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A New Species of *Peropteryx* (Chiroptera: Emballonuridae) from Western Amazonia with Comments on Phylogenetic Relationships within the Genus

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ABSTRACT

We report the discovery of a new species of doglike bat (*Peropteryx*) from the lowland Amazonian forests of Ecuador and Peru. It has transparent wing membranes that are faintly tinged brown with pale-brown arms and digits; ears that are separated on the forehead; and a skull with small, shallow pterygoid pits that are anterolateral to an undivided basisphenoid pit and that are separated by a mesopterygoid extension. These characters distinguish the new species from morphologically similar species with which it was previously confused (*P. leucoptera* and *P. macrotis*). A molecular phylogenetic analysis of unlinked loci from each of the four genetic transmission systems of mammals (mitochondrial, nuclear-autosomal, *X*, and *Y* chromosomes) independently corroborated the placement of the new species as the sister taxon to a clade that includes *P. kappleri*, *P. macrotis*, and *P. trinitatis*; the basal lineage for the genus is *P. leucoptera*. This phylogeny suggests that transparent wings (sometimes described as “white” but actually lacking pigment), the traditional character used to diagnose *Peronymus*, is not a unique synapomorphy. Furthermore, based on a molecular dating analysis, the depth of divergence of *Peropteryx* is equivalent to that of another New World emballonurid genus (*Balantiopteryx*). Therefore, *Peronymus* does not warrant higher-level recognition as a subgenus or genus.

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INTRODUCTION

There are four species of doglike bats currently recognized in the genus *Peropteryx* Peters, including *P. kappleri* Peters, *P. leucoptera* Peters, *P. macrotis* (Wagner), and *P. trinitatis* Miller (Simmons, 2005). This genus belongs to the tribe Diclidurini Robbins and Sarich, which is the only group of sheath-tailed bats (family Emballonuridae Gervais) that is endemic to the Neotropics (Robbins and Sarich, 1988; Lim et al., 2008). *Peropteryx* is one of four genera of emballonurids (the others being *Balantiopteryx* Peters, *Cormura* Peters, and *Saccopteryx* Illiger) that have a distinctive saclike structure in the wing membrane between the leading edge of the upper and lower arm (propatagium). Each genus has a different-sized sac that is uniquely positioned in the propatagium, and these structures are typically better developed in adult males than in females. The sac is comparatively large and located adjacent to the forearm in *Saccopteryx*, whereas it is medium sized and located in the middle of the propatagium in *Balantiopteryx*. In contrast, the sac is located near the leading edge of the propatagium in *Cormura* and *Peropteryx*. In *Cormura* the sac is small but moderately well developed, whereas in *Peropteryx* it is small and poorly developed (Sanborn, 1937; Lim and Dunlop, 2008). *Peropteryx* is also differentiated from *Cormura*, the genus to which it is most morphologically similar, by a combination of other characters including having a paler medium-brown fur color (darker in *Cormura*), a naked face, wing attachment at the ankle (attachment at base of toe in *Cormura*), and less robust body proportions (Emmons and Feer, 1997; Reid, 1997; Lim and Engstrom, 2001).

New World emballonurids roost in a variety of habitats in lowland forests including tree trunks, tree hollows, rotted logs, palm fronds, caves, and buildings (Emmons and Feer, 1997; Reid, 1997; Simmons and Voss, 1998). However, most species are seldom documented during faunal surveys, and they are relatively understudied because of their typically agile, high-flying behavior and a sensitive echolocation system that lessens the chance of capture in mist nets. There is a better possibility of encountering them by actively searching for roosts (Simmons and Voss, 1998). Acoustic monitoring is another approach for detecting

emballonurids by comparing species-specific echolocation search-call parameters, such as peak frequency, call duration, and pulse interval (Kalko, 1995; Jung et al., 2007). Although the widely distributed *Peropteryx macrotis* can be locally common in limestone caves of the Yucatan Peninsula of Mexico, they are sporadically documented and poorly known across the vast expanse of the Amazon basin. Similarly, *P. trinitatis* sometimes roosts in large colonies among granite outcrops in the Venezuelan Llanos, but its occurrence throughout the Guiana Shield of northern South America is rarely reported. Our understanding of the relative abundance, distribution, and general biology of the other species of *Peropteryx* is even sparser. During biodiversity studies in Amazonian Ecuador and Peru, we discovered another species in this genus that is new to science. Herein we describe its diagnostic characters, analyze its phylogenetic relationships, and summarize what little is known about its natural history.

MATERIALS AND METHODS

Mammals were surveyed in 1995 and 1996 as part of a larger faunal and floral inventory of the Block 16 oil concession in Orellana province, Ecuador, by MAXUS Inc. (Reid et al., 2000). Sampling was concentrated along the main access road through predominantly terra firma primary forest ranging between 200 and 350 m above sea level west of Yasuni National Park. The main method of capturing bats was by mist net, either 6 m or 12 m long, with a mesh diameter of 36 mm set at a height of 3 m above the ground in different situations (such as across trails, over streams, in clearings, and near roosts). Nets were opened at dusk and checked on a regular basis, typically until midnight.

Surveys were also conducted at the Matses Indian village of Nuevo San Juan (5°14'50"S, 73°9'50"W, ca. 150 m above sea level) on the Río Gálvez, a left-bank tributary of the Río Yavari, in the Peruvian department of Loreto. Mist-netting was carried out by Voss on 21 nights from May to July of 1998, when an average of 40.9 m of nets were deployed at ground level (0–3 m) for 2.6 hr per night, for a total of 2309 net/meter/hour. Nets (in 6 m and

12 m lengths, both with 36 mm mesh) were usually opened just before dusk and were tended continuously until they were closed, usually before midnight. Local habitats sampled by mist-netting included gardens and clearings around Matses houses, secondary growth (abandoned swiddens), well-drained primary forest, palm swamps, mineral licks, and river beaches. Bats were also surveyed at Nuevo San Juan by searching for roosts (Voss and Emmons, 1996: 20–22). Voss searched for roosts from May to June of 1998, and several Matses men were trained to search for roosts by Fleck from September to November of 1999 (for details of this operation, see Fleck et al., 2002). Bats observed at roosts were collected by hand or by shooting.

Specimens examined (appendix 1) are deposited at the American Museum of Natural History (AMNH; New York, USA); the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (MUSM; Lima, Peru); and the Royal Ontario Museum (ROM; Toronto, Canada). External measurements (mm) and mass (g) were taken from specimen labels including total length (TL), length of tail (TV), length of hind foot (HF), length of ear (EAR), length of tragus (TR), and length of forearm (FA). Cranial measurements were recorded with digital calipers to the nearest 0.1 mm including greatest length of skull (GLS), condylo-incisive length (CIL), breadth across zygomatic arches (ZB), breadth across mastoids (MB), breadth of braincase (BBC), breadth across postorbital constriction (POC), length of maxillary tooth row (CM3), and breadth across upper molars (M3M3; Reid et al., 2000). One-tailed Student's t-tests were used to evaluate sexual size dimorphism in our measurement data.

RESULTS

Peropteryx pallidoptera, new species

Pale-winged Doglike Bat

Figures 1, 2, 3

HOLOTYPE: An adult male (ROM 104396) collected 66 km S of Pompeya Sur (00°48'S, 76°24'W), Orellana Province, Ecuador by F.A. Reid, and F. Sornoza (field number

F37227) on 8 May 1995. The holotype was prepared as a skin, skull, and partial skeleton.

