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Tent Construction by Bats of the Genera *Artibeus* and *Uroderma*

Robert M. Timm

ABSTRACTS

Herein, I describe new styles of tents cut and utilized by *Artibeus anderseni, A. glaucus, A. gnomus, A. phaeotis, A. toltecus, A. watsoni, Uroderma bilobatum,* and *U. magnirostrum*; review and summarize the literature on tent use by *Artibeus* and *Uroderma*; and discuss the effectiveness of tents as diurnal roosts. *Artibeus anderseni* alters the shape of *Heliconia* leaves by cutting the lateral nerves and interconnected tissue extending out from the midrib. *Artibeus glaucus* cuts the basal lateral nerves in *Xanthosoma,* causing the two sides of the leaf to collapse downward around the midrib. *Artibeus phaeotis* cuts the lateral nerves and interconnected tissues in both banana and *Heliconia imbricata*; the basal cuts veer out from the midrib such that a distinctive V-shaped enclosure is formed by the hanging leaf. *Artibeus toltecus* cuts the basal nerves on *Anthurium,* causing the sides of the leaf to fold down around the midrib to form a pyramid-shaped tent. *Artibeus watsoni* was found to make four distinctive styles of tents, including simple V-shaped cuts on bifurcated palms, cuts of a few side veins on aroids to produce a rounded pyramid, elongate J-shaped cuts on banana and *Heliconia,* and polygonal cuts on *Carludovica palmata. Artibeus watsoni* has the greatest repertoire in tent styles, and uses the most diverse array of plant species and leaf shapes. Two styles of tents constructed by *Uroderma bilobatum* are reported for the first time, one on the large pinnately leafed palm *Scheelea rostrata* and the second on banana. The common denominator between the *Uroderma bilobatum* tents reported herein and those previously described is that all are on large, broad leaves and all have a distinctive V-shaped pattern cut by the bats. *Uroderma magnirostrum* also creates an inverted elongate V-shaped tent on pinnately leafed palms.

All New World tent-makers described to date are tropical members of the phyllostomid subfamily Stenoderminae. Each species of tent-making bat has one or more distinctive style of tent. Bats select leaves of specific shapes, sizes, and angles for tent construction. Most species appear to be obligate tent-roosters. Tents provide bats with a cryptic diurnal roost site, in addition to providing shelter from both the sun and rain and an early warning to the approach of predators.

Aqui yo describo nuevos estilos de carpas cortadas y utilizadas por *Artibeus anderseni, A. glaucus, A. gnomus, A. phaeotis, A. toltecus, A. watsoni, Uroderma bilobatum,* y *U. magnirostrum* reviso y hago un sumario de la literatura acerca del uso de carpas por filostomidos; y discuto la efectividad de las carpas como perchas diurnas. *Artibeus anderseni* altera la forma de las hojas de *Heliconia* cortando las nervaduras centrales y tejido interconectado que se extiende

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exteriormente desde la nervadura central. *Artibeus glaucus* corta la base de las nervaduras laterales en *Xanthosoma,* causando asi que los dos lados de la hoja colapsen hacia abajo al rededor de la nervadura central. *Artibeus phaeotis* corta las nervaduras laterales y tejidos interconectados en banana y *Heliconia imbricata*; los cortes basales viran hacia afuera desde la nervadura central de tal modo que una distintiva cavidad en forma de V es formada por la hoja colgante. *Artibeus toltecus* corta las nervaduras basales de *Anthurium,* adi que los lados de la hoja doblen en redor de la nervadura central de tal modo que una cavidad es formada en forma de una piramide. *Artibeus watsoni* fue encontrada haciendo cuatro distintos estilos de carpas, incluyendo simples cortes en forma de V en palmas bifurcadas, cortes en unas pocas nervaduras laterales en araceas para producir una piramide redondeada, cortes alargados en forma de J en banana y *Heliconia,* y cortes poligonales en *Carludovica palmata. Artibeus watsoni* tiene el mas grande repertorio en estilos de carpas y usa la mas diversa serie de plantas y formas de hojas. Dos estilos de carpas construidas por *Uroderma bilobatum* son reportadas por primera vez; una en la larga y pinnada hoja de palma *Scheelea rostrata* y la segunda en banana. El comun denominador entre carpas de *Uroderma bilobatum* reportadas aqui y aquellas previamente descritas es que todas usan hojas grandes y anchas y todas tienen un distintivo patron en forma de V cortado por los murciélagos. *Uroderma magnirostrum* también corta una carpa en forma de V-invertido en hojas pinnadas de palmas.

Todos los filostomidos cortadores y utilizadores de carpas descritos del Nuevo Mundo son membros tropicales de la subfamilia Stenoderminae. Cada especie tiene uno o mas estilos distintos de carpas. Los murciélagos escogen hojas de formas especificas, y constróen sus carpas en angulos peculiares. La mayor parte de las especies parecen utilizar las carpas obligatoriamente. Las carpas oferecen una percha oculta durante el dia, asi como un abrigo del sol, de la lluvia, y de predadores.

Neste trabalho, (1) descrevo novos estilos de tendas cortadas e utilizadas por *Artibeus anderseni, A. glaucus, A. gnomus, A. phaeotis, A. toltecus, A. watsoni, Uroderma bilobatum,* e *U. magnirostrum*; (2) reviso e resumo a literatura sobre o uso de tendas pelos morcegos da família Phyllostomidae, e (3) discuto a eficiência de tendas como alojamentos diurnos. *Artibeus anderseni* altera a forma das fôlhas de *Heliconia,* cortando as veias laterais e os tecidos interligados que estendem da veia central. *Artibeus glaucus* corta as veias basilares laterais em *Xanthosoma,* causando com que os dois lados da fôlha caiam contra o centro. *Artibeus phaeotis* corta as veias laterais e os tecidos interligados nas fôlhas de bananas e de *Heliconia imbricata.* Os cortes basilares partem da veia central, formando um abrigo distinto em forma de "V". *Artibeus toltecus* corta as veias basilares de *Anthurium,* causando com que os lados da fôlha dobrem em volta da veia central, criando um abrigo em forma de pirâmide. *Artibeus watsoni* constrói quatro tipos diferentes de tendas, incluindo simples cortes em forma de "V" em fôlhas de palmeiras bifurcadas; cortes em algumas das veias laterais em fôlhas de trepadeiras (resultando em pirâmides redondas); cortes alongados, em forma de "J", em fôlhas de bananas e de *Heliconia*; e cortes polígonos em fôlhas de *Carludovica palmata. Artibeus watsoni* possue o maior repertório de estilos de tendas, e usa o conjunto mais diverso de espécies de plantas e de configurações de fôlhas. Dois estilos de tendas construídas por *Uroderma bilobatum* são descritos pela primeira vez; um nas fôlhas grandes da palmeira *Scheelea rostrata,* e outro nas fôlhas de bananas. Fatôres comuns entre as tendas construídas por *Uroderma bilobatum* aqui descritas, e as descritas prèviamente, são a forma distinta em "V" cortada pelos morcêgos, e o uso de fôlhas grandes e largas para a construção das tendas. *Uroderma magnirostrum* também constróe tendas em forma de "V" invertido nas fôlhas de palmeiras.

Todos morcêgos construidores de tendas no Novo Mundo pertencem à subfamília Stenoderminae (família Phyllostomidae), e cada espécie exibe um ou mais estilos característicos de construção. A maioria destas espécies de morcêgos parecem alojar-se obrigatòriamente em tendas, as quais oferecem não só um abrigo diurno camuflado, mas também proteção contra sol, chuva, e predadores.

Introduction

The use of cut leaves for diurnal roosting sites by bats was first described by Thomas Barbour (1932), who reported on diurnal roosts of *Uroderma bilobatum* near the Panama Canal. He found these bats roosting under the leaves of two cultivated palms identified as *Livistona chinensis* and *Prichardia pacifica*. Not only were these bats found roosting under palm fronds, but they had also altered the leaf to produce a diurnal roosting structure. Barbour (1932, p. 307) stated that "by nipping the ridges of the plications on the under side the leaf is weakened and as the bitten spots are skillfully and serially distributed the leaf finally is sufficiently weakened so that the distal portion droops sharply downward." Chapman (1932, p. 555) discovered *Artibeus watsoni* roosting under the cut veins of a bifurcated palm, *Geonoma cuneata* (reported as *G. decurrens*), on Barro Colorado Island, Panama, and first called these modified leaves "tents." Ingles (1953) also reported *A. watsoni* constructing tents in the palm *Geonoma oxycarpa* (reported as *G. binervia*) on Barro Colorado Island. Goodwin and Greenhall (1961, p. 262) found *Artibeus cinereus* roosting "under cut leaves of palm trees and on the under side of banana leaves" and *Uroderma bilobatum* roosting under cut leaves of the carat palm, *Sabal glaucescens*, and coconut palm, *Cocos nucifera*, on Trinidad. *Ectophylla alba* was reported by Timm and Mortimer (1976) to alter the leaves of five species of *Heliconia* in Costa Rica; the bats selected specific leaves for both size and angle to the ground. *Artibeus jamaicensis* was found by Foster and Timm (1976) roosting under the cut leaflets on a pinnately leafed palm, *Scheelea rostrata*, in a tropical dry forest in Costa Rica. Recently, Timm (1984) reported tent construction by another phyllostomid, *Vampyressa pusilla*, in Costa Rica, and Koepcke (1984) found *Mesophylla macconnelli* utilizing similar tents in Peru. Only one Old World bat, *Cynopterus sphinx* (Pteropodidae), has been reported to alter the shape of palm leaves to produce a diurnal roosting structure (Goodwin, 1979). Reviews of roosting site selection by bats were provided by Tuttle (1976) and Kunz (1982).

To date, seven species of phyllostomids (*Artibeus cinereus, A. jamaicensis, A. watsoni, Ectophylla alba, Mesophylla macconnelli, Uroderma bilobatum,* and *Vampyressa pusilla*) have been reported to modify leaves of plants to produce diurnal roosting sites herein referred to as tents. All are tropical members of the phyllostomid subfamily Stenodermatinae.

The phyllostomid genus *Artibeus*, which includes some 15 species, is widespread in the Neotropics from northern Mexico southward to Argentina and Chile. These bats range in size from 10 g (*A. anderseni* and *A. watsoni*) to 70 g (*A. lituratus*). *Uroderma*, a closely related genus of medium-sized stenodermatines that includes only two species, is found from southern Mexico through the Amazon Basin of South America. The better known of the two species, *U. bilobatum*, weighs from 13 to 21 g.

Herein I describe tent construction and utilization by *Artibeus anderseni, A. glaucus, A. gnomus, A. phaeotis, A. toltecus, A. watsoni, Uroderma bilobatum,* and *U. magnirostrum*; describe several new styles of tents; review and summarize the literature on tent use by *Artibeus* and *Uroderma*; discuss the effectiveness of tents as diurnal roosts; and suggest directions for future research.

