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WOODY VEGETATION OF TROPICAL LOWLAND DECIDUOUS FORESTS AND MAYAN RUINS IN THE NORTH-CENTRAL YUCATAN PENINSULA, MEXICO

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POPULATION STRUCTURE AND CLONAL GROWTH IN *BROMELIA PINGUIN* L. (BROMELIACEAE) IN DRY FORESTS OF COASTAL VERACRUZ, MEXICO

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THE CYCLOPOID COPEPOD (CRUSTACEA) FAUNA OF NON-PLANKTONIC CONTINENTAL HABITATS IN LOUISIANA AND MISSISSIPPI

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Abstract

Quadrats were sampled at five dry-forest and two Mayan ruin sites in the north-central Yucatan Peninsula of Mexico. A total of 149 woody species were found, and data for the 81 most important species were analyzed (Importance Values ≥1.0; DBH ≥3.0 cm). Their distribution correlates with dry season precipitation patterns (polar ordination). Average basal area is 20.2 sq. m per ha for forest sites and 28.2 sq. m per ha for ruin sites. Average density is 3344 stems per ha in forests and 1432 stems per ha on ruins. The Shannon-Weaver Diversity Index varies from 1.76 to 2.25 for forests and 0.94 to 1.25 for the two ruins. Important forest species are *Bursera simaruba, Thouinia paucidentata, Piscidia piscipula, Gymnopodium floribundum*, and *Caesalpinia gaumeri.* Leguminous species are more common in the drier, western forests than in the eastern forests, but are rare on the ruins. The two Mayan ruin sites have a vegetation that is distinct from that of the central peninsula and is dominated by *Brosimum alicastrum.*

Introduction

According to the Holdridge (1967) system of vegetation classification, the Yucatan Peninsula of Mexico is dominated by dry tropical forests (Holdridge et al., 1971). Until the middle 1900s, most botanical work on the peninsula was floristic and survey-type, conducted by Lundell (1934, 1937, 1938), Millspaugh (1895, 1896, 1898), Standley (1930), and others with ties to the Carnegie Institute in Washington, D.C. Miranda (1958) divided the Yucatan forests into five types based upon woody species presence, canopy height, and deciduousness. The boundaries of his forest types correspond precisely with isohyets of increasing precipitation across the peninsula from northwest to southeast (García, 1964; Isphording, 1975). The first quantitative ecological study of a forest on the peninsula was by Thien et al. (1982) near and on the ruins of Dzibilchaltun in the very northwest of the peninsula. Others have quantified the woody vegetation of old-growth forest in the north-central peninsula (Rico-Gray et al., 1988) and have described the relationships of the local people, descendants of the Maya, to the present vegetation of the region (Rico-Gray et al., 1990; Rico-Gray and García-Franco, 1991, 1992). Whigham et al. (1990, 1991) studied a north-

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eastern forest, quantifying woody plant growth, litter production, and impacts of hurricanes. No quantitative vegetation study ofthe central peninsular forests has been published, although this is a large region under intense human pressure (Brown and Lugo, 1990; Sabogal, 1992).

Most scientific studies conducted in the region have focused on the archaeology of Mayan sites, and have spawned some ancillary descriptions of vegetation associated with ruins (Lundell, 1937; Folan et al., 1979; Orejuela, 1980; Lambert and Arnason, 1982; Peters, 1983). A paradox exists as to why the vegetation of ruin sites is often different from neighboring forest vegetation. This study describes and quantifies extant old natural forest vegetation, compares it to the vegetation on two collapsed ruins, and then compares it in general to dry tropical vegetation of the world. The variation in the peninsula's forest vegetation is then related to known climatological patterns in Yucatan.