PARATYPES: An adult male (AMNH 74107) prepared as a skin and skull collected at Orosa (03°26'S, 72°08'W), Amazon River, Loreto, Peru, by Alfonso and Ramón Olalla on 28 November 1926. Seventeen individuals prepared as fluid-preserved specimens collected at Nuevo San Juan (05°14'50"S, 73°09'50"W, 150 m above sea level), Río Gálvez, Loreto, Peru, by Robert S. Voss and David W. Fleck in 1998 and 1999, including 1 adult male (MUSM 13226), 14 adult females (AMNH 272671, AMNH 272726, AMNH 272854, AMNH 272855, AMNH 272827, AMNH 273042, AMNH 273116, AMNH 273185, MUSM 13228, MUSM 13230, MUSM 15246, MUSM 15249, MUSM 15250, MUSM 15252) and 2 subadult females (MUSM 13227, MUSM 13229).

DISTRIBUTION: The new species is currently known from just three localities in primary lowland forests of eastern Ecuador and northern Peru at elevations <400 m above sea level. It is found sympatrically with *P. kappleri* and *P. leucoptera* at Nuevo San Juan. The new species and *P. macrotis* have overlapping distributions in the western Amazon but their closest points of documented occurrence are approximately 50 km apart (between Orosa and Puerto Indiana on the Amazon River of Peru).

ETYMOLOGY: The specific epithet refers to the pale wings and is compounded from the Latin words *pallidus* ("pale") and *ptera* ("wing").

MEASUREMENTS: External measurements are presented in table 1 and cranial measurements are presented in table 2 for *Peropteryx pallidoptera* and other congeneric species.

DIAGNOSIS: Superficially, *Peropteryx pallidoptera* appears most similar to *P. leucoptera* because they both have transparent wings. However, the new species has paler brown arms and digits (dark brown in *P. leucoptera*), the skin from the wing tip to the elbow is translucent and evenly colored with a tinge of brown (gradually darkens in color from wing tip to body in *P. leucoptera*; fig. 1), the ears are not connected by a band of skin, the rostrum of the skull is not broad, and the lateral pterygoid pits are not as large and deep as they are in *P. leucoptera* (fig. 2). In



Fig. 1. The contrasting color patterns of the wings spread on the left and closed on the right for three species of *Peropteryx*: **top**, *P. leucoptera* (ROM 112531) with white wing tips, brown toward the elbow and brown digits; **middle**, *P. pallidoptera* (ROM 104396) with uniform white from the wing tips to the elbow and light brown digits; and **bottom**, *P. macrotis* (ROM 108523) with uniform brown from the wing tips to the elbow and brown digits.

contrast, *P. pallidoptera* is morphologically similar to *P. kappleri*, *P. macrotis*, and *P. trinitatis* with the ears separated, rostrum of the skull not broad, and the lateral pterygoid

pits small and shallow (fig. 2). However, the new species does not have dark brown wings and digits, the rostrum is not inflated dorsally, and the posterior border of the mesopterygoid



Fig. 2. Differences in basisphenoid pit and lateral pterygoid pits at the anterior end (toward the top) for three species of *Peropteryx*: **top**, *P. leucoptera* (ROM 112531) with large pterygoid pits separated by a mesopterygoid extension; **middle**, *P. pallidoptera* (ROM 104396) with small pterygoid pits separated by a mesopterygoid extension; and **bottom**, *P. macrotis* (ROM 108467) with small pterygoid pits separated by the basisphenoid pit.



Fig. 3. Skull of the holotype of *Peropteryx pallidoptera* (ROM 104396) with dorsal, ventral, and lateral views of the cranium, and lateral view of the left mandible from top to bottom. The greatest length of the skull is 14.1 mm.

extension is not level with the anterior border of the basisphenoid and lateral pterygoid pits, all of which are characters seen in *P. kappleri*, *P. macrotis*, and *P. trinitatis*. Furthermore, *P. pallidoptera* has a tiny peglike upper anterior premolar similar to that of *P. trinitatis* but different from those of *P. kappleri* and *P. macrotis*; the latter two species have a slightly larger tooth, bearing a distinct posterior cusp. *Peropteryx kappleri* is the largest species in the genus with no overlap in forearm length and

TABLE 1
External measurements (in mm) and weight (in g) for adult specimens of *Peropteryx*
 The average and range of measurements for each sex of the five species of *Peropteryx* and the probability ($* < 0.05$) of sexual dimorphism within each species with sample sizes > 2 are summarized in boldface. Abbreviations of measurements are listed in the Materials and Methods section, and localities of specimens examined are listed in appendix 1.

Species	Specimen	Sex	TL	TV	HF	EAR	TR	FA	WT	Country
<i>P. pallidoptera</i>	ROM 104396	male	57	15	9	15	5	40	4	Ecuador
<i>P. pallidoptera</i>	MUSM 13226	male	62	11	9	15	—	39	4.3	Peru
			59.5	13	9	15	5	39.5	4.15	
			57–62	11–15	9	15	5	39–40	4–4.3	
<i>P. pallidoptera</i>	AMNH 272671	female	65	11	9	15	—	41	5.2	Peru
<i>P. pallidoptera</i>	AMNH 272726	female	65	13	9	15	—	41	5.6	Peru
<i>P. pallidoptera</i>	AMNH 272854	female	59	14	9	15	—	—	5.5	Peru
<i>P. pallidoptera</i>	AMNH 272855	female	60	13	8	15	—	—	5.0	Peru
<i>P. pallidoptera</i>	AMNH 272827	female	65	14	10	15	—	42	5.2	Peru
<i>P. pallidoptera</i>	AMNH 273042	female	62	12	9	15	—	41	5.2	Peru
<i>P. pallidoptera</i>	AMNH 273116	female	64	13	10	16	—	43	7.1 ¹	Peru
<i>P. pallidoptera</i>	AMNH 273185	female	66	12	10	16	—	42	6.0	Peru
<i>P. pallidoptera</i>	MUSM 13228	female	61	13	10	15	—	43	4.5	Peru
<i>P. pallidoptera</i>	MUSM 13230	female	58	13	9	15	—	—	4.9	Peru
<i>P. pallidoptera</i>	MUSM 15246	female	61	13	9	16	—	—	5.9	Peru
<i>P. pallidoptera</i>	MUSM 15249	female	63	12	9	17	—	42	6.7 ¹	Peru
<i>P. pallidoptera</i>	MUSM 15250	female	67	14	9	16	—	43	7.6 ¹	Peru
<i>P. pallidoptera</i>	MUSM 15252	female	66	11	10	15	—	43	5.2	Peru
			63.0	12.7	9.3	15.4	—	42.1	5.3	
			58–67	11–14	8–10	15–17	—	41–43	4.5–6.0	
			—	—	—	—	—	—	—	
<i>P. l. leucoptera</i>	AMNH 273182	male	69.0	13.0	10.0	19.0	—	45.0	8.0	Peru
<i>P. l. leucoptera</i>	AMNH 273197	male	66.0	16.0	10.0	20.0	—	45.0	8.5	Peru
<i>P. l. leucoptera</i>	MUSM 15247	male	66.0	16.0	10.0	20.0	—	46.0	8.1	Peru
<i>P. l. leucoptera</i>	MUSM 15251	male	69.0	13.0	9.0	19.0	—	46.0	8.5	Peru
<i>P. l. leucoptera</i>	AMNH 267838	male	63.0	13.5	8.0	16.5	—	41.0	6.4	French Guiana
<i>P. l. leucoptera</i>	AMNH 266012	male	63.0	13.0	9.0	16.0	—	43.0	6.0	French Guiana
<i>P. l. leucoptera</i>	AMNH 267280	male	69.0	15.0	8.0	16.0	—	43.0	6.1	French Guiana
<i>P. l. leucoptera</i>	AMNH 267088	male	65.0	14.0	9.0	15.0	—	42.0	6.2	French Guiana
<i>P. l. leucoptera</i>	ROM 41530	male	56	5	8	16	7	43	—	Guyana
<i>P. l. leucoptera</i>	ROM 107458	male	61	11	9	16	5	44	6	Guyana
<i>P. l. leucoptera</i>	ROM 112530	male	57	10	9	16	6	42	4	Guyana
<i>P. l. leucoptera</i>	ROM 112531	male	60	11	9	16	6	42	5	Guyana