Methods

Descriptions of Study Areas

Costa Rica—Bosque Brrancia, also known locally as Bosque Blanco, is located 0.8 km west of Cuarto Cruces on the south side of the Pan American Highway (Route 1) in Guanacaste Province, in the Pacific lowlands of western Costa Rica. Bosque Brrancia is a restricted area of undisturbed lowland forest classified as Tropical Moist Forest; the dominant vegetation includes *Anacardium excelsum* and *Scheelea rostrata*. This stand of forest probably has not been logged previously, and represents a close approximation to the original (pre-Columbian) forests of this part of Guanacaste. Further descriptions of this forest can be found in Janzen (1971) and Wilson and Janzen (1972).

Parque Nacional de Corcovado is located on the Osa Peninsula of southwestern Costa Rica, Puntarenas Province (between 08°27′N and 08°39′N, and 83°25′W and 83°45′W); the elevation ranges from sea level to 400 m. Corcovado lies within the Tropical Wet Forest Life Zone (Holdridge, 1967), with lowland evergreen forest being the dominant forest type. Mean annual rainfall is 3,800+ mm and the wettest months are from August through November; mean monthly temperatures range from 25.0°C to 26.5°C. Vegetation and habitat types at Corcovado have been described by Herwitz (1981) and Hartshorn (1983). Areas surveyed included both primary forest and secondary scrub along the coast.

The La Selva Biological Station is the field station of the Organization for Tropical Studies located 1 km SW of Puerto Viejo de Sarapiquí, Heredia Province in the Caribbean lowlands of northeastern Costa Rica (10°27'N,84°00'W); elevation ranges from 29 to 100 m. Mean annual rainfall is 3,990 mm, with the wettest months being November, December, and February; mean monthly temperatures range from 24.5°C (December) to 26.1°C (April). La Selva lies within the Tropical Wet Forest Life Zone, with lowland evergreen forest being the dominant forest type. Vegetation and habitat types of La Selva have been described by Slud (1960), Holdridge et al. (1971), Sawyer and Lindsey (1971), and Hartshorn (1983). One unusual feature of the subcanopy of the La Selva forest is the diversity and abundance of dwarf palms (Hartshorn, 1983), especially the broad-leaved species, *Geonoma congesta* and *Asterogyne martiana.* These species are regularly utilized by *Artibeus watsoni* for tent construction. The transect surveys, which included all *Artibeus* tents observed, were restricted to primary forest. The *Uroderma* tents described from this site were restricted to an open banana patch.

Palo Verde (Refugio Nacional de Fauna Silvestre Dr. Rafael Lucas Rodríguez Caballero) is a wildlife refuge located 2 km S and 12 km E of Bolsón, in the Pacific lowlands of Guanacaste Province, northwestern Costa Rica (10°30'N, 85°20'W); the elevational range is from 3 to 183 m. Palo Verde lies within the Tropical Dry Forest Life Zone, with lowland deciduous forest and riverine swamp forest being the dominant forest types. The vegetation and habitat types of Palo Verde have been described by Slud (1980) and Hartshorn (1983). Mean annual rainfall is 1,700+ mm, with the wettest months being April, May, September, and October; mean monthly temperatures range from 26.0°C (November) to 29.7°C (April). The immediate vicinity of the survey at this site was in a mosaic of primary forest and secondary scrub that included considerable bananas scattered throughout.

The newly expanded Parque Nacional Braulio Carrillo is located in northeastern Costa Rica (between 10°05'N and 10°25'N, and 83°54'W and 84°05'W); the elevation of the park ranges from 100 to 2600 m. Braulio Carrillo is located on the eastern, Caribbean slope of Volcan Barba in Heredia Province. The elevational range at which *Artibeus toltecus* and associated tents were observed was from 700 to 1400 m, within the Premontane Rain Forest Zone with midelevational evergreen forest and tall palms being the dominant forest types. Mean annual rainfall at this elevational range is perhaps as much as 5,000 mm, although no exact measurements are yet available. The vegetation and habitat types at the midelevational ranges also have yet to be described. On 14–15 April 1986, 3 km of trail ranging from 700 to 1100 m were surveyed for bat tents. Additionally, an intensive netting effort with Richard K. LaVal and Don E. Wilson was conducted in this area over a 7-day period to determine what species of bats were present and their relative abundance.

At Finca Las Cruces (2 km S of San Vito, Puntarenas Province, 08°45'N, 82°58'W, 1200 m) in the Premontane Wet Forest–Rain Forest transition area, approximately 2 km of trail leading down to the Río Jaba was surveyed for tents on 13 August 1982.

ECUADOR—Cascada San Rafael lies 17 km (by road) west of the village of Reventador, Napo Province, in northeastern Ecuador (00°5.8'S, 77°34.4'W). Rainfall averages 1,500 to 2,000 mm; average temperatures range from 18°C to 22°C. The elevation is 1200 m. Reventador lies within the Humid Subtropical Life Zone.

Lagarto Cocha and Zancudo Cocha are military encampments along the Río Aguarico of Amazonian Ecuador named for prominent lagoons. Both areas are undisturbed primary lowland rain forests classified as Moist Forest, with an annual rainfall averaging from 2,000 to 3,000 mm; the elevation is approximately 200 m.

PERU—Hacienda Amazonia lies just north of the confluence of the Alto Río Madre de.Dios and the Río Pinipini in the department of Madre de Dios, southeastern Peru (12°58'S, 71°09'W), just north of Atalaya. The Hacienda is located just east of Parque Nacional del Manu in the Upper Tropical Zone on the eastern foothills of the Andes. On 25 July 1985 Barbara L. Clauson searched the ridge above the Hacienda for bat tents at an elevation of 825 m in primary rain forest that had received some selective timber harvest; she returned to this site again on 3 November 1985.

Cerro de Pantiacolla lies above the Río Palotoa, 10–15 km NNW of Shintuya, in the department of Madre de Dios, southeastern Peru (12°35'N, 71°18'W). On 15 November 1985 Clauson searched a steep sloping ridge at 600 m. The sur-

TABLE 1. Individual measurements (in cm or degrees) collected from four tents constructed by *Artibeus anderseni* on *Heliconia* in Ecuador.

Blade			Petiole		Basal height	Remarks
Length	Width	Angle	Length	Angle		
176	34	40	80	80	200	1 adult male *A. anderseni*
158	38	15	75	55	220	3 male *A. anderseni*
154	36	50	88	80	260	...
140	27	...	60	70	140	...

rounding forest was primary rain forest in the Upper Tropical Zone on the eastern Andean foothills.

Reference specimens of the bats have been deposited at Field Museum of Natural History, Chicago; Escuela Politécnica Nacional, Quito, Ecuador; and Universidad Nacional de Costa Rica and Servicio de Parques Nacionales, San José, Costa Rica. Voucher specimens of plants have been deposited in the herbaria at Field Museum, Duke University, Missouri Botanical Garden, and/or University of Wisconsin.

Accounts of Species

Artibeus

Artibeus anderseni Osgood, 1916

Artibeus anderseni occupies an extensive range in western Amazonia; however, little is known of its biology. This species has long been considered a junior synonym of *A. cinereus.* In resurrecting *A. anderseni* as a distinct species, Koopman (1978, p. 14) stated, "Besides its shorter face and more abrupt forehead, *A. anderseni* apparently always lacks the last lower molars, which *A. cinereus* in western Amazonia almost always has." I concur with Koopman in recognizing *A. anderseni* as a distinct species.

In late October and early November of 1983, the trails and forest surrounding the military encampments were searched at Lagarto Cocha and Zancudo Cocha in eastern Ecuador. *Artibeus anderseni* was found to alter the shape of leaves of several small, forest *Heliconia* species to produce diurnal roosting structures. To create a tent from a *Heliconia* leaf, the bat severs the lateral nerves and interconnecting veins that extend along both sides of the midrib. The cuts ran along the central 90% of the leaf from near (0 to 14 cm) the base to near (10 to 20 cm) the tip. Nerves and interconnected tissues were severed, but not completely, so that they did afford some support for the sides of the leaf. Cuts ran parallel to the midrib for most of its length, but did flare outward slightly toward the base. The lateral nerves were cut from 3 to 8 mm from the midrib; the midrib was not cut. Claw marks where the bats roosted started 50 cm from the base in one tent and ran for 16 cm distally; in another they started at 70 cm and ran for 10 cm distally. Measurements of the blade length, blade width, blade angle, petiole length, petiole angle, and basal height of four tents are provided in Table 1.

At Zancudo Cocha one *Heliconia* tent was unoccupied for two days in succession, then on the third day was occupied by an adult male with enlarged testes, an adult lactating female, and a juvenile male *Artibeus anderseni* (fig. 1). Another *Heliconia* tent was unoccupied.

At Lagarto Cocha 13 tents were found in *Heliconia.* One was occupied by three subadult males not in breeding condition; a second tent contained a single adult male with enlarged testes.

Artibeus cinereus (Gervais, 1856)

Artibeus cinereus, Gervais's fruit-eating bat, is found on the islands of Grenada, Trinidad, and Tobago, and throughout the Amazon Basin and adjacent coastal areas. Surprisingly little has been published on roosting behavior or ecology of this widely distributed species. On Trinidad, Goodwin and Greenhall (1961, p. 262) stated, "It roosts in small colonies of a few individuals under the cut leaves of palm trees and on the under side of banana leaves." On Tobago, Husson (1954, p. 64) reported a single male *Artibeus cinereus* "hanging in a banana tree in cultivated country near the shore."