MATERIALS AND METHODS

STUDY REGION. The northern Yucatan Peninsula of Mexico (states of Campeche, Yucatán, Quintana Roo) consists of limestone bedrock of Tertiary age, flat and without surface runoff (streams are absent). The average annual temperature is 27°C, with a July average of 29°C and a January average of 24°C. The lowest recorded temperature is 6°C. Total annual precipitation across the peninsula averages 1100 mm, with a dry season from October to May (average total = 300 mm) and a wet season from June to September (average total = 800-900 mm) due to adiabatic heating. The northern peninsula has no significant topographic features to create unusual localized rainfall or temperature conditions. There is a noticeable west to east, dry to wet gradient over the peninsula (Figure 1), the prevailing winds being from the Caribbean Sea in the east. For several thousand years, an extensive Mayan civilization with enormous cities occupied the region (Morley and Brainerd, 1983). The current inhabitants of the peninsula are Mayan subsistence farmers who practice a type of slash-and-burn agriculture principally in the northern and central portion of the State of Yucatán.

Near and almost parallel to the southwestern border of the state of Yucatán is a small but topographically significant anticlinal hill range (the Puuc, 100 m maximum elevation; Isphording, 1975), which emerges from the flat landscape of the north. This range begins about 50 km from the western coastline and its fault-line is continuous for 160 km before disappearing near the southeastern border of the state of Yucatán and the state of Quintana Roo. Because it is easier for the inhabitants to cultivate the surrounding flatter land, some of the least disturbed vegetation in the north-central part of the peninsula are found on the slopes of these hills. By local estimates, forests on some slopes have grown for 50 to more than 100 years without disturbance from cultivation. This is likely a significant amount of time for recovery from disturbance, since it has been estimated that dry tropical forests generally require only 150 years for total recovery (Opler et al., 1977), and species composition may not change over that period (Miranda, 1958).

STUDY SITES. Three forest study sites 40 to 75 years old were established along the Puuc range, one at each end and one near the middle. The Calcehtok site was the western site (20°33'N, 89°54'W) near the village of Calcehtok (Figure 1). The eastern site (20°02'N, 89°04'W) was just south of the town of Tzucacab and