TABLE 1
(Continued)

Species	Specimen	Sex	TL	TV	HF	EAR	TR	FA	WT	Country
<i>P. l. leucopeura</i>	ROM 113612	male	60	11	7	13	6	42	6	Guyana
<i>P. l. cyclops</i>	BM 24.3.1.6 ²	male	65	15	—	17	—	45	—	Peru
			63.5	12.6	8.8	16.8	6.8	43.5	6.6	
			56-69	5-16	7-10	13-20	5-7	41-46	4-8.5	
<i>P. l. leucopeura</i>	AMNH 267837	female	64.0	17.0	8.0	18.5	—	44.0	6.0	French Guiana
<i>P. l. leucopeura</i>	AMNH 267839	female	66.0	14.0	8.5	17.0	—	43.0	7.8	French Guiana
<i>P. l. leucopeura</i>	AMNH 266010	female	63.0	14.0	9.0	16.0	—	42.0	5.5	French Guiana
<i>P. l. leucopeura</i>	AMNH 266011	female	61.0	12.0	10.0	17.0	—	45.0	7.0	French Guiana
<i>P. l. leucopeura</i>	AMNH 266013	female	64.0	14.0	9.0	16.5	—	45.0	6.5	French Guiana
<i>P. l. leucopeura</i>	AMNH 267087	female	66.0	13.0	9.0	15.0	—	44.0	6.2	French Guiana
<i>P. l. leucopeura</i>	ROM 113611	female	66	13	8	16	7	44	7	Guyana
			64.3	13.9	8.8	16.6	7	43.9	6.6	
			61-66	12-17	8-10	15-18.5	7	42-45	5.5-7.8	
			0.3084	0.1246	0.4397	0.3919	—	0.2536	0.4968	
<i>P. kappleri</i>	MUSM 15245	male	70.0	14.0	12.0	19.0	—	48.0	8.0	Peru
<i>P. kappleri</i>	AMNH 272797	male	76.0	17.0	12.0	17.0	—	50.0	8.5	Peru
<i>P. kappleri</i>	AMNH 272799	male	71.0	14.0	11.0	17.0	—	50.0	8.7	Peru
<i>P. kappleri</i>	AMNH 267863	male	69.0	15.0	10.0	20.0	—	47.5	7.2	French Guiana
<i>P. kappleri</i>	AMNH 265989	male	74.0	14.0	11.0	19.0	—	51.0	7.5	French Guiana
<i>P. kappleri</i>	AMNH 265993	male	68.0	13.0	10.0	18.0	—	49.0	8.0	French Guiana
<i>P. kappleri</i>	AMNH 265995	male	73.0	13.0	11.0	18.0	—	50.0	8.5	French Guiana
<i>P. kappleri</i>	AMNH 265997	male	70.0	14.0	12.0	18.0	—	47.5	8.5	French Guiana
<i>P. kappleri</i>	AMNH 267084	male	68.0	11.0	11.0	17.0	—	49.0	8.0	French Guiana
<i>P. kappleri</i>	AMNH 267085	male	65.0	11.0	11.0	18.0	—	49.0	7.2	French Guiana
<i>P. kappleri</i>	AMNH 267291	male	74.0	14.0	9.0	18.0	—	47.0	6.7	French Guiana
<i>P. kappleri</i>	AMNH 267392	male	68.0	9.0	10.0	18.0	—	47.0	7.9	French Guiana
<i>P. kappleri</i>	ROM 78055	male	—	—	—	—	—	49	—	Mexico
<i>P. kappleri</i>	ROM 101123	male	67	13	11	18	8	50	7	Guyana
			70.2	13.2	10.8	18.1	8	48.9	7.8	
			65-76	9-17	9-12	17-20	8	47-51	6.7-8.7	
<i>P. kappleri</i>	AMNH 273086	female	76.0	15.0	12.0	15.0	—	54.0	11.4	Peru
<i>P. kappleri</i>	AMNH 273174	female	76.0	15.0	11.0	19.0	—	52.0	10.3	Peru
<i>P. kappleri</i>	AMNH 272798	female	82.0	17.0	11.0	17.0	—	53.0	10.5	Peru
<i>P. kappleri</i>	AMNH 267835	female	73.0	17.0	9.0	19.0	—	51.0	7.1	French Guiana
<i>P. kappleri</i>	AMNH 267086	female	71.0	13.0	10.0	19.0	—	51.0	11.6	French Guiana

TABLE 1
(Continued)

Species	Specimen	Sex	TL	TV	HF	EAR	TR	FA	WT	Country
<i>P. kappleri</i>	AMNH 265990	female	74.0	16.0	13.0	18.0	—	52.0	8.0	French Guiana
<i>P. kappleri</i>	AMNH 265991	female	70.0	17.0	11.0	19.0	—	51.0	8.0	French Guiana
<i>P. kappleri</i>	AMNH 265992	female	75.0	14.0	12.0	18.0	—	52.5	9.0	French Guiana
<i>P. kappleri</i>	AMNH 265996	female	70.0	15.0	12.0	18.0	—	51.0	8.5	French Guiana
<i>P. kappleri</i>	AMNH 265998	female	78.0	12.0	12.0	18.0	—	51.0	9.5	French Guiana
<i>P. kappleri</i>	AMNH 265999	female	76.0	14.0	12.0	18.0	—	[50]	9.5	French Guiana
<i>P. kappleri</i>	AMNH 267080	female	74.0	12.0	11.0	17.0	—	—	8.0	French Guiana
<i>P. kappleri</i>	AMNH 267081	female	69.0	10.0	11.0	18.0	—	50.0	8.4	French Guiana
<i>P. kappleri</i>	AMNH 267082	female	74.0	11.0	11.0	18.0	—	—	9.9	French Guiana
<i>P. kappleri</i>	AMNH 267833	female	78.0	15.0	11.0	19.0	—	50.5	9.1	French Guiana
<i>P. kappleri</i>	AMNH 267834	female	74.0	13.0	11.0	18.0	—	50.5	7.3	French Guiana
<i>P. kappleri</i>	ROM 100910	female	68	13	12	14	5	53	7	Guyana
			74.0	14.1	11.3	17.8	5	51.5	9.0	
			68–82	10–17	9–13	14–19	5	50–54	7–11.6	
			0.0032*	0.1427	0.0963	0.2420	—	0.000002*	0.0046*	
<i>P. trinitatis</i>	ROM 107822	male	55	16	8	13	5	39	3	Venezuela
<i>P. trinitatis</i>	ROM 107922	male	56	11	7	13	5	38	4	Venezuela
<i>P. trinitatis</i>	ROM 107823	male	57	13	7	13	5	37	3	Venezuela
<i>P. trinitatis</i>	ROM 107824	male	54	15	8	14	6	38	3	Venezuela
<i>P. trinitatis</i>	ROM 107825	male	60	16	8	14	6	38	3	Venezuela
<i>P. trinitatis</i>	ROM 107827	male	59	12	5	11	3	36	3	Venezuela
<i>P. trinitatis</i>	ROM 107828	male	55	18	6	12	2	39	4	Venezuela
<i>P. trinitatis</i>	ROM 107829	male	57	16	5	12	2	39	4	Venezuela
<i>P. trinitatis</i>	ROM 107835	male	55	15	8	14	5	40	4	Venezuela
<i>P. trinitatis</i>	ROM 107923	male	57	14	7	13	5	39	5	Venezuela
			56.5	14.6	6.9	12.9	4.4	38.3	3.6	
			54–60	11–18	5–8	11–14	2–6	36–40	3–5	
<i>P. trinitatus</i>	AMNH 7496 ³	female	—	—	—	—	—	41.9	—	Trinidad
<i>P. trinitatis</i>	ROM 107831	female	64	16	9	15	6	41	4	Venezuela
<i>P. trinitatis</i>	ROM 107921	female	59	14	8	15	6	40	5	Venezuela
<i>P. trinitatis</i>	ROM 107826	female	60	18	9	13	3	42	4	Venezuela
<i>P. trinitatis</i>	ROM 107830	female	57	15	9	14	5	40	4	Venezuela
<i>P. trinitatis</i>	ROM 107832	female	60	15	8	14	5	42	4	Venezuela
<i>P. trinitatis</i>	ROM 107833	female	62	15	9	15	6	43	5	Venezuela
<i>P. trinitatis</i>	ROM 107834	female	62	14	8	14	5	42	4	Venezuela
<i>P. trinitatis</i>	ROM 107916	female	63	14	8	14	5	41	5	Venezuela