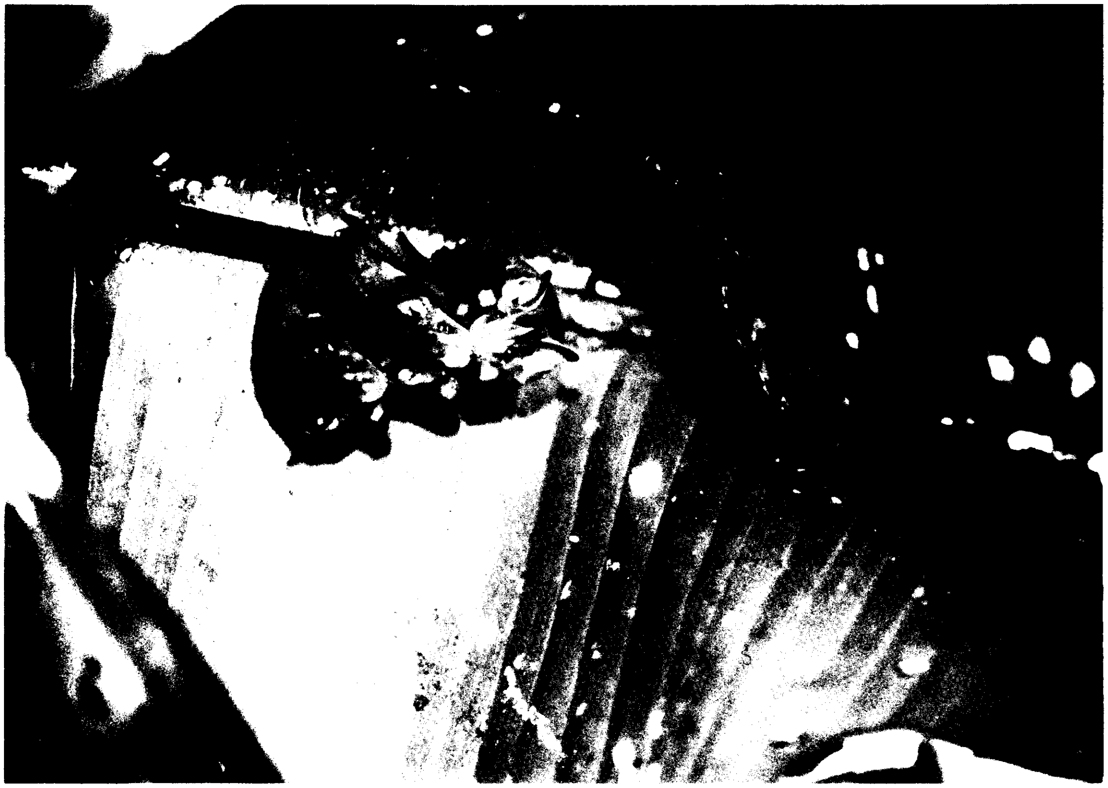

FIG. 1. Photograph of an adult male, adult female, and juvenile *Artibeus anderseni* roosting in a *Heliconia* leaf tent. Details of the cut side nerves can be seen along the midrib of the leaf.

Artibeus glaucus Thomas, 1893

Artibeus glaucus is found at midelevations along the eastern slopes of the Andes from Venezuela to Peru. The status of the name *glaucus* has long been in a state of flux; it often has been considered a subspecies of *A. cinereus.* I concur with Handley (1987) in regarding *A. glaucus* as a distinct species.

A single old adult male *Artibeus glaucus* (FMNH 124844) was observed roosting under a cut *Xanthosoma* leaf at Cascada San Rafael, Ecuador, on 21 September 1983. Four cut leaves on separate plants were observed in close proximity to each other; a fifth cut leaf was observed approximately 10 to 15 m to the south. Only the one cut leaf was occupied by the single bat. An adult female *A. glaucus* was netted in the vicinity that evening. All tent leaves were cut down at the time and four were measured. On 26 November, two more cut leaves were found in this *Xanthosoma* population; one contained three *A. glaucus.* The *Xanthosoma* in which the bats were roosting were part of a population of *Xanthosoma* that occupied approximately 1 ha on a steep east-facing hillside.

The basal lateral nerves from 2 to 5 (usually 3) of the *Xanthosoma* leaves were severed near the midrib, causing the two sides of the leaf to collapse downward around the midrib. The midrib was not cut. Four of the five cut leaves were measured in September; one found in November was measured (table 2). The leaves that were selected by *Artibeus glaucus* for tents all had the midrib running approximately parallel to the ground, whereas the majority of unaltered leaves in the population stood at more vertical angles.

Artibeus gnomus (Handley, 1987)

Artibeus gnomus, the dwarf fruit-eating bat, is found in a peculiar circular range ringing the western edge of the Amazon Basin. Although this species has a wide distribution from Venezuela and Guyana to Peru, it was only recently recog-

TABLE 2. Individual measurements (in cm or degrees) collected from five tents constructed by *Artibeus glaucus* on *Xanthosoma* in Ecuador.

Blade			Petiole	Basal	
Length	Width	Angle	length	height	Remarks
57	68	60	140	230	3 basal cut veins on each side, 2–3 cm from midrib
53	...	40	...	230	3 basal cut veins on each side, 1.5–3.0 cm from midrib
55	62	40	...	230	2 veins cut left, 4 cut right side, 2–3 cm from midrib
64	36	45	137	300	3 basal veins cut on each side, 1.5–3.0 cm from midrib; adult male *A. glaucus* hanging 16 cm from base
61	66	20	145	275	5 basal veins cut on each side, 3.5–4.0 cm from midrib; 3 *A. glaucus*

nized as a distinct species, and little biological information is available (Handley, 1987).

On 15 November 1985 Barbara L. Clauson found a single adult male *Artibeus gnomus* roosting under a cut *Monstera lechleriana* leaf. The *Monstera* was growing as an epiphyte approximately 10 m off the ground on a tree on a sloping hillside at 600 m elevation at Cerro de Pantiacolla, southeastern Peru. The single cut leaf was green and healthy and hung horizontally. No other cut leaves were observed in the immediate vicinity.

The altered leaf was 70 cm long and 38.5 cm at its widest point. All lateral nerves along the basal nearly two-thirds of the leaf were severed immediately adjacent to the thick midrib; this included the basal 12 nerves on one side and 14 on the other. The midrib was severed at 44.5 cm from the base which caused the apical third of the leaf to droop downward perpendicular to the midrib. All nerves proximal to the midrib cut were severed. The lateral nerves along the apical, drooping 25.5 cm were unaltered.

The tent resulting from these cuts was quite enclosed, being formed by the sides of the leaf collapsing downward around the midrib and the distal third of the leaf folding down, perpendicularly to the midrib. The lone *Artibeus gnomus* was roosting 9 cm toward the base from the severed midrib of the leaf.

Artibeus jamaicensis Leach, 1821

Artibeus jamaicensis, the Jamaican fruit-eating bat, is found throughout much of tropical Central America, the northern half of South America, and the Greater and Lesser Antilles. At many localities this is one of the most common species of bats encountered and consequently has received more study than any other phyllostomid.

Artibeus jamaicensis was reported roosting under the cut leaflets of *Scheelea rostrata* in Costa Rica by Foster and Timm (1976). *Scheelea rostrata* is a large, pinnately leafed palm with the leaflets extending out at right angles from the horizontal rachis. Leaflets within the middle 1.3 m region of the frond were cut at varying distances that increased going up to the center of the cut area, then decreased. "As a result . . . the distal parts of the leaflets folded perpendicularly, hung vertically below the frond, and formed a broadly lanceolate tent" (Foster & Timm, 1976, p. 266).

Although several *Artibeus jamaicensis* occupied the roost, only two males were captured, one an adult with enlarged testes, and the second a smaller male not in breeding condition. *Artibeus jamaicensis* apparently has a harem mating system, in which a single breeding male defends a roost used by several females and their offspring; nonbreeding males may be found either singly or in small groups (Morrison, 1979; Kunz et al., 1983). *Artibeus jamaicensis* has been found roosting in a wide variety of situations, including caves, hollow trees, buildings, and under unaltered leaves (Tuttle, 1976), and thus is certainly not an obligate tent-roosting species, as apparently are the smaller species of *Artibeus.*

Artibeus phaeotis (Miller, 1902)

Artibeus phaeotis, the pygmy fruit-eating bat, is found from central Mexico to northern South America (Timm, 1985). Most accounts of habitat for pygmy fruit-eating bats mention their being netted in close proximity to stands of bananas, *Musa* × *paradisiaca* (Ramírez-Pulido et al., 1977; Watkins et al., 1972). Davis (1970) suggested that they might roost under the leaves of bananas.

During the summer of 1982, *Artibeus phaeotis*

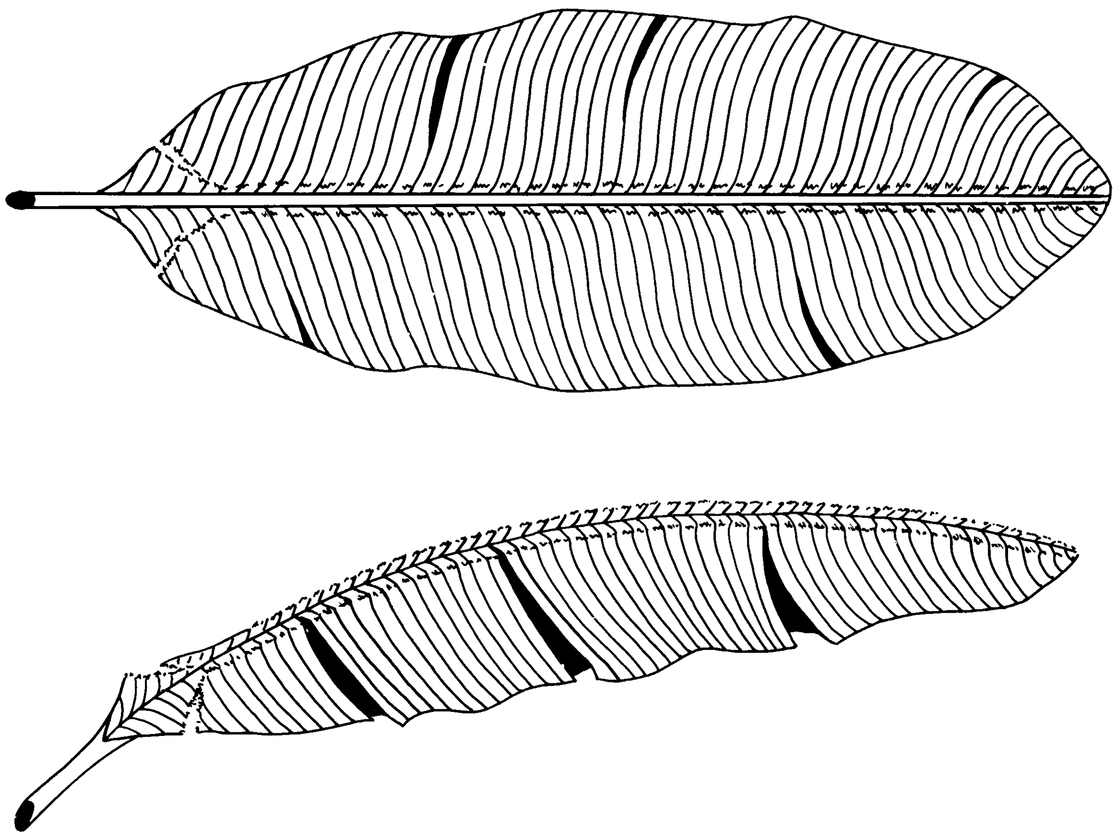

FIG. 2. **Top,** Dorsal view of a banana leaf (*Musa* × *paradisiaca*) showing the cut nerves running along the midrib and flaring out toward the base; **bottom,** tent of *Artibeus phaeotis* made from a banana leaf.

was observed roosting under the leaves of banana and *Heliconia imbricata* at Palo Verde and La Selva, respectively, in Costa Rica. In all cases the leaves had been altered to produce tents.