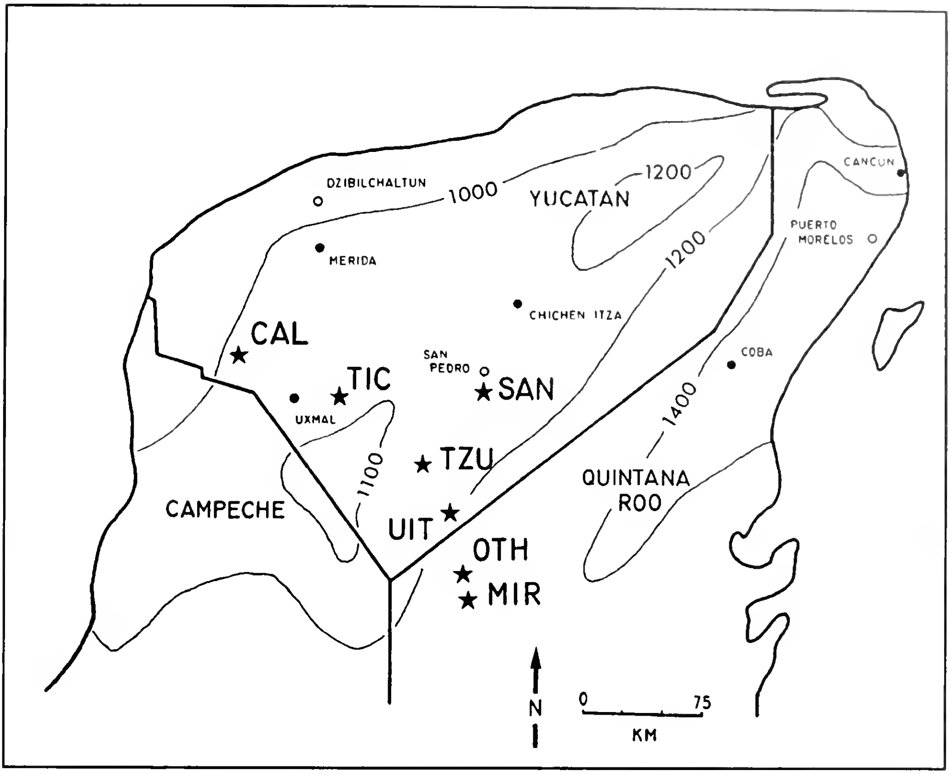

Figure 1. Map of the northern Yucatan Peninsula, Mexico, showing state boundaries, principal cities, archaeological sites (solid circles), location of the seven study sites (stars), three study sites cited in the literature (open circles), and isohyets (mm) adapted from García (1965). CAL = Calcehtok forest; TIC = Ticul forest; TZU = Tzucacab forest; SAN = San Mateo forest; OTH = Othon Blanco forest; UIT = Uitizina ruin; MIR = Mirador ruin.

given that name. The third site was located about equidistant between the other two (20°22'N, 89°34'W), southwest of Ticul. In addition to those sites within the Puuc, two others were studied because of their unusually old age. The Othon Blanco site (19°37'N, 89°00'W), is of older growth (more than 150 years), with a closed forest canopy and by appearance representative of the extensive forest in the east-central part of the peninsula. It is located near the village of Othon Blanco in western Quintana Roo, about the same distance (50 km) from the Tzucacab site as the distance separating the other forest sites. The San Mateo site (20°24'N, 88°49'W) was chosen for study because Rico-Gray et al. (1988) found that forests in this region show almost no evidence of human occupation or disturbance. These last two sites are on limestone substrate and a considerable distance from the Puuc area.

Two other sites were chosen because they were the least disturbed closed canopy forests found growing on the rubble of collapsed Mayan ruins. At each site the clearly visible rubble occupies an area less than 0.20 sq. km and forms small hills up to 20 m high in the otherwise flat landscape. The Uitizina ruin site (19°52'N, 88°58'W) is located 15 km southeast of the town of Tzucacab. The forests growing on the ruin are striking in their lushness, contrasting with the surrounding cattle ranches of savanna-like fields. The Mirador ruin site is approximately 5 km south from the Othon Blanco site and a considerable distance from any village or cultivated land. The structure of the closed-canopy forest around it is similar to that of the Othon Blanco site.

All seven sites were identified by local people as the oldest forests within their region. At all but the San Mateo and Mirador sites, culling of trees occurs for firewood and house construction with increasing frequency from east to west.

VEGETATION COMPOSITION AND STRUCTURE. At each site, the vegetation was sampled using sets of three 10 m × 20 m plots placed along 50 m transects. The total number of transects, and thus of plots, varied at each site from three to nine depending upon species-area curve calculations. The transects were spaced at least 25 m apart on flat land and were oriented east-west; on land with relief, the transects were oriented along the cardinal direction most parallel to the slope. The long axis of each plot was perpendicular to the transect. Within the plots, all woody stems (including coppiced stems)$\geq$3.0 cm DBH were measured and identified with the Mayan vernacular name supplied by one or several of six remarkably knowledgeable local field assistants. To be sure of their abilities and consistency in applying names, we repeatedly collected multiple samples of sterile specimens identified by the Mayans to compare with vouchers. Very rarely were mistakes made.

Voucher collections were made for each species, most of which were eventually found with flowers or fruits. Identification to species was tedious because the flora of the peninsula is not well known. Collections were identified at Tulane University (NO), with questionable and unnamed specimens taken for scrutiny to the Field Museum (F), or the Missouri Botanical Garden (MO). Nomenclature follows the floras of Panama (Woodson and Schery, 1943-1980), Guatemala (Standley and Williams, 1946-1977), and Mexico (Standley, 1920-1926, 1930; Gómez-Pompa, 1978-; Cano et al., 1982; Sosa et al., 1985), or recent monographic studies. All vouchers have been deposited in the Tulane University Herbarium, with duplicates sent to other institutions.