TABLE 1
(Continued)

Species	Specimen	Sex	TL	TV	HF	EAR	TR	FA	WT	Country
<i>P. trinitatis</i>	ROM 107918	female	61	15	8	13	6	43	6	Venezuela
<i>P. trinitatis</i>	ROM 107920	female	58	14	8	14	6	42	5	Venezuela
			60.6	15.0	8.4	14.1	5.3	41.6	4.6	
			57–64	14–18	8–9	13–15	3–6	40–43	4–6	
			0.0002*	0.3066	0.0012*	0.0033*	0.0636	0.000002*	0.0025*	
<i>P. macrotis</i>	AMNH 266005	male	58.0	12.0	7.0	14.0	—	39.7	4.3	French Guiana
<i>P. macrotis</i>	AMNH 266007	male	53.0	12.0	8.0	14.0	—	40.1	3.8	French Guiana
<i>P. macrotis</i>	AMNH 267395	male	59.0	11.0	8.0	14.0	—	42.2	4.6	French Guiana
<i>P. macrotis</i>	ROM 95945	male	60	11	8	16	6	45	5	Mexico
<i>P. macrotis</i>	ROM 96442	female	55	13	8	14	5	45	5	Mexico
<i>P. macrotis</i>	ROM 96443	female	59	14	9	14	5	45	4	Mexico
<i>P. macrotis</i>	ROM 96446	female	59	13	10	15	6	45	5	Mexico
<i>P. macrotis</i>	ROM 97765	male	55	12	8	15	5	43	5	Mexico
<i>P. macrotis</i>	ROM 107126	male	62	15	8	15	6	46	4	Guyana
<i>P. macrotis</i>	ROM 108467	male	62	15	9	14	6	43	5	Guyana
			58.2	12.8	8.3	14.5	5.6	43.4	4.6	
			53–62	11–15	7–10	14–16	5–6	39.7–46	3.8–5	
<i>P. macrotis</i>	AMNH 266006	female	60.0	12.0	8.0	14.0	—	—	5.3	French Guiana
<i>P. macrotis</i>	AMNH 267396	female	64.0	13.0	8.0	15.0	—	45.2	5.4	French Guiana
<i>P. macrotis</i>	ROM 95946	female	65	12	8	15	5	46	6	Mexico
<i>P. macrotis</i>	ROM 95947	female	65	12	9	16	6	47	6	Mexico
<i>P. macrotis</i>	ROM 96444	female	65	14	9	15	5	48	7	Mexico
<i>P. macrotis</i>	ROM 96445	female	63	13	9	16	5	47	6	Mexico
<i>P. macrotis</i>	ROM 96447	female	64	12	10	16	5	48	5	Mexico
<i>P. macrotis</i>	ROM 96448	female	65	13	9	15	5	47	7	Mexico
<i>P. macrotis</i>	ROM 96449	female	62	14	9	15	6	45	5	Mexico
<i>P. macrotis</i>	ROM 96450	female	60	15	9	15	5	45	5	Mexico
<i>P. macrotis</i>	ROM 96451	female	59	15	10	15	5	46	5	Mexico
<i>P. macrotis</i>	ROM 108523	female	63	18	9	16	6	46	5	Guyana
<i>P. macrotis</i>	ROM 117527	female	64	14	8	15	6	45	5	Suriname
			63.0	13.6	8.8	15.2	5.4	46.3	5.6	
			59–65	12–18	8–10	14–16	5–6	45–48	5–7	
			0.0001*	0.1215	0.0489*	0.0070*	0.2086	0.0004*	0.0006	

¹ Pregnant (not included in mean or range).
² Measurements of holotype from Thomas (1924).
³ Holotype.

TABLE 2

Cranial measurements (in mm) for adult specimens of *Peropteryx*

The average and range of measurements for each sex of the five species of *Peropteryx* and the probability (* < 0.05) of sexual dimorphism within *P. macrotis* (other species have small sample sizes) are summarized in boldface. Abbreviations of measurements are listed in the Materials and Methods section, and localities of specimens examined are listed in appendix 1.

Species	Specimen	Sex	GLS	CIL	ZB	MB	BBC	POC	CM3	M3M3
<i>P. pallidoptera</i>	ROM 104396	male	14.1	12.5	8.2	7.3	6.4	2.8	5.3	5.9
<i>P. pallidoptera</i>	AMNH 74107	male	—	—	8.1	7.2	6.5	2.9	5.0	5.9
<i>P. pallidoptera</i>	MUSM 13226	male	—	—	—	—	—	2.6	5.2	5.8
			14.1	12.5	8.2	7.3	6.5	2.8	5.2	5.9
			14.1	12.5	8.1–8.2	7.2–7.3	6.4–6.5	2.6–2.9	5.0–5.3	5.8–5.9
<i>P. pallidoptera</i>	AMNH 272671	female	14.1	12.8	8.3	7.1	6.5	2.6	5.3	6.1
<i>P. pallidoptera</i>	AMNH 272726	female	—	—	8.4	7.3	6.7	2.9	5.5	6.1
<i>P. pallidoptera</i>	AMNH 272827	female	14.1	12.7	8.7	7.4	6.6	2.9	5.3	6.4
<i>P. pallidoptera</i>	MUSM 13227	female	13.7	12.2	8.0	6.9	6.6	2.7	5.1	5.8
<i>P. pallidoptera</i>	MUSM 13228	female	13.8	12.5	8.1	7.2	6.5	2.6	5.2	6.1
<i>P. pallidoptera</i>	MUSM 13229	female	13.9	12.7	8.3	7.2	6.4	2.8	5.5	6.1
<i>P. pallidoptera</i>	MUSM 13230	female	13.6	12.4	8.1	7.1	6.3	2.6	5.0	5.7
			13.9	12.6	8.3	7.2	6.5	2.7	5.3	6.0
			13.6–14.1	12.2–12.8	8.0–8.7	6.9–7.4	6.3–6.7	2.6–2.9	5.0–5.5	5.7–6.4
<i>P. l. leucoptera</i>	ROM 41530	male	—	—	9.5	8.0	7.2	3.3	6.2	7.0
<i>P. l. leucoptera</i>	ROM 107458	male	15.6	14.1	9.5	7.9	7.3	3.1	6.1	6.9
<i>P. l. leucoptera</i>	ROM 112531	male	15.5	14.1	9.6	7.8	7.2	3.3	6.1	6.7
<i>P. l. leucoptera</i>	ROM 113612	male	14.9	13.9	9.3	7.6	7.0	3.3	6.1	6.8
			15.3	14.0	9.5	7.8	7.2	3.3	6.1	6.9
			14.9–15.6	13.9–14.1	9.3–9.6	7.6–8.0	7.0–7.3	3.1–3.3	6.1–6.2	6.7–7.0
<i>P. l. cyclops</i>	BM 24.3.1.6 ¹	male	16.2²	14.5³	—	9.2	7.8	3.2	6.5	—
<i>P. kappleri</i>	ROM 78055	male	—	—	9.9	8.4	7.7	2.9	6.6	7.5
<i>P. kappleri</i>	ROM 101123	male	18.2	16.4	10.3	8.6	7.7	2.8	7.2	7.8
			18.2	16.4	10.1	8.5	7.7	2.9	6.9	7.7
			18.2	16.4	9.9–10.3	8.4–8.6	7.7	2.8–2.9	6.6–7.2	7.5–7.8
<i>P. kappleri</i>	AMNH 272798	female	17.5	16.2	10.4	8.5	7.5	3	7.1	7.7
<i>P. kappleri</i>	ROM 100910	female	17.5	16.3	10.2	8.3	7.4	2.8	7.5	8.1
			17.5	16.3	10.3	8.4	7.5	2.9	7.3	7.9
			17.5	16.2–16.3	10.2–10.4	8.3–8.5	7.4–7.5	2.8–3.0	7.1–7.5	7.7–8.1
<i>P. trinitatis</i>	ROM 107822	male	12.4	11.2	7.2	6.7	6	2.8	4.4	5.1