Artibeus phaeotis constructs roosts in both bananas and *Heliconia imbricata* by biting the lateral nerves and interconnecting tissue that extend at right angles from the midrib, causing the blade to fold over in a V-shaped enclosure. The two sides of the leaf collapse downward, hanging beneath the midrib (fig. 2). Nerves and interconnected tissues are not completely severed, thus the sides of the leaf provide some support for the entire length of the cut. The cuts ran from the base of the leaf to near the tip (table 3). Near the base, the cuts flared out from the midrib to the sides to form an elongate J-shaped pattern. The uncut tip and basal portion of the leaf provide additional strength. The undersides of roost leaves are obscured from view from almost all angles except from directly beneath the tent.

To characterize *Musa* clumps, each of which presumably represented an individual plant, the number of stalks (ramets) per clump was counted; the height of each ramet was estimated to the nearest half meter. This was done for all clumps of *Musa* in the patches that could be located, both those with tents and without bat tents. When a bat tent was located, the following measurements were taken in centimeters: the angle of the petiole (midway from stalk to blade), angle of blade (midway on blade), petiole length, blade length, blade width, height of base of blade, height of tip of blade, height of roost, isolation distance (distance from nearest solid object on the same vertical level), length of uncut basal portion of blade, and length of uncut distal portion. I also noted whether the roosts were in direct sunlight or in shade (table 3). Also for all tents the number of stalks on that column was counted, and the age of the leaf relative to other expanded leaves was recorded. The oldest (lowest leaf) on a plant was assigned the number 1, then the rest counted up from there.

I scored 232 individual stalks of *Musa*, which

TABLE 3. Individual measurements (in cm or degrees) collected from 19 tents constructed by *Artibeus phaeotis* on leaves of banana, *Musa* × *paradisiaca*, in Costa Rica.

Petiole		Blade			Basal	Height			Uncut	
Length	Angle	Length	Angle	Width	height	Tip	Roost	Isolation	Base	Tip
43	40	110	−27	20	196	156	182	81	0	15
53	38	136	−14	19	230	146	225	120	10	45
43	42	146	−40	22	213	170	228	125	1.5	48
49	12	120	−55	23	250	180	240	53	5	8
45	52	100	−16	18	205	···	200	70	0	30
50	55	120	−3	21	200	165	210	25	3	8
54	50	142	−36	20	235	160	230	115	1	44
40	75	80	+15	19	190	195	206	80	0, 25	20
36	68	175	−12	26	320	260	320	> 300	0	1.5
60	70	195	+25	30	360	400	400	> 300	0, 35	0
44	66	130	+23	25	250	260	290	120	0	40
41	50	94	+5	20	140	155	170	40	0, 40	25
34	45	97	−22	20	205	175	200	100	0	0
50	68	130	0	23	180	220	230	60	0	2
56	60	147	−37	27	260	180	240	35	0	28
33	55	85	−12	21	205	215	220	18	0	5
16	52	60	+28	13	130	···	140	35	0	12
46	50	129	+15	21	250	220	260	120	0	65
40	54	88	+15	14	170	···	180	220	0	3

were in 41 clumps scattered in 100 m of second growth forest. The mean number of ramets per clump was 5.4; the range from 1 to 23. I located 26 leaves that were cut by bats, a ratio of roughly one tent per 8.1 ramets. Fourteen clumps had cut leaves; if a clump had cut leaves it had a mean of 1.9 cut leaves (range 1 to 2). Of the 26 altered leaves, complete data were taken on 19. The remaining tents were decomposing; in a few cases the bats had not completed the tents. On the partially completed tents, only one side of the midrib was cut along one-quarter to one-third the distance of the blade, but did not cause the side to collapse. Only 2 of the 19 complete tents were located directly in the sun. Bat tents were found in clump sizes ranging from 1 to 23 (mean = 6.2). The average height of all plants (N = 232) was 2.3 m. The average height of plants with tents was 2.0 m (N = 16).

One adult male with enlarged testes and six pregnant females were watched over a 3-day period in one of the roosts. Additionally, two solitary nonpregnant female *Artibeus phaeotis* roosted under separate leaves (fig. 3).

Artibeus phaeotis appears to select banana leaves with specific characteristics. Usually these are the oldest fully expanded leaves, just over 2 m above the ground, with the center of the midrib nearly horizontal to the ground and positioned far enough from nearby stems and branches to limit access by predators. Roost sites generally are located in the shade of surrounding forest trees where apparently they are protected by the forest overstory from wind, blowing rain, and sunlight.

Although bananas are not native to the New World, they are now common throughout the range of *Artibeus phaeotis* and probably provide roost sites in other localities. *Heliconia, Calathea,* and broad-leafed palms are uncommon at Palo Verde, hence are not readily available to *A. phaeotis* for tent sites there. *Artibeus phaeotis* used only banana leaves for tent making at Palo Verde, but constructed similar tents in *Heliconia imbricata* at La Selva. *Heliconia imbricata* is the largest species of *Heliconia* in Costa Rica, and its leaves are similar in size and shape to banana. The tents in *Heliconia* were similar in all respects to those in banana leaves. An adult male and adult female were found roosting together under a single *Heliconia* leaf in late June.

Villa-R. (1967) found a single specimen roosting near the mouth of a small cave in Mexico.

Artibeus toltecus (Saussure, 1860)

Artibeus toltecus, the lowland fruit-eating bat, is found along the coasts of eastern and western Mexico from Nuevo León and Sinaloa south through Central America and perhaps to extreme northwestern Colombia. This species appears to be restricted to midelevational slopes, and in Costa Rica

FIG. 3. Photograph of an adult female *Artibeus phaeotis* roosting in a banana leaf tent. Details of the cut side nerves can be seen along the midrib of the leaf.

I have found it only from 650 to 1500 m in elevation.

In April 1986 I observed a single *Artibeus toltecus* roosting under a cut leaf of *Anthurium caperatum* in Braulio Carrillo National Park, northeastern Costa Rica. The *Anthurium* was growing as an epiphyte on a small tree at 800 m (2½ km S, 11 km E of San Miguel, 10°17′N, 84°05′W). One leaf on the plant was altered; it was 2½ m off the ground and the midrib hung parallel to the ground. Four or five lateral nerves were cut basally on each side, causing the sides of the leaf to fold down around the midrib. A break of the midrib at its midpoint caused the distal half of the leaf to droop down (fig. 4). Seven additional tents of this style were observed on *Anthurium* in this area, ranging in elevation from 700 to 1400 m. It is assumed that they were made by *A. toltecus*, the only small species of *Artibeus* we netted there, although these tents were not occupied. Six tents were observed in a 3-km transect ranging from 700 to 1100 m in elevation.

Davis (1944) reported that *Artibeus toltecus* roosts under banana leaves, although he did not indicate that the bats were modifying the leaves. Davis (1944, p. 378) stated:

> . . . they had regularly established roosts under the large, drooping leaves of the banana trees, each one easily recognized by the manner in which the vane of the leaf hung limply suspended from the midrib. The closely appressed vanes of the leaf, plus the natural darkness within the depths of the grove, afforded good concealment. These bats, too, were wary and that feature coupled with the nature of their retreat caused considerable difficulty in procuring specimens.

In light of Davis's description of the roost sites of *A. toltecus* in banana leaves and my own observations on *A. toltecus*, I suspect that this species was creating tents similar to those I observed for *A. phaeotis* in Costa Rica. The tents formed by *A. phaeotis* in *Musa* (see fig. 2) are similar in ap-

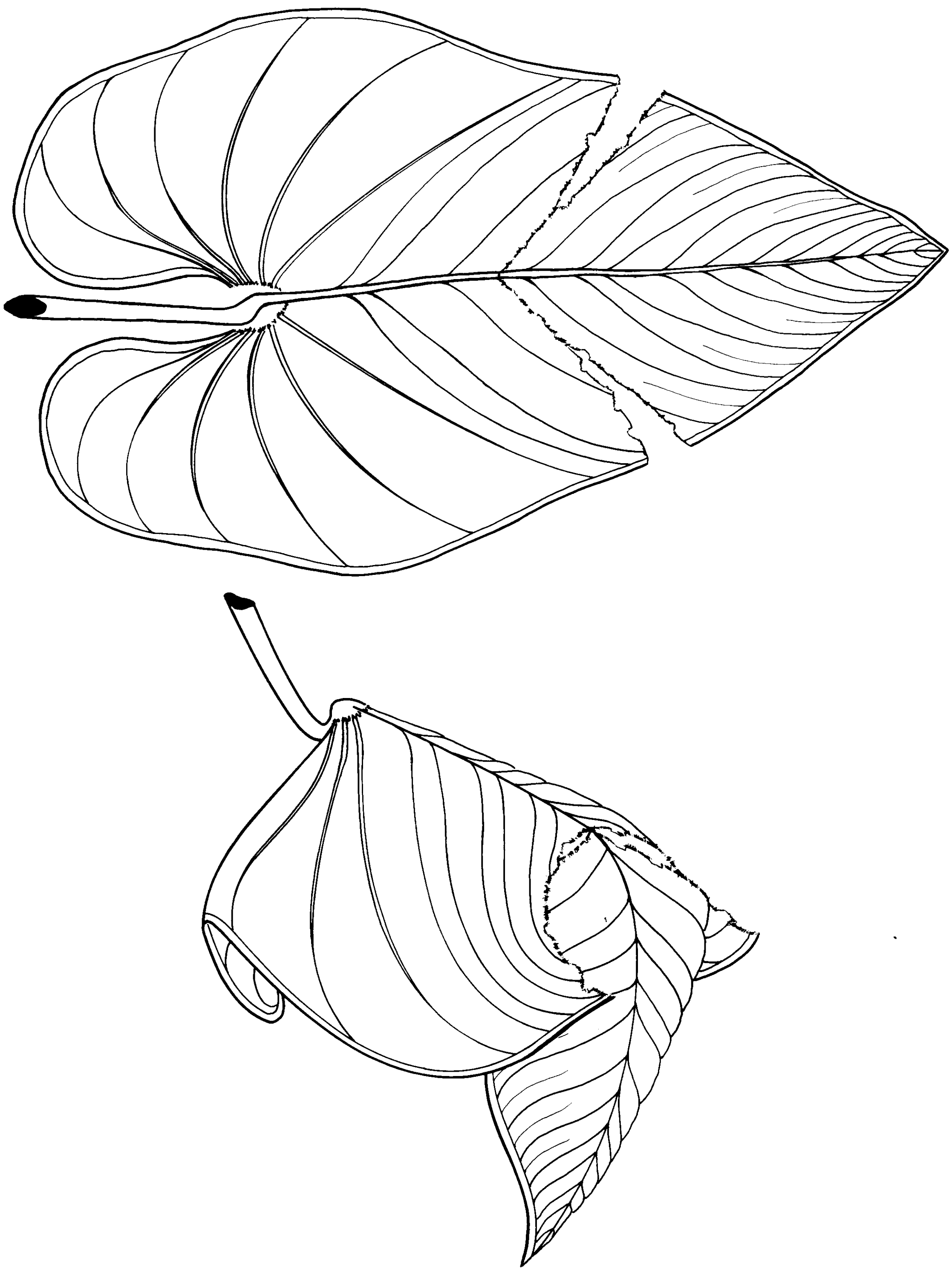

FIG. 4. **Top,** Ventral view of an *Anthurium caperatum* leaf showing the cut nerves along the base of the leaf and the broken midrib; **bottom,** tent of *Artibeus toltecus.*

pearance to those described by Davis (1944) for *A. toltecus.*

Artibeus toltecus has also been reported in caves (Davis et al., 1964; Jones, 1966; Jones & Alvarez, 1964), and Goodwin (1934, p. 12) reported a single specimen collected "in one of the buildings (church?) at San Lucas . . . [the] rest of the congregation seemed to be *Glossophaga.*"

Artibeus watsoni Thomas, 1901

Artibeus watsoni, Thomas's fruit-eating bat, is one of the smaller members of the genus *Artibeus* and found from southern Veracruz south through Central America to northern South America. It appears to be restricted to lowland and midelevation humid forests.