For each site, Importance Values were calculated using relativized values of density, total basal area, and frequency of occurrence in the plots (Mueller-Dombois and Ellenberg, 1974). The vegetation data were analyzed using the BCORD program on the PC-ORD system (McCune, 1987). This program performs the Bray-Curtis (polar) ordination. The Euclidean dissimilarity measurement was used with endpoints selected by the variance-regression method (Beals, 1985); all other options were defaulted. The polar ordination technique was employed instead of detrended correspondence analysis and other techniques following Causton (1988); with the small number of sites, all multivariate techniques would likely give insignificantly different results. Species diversity was estimated as Richness (S), Evenness (E), and Diversity (H'). S is defined as the total number of species present, and E as H'/ln S (Pielou, 1969), where H' is $\sum(p_i \log p_i)$ (Shannon and Weaver, 1949).

RESULTS

General Vegetational Characteristics

A total of 123 plots were sampled, 99 at the five forest sites and 24 at the two ruin sites (Table 1), giving a sample area of 1.98 ha of forest and 0.48 ha on

TABLE 1. Summary of woody vegetation data from five forest sites and two ruin sites within the north-central Yucatan Peninsula, Mexico. Data are from all woody stems ≥3.0 cm DBH in 10 × 20 m plots. CAL = Calcehtok forest; TIC = Ticul forest; TZU = Tzucacab forest; SAN = San Mateo forest; OTH = Othon Blanco forest; UIT = Uitizina ruin forest; MIR = Mirador ruin forest.

	CAL	TIC	TZU	SAN	OTH	UIT	MIR	FOREST*	RUIN*
Number of plots	24	9	27	12	27	12	12	99	24
Total Area Sampled (ha)	0.48	0.18	0.54	0.24	0.54	0.24	0.24	1.98	0.48
Basal Area per Stem (dm^2)	0.59	0.33	0.37	0.73	1.40	2.03	1.93	0.68	1.98
Total Basal Area (m^2/ha)	20.9	11.9	17.4	18.4	32.5	29.8	26.9	20.2	28.4
Stems/ha	3525	3611	4748	2513	2324	1467	1396	3344	1432
Stems/Plot	71	72	95	50	46	29	28	67	29
Plot Richness	13.8	15.6	21.2	18.5	15.6	8.8	8.3	16.9	8.6
Shannon-Weaver Index	1.76	2.00	2.25	2.23	2.14	0.94	1.25		
Site Richness	64	46	93	53	67	23	32	65	28
Site Evenness	0.681	0.731	0.739	0.767	0.782	0.434	0.608		
Total Tallied Stems	1692	650	2564	603	1255	352	335	6764	687

* Data are either averages or totals depending upon the parameter.

ruins. The species × area plots for the seven sites have a slope near zero after 12 plots or a sample area of 0.18-0.24 ha (Figure 2). A total of 149 species from 7451 stems ≥3.0 cm DBH were identified in one or more sites.

A summary of important vegetation parameters for the seven sites is presented in Table 1. The mean Richness of the forest sites is 65 species, whereas the ruin sites have an average of 28 species. The average Richness in each forest quadrat varies from 13.8 species at Calcehtok to 21.2 at Tzucacab, with an average of 17 for each plot over the five sites. Both of the ruin sites have fewer species in each plot (S = 8.6), and little intersite variability (alpha-diversity). The Shannon-Weaver Diversity Index is usually much higher for the forest sites (H' >2.00) than for the ruin sites (H' ca. 1.00). The density in the forest sites is much greater (3344 stems per ha) than in the ruin sites (1432 stems per ha). However, stem diameters are on average greater (15.9 cm) in ruin sites than in forest sites (9.3 cm). This translates into an average of 28.2 sq. m per ha total basal area for the two ruin sites and 20.2 sq. m per ha total basal area for the five forest sites.

Of the 149 species identified, 81 may be considered ecologically common because their Importance Values are ≥1.00 (out of a total of 100.00) in at least one of the seven study sites. The 68 remaining species are ecologically rare and were not included in these data analyses. In Appendix I, we present the frequency, density, and basal area data for the 81 common species at the seven sites; these data represent 93% of the total tallied stems. Appendix II is a list of the 68 rare species by site.