TABLE 2
(Continued)

Species	Specimen	Sex	GLS	CIL	ZB	MB	BBC	POC	CM3	M3M3
<i>P. trinitatis</i>	ROM 107922	male	12.8 12.6 12.4–12.8	11.6 11.4 11.2–11.6	7.6 7.4 7.2–7.6	6.8 6.8 6.7–6.8	5.9 6.0 5.9–6.0	2.8 2.8 2.8	4.7 4.6 4.4–4.7	5.5 5.3 5.1–5.5
<i>P. trinitatis</i>	ROM 107831	female	13.2	11.8	7.7	7.0	6.1	2.4	4.9	5.8
<i>P. trinitatis</i>	ROM 107921	female	13.5 13.4 13.2–13.5	12.2 12.0 11.8–12.2	8.0 7.9 7.7–8.0	7.1 7.0–7.1	6.2 6.2 6.1–6.2	2.5 2.5 2.4–2.5	5.1 5.0 4.9–5.1	5.7 5.8 5.7–5.8
<i>P. macrotis</i>	ROM 107126	male	14.5	13.1	8.1	7.2	6.6	2.4	5.5	5.9
<i>P. macrotis</i>	ROM 108467	male	14.3	13.1	8.1	7.2	6.6	2.4	5.5	5.9
<i>P. macrotis</i>	ROM 95945	male	15.2	13.7	8.4	7.5	6.8	2.9	5.9	6.4
<i>P. macrotis</i>	ROM 96442	male	—	—	8.4	7.8	7.0	3.1	5.7	6.3
<i>P. macrotis</i>	ROM 96443	male	15.0	13.6	—	7.8	6.8	2.9	5.7	6.3
<i>P. macrotis</i>	ROM 96446	male	15.5	14.2	8.4	7.8	6.9	3.0	5.8	6.3
<i>P. macrotis</i>	ROM 97765	male	14.6	13.2	8.3	7.5	6.7	2.9	5.6	6.2
<i>P. macrotis</i>	AMNH 73502	male	—	—	7.6	7.0	6.2	3.1	4.5	5.2
<i>P. macrotis</i>	AMNH 73503	male	—	—	—	7.2	6.9	3.0	—	5.8
<i>P. macrotis</i>	AMNH 266005	male	14.1	12.7	8.2	7.1	6.7	2.8	5.4	5.9
<i>P. macrotis</i>	AMNH 266007	male	—	—	—	—	—	2.7	5.1	5.7
			14.5 14.3–15.2	13.2 12.7–13.7	8.1 7.6–8.4	7.2 7.0–7.5	6.6 6.2–6.9	2.8 2.4–3.1	5.4 4.5–5.9	5.9 5.7–6.4
<i>P. macrotis</i>	ROM 108523	female	15.3	13.8	8.6	7.4	6.7	2.6	5.7	6.3
<i>P. macrotis</i>	ROM 95946	female	15.2	13.9	8.5	7.6	6.7	3.0	6.0	6.7
<i>P. macrotis</i>	ROM 96444	female	15.5	14.1	8.7	7.9	7.0	2.9	5.8	6.8
<i>P. macrotis</i>	ROM 96445	female	15.5	14.1	8.9	7.8	7.0	3.0	5.9	6.7
<i>P. macrotis</i>	ROM 96447	female	15.9	14.6	8.7	8.0	6.9	3.0	6.2	6.7
<i>P. macrotis</i>	ROM 96448	female	15.3	14.2	8.6	7.9	6.9	2.9	6.0	6.5
<i>P. macrotis</i>	ROM 96449	female	15.1	13.7	8.7	7.7	6.9	2.9	5.9	6.6
<i>P. macrotis</i>	AMNH 266006	female	—	—	8.3	—	—	2.9	5.7	6.2
			15.4 15.0–15.9 0.0051*	14.0 13.6–14.6 0.0043*	8.6 8.3–8.9 0.0009*	7.8 7.4–8.0 0.0106*	6.9 6.7–7.0 0.0647	2.9 2.6–3.1 0.3016	5.9 5.7–6.2 0.0067*	6.5 6.2–6.8 0.0004*

¹ Measurements of holotype from Thomas (1924).

² Greatest length of skull to front of canine.

³ Length from condyle to front of canine.

cranial measurements (except postorbital constriction) with the other species (tables 1 and 2). In general, *P. pallidoptera* is smaller in cranial size than *P. leucoptera*, *P. macrotis*, and *P. kappleri*, but it is larger than *P. trinitatis*. This size gradation is most evident in same-sex comparisons of condyloincisive length (table 3).

DESCRIPTION: The new species is a medium-sized *Peropteryx* (table 2). The dorsal fur is relatively long (approximately 8 mm) and is a uniform medium brown with slightly paler hair bases. The ventral fur is similar but slightly lighter in color. The ears are brown and are not in contact with each other, although they are close together on the forehead. The interfemoral membrane is brown, as is the wing membrane from the body to the elbow, but the distal portion is translucent with a tinge of brown (fig. 1). The arms and digits of the wings are medium brown. There is a poorly developed wing sac situated on the leading edge of the propatagium with an outward lateral opening.

The skull of *P. pallidoptera* has slender postorbital processes and a relatively narrow rostrum, but the rostrum is not dorsally inflated. The relatively shallow, undivided basisphenoid pit has two small anterolateral pterygoid pits and the mesopterygoid extension protrudes posteriorly into the basisphenoid region (fig. 2). The upper anterior premolar is tiny and peglike. The dental formula is $i\ 1/3$, $c\ 1/1$, $p\ 2/2$, $m\ 3/3$ with a total of 32 teeth.

COMMENTS: The cranial measurements for males of *P. pallidoptera* are all within the observed range of variation for females (table 2), which suggests that there is little or no sexual dimorphism in skull size. However, although the sample size for male *P. pallidoptera* is small ($N = 2$), males are smaller than females with no overlap in forearm length and weight (table 1). In contrast, females of *P. macrotis* are significantly larger than males ($p < 0.02$) for all cranial measurements except breadth of braincase and postorbital constriction. Similarly, females of *P. macrotis* are significantly larger than males ($p < 0.05$) for all external measurements except length of tail and length of tragus. Brosset and Charles-Dominique (1990) did not observe sexual dimorphism for *P. trinitatis* but they only

compared 1 male and 1 female. Although our sample size was not much better (at 2 males and 2 females), females were larger for all cranial measurements except postorbital constriction and there was no overlap in range (table 2). The male *P. trinitatis* reported by Brosset and Charles-Dominique (1990) was large and similar to our females except for maxillary tooth-row length. However, with larger sample sizes for external measurements (10 males and 10 females), females of *P. trinitatis* are significantly larger ($p < 0.003$) than males except for length of tail and length of tragus. The sample sizes for *P. kappleri* and *P. leucoptera* were too small for making meaningful comment on cranial sexual size dimorphism. External measurements suggest that females of *P. kappleri* are larger than males ($p < 0.005$ for total length, forearm length, and weight), but there is no indication of sexual dimorphism in any of the external measurements for *P. leucoptera*.