During the summers of 1974, 1982, 1984, and 1986, numerous individuals of *Artibeus watsoni* were seen roosting under 19 different species of broadleafed plants at several localities in Costa Rica. At Parque Nacional de Corcovado, Costa Rica, trails were surveyed on three separate occasions for the presence of tents made by *Artibeus watsoni,* in June and August 1982 and again in August 1984. In mid-June 1982, the following groupings of *Artibeus watsoni* were observed: two (both adults, a male and pregnant female), two (pregnant female and one not captured), two (not captured), and six hanging singly (of which two were captured and found to be adult males). Additionally, several tents on banana and *Heliconia* were marked for relocation later in the summer. A tent marked on *Heliconia imbricata* was relocated 60 days later. The tent was still intact, although it was beginning to break down; a single *A. watsoni* was using it. All other marked tents had decomposed.

On 10 August 1982 I found 90 tents constructed by *Artibeus watsoni* along the trail through Corcovado's "Monkey Woods." These tents were made from the following species of plants: *Musa × paradisiaca* (49, 54%), *Anthurium ravenii* (13, 14%), unidentified aroid (11, 12%), *Heliconia imbricata* (9, 10%), *Heliconia latispatha* (1, 1%), *Heliconia* sp. (3, 3%), and *Calathea insignis* (4, 4%). Tents located on *Anthurium ravenii* were most often found clumped, with an average of 2.6 tents per plant, whereas in the other species of plants it was uncommon to find more than one tent per individual plant. Bats were found singly (five) or in three groupings of four, three, and two individuals. Four of the single bats were all adult males.

A trail running up to a ridge top was surveyed from 9 through 11 August 1982, with the following results: 25 tents found of which 16 were on *Heliconia imbricata* (64%), 8 on *Calathea insignis* (32%), and 1 on *Carludovica palmata* (4%). Three tents were occupied by two (sexes unknown), one male, and one female. Near the mouth of the Río Llorona on 8 and 9 August I counted the following groups of bats: eight (three adult females, three young, and two not caught), two (adult female with volant young), two (sexes unknown), and three singles (one a nonreproductive adult female). Additional tents were observed in banana, coconut palm (*Cocos nucifera*), *Calathea insignis,* and *Carludovica* cf. *drudei.*

In August 1984, I found 63 tents constructed by *Artibeus watsoni.* These were distributed on the following plants: *Anthurium ravenii* (36, 57%), *Heliconia* sp. (14, 22%), *Musa × paradisiaca* (7, 11%), *Calathea insignis* (3, 5%), *Carludovica palmata* (1, 1.6%), *Welfia georgii* (1, 1.6%), and *Geonoma* sp. (1, 1.6%). Only 3 of the 63 tents were occupied; one had two bats and two each had single bats. As I noted in 1982, tents on *Anthurium ravenii* were often clumped on the same plant with an average of 2.5 tents per plant.

At La Selva in July 1982, 43 *Artibeus watsoni* tents were located over a 5-day period in the following species of plants: *Asterogyne martiana* (33, 77%), *Geonoma congesta* (6, 14%), *Geonoma cuneata* (2, 5%), and an unidentified species of Cyclanthaceae (2, 5%). One adult male *A. watsoni* was found under an *Asterogyne martiana* tent on the first day. On the fifth day an adult female with young was found under another *A. martiana* tent that had been unoccupied for the previous four days, as was a third adult (not captured) under another *A. martiana* tent. All other tents were unoccupied.

In 1974 I surveyed approximately 10 km of trails at La Selva and found 29 tents on the following species of palms: *Asterogyne martiana* (19, 66%), *Bactris wendlandiana* (1, 3%), *Geonoma congesta* (2, 7%) and *Geonoma cuneata* (7, 24%); all were unoccupied. Foster and Timm (1976) reported tents in these palms, although they were not able to associate bats with the tents. My recent studies at La Selva have confirmed that these tents were made by *A. watsoni.*

At Finca Las Cruces in mid-August 1982, 13 tents constructed by *Artibeus watsoni* were located;

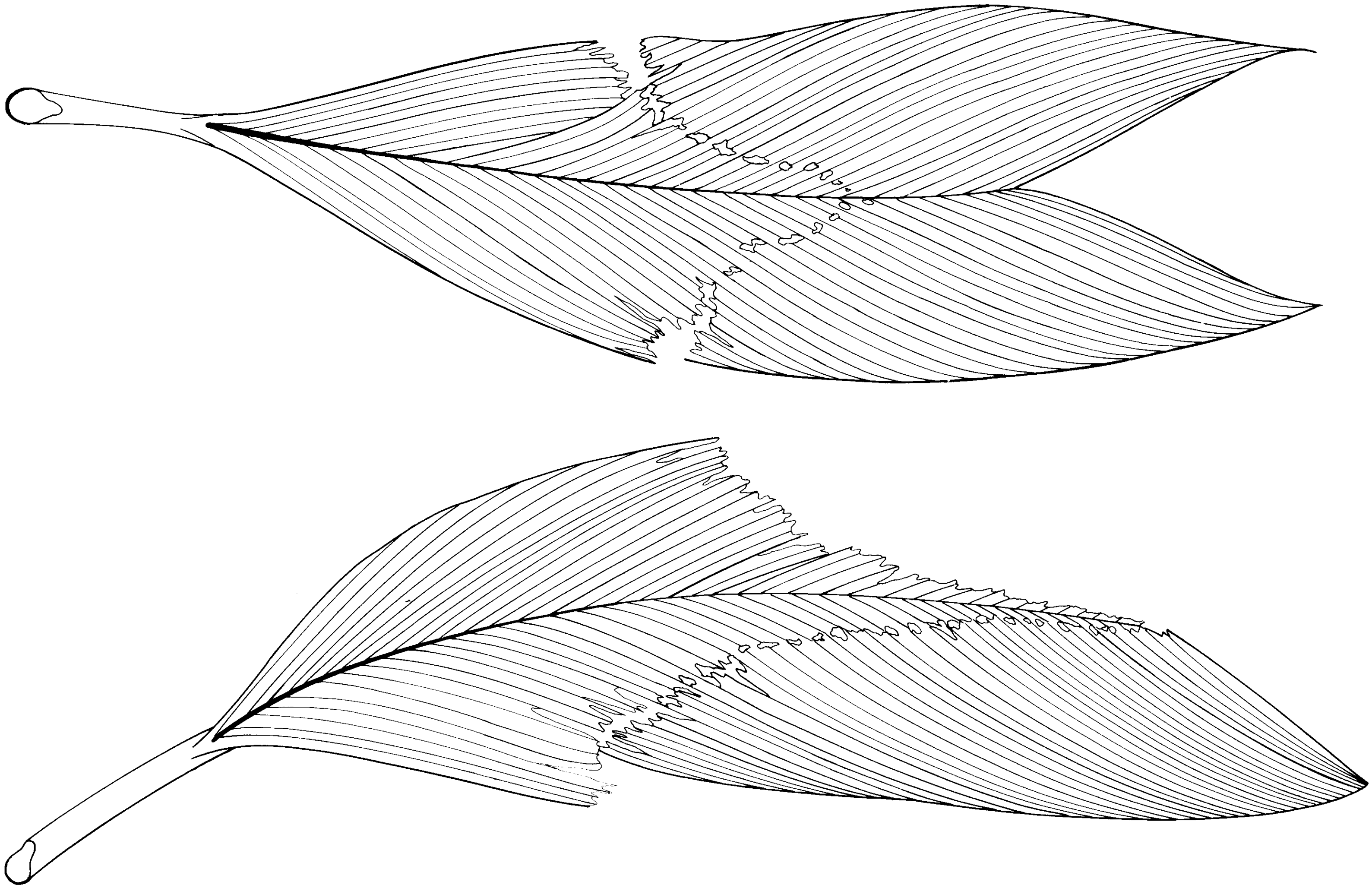

FIG. 5. **Top,** Dorsal view of the ground palm, *Asterogyne martiana,* showing the cut nerves running along the midrib and swinging out to the sides about midway in the leaf (described in the text as the J-shaped cut); **bottom,** tent of *Artibeus watsoni* on *A. martiana.*