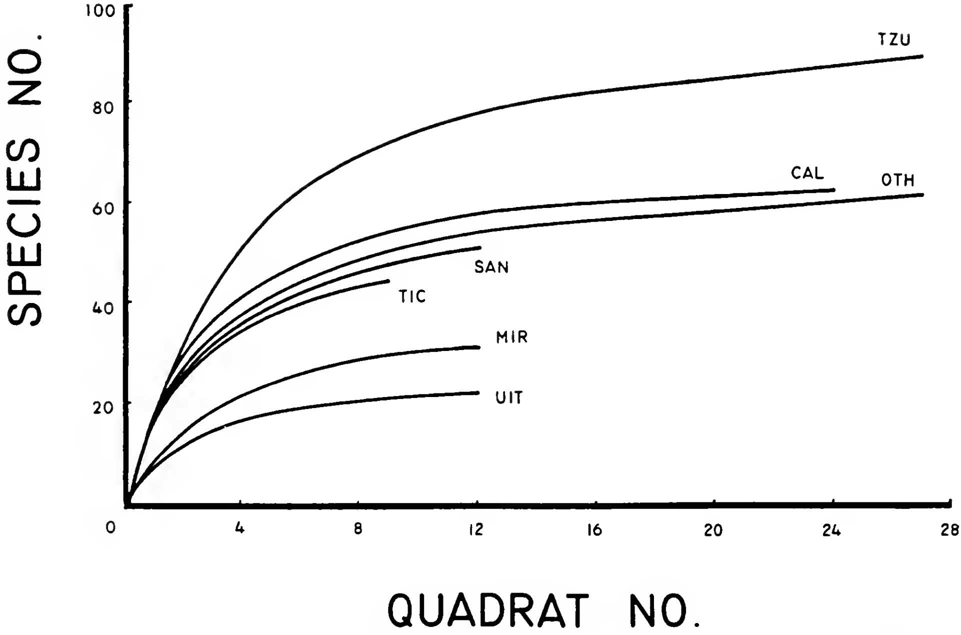

Figure 2. Species-area curves for the seven study sites in the northern Yucatan Peninsula, Mexico. The x-axis is the number of 200 sq. m quadrats sampled. The y-axis is the cumulative number of species measured. CAL = Calcehtok forest; TIC = Ticul forest; TZU = Tzucacab forest; SAN = San Mateo forest; OTH = Othon Blanco forest; UIT = Uitizina ruin; MIR = Mirador ruin.

The ordination (Figure 3) indicates the distinctiveness of the ruin sites. The spatial position of the forest sites in the two-axis ordination corresponds exactly to a northwest to southeast transect paralleling the northern boundary of the state of Campeche (Figure 1), with Calcehtok the westernmost site and Othon Blanco the easternmost site, and the San Mateo site close to the Tzucacab site. The first two axes explain 78% of the variation in the data. No new relationships are revealed if the ruin sites are eliminated and only the five forest sites ordinated; four sites are positioned as endpoints, with the San Mateo site in the center of the two-axis plot.

Forests of Central Yucatan

Calcehtok forest.– In the Calcehtok forest, *Bursera simaruba* and *Gymnopodium floribundum* are the most frequently found woody plants; they were in 88% and