NATURAL HISTORY

ECUADOR: *Peropteryx pallidoptera* was one of 66 species of bats that we captured in Block 16 in 1995 and 1996 (Reid et al., 2000). The holotype was caught in a mist net set at the entrance to a small cave next to a muddy, spring-fed *saladero* (mineral-rich seep) that periodically flooded the surrounding forest. The cave appeared to have been used primarily as a night roost, because few bats were found to occupy it in the daytime.

Another six specimens of *Peropteryx pallidoptera* (easily recognized as such by their transparent wing tips) were captured and released by Engstrom, who netted them over a larger *saladero* (at least 1 km in diameter) located near the edge of the Tiputini River about 10 minutes by boat north of the Tiputini Biodiversity Station (00°38'S, 76°09'W). The small stream that fed this *saladero* tumbled over the edge of a cliff ca. 10 m high, and a shallow cave was present behind the waterfall. The bats apparently used the cave as a diurnal roost: Engstrom saw small, brown emballonurids in the cave before it got dark, and he caught the six *P. pallidoptera* in the net nearest the cave exit at dusk.

PERU: We recorded a total of 58 species of bats at Nuevo San Juan in 1998 and 1999

TABLE 3
Morphological comparison among the five species of *Peropteryx*

	<i>P. kappleri</i>	<i>P. leucoptera</i>	<i>P. macrotis</i>	<i>P. pallidoptera</i>	<i>P. trinitatis</i>
Wings	Uniformly brown	Translucent, gradually darkening to brown from wing tips to body	Uniformly brown	Translucent and evenly tinged pale brown	Uniformly brown
Arms and digits	Dark brown	Dark brown	Dark brown	Medium brown	Dark brown
Ears	Not connected	Connected	Not connected	Not connected	Not connected
Rostrum of skull	Not broad	Broad	Not broad	Not broad	Not broad
Lateral pterygoid pits	Dorsally inflated	Not dorsally inflated	Dorsally inflated	Not dorsally inflated	Dorsally inflated
Mesopterygoid posterior extension into basisphenoid region	Small and shallow	Large and deep	Small and shallow	Small and shallow	Small and shallow
Upper anterior premolar	Does not extend	Extends	Does not extend	Extends	Does not extend
Overall size	With posterior cusp Large	Peglike Medium	With posterior cusp Small	Peglike Small	Peglike Small
Condylolincisive length	Forearm 47–54 16.4 (males, $N = 1$) 16.2–16.3 (females, $N = 2$)	Forearm 41–46 13.9–14.1 (males, $N = 3$)	Forearm 39–45 12.7–13.7 (males, $N = 5$) 13.6–14.6 (females, $N = 9$)	Forearm 39–43 12.5 (males, $N = 1$) 12.2–12.8 (females, $N = 6$)	Forearm 41.9 11.2–11.6 (males, $N = 2$) 11.8–12.2 (females, $N = 2$)

(Fleck et al., 2002). Of 503 recorded bat captures at this locality, 372 were in mist nets and 311 were made at diurnal roosts. All 17 specimens of *Peropteryx pallidoptera* from Nuevo San Juan were taken from roosts. In total, we found 10 roosts occupied by this species in a variety of circumstances as described below (numbers refer to entries in a field catalog of bat roosts).

Roost 2: Dark cavities among the roots and buttresses of a fallen tree in well-drained primary forest. Exactly where the bats were roosting is unknown because they had been spooked by kids who were shooting at them with arrows. A total of eight bats were collected as they perched on nearby tree trunks. Three (one adult male, one adult female, and one subadult female) were *Peropteryx pallidoptera* and five were *Saccopteryx bilineata*; an unknown number of either or both species might have escaped (22 May 1998).

Roost 6: A half-open hollow log (about 50 cm inside diameter) in old secondary growth near a stream. Two bats were found roosting here, only one of which (an adult female *Peropteryx pallidoptera*) was collected (11 June 1998).

Roost 15: An undercut earth bank in the side of a stream gully in well-drained primary forest. Two adult female and one subadult female *Peropteryx pallidoptera* occupied this roost, where they were found hanging well apart from one another (30 June 1998).

Roost 20: A small dark cavity of roots and earth at the base of a large fallen tree in well-drained primary forest. Two bats were found roosting here about 50 cm above the ground, of which only one (an adult female *Peropteryx pallidoptera*) was collected (8 July 1998).

Roost 22: A dark horizontal chamber under a buttress of a fallen tree in well-drained primary forest. Two adult female *Peropteryx pallidoptera* were found roosting here, about 80 cm above the ground (8 July 1998).

Roost 31: A deep armadillo burrow in the side of a stream headwater gully in well-drained primary forest. One adult female *Peropteryx pallidoptera* was found roosting

here in the company of at least two *Micronycteris matses* and three *Carollia brevicauda*. No bats were seen to escape this roost by flying out of it, but some might have escaped by flying deeper inside (4 September 1999).

Roost 56: The unmodified leaf of a wild banana plant in hilltop primary forest. The single bat (a pregnant female *Peropteryx pallidoptera*) observed and collected here was hanging from the middle of the leaf about 1 m above the ground (16 September 1999).

Roost 73: A hole in the ground in the side of a stream headwater gully on a hillside in well-drained primary forest. Two bats were observed roosting here, of which one (a pregnant female *Peropteryx pallidoptera*) was collected (22 September 1999).

Roost 77: A hole in the side of a stream headwater gully in hilltop primary forest. Four bats were observed using this roost, of which two were collected. One of those collected was an adult female *Peropteryx pallidoptera*, and the other was an adult male *P. leucoptera* (23 September 1999).

Roost 102: The undercut bank of a small stream in well-drained primary forest. Only a single bat (an adult female *Peropteryx pallidoptera*) was observed and collected here (11 October 1999).

Roost 147: The “underside of a log” [as described by the Matses collector; presumably elevated somehow above the ground] in well-drained primary forest in a valley bottom. A single lactating adult female *Peropteryx pallidoptera* was collected here, but it seems likely that one or more nursing young may have been present but unobserved (27 October 1999).

Roost 154: The underside of a fallen tree in primary upland forest near a small stream. A single female *Peropteryx pallidoptera* was in the roost (2 November 1999).

The specimen from Orosa was collected by Alfonso and Ramón Olalla, members of an Ecuadorean family of professional collectors employed by the American Museum of Natural History, who worked at or near the mouth of the Río Orosa on the right (south) bank of the Amazon from 30 August to 11 December 1926. According to Wiley (in press),

the Olallas' camp at Orosa must have been in the floodplain of the Amazon, which is so wide at this point (about 15 km) that most of their specimens certainly came from floodplain habitats. Although the forest within several kilometers of the riverbank at the Olallas' presumed campsite (ca. 3°31'31"S, 73°11'22"W; Wiley, in press) is seasonally flooded *varzea*, the river was probably at or near its lowest annual stage in August–December, so this habitat would have been easy to traverse on foot.