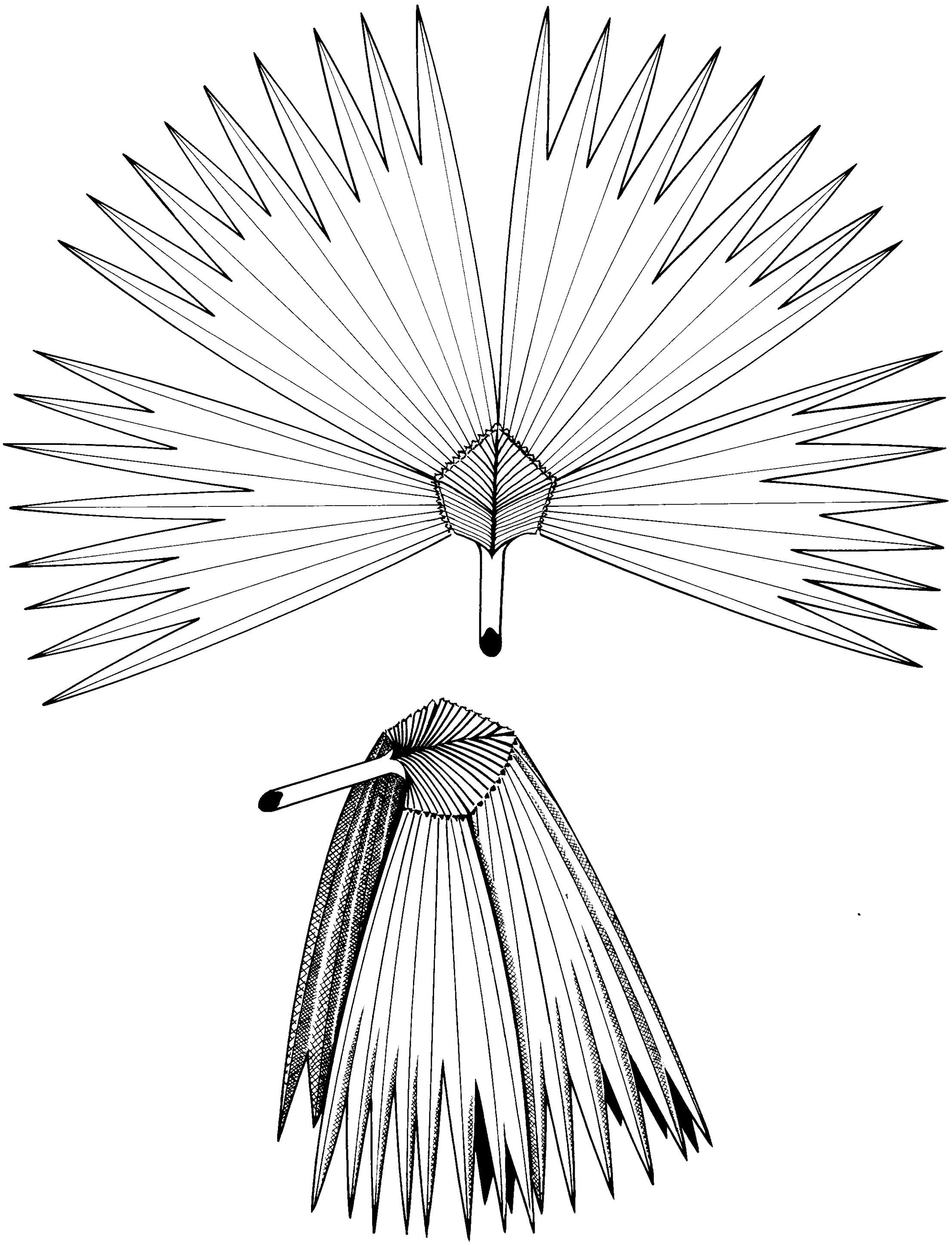

FIG. 6. **Top,** Dorsal view of the cyclanth, *Carludovica palmata,* showing the polygonal cuts; **bottom,** tent of *Artibeus watsoni* on *C. palmata.*

FIG. 7. Photograph of adult female *Artibeus watsoni* and her subadult offspring roosting in a *Carludovica* leaf tent. Details of the polygonal cuts and folds can be seen in the background.

one was occupied by an adult male. The tents were distributed on the following species of cyclanths: *Asplundia euryspatha* (6, 46%), *Carludovica drudei* (4, 31%), and *Cyclanthus bipartitus* (3, 23%).

Artibeus watsoni uses a variety of species of plants and a wide array of leaf shapes for diurnal roosts. I have found four distinct styles of tents at a single locality (Corcovado). These styles include the simple V-shaped cuts on bifurcated palms (fig. 5), cutting a few side veins on aroids to produce a rounded pyramid, the elongated J-shaped cuts on banana and *Heliconia* leaves, and the polygonal cuts on *Carludovica* (figs. 6–7). For each distinct leaf shape, the cuts create a well-concealed diurnal roost. *Artibeus watsoni* probably is an obligate tent-rooster, as it has only been found roosting under cut leaves.

On several instances a bat occupied the same tent, or tents in close proximity, for two to three days in succession. Those tents might then remain unoccupied for several days in succession. Disturbed bats generally flew directly to another tent from 20 to 50 m away, or attempted to return to the tent where originally found.

Tents generally are found clumped, both on a single plant if leaf morphology and age are appropriate, and in restricted areas. Up to five tents have been found on a single *Anthurium ravenii,* and when present the mean number of tents was 2.5.

At Parque Nacional de Corcovado, Choe and Timm (1985) found that *Artibeus watsoni* showed strong preference for *Anthurium ravenii* leaves that were medium sized, low within the plant, and grew closer to the ground than average *A. ravenii* leaves. Also at this site, Boinski and Timm (1985) documented that squirrel monkeys (*Saimiri oerstedi*) were major predators on *A. watsoni,* with the adult male monkeys being the most successful at capturing bats. Additionally, double-toothed kites (*Harpagus bidentatus*) followed troops of foraging squirrel monkeys, using them as "beaters." When tent-making bats were flushed by the monkeys and escaped, they were routinely captured and consumed by the attending double-toothed kites.

Artibeus watsoni has long been known to cut palm tents for diurnal roosts, although prior to this study little had been published on roosting

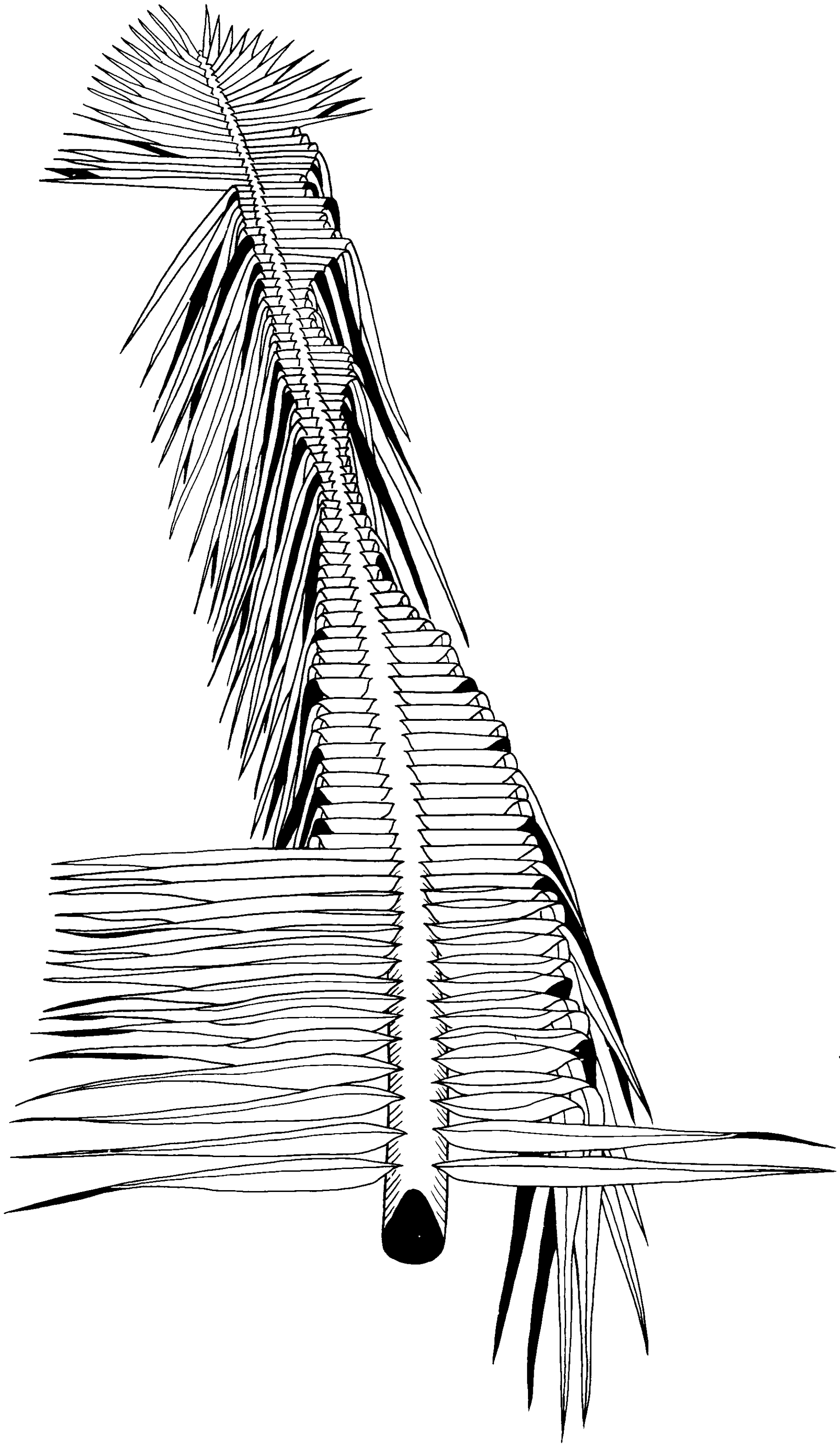

FIG. 8. Dorsal view of *Scheelea rostrata* showing the leaflets cut by *Uroderma bilobatum* to form a tent.

behavior of this species. The elongate J-shaped cuts made on bifurcated palms were first described and illustrated by Chapman (1932, p. 555). He stated that "both vanes of the leaf whence the bat flew were cut diagonally to the midrib of the leaf, so that their terminal portions drooped downward to form a tentlike shelter." Chapman appropriately termed these three-sided diurnal roosts "tents," and I have expanded the use of the word tents to include all modified leaves by bats.

Barbour's (1932) original description of *Uroderma bilobatum* cutting palm leaves for roosts also provides a secondhand report (p. 308) by H. C. Clark stating that "Clark has just found for the first time a youngish coconut palm, a single leaf of which was being cut by bats of the genus Uroderma in a very similar way." The common use of young coconut palms (*Cocos nucifera*) by *Artibeus watsoni* in Costa Rica, coupled with the total lack of evidence that *Uroderma bilobatum* uses juveniles of this palm, leaves that small, or roosts that close to the ground, suggests that the tents seen by Clark were in fact made by *A. watsoni. Artibeus watsoni* also is abundant on Barro Colorado Island, Panama. Apparently no voucher specimens of the bats were preserved at the time. Allen (1939, p. 69) reported "a specimen of *A. watsoni* that was hanging by day from the underside of a banana leaf." Perhaps the natural-looking folds caused by the cuts running parallel to the midrib were not noticed at the time. Ingles (1953) reported on tents of *A. watsoni* in two species of *Geonoma* on Barro Colorado Island; one tent was occupied by three individuals. Thomas's fruit-eating bat has been found roosting in an artificial tent, an inverted hanging box. Wilson (1970) reported that several females raised young in the corner of a suspended box on Barro Colorado Island.

Uroderma

Uroderma bilobatum Peters, 1865

Uroderma bilobatum has been given the distinctive "common" name of Peters's tent-making bat. Tents constructed by *Uroderma bilobatum* were seen at three separate localities in Costa Rica during the summers of 1982, 1984, and again in 1986, the first at Bosque Brrancia near Cuarto Cruces in the Pacific lowlands of northwestern Costa Rica, the second at Corcovado on the Osa Peninsula, and the third at La Selva in the Caribbean lowlands.

On 25 August 1982 a colony of *Uroderma bilobatum* was roosting under a modified frond of the palm *Scheelea rostrata* at Bosque Brrancia. The colony included an adult male with enlarged testes and four adult females.