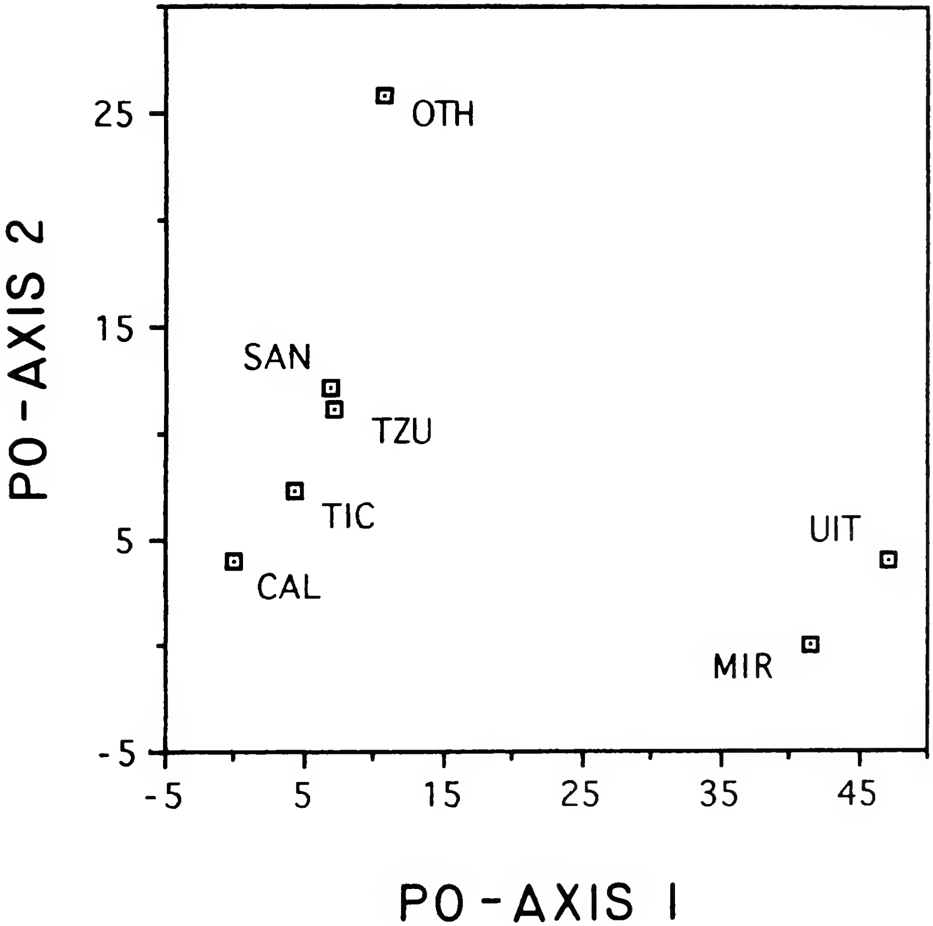

Figure 3. Polar ordination of five forest and two Mayan ruin sites in northern Yucatan Peninsula, Mexico. CAL = Calcehtok forest; TIC = Ticul forest; TZU = Tzucacab forest; SAN = San Mateo forest; OTH = Othon Blanco forest; UIT = Uitizina ruin; MIR = Mirador ruin.

75% of the plots, respectively (Appendix 1). *Gymnopodium floribundum, Machaonia lindeniana,* and *Bursera simaruba* are most abundant, accounting for 49% of the stems. *Caesalpinia gaumeri, Guettarda elliptica, Lysiloma bahamense,* and *Thouinia paucidentata* also have high densities, totalling 20% of the stems. They are also frequent species, found in about 70% of the plots. Together these seven species contribute 69% of the total density, and in some portions of this forest *G. floribundum* is found in large, nearly monotypic stands. *Gymnopodium floribundum* is the most abundant species and represents 26% of the density, but it contributes only a third of the total basal area, a reflection of the small average stem diameter. *Bursera simaruba* is the largest tree, with a basal area of 6.70 sq. m per ha (32% of the total). Those two species, plus *C. gaumeri* and *L. bahamense,* contribute 13.9 sq. m per ha, or 67% of the basal area. The average DBH at the site is a small 8.7 cm. The Calcehtok site is the least diverse of the forest sites (H' = 1.76), but has a relatively large total number of species (64). The canopy height varies from 8 to 15 m. *Bursera simaruba, Lysiloma bahamense,* and *Vitex gaumeri* are usually the tree species of any size in this forest.