DISCUSSION

TAXONOMY

Several genera of New World emballonurids (including *Balantiopteryx*, *Cormura*, *Peropteryx*, and *Rhynchonycteris*) were described by Peters (1867) based primarily on the presence or absence of a wing sac and the position of this sac in the propatagium. In addition to *Balantiopteryx plicata* and *Peropteryx kappleri*, Peters (1867) also described the white-winged doglike bat (*P. leucoptera*) with the type locality from Suriname. The following year, Peters (1868) described a new subgenus (*Peronymus*) for this species. Dobson (1878) subsequently synonymized *Balantiopteryx*, *Centronycteris*, and *Peropteryx* with *Saccopteryx* (treating them as subgenera) based primarily on the shared presence of a wing sac. He considered this taxonomic grouping of species with wing sacs in *Saccopteryx* as analogous to the grouping of taxa with throat pouches in *Taphazous* and to the grouping of taxa with frontal sacs in *Rhinolophus*. However, Dobson's (1878) speculation that wing sacs were present in *Centronycteris* was a misinterpretation of Peters (1867) and further exasperated by the examination of only two females, the gender that typically has poorly developed sacs. The absence of wing sacs in *Centronycteris* was eventually correctly documented by Sanborn (1937) in his taxonomic revision of New World emballonurids. Dobson (1878) apparently considered *Cormura* part of *Saccopteryx*, but did not formally classify it in his synopsis of groups and genera of Emballonurinae because the presence of wing sacs could not be conclusively documented in the poorly preserved holotype.

The subgenera of *Saccopteryx* proposed by Dobson (1878) were subsequently reinstated as full genera by Miller (1907) based on cranial differences. Miller (1907) additionally elevated *Peronymus* to generic rank. The primary characters for distinguishing *Peronymus* from *Peropteryx* include a broad rostrum, ears connected across the top of the head, and white wings (Miller, 1907). In total, Miller recognized eight genera of Neotropical emballonurines: *Rhynchiscus* (= *Rhynchonycteris*), *Centronycteris*, *Balantiopteryx*, *Saccopteryx*, *Cormura*, *Peropteryx*, *Peronymus*, and *Myropteryx*. *Myropteryx*, described as new by Miller (1907), is now considered a junior synonym of *Cormura*.

Peronymus was considered monotypic until Thomas (1924) described a second species of white-winged doglike bat as *Peronymus cyclops* from Peru. Thomas (1924: 531) diagnosed *cyclops* as "very closely allied to the *P. leucoptera* of Guiana and the lower Amazon, but distinguished by its larger skull." Although Thomas (1924) did not consider that the differences in rostral inflation and scarcely perceptible ear connection in *Peronymus* warranted higher-level recognition, he grudgingly followed the generic classification of Miller (1907) because of differences in the structure of the basisphenoid pits. Likewise, Sanborn (1937) retained *Peronymus* as a distinct genus but regarded *cyclops* as a larger upper Amazon subspecies of *P. leucoptera*. *Peronymus* was again demoted to a subgenus of *Peropteryx* by Cabrera (1958) following the classification of Peters (1868), but its taxonomic rank remained contentious. Subsequent authorities have treated *Peronymus* as a distinct genus (Husson, 1962, 1978; Linares, 1986; Brosset and Charles-Dominique, 1990; Corbet and Hill, 1991), as a subgenus of *Peropteryx* (Honaki et al., 1982; Koopman, 1982, 1984; Jones and Hood, 1993; Koopman, 1993, 1994; McKenna and Bell, 1997; Simmons and Voss, 1998; Simmons, 2005), or as a junior synonym of *Peropteryx* (Hood and Gardner, 2007).

SYSTEMATICS

Separate molecular phylogenetic analyses representing loci from each of the four genetic transmission systems in mammals (mitochon-

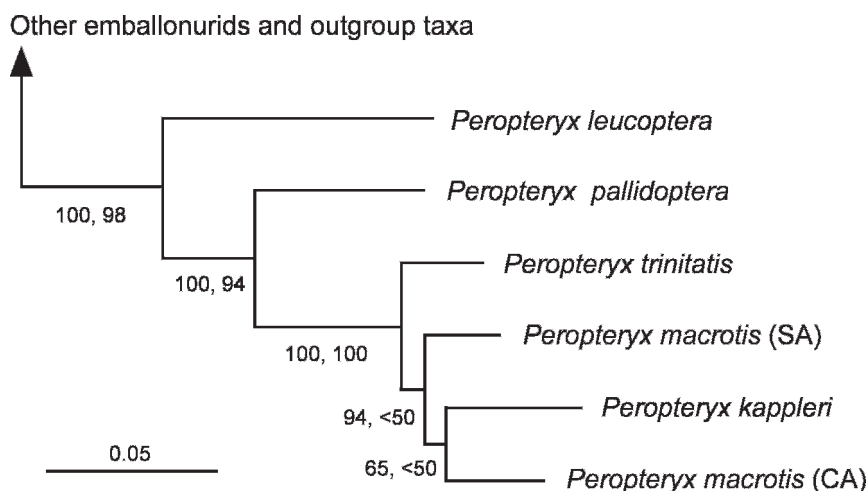


Fig. 4. Topology within *Peropteryx* from a phylogenetic analysis of Emballonuridae (Lim, 2009). The tree is a Bayesian analysis of combined genes representing each of the four genetic transmission systems in mammals. First number along the branch is the Bayesian posterior probability percentage and the second number is the bootstrap percentage from a parsimony analysis. There are two populations of *P. macrotis* from Central America (CA) and South America (SA).

drial, autosomal, X, and Y chromosomes) for New World emballonurids resulted in trees with congruent topologies in which *P. pallidoptera* and *P. leucoptera* appear as successively basal lineages to a clade comprised of *P. kappleri*, *P. macrotis*, and *P. trinitatis* (Lim et al., 2008; *P. pallidoptera* was identified as "*Peropteryx* sp." in that publication). Although the relationships among *P. kappleri*, populations of *P. macrotis* from Central America and South America, and *P. trinitatis* were poorly supported, a combined analysis of the four unlinked genes (cytochrome *b*, *chd1*, *usp9x*, and *dby*) corroborated the more basal systematic relationships including the phylogenetic position of the new species (fig. 4; Lim, 2009).

Parsimonious optimizations of wing pigmentation on this phylogeny suggest that transparent ("white") wings, the principal trait used to distinguish *Peronymus* from *Peropteryx*, is not a unique synapomorphy that diagnoses that taxon. Either transparent wings evolved once in the common ancestor of *Peronymus* + *Peropteryx* and subsequently reversed on the branch that subtends the dark-winged species of *Peropteryx*, or transparent wings evolved independently in *leucoptera* and *pallidoptera*. Furthermore, a molecular dating study estimat-

ed a similar age of diversification for *Balan-tiopteryx* and *Peropteryx* (including *P. leucoptera*) beginning 10.8 mya and 11.7 mya, respectively (Lim, 2007). In contrast, the most recent split of genera in the subtribe Diclidurina was *Cyttarops* and *Diclidurus*, which occurred much earlier at 14.6 mya (Lim, 2007). Because *Peronymus* no longer appears notably distinct from all other species of *Peropteryx* in morphology, and because its age of divergence from other *Peropteryx* is similar to that seen within other emballonurid genera, we see little value in recognizing *Peronymus* as distinct at the generic or subgeneric level. Accordingly, we follow Hood and Gardner (2007) in treating *P. leucoptera* as a species of *Peropteryx* and in not recognizing any subgenera within that taxon.