The *Scheelea rostrata* frond in which the colony of *Uroderma bilobatum* roosted was a mature leaf, approximately 6.5 m in length. The bats were hanging approximately 4.5 m off the ground; most were clustered together, although a few were spread out over 50 cm of the frond. The cut leaflets started at about 3.5 m off the ground and proceeded up the frond for the next 2.5 m (fig. 8). The general pattern of the cut leaflets was a tapering effect, with the cuts on the lowermost leaflets being farthest from the midrib. Leaflets along the proximal 2 m and the distal 50 cm were unmodified. Only the midrib of the leaflets was cut. Each leaflet had a distinctive V-shaped fold at its base where it was attached to the midrib. The bats were hanging from the leaflets rather than the midrib.

From the dorsal aspect of the leaf, the proximal portion of the tent (cut leaflets) extended 50 cm further down on the right side than on the left to include 10 basal leaflets whose opposites on the left were unaltered. The basalmost cut leaflet was cut 34 cm from the midrib. Proceeding distally, the length of the unmodified basal portion of each leaflet decreases. The basalmost cut leaflet on the left was cut 19 cm from the midrib. The overall appearance of the tent was a sharp, convergent taper for the next meter. Following this section, there was a 75-cm section in which the cuts were close to the midrib (within 3 cm). On the distalmost 30 cm of the tent, the leaflets were cut closer to the midrib on the left side than on the right. Similar tents, each housing a colony of *Uroderma bilobatum,* were found in a large stand of *Scheelea rostrata* at Corcovado in 1984, and William A. Haber (pers. comm.) informed me that he has seen similarly cut leaves in the same species of palm at Cahuita (09°44′N, 82°49′W) in the Caribbean lowlands of southeastern Costa Rica in 1984.

In June of 1982 and again in March of 1986, I found numerous banana leaves cut by *Uroderma bilobatum* just to the north of the field station at La Selva. The midrib on vertical leaves was cut to the extent that the distal portion of the leaf collapsed downward to form a two-sided tent (fig. 9). Severing the midrib on vertical leaves had the effect of folding the leaf back upon itself creating a tight, dark crevice at the fold where the bats roosted (fig. 10). In addition to severing the midrib, the bat cut a large V-shaped pattern running

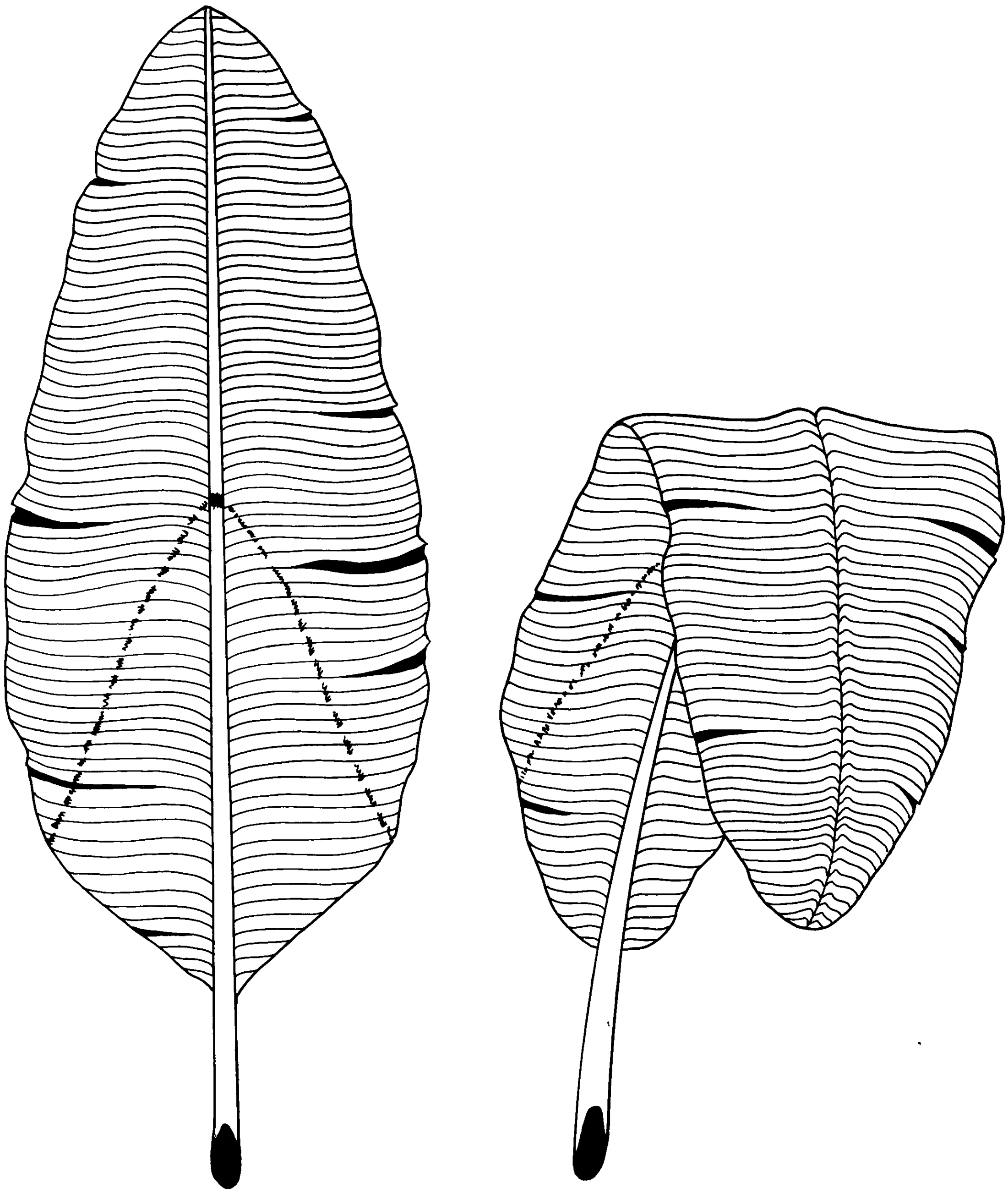

FIG. 9. **Left,** Dorsal view of a banana leaf showing the cut midrib and the large V-shaped cuts through the side nerves; **right,** tent of *Uroderma bilobatum* made from a banana leaf.

from the midrib to the base of the leaf. The side veins and interconnected tissues were partly severed. However, because the leaf stood nearly vertical, these V-shaped cuts did not cause further folding of the leaf. The only cut creating the tent was that of the midrib.

In 1982 five tents in widely separated banana leaves were located (table 4). One was occupied by eight *Uroderma bilobatum,* which included one adult male with enlarged testes and seven females. In 1986 eight tents were observed in the same banana patch. On this occasion eight *U. bilobatum*

FIG. 10. Photograph of a colony of *Uroderma bilobatum* roosting in a banana leaf tent. The bats are roosting in the fold of a leaf that was created by the distal half of the leaf collapsing downward at the severed midrib.

tents were clustered in three clumps of bananas. Only one tent was occupied; it contained 13 bats.

This folded broad-leaved style of tent is undoubtedly the tent style illustrated by Walker (1960, p. 30) in his photograph of roosting *Uroderma bilobatum*, although he did not describe it nor mention where it was observed. Interestingly, I have searched several dozen banana and larger *Heliconia* groves throughout Costa Rica and Ecuador specifically looking for this style of tent, and none were observed. *Uroderma bilobatum* is an abundant and widespread species in the lowlands, but employment of this particular style of tent appears spotty as I have not observed it elsewhere.

In Panama, Barbour (1932) found that colony size under a single cut leaf of *Prichardia pacifica* varied from a few bats to 56. Prior to Barbour's discovery that *Uroderma* altered leaves, Goldman (1920, p. 199) stated of these bats in Panama.

> In the forest near Gatun *Uroderma bilobatum* was located several times, a few in a place, clinging during the day in clusters to the midribs on the under sides of large palm leaves. They usually choose darkened spots where the leaf was folded over, or overhanging pinnae shut out much of the light.

Burt and Stirton (1961) reported *U. bilobatum* in El Salvador roosting beneath the leaves of bananas and coconut palms. I strongly suspect that the bats had altered these leaves and that these authors had failed to notice it or failed to associate the hanging bats with the damage to the leaves. Bloedel (1955, p. 234) stated of *Uroderma bilobatum* in Panama that:

> I observed these bats only in their palm-leaf tents. . . . In the latter part of March most females have nursing young, and are roosting in clusters of 20 to 40, while the males are separated from them, usually solitary or in small groups of from 2–5.

In Trinidad, Goodwin and Greenhall (1961, p. 254) found them

> on the under side of the fan-shaped leaves of certain palm trees, especially the carat palm (*Sabal glaucescens*). . . . The bat makes a series of cuts across the pleated surface of a leaf, causing half of the leaf to bend at an angle to form a protected retreat.

TABLE 4. Individual measurements (in cm or degrees) collected from four tents constructed by *Uroderma bilobatum* on banana, *Musa* × *paradisiaca*, in Costa Rica.

Blade		Petiole	Cut midrib	
Length	Width	angle	from base	Remarks
210	95	40	117	Not occupied
220	90	70	90	8 *U. bilobatum*
. . .	. . .	80	. . .	1 *U. bilobatum*
. . .	. . .	80	. . .	Not occupied
210	95	. . .	. . .	Not occupied

They were found roosting in colonies of 10 or more individuals. In Suriname, Husson (1962, p. 161; 1978, p. 143) collected three pregnant female *U. bilobatum* "in a plantation where they were found hanging on the under side of a leaf of [a] so-called 'paloeloe,' *Ravenala guyanensis*." In Nicaragua, Jones (1964, p. 507) collected four female *U. bilobatum* that "hung together about 10 feet above the ground in the 'tent' formed by a cut palm frond. Each was pregnant with a single embryo." In Guatemala, Dickerman et al. (1981, p. 409) reported, "Palm leaf tents were frequently found occupied by one to seven individuals, but nursing females were usually found alone or with juveniles."

Leaves selected by *Uroderma bilobatum* for tents are all large, and of a variety of shapes. The large V-shaped pattern cut into the leaves is a characteristic of *Uroderma* tents. *Artibeus watsoni* also uses a variety of leaf shapes for tents; however, the nature of the cuts and style of tent created vary with leaf shape. *Uroderma bilobatum*, on the other hand, makes patterned cuts that appear to be an innate response to large leaves, regardless of the shape. As noted in the banana tents, a single cut across the midrib creates the tent, and the V-shaped pattern had no effect upon tent shape; this perhaps represents wasted effort by the bats.