Ticul forest.– In the Ticul forest, 650 stems were measured, and these have the lowest average diameter (6.5 cm) of any site (Table 1). *Bursera simaruba* and *Thouinia paucidentata* were found in every plot, while *Guettarda elliptica* and *Caesalpinia gaumeri* were relatively abundant, present in eight and six of the nine plots, respectively (Appendix I). *Gymnopodium floribundum* is clumped in this forest, found in four plots. These five species are the most abundant at the site, comprising 54% of the total number of stems (Table 1). Each is found at about the same density. As at the Calcehtok site, *B. simaruba* is, by a factor of three, the largest contributor (3.13 sq. m per ha or 26%) to the total basal area of 11.9 sq. m per ha. *Caesalpinia gaumeri, Piscidia piscipula,* and *Thouinia paucidentata* contribute 34% to the basal area. *Piscidia piscipula* is the largest tree at this site with a mean DBH of 12.9 cm. As in forests to the east, the Diversity Index (H' = 2.00) is significantly greater than at the Calcehtok site. The average canopy height is from 8 to 15 m, but broken with taller individual trees of *Lysiloma bahamense* and *Spondias mombin.*

Tzucacab forest.– The Tzucacab forest has the largest number of recorded species (93) and the greatest Diversity (H' = 2.25; Table 1). The six most frequent species are *Bursera simaruba, Piscidia piscipula, Diospyros cuneata, Croton reflexifolius, Lonchocarpus rugosus,* and *Coccoloba spicata* (Appendix I). *Bursera simaruba* is the most dense species with 574 stems per ha; *Croton reflexifolius* and *Diospyros cuneata* are also very abundant, yet they comprise only 29% of total density. Other relatively dense species include *Eugenia axillaris, Lonchocarpus rugosus, Lysiloma bahamense, Neea choriophylla, Piscidia piscipula,* and *Vitex gaumeri,* with a combined density of 1204 stems per ha, or 25% of the total. As in the other forests, *Bursera simaruba* is the largest contributor (3.39 sq. m per ha or 19%) to the total basal area. *Lysiloma bahamense* and *Vitex gaumeri* contribute 4.51 sq. m per ha, or 26% of the total. The ten species just mentioned make up 65% of the basal area in this forest; the other 84 species found in the Tzucacab forest contribute 35%. Average stem diameter at this site is 6.8 cm, slightly larger than in the Ticul forest. Canopy height is 15 to 25 m, broken and very plot-dependent, with no single or group of species consistently tall.

San Mateo forest.– Trees of the San Mateo forest have a mean stem diameter of 9.6 cm. This site has a high Diversity Index (H' = 2.23), very similar to that of the Tzucacab forest, and a relatively low total density of 2513 stems per ha (Table 1).

Thouinia paucidentata is most frequent (92%; Appendix I), while *Bursera simaruba* has a frequency of 83%, and *Diphysa carthagenensis*, *Eugenia buxifolia*, and *Piscidia piscipula* each with a frequency of 75%. *Gymnopodium floribundum* is the most commonly encountered species with 288 stems per ha, but it only accounts for 12% of the total number of stems. The other relatively abundant species, *Thouinia paucidentata, Malpighia punicifolia, Diphysa carthagenensis,* and *Eugenia buxifolia* contribute an additional 30% to the density. The total basal area of 18.4 sq. m per ha is not very different from that of the previously described sites. *Bursera simaruba* and *Caesalpinia gaumeri* are the largest trees and contribute 24% of total basal area. *Thouinia paucidentata, Piscidia piscipula, Gymnopodium floribundum, Lysiloma latisiliquum,* and *Vitex gaumeri* are also significant species and about equal in their basal area contributions, a combined 34% of the total. The tallest trees in this forest reach 20 m, with *Caesalpinia gaumeri, Bursera simaruba, Talisia olivaeformis,* and *Vitex gaumeri* the usual species with an average diameter of approximately 18 cm. An occasional large crown of *Lysiloma latisiliquum* (32.5 cm average DBH) protrudes through the uneven canopy.

