	92.38***	34.25***
Condylomolar length	6.1 ± 0.07 (6.0–6.2) 1.90	6.1 ± 0.10 (5.8–6.6) 4.41	5.8 ± 0.03 (5.5–6.1) 2.56	6.0 ± 0.03 (5.4–6.4) 3.02	20.94***	11.68**
Temporal moment arm length	4.6 ± 0.19 (4.2–4.8) 7.04	4.6 ± 0.08 (4.3–5.0) 4.88	4.2 ± 0.03 (4.1–4.5) 3.31	4.5 ± 0.03 (4.2–4.8) 3.76	35.39***	11.96***
Masseter moment arm length	2.4 ± 0.00 (2.4–2.4) 0.00	2.5 ± 0.05 (2.3–2.7) 5.80	2.3 ± 0.02 (2.1–2.5) 5.10	2.5 ± 0.02 (2.2–2.8) 4.36	37.44***	4.76*
Coronoid process height	5.3 ± 0.22 (4.9–5.6) 7.10	5.9 ± 0.11 (5.2–6.2) 5.23	5.4 ± 0.04 (5.1–5.6) 3.23	5.7 ± 0.04 (5.3–6.3) 4.15	44.92***	2.40
Angular process length	3.4 ± 0.22 (3.0–3.7) 11.03	3.6 ± 0.07 (3.3–4.0) 5.81	3.4 ± 0.05 (3.1–4.1) 6.69	3.5 ± 0.03 (3.1–4.1) 5.55	5.66*	0.64
Dentary height at M2	2.8 ± 0.07 (2.7–2.9) 4.17	2.8 ± 0.04 (2.6–2.9) 3.56	2.6 ± 0.03 (2.2–2.8) 5.84	2.7 ± 0.02 (2.5–2.9) 4.37	18.13***	8.93**
Lower canine height[f]	2.7 ± 0.06 (2.6–2.8) 3.70	2.8 ± 0.05 (2.5–2.9) 5.07	2.5 ± 0.02 (2.3–2.6) 3.27	2.6 ± 0.02 (2.4–2.9) 4.15	27.18***	16.81***
Mandibular condyle width	2.1 ± 0.17 (1.8–2.3) 13.53	2.4 ± 0.04 (2.2–2.5) 4.36	2.2 ± 0.03 (1.8–2.5) 6.32	2.3 ± 0.02 (2.0–2.7) 6.34	14.39***	0.05

[a] Two-way analysis of variance: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.
[b] 9 specimens from Bolivia-Argentina (2 ♂♂, 7 ♀♀); 59 from Paraguay-Brazil (20 ♂♂, 39 ♀♀).
[c] 63 specimens from Paraguay-Brazil (21 ♂♂, 42 ♀♀); interaction effect, $F = 6.56$*.
[d] 63 specimens from Paraguay-Brazil (22 ♂♂, 41 ♀♀).
[e] 10 specimens from Bolivia-Argentina (3 ♂♂, 7 ♀♀); 64 from Paraguay-Brazil (22 ♂♂, 42 ♀♀).
[f] 10 specimens from Bolivia-Argentina (3 ♂♂, 7 ♀♀).

western Argentina; possibly occurring throughout the transitional forest that is located between the Gran Chaco and the eastern slopes of the Andean Cordillera.

Diagnosis.—Externally similar to *P. b. bilabiatum*; dorsal pelage tricolored, the middle band the palest; uropatagium and forearm densely furred; dactylopatagium minus well developed and permanently open; noseleaf large. The skull of *P. b. magna* is more robust than that of the nominate subspecies, the rostrum is large and cuboid, the zygoma converge anteriorly, and the sagittal and lamboidal crests are well developed. Tooth morphology is detailed in Husson (1962, 1978).

Comparisons.—As noted above, *P. b. magna* averages larger than *P. b. bilabiatum* in most cranial measurements (Table 1). The posterior palatal processes tend to be broad and poorly developed in *P. b. magna*, but narrow and elongate in *P. b. bilabiatum*. Also, the outer upper incisors are larger and the basisphenoid pits average deeper in *P. b. magna*.

Remarks.—*Pygoderma bilabiatum* is known in Argentina from two disjunct populations; these currently are under study by R. A. Ojeda and R. D. Owen. The northwestern specimens are herein assigned to *P. b. magna*, but individuals from the northeastern part of the country are probably referable to *P. b. bilabiatum*. Reproductive information is scanty. Female *P. b. magna* with enlarged nipples have been collected in April in Argentina and July in Bolivia, but this condition may not imply lactation (see Myers, 1981).

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Specimens examined (78).—ARGENTINA. *Salta:* Piquirendo Viejo, 30 km N Tartagal, 1 (CMNH). BOLIVIA. *Santa Cruz:* Ichilo and Sara, 7 km N Santa Rosa, 800 m, 10 (AMNH). BRAZIL. *Minas Gerais:* Rio Doce, Parque Est., Coronel Fabriciano, 1 (ROM). *São Paulo:* Itapetininga, 1 (USNM); Primeiro Morro, 1 (FMNH). PARAGUAY. *Caaquozú:* Igatimí (Ygatimí), 10 (AMNH). *Canendiyú:* 6.3 km NE Curuguaty, 5 (UMMZ); 13.3 km N Curuguaty, 28 (UMMZ); Río Yuqueri, 1 (MCZ); Pastenea, Río Yuqueri, 1 (MCZ). *Concepción:* 8 km E Concepción, 1 (MVZ). *Cordillera:* Sapucay (Sapucai), 2 (USNM); 12 km N Tobatí, 1 (MVZ). *Itapúa:* 8 km N San Rafael, 8 (UMMZ); 2 km NNW San Rafael, 4 (UMMZ); 3.5 km E San Rafael, 2 (UMMZ). SURINAM. 1 (USNM).

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