There are a few records of *Uroderma bilobatum* being found roosting in a hollow tree and one "under the eave of house" (Davis, 1968, p. 695). In all cases these have been of single individuals, and I suspect represent either recently dispersed young that have yet to join a breeding colony or bachelor males. *Uroderma bilobatum* roosting under a cut *Prichardia* leaf was illustrated by Kunz (1982). A colony of *U. bilobatum* roosting under a banana leaf tent was illustrated by Keller (1986). Macdonald's (1984, p. 806) photograph of two tent-making bats under a *Heliconia* tent is erroneously labeled *Uroderma bilobatum*. These bats are ac-

FIG. 11. Tent of *Uroderma magnirostrum* on the pinnately leafed palm *Astrocaryum murumuru*.

tually a small species of *Artibeus*, probably *A. phaeotis*; the tent style and size and coloration of the bats are typical of *A. phaeotis*.

Uroderma magnirostrum Davis, 1968

Although *Uroderma magnirostrum* is a widely distributed bat found from Mexico to Bolivia, it was not recognized as a species distinct from *U. bilobatum* until 1968 (Davis, 1968), and few specimens are represented in collections. When W. B. Davis described this new species he commented that although it was widely distributed only seven specimens had been collected prior to the widespread use of mist nets in the 1960s, and that all specimens available to him had come from localities less than 1000 feet in elevation. He stated that "These facts strongly suggest basic differences in the habits of the two species and that those bats with a deep rostrum are not 'tent-makers' as are members of the species *Uroderma bilobatum*" (Davis, 1968, p. 678). There have been no reports on the behavior or ecology of *U. magnirostrum*.

On 25 July 1985 Barbara L. Clauson discovered a colony of two male and three female *Uroderma* *magnirostrum* roosting under the cut leaflets of the pinnately leafed palm, *Astrocaryum murumuru*. The single occupied tent found was on the ridge above Hacienda Amazonia at 825 m in southeastern Peru. The entire colony was collected by John W. Fitzpatrick. On 3 November Clauson returned to the site to measure the leaf and noted an additional cut leaf in the same plant.

When first observed, four bats were hanging together and one was hanging several centimeters away. When observed an hour later, all five were hanging together in a tight cluster approximately 7.5 m off the ground. The bats were hanging from the leaflets rather than the midrib, approximately 200 cm from the tip of the leaf. The colony included one adult male with enlarged testes, two adult females, and two subadults, one female and one male.

The roosting structure of *Uroderma magnirostrum* was in a pinnately leafed palm (fig. 11). The bats severed the leaflets along the upper two-thirds of the leaf; those along the lower third were unaltered, as were the leaflets at the very tip. As the leaflets proceeded up the tent they were severed closer to the midrib forming an elongate, convergently tapering tent (fig. 11). The general appearance of the *U. magnirostrum* tent is similar to that described herein for *U. bilobatum* on the pinnately leafed palm *Scheelea rostrata*.

The *Astrocaryum* frond in which the colony of *Uroderma magnirostrum* roosted was a mature leaf, approximately 6.1 m in length and 1.9 m in width at the widest point, with the petiole 1.1 m long. The leaf left the trunk (d.b.h. .4 m) at 3 m from the ground and hung at an angle of approximately 50°. The bats were hanging approximately 7.5 m off the ground. The cut leaflets started at 1.5 m from the lowest leaflet and proceeded up the frond for the next 2.9 m to nearly the tip (fig. 11). The cuts on the lowermost leaflets were furthest from the midrib. The lowest severed leaflets were cut up to 34 cm from the midrib, whereas the distal leaflets were severed only 2 cm from the midrib of the leaf. The midribs of the leaflets were cut causing the distal portion of the leaflets to fold downward. Leaflets along the proximal 1.5 m and the distal .5 m were unmodified. The trunk, petiole, and midrib of this palm were covered with sharp, penetrating spines several centimeters in length. After 14½ weeks this tent was still alive and green, most of the leaflets appearing as fresh in November as they did in July.

This *Astrocaryum* contained a second cut leaf that was unoccupied. This roost was also in a mature leaf which was an older leaf than the occupied tent, with many broken, yellowed, and brown leaflets. The leaf was approximately 6 m in length and 2 m in width at the widest point, with a petiole .8 m long. The leaf left the trunk at 2.9 m from the ground and hung at an angle of approximately 60°. Cuts were distributed asymmetrically along the length of the leaf. The cut leaflets on the left side of the leaf started 3.05 m from the lowest leaflet and proceeded up the frond for the next 1.3 m, to .88 m from the tip. The cut leaflets on the right side of the leaf started 3.25 m from the lowest leaflet and proceeded up the frond for the next 1.49 m, to .49 m from the tip. The cuts on the lower leaflets were farthest from the midrib. The lowest severed leaflets were cut up to 35 cm from the midrib, whereas the distal leaflets were severed as close as 1.5 cm from the midrib. Leaflets along the proximal 3.05 m and 3.25 m and the distal .88 m and .49 m were unmodified.

I propose the common name of Davis's tent-making bat for this species.

Conclusions

A review of the literature on tent-making bats contains some 32 primary references covering the 55-year period from 1932 through 1986. Surprisingly, we actually know very little about the biology of these bats.

As late as 1975 Eisentraut was yet doubting that bats were cutting leaves to make tents, stating:

> . . . observers maintain that the bats form these tentlike structures themselves, by making a series of holes running across the middle of a large palm leaf. The bats then supposedly bend the outer half of the leaf around, so they can then rest inside this 'tent'. . . . On the basis of personal observations in tropical regions in Africa, I tend to believe instead that these holes were made by insect larvae while the leaves were still rolled up. A storm can then easily break the leaf along the line of holes and form the tent roof which is so convenient for the bats (Eisentraut, 1975, p. 142).

Eisentraut, by his own admission, had never seen a bat tent. I believe that if he had, he would have come to the same conclusion Thomas Barbour did nearly a half century earlier, that the bats and not insects were making the cuts.

Although we have yet to actually observe bats cutting leaves to form the roosting structures described herein, I hope the volume of data presented here and in my other works establishes for a fact that many species of small and medium sized stenodermines are indeed tent-makers. The observations presented represent data collected from several hundred tents located over a 15-year period. Several facts consistently emerge between my observations and those independently corroborated by others. Bats of the genera *Artibeus* and *Uroderma* (as well as *Ectophylla, Mesophylla,* and *Vampyressa*) roost under cut leaves. These leaves may be on a wide variety of species of plants, but generally the shape of the leaves is similar. The shape of the cuts is very characteristic for each species of bat and the patterns and styles of tents created by the bat species are consistent.

The behavioral repertoire associated with tent-making in bats certainly evolved more than once, as evidenced by the patchy distribution of tent-making species with the chiropteran suborders Megachiroptera and Microchiroptera. Within the Megachiroptera, a single species of tent-maker is known, *Cynopterus sphinx*. Within the Microchiroptera, tent-makers are known only from one subfamily of the Phyllostomidae, the Stenoderminae. The Stenoderminae constitute an extremely speciose and diverse group of bats, with more than 30 species currently recognized. Tent construction within stenodermines may be a trait that evolved once, twice, or as many as three times. The *Artibeus-Uroderma* group are sister genera and form one clade of the tent-making repertoire. Secondly, the *Mesophylla-Vampyressa* group are sister genera (and perhaps should be considered congeneric) and would constitute the second clade. Finally, *Ectophylla* would constitute a third lineage. The relationship between these three lineages is uncertain and warrants further investigation.

Knowing that bats modify the leaves of several species of plants to produce diurnal roosting structures led to the following questions: (1) Are bats selecting specific species of plants for tents? (2) What styles of tents are cut by bats and do these differ between species? (3) Do bats select for a particular angle, size, or shape of leaf for diurnal tents? (4) Are leaves selected preferably in larger clumps or smaller clumps? (5) Are older or younger leaves selected? (6) Are leaves of a particular height class selected? (7) Are leaves that are not adjacent to solid objects selected? (8) What do typical tents look like? (9) How and why did tent construction evolve?

On occasion I have found "cheaters," species of bats roosting in a tent made by another species. Is cheating an evolved strategy of roost site selection of some bats?

Bats of the genera *Artibeus* and *Uroderma* actively modify leaves to produce diurnal roosting structures, but by biting the tissue between veins along the midrib and leaving the midrib and most veins intact, do not kill the leaves. The resulting tent is available for use as a roost for an extended period of time; one was observed in use for more than 60 days. Bats select for specific sizes and shapes of leaves. Tents provide concealment from predators and protection from the rain, wind, and sun. This type of roost offers the additional advantage that the bats are warned about the approach of a potential predator, because even slight movements of the leaf stem or the leaf itself are transmitted as magnified vibrations to the roosting bat. Tents may provide bats with suitable roosting sites that would not otherwise be available in close proximity to prime food resources.

One of the most productive areas for future research will be exploring aspects of the biology of these bats from an evolutionary perspective. Future subjects I will be addressing include the role of tent roosting in controlling ectoparasites and the correlation between complexity of tents and social systems in these bats. I believe that tent-making originated as an antipredation strategy and has since, secondarily, evolved to play a major role in controlling ectoparasites and in social behavior.

Many factors influence the choice of roost site selection by bats. Included among these are vulnerability to predation, physical stability of the site, proximity to food sources, and general appropriateness of the nest microenvironment for the rearing of young. It seems likely that tent construction requires considerable time and energy expenditure by bats, attesting to intense selection pressures involved.

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Appendix

List of scientific names of plants mentioned in the text and used by Neotropical bats for tent construction.

Anacardiaceae

Anacardium excelsum (Bertero & Balbis) Skeels

Araceae

Anthurium caperatum Croat & Baker
Anthurium ravenii Croat & Baker

Araceae (cont'd.)
Monstera lechleriana Schott
Xanthosoma sp.

Cyclanthaceae

Asplundia euryspatha Harl.
Carludovica drudei Masters

Cyclanthaceae (cont'd.)
Carludovica palmata R. & P.
Cyclanthus bipartitus Poit.

Marantaceae

Calathea insignis Petersen

Musaceae

Heliconia imbricata (Kuntze) Baker
Heliconia latispatha Benth.
Musa × *paradisiaca* L.
Plenakospermum guyanense Endl. (syn. *Ravenala guyanensis* Petersen)

Palmae

Asterogyne martiana (H. Wendl.) H. Wendl. ex Hemsley
Astrocaryum murumuru Mart.
Bactris wendlandiana Burret
Cocos nucifera L.
Geonoma congesta H. Wendl. ex Spruce
Geonoma cuneata H. Wendl. ex Spruce (syn. *G. decurrens* H. Wendl.)
Geonoma oxycarpa Martius (syn. *G. binervia* Oerst.)
Livistona chinensis (Jacq.) R. Br. ex. Mart.
Prichardia pacifica Seem. & H. Wendl.
Sabal mauritiiformis (Karsten) Griseb. & H. Wendl. ex Griseb. (syn. *S. glaucescens* Lodd. ex H. E. Moore)
Scheelea rostrata (Oersted) Burret
Welfia georgii H. Wendl. ex Burret