WING SACS

The wing sac of New World emballonurids is a nonglandular structure (Scully et al., 2000) that is apparently a receptacle for various bodily secretions used in the scent-marking behavior (salting) of *Saccopteryx* (Voigt and von Helversen, 1999). *Saccopteryx* is the only genus known to exhibit the complex social behavior of salting, which is apparently associated with its

harem mating system (Bradbury and Vehrencamp, 1977). Although the behavioral function of the wing sac in the other genera has not been thoroughly studied, the distinctive folding of the internal surface in *Saccopteryx* is lacking in *Peropteryx* (Scully et al., 2000). This suggests the possibility of a use other than scent holding, and possibly a different ecological role for the wing sac. Based on a study of evolutionary patterns in morphology, wing sacs evolved independently in each of the two subtribes of New World emballonurid bats: once in the lineage leading to *Peropteryx*, *Cormura*, and *Balantiopteryx* in Diclidurina, and independently in the ancestral lineage leading to *Saccopteryx* in Saccopterygina (Lim and Dunlop, 2008). Furthermore, each genus has a different-sized sac that is uniquely positioned in the propatagium. The variation of the wing sac position, degree of internal folding, and social behavior map consistently on the phylogeny suggesting a potential phylogenetic basis for these character systems. More detailed study and comprehensive taxonomic coverage of the ecology and systematics of Emballonuridae may yield additional insights about the adaptive significance and evolution of these interesting structures.

NATURAL HISTORY AND BIOGEOGRAPHY

Several aspects of our sparse capture data are noteworthy. First, *Peropteryx pallidoptera* does not appear to be a roost specialist, as it uses a variety of diurnal refugia including caves, fallen trees, holes in the ground, undercut stream banks, and leaves. Second, at least some of these roosts are shared with several other species of bats, including phyllostomids and emballonurids. Lastly, nothing about the localities where these bats were captured leads us to believe the species is rare in any ecologically meaningful sense.

The three known capture sites of *Peropteryx pallidoptera* (Block 16, Nuevo San Juan, and Orosa) do not appear to share any ecological characteristics that are not also present throughout much of western Amazonia. For example, all three sites are <400 m above sea level and probably receive >2800 mm of annual precipitation; lowland rainforest, including both riparian and upland formations, is the predominant vegetation type at each site

(Reid et al., 2000; Fleck et al., 2002; Wiley, in press). Most of the roosts we found near Nuevo San Juan were in upland (well-drained, nonriparian) forest, which is by far the most abundant macrohabitat throughout the region. It is also relevant that *P. pallidoptera* occurs north and south of the Amazon, one of the most significant zoogeographic barriers in the region. Therefore, it seems probable that the species is very widely distributed and will soon turn up at other sites where appropriate survey methods are used to inventory bat diversity. It also seems likely that additional specimens may be found in museum collections where they may have been misidentified as *P. leucoptera* because of their similar transparent wing membranes.

The relative abundance of *Peropteryx pallidoptera* among the bats we collected at roosts near Nuevo San Juan (17 out of 311 specimens, about 5%) contrasts with the total absence of this species among the bats we captured in mist nets at the same locality ($N = 372$). Although all of the Ecuadorean specimens were taken in mist nets, the mist nets that caught *P. pallidoptera* were set to intercept bats flying into or out of caves. Although it is not known how the Orosa specimen was captured, the Olallas did not have mist nets, and most of the other bats they obtained at Orosa belong to species that are readily taken at diurnal roosts (e.g., *Glossophaga soricina*, *Mesophylla macconnelli*, *Furipterus horrens*, *Thyroptera tricolor*), so it seems probable that they also collected *P. pallidoptera* by this method. Thus, searching for roosts would appear to be the method of choice for collecting additional material of this species, which either is adept at avoiding nets or forages in situations where nets are hard to set.

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APPENDIX 1

SPECIMENS EXAMINED

Locality information of specimens examined of *Peropteryx*. Museum acronyms are listed in the Materials and Methods section. Specimens marked with an asterisk (*) were sequenced in the molecular phylogenetic study of Lim et al. (2008).

Peropteryx pallidoptera—**Ecuador**: Orellana; 66 km S of Pompeya Sur, 00°48'S, 76°24'W (ROM 104396*; holotype). **Peru**: Amazon River, Orosa, 03°26'S, 72°08'W (AMNH 74107); Rio Galvez, Nuevo San Juan, 05°14'50"S, 73°09'50"W, 150 m (AMNH 272671, 272726, 272827, 272854, 272855, 273042, 273116, 273185; MUSM 13226, 13227, 13228*, 13229, 13230, 15246, 15249, 15250, 15252).

Peropteryx kappleri—**French Guiana**: Paracou, 5°16'31"N, 52°55'25"W (AMNH 265990, 265991, 265292, 265989, 265993, 265995, 265996, 265997, 265998, 265999, 267080, 267081, 267082, 267084, 267085, 267086, 267291, 267392, 267833, 267834*, 267835, 267863). **Guyana**: Barima-Waini; Baramita, 07°22'N, 60°29'W (ROM 100910*, 101123*). **Mexico**: Tabasco; 2 km E of Teapa, 17°35'N,

92°56'W (ROM 78055). **Peru**: Loreto; Rio Galvez, Nuevo San Juan, 05°14'50"S, 73°09'50"W, 150 m (AMNH 272797, 272798, 272799, 273086, 273174; MUSM 15245).

Peropteryx leucoptera—**French Guiana**: Paracou, 5°16'31"N, 52°55'25"W (AMNH 266010, 266011, 266012, 266013, 267087, 267088, 267280, 267837, 267839*, 267838). **Guyana**: Demerara-Mahaica; Ceiba Biological Center, 06°30'N, 58°13'W, 50 m (ROM 112530, 112531*, 113611, 113612*). Potaro-Siparuni; Iwokrama Forest Field Station, 04°40'N, 58°51'W, 70 m (ROM 107458*). Upper Essequibo-Upper Takutu; Illiwa River, 3 days below Kuitaro River Mouth, approximately 02°40'N, 58°40'W (ROM 41530). **Peru**: Loreto; Rio Galvez, Nuevo San Juan, 05°14'50"S, 73°09'50"W, 150 m (AMNH 273182, 273197; MUSM 15247, 15251).

Peropteryx macrotis—**French Guiana**: Paracou, 5°16'31"N, 52°55'25"W (AMNH 266005, 266006, 266607, 267395, 267396). **Guyana**: Potaro-Siparuni; Iwokrama Forest, Cow Fly Camp, 04°20'N, 58°49'W, 100 m (ROM 108523*), Giaconda Camp, 04°38'N, 58°43'W, 75 m (ROM 107126*), 38 Mile Camp, 04°20'N, 58°51'W, 100 m (ROM 108467*). **Mexico**: Quintana Roo, Tulum, 20°10'N, 87°29'W (ROM FN33843*). Yucatan; Loltun,

20°15'N, 89°29'W (ROM 96442, 96443, 96444, 96445, 96446*, 96447, 96448, 96449, 96450, 96451), Ruinas Kabah, 20°15'N, 89°40'W (ROM 95945, 95946, 95947, 97765). **Peru:** Loreto; Amazon River, Puerto Indiana, 03°20'S, 72°40'W, 100 m (AMNH 73502, 73503). Pasco, San Pablo, 10°27'S, 74°52'W, 300 m (AMNH 230096). **Suriname:** Sipaliwini; Bakhuis, Area 8 Recon Fly Camp, 04°27'13"N, 56°52'00"W, 248 m (ROM 117527).

Peropteryx trinitatis—**Trinidad and Tobago:** Trinidad; Saint George County, Port of Spain, 10°40'N, 61°31'W (AMNH 7496; holotype). **Venezuela:** Amazonas; Pozon, 06°03'N, 67°25'W (ROM 107822*, 107823, 107824, 107825, 107826, 107827, 107828, 107829, 107830, 107831, 107832, 107833, 107834, 107835). Bolivar; Hato La Florida, 07°34'N, 65°52'W (ROM 107916, 107918, 107920*, 107921, 107922, 107923).

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