Othon Blanco forest.– Of all the forest sites, the Othon Blanco forest has the largest total basal area (32.5 sq. m per ha; Table 1); *Manilkara zapota* is the largest contributor (13%). *Bursera simaruba, Gymnanthes lucida, Caesalpinia gaumeri,* and *Metopium brownei* are the other major contributors to basal area (ca. 7% each; Appendix I). Six other species, *Drypetes laterifolia, Coccoloba spicata, Gymnopodium floribundum, Lysiloma latisiliquum, Psidium sartorianum,* and *Thouinia paucidentata* are also important in this forest, with a combined basal area of 24%. *Gymnanthes lucida, Drypetes laterifolia,* and *Manilkara zapota* are strikingly abundant and contribute 45% of the total number of stems (Table 1). Here, the two most widespread species are *Manilkara zapota,* found in 93% of the plots, and *Drypetes laterifolia,* found in 89% of the plots. *Gymnanthes lucida, Gymnopodium floribundum,* and *Cosmocalyx spectabilis* are also frequently encountered. *Bursera simaruba* is not so frequent as in the more western forests, here found in 44% of the plots. The Othon Blanco forest has twice the average stem basal area (1.40 sq. dm per stem, or DBH = 13.4 cm; Table 1) of any of the other forests studied. This is the only forest with a persistent, well-defined canopy and understory. The canopy height is uniformly 30 to 35 m with *Lysiloma latisiliquum* (45.6 cm DBH), *Bursera simaruba* (28.7 cm DBH), *Metopium brownei* (30.3 cm DBH), and *Spondias mombin* (31.3 DBH) the largest, most common, and tallest trees. Some individuals of *Guettarda combsii, Luehea speciosa, Piscidia piscipula, Vitex gaumeri,* and *Zuelania guidonia* are at canopy level also.

Forests on Ruins

The two ruin-associated forests are remarkable in their similar differences from the five other forest sites (Table 1). Both exhibit low Diversity, low Richness, low total density, high basal area coverage, and tall canopies (30 m). They are also similar in species composition, sharing nine species, particularly the dominant *Brosimum alicastrum* in the overstory, and *Croton lundelii* in the understory (Appendix I). *Brosimum alicastrum* is the most frequent, most dense, and largest tree in the ruin sites; it was found in all plots at both sites, accounting for 32% of the total stems encountered at the Uitizina site and 43% at the Mirador site. Trees of *Brosimum alicastrum* comprise 69% of the basal area at the Uitizina site and 50% at the Mirador, site, with average diameters of 23.9 cm and 26.9 cm, respectively. In both forests, *Croton lundelii* is the second most abundant species (Uitizina, 19%; Mirador, 17% of total density), but only in the understory. It is frequently encountered, found in 100% of the Uitizina and 75% of the Mirador plots.

Both ruin-site forests are unique in the presence of *Urera baccifera* in the understory. It is common at the Uitizina site (16% of total density) and small, with an average diameter of 3.5 cm. *Bursera simaruba* and *Thouinia paucidentata* are important overstory species at both sites, both species being larger at Uitizina. The sites differ in other overstory species. The Uitizina forest has the overstory species *Ehretia tinifolia* and *Talisia olivaeformis*, while the Mirador overstory is much richer and includes *Karwinskia humboldtiana, Chlorophora tinctoria, Spondias mombin, Piscidia piscipula,* and *Ficus cotinifolia,* all with average diameters between 38 cm and 22 cm. In addition, there are several unidentified species of large *Ficus* growing over the rubble of this ruin.

Forest Phytosociology

In Table 2 the Importance Values (I.V.) for the 81 most common species are listed by forest; to show patterns of distributions, the species are separated into eight groups. By studying only the ecologically common species (those with I.V. ≥1.0), intersite phytosociological relationships become clear. The elimination of the 68 rare species should not affect the robustness of the data; the combined Importance Values for the rare species averaged 6% across all seven forests (Table 2, bottom), and was never greater than 14%.

Of the 81 more important species in the central Yucatan forests, 13 are especially common; three (*Bursera simaruba, Thouinia paucidentata, Bunchosia swartziana*) are present in all seven forests, and one, *Spondias mombin,* is found in five forests but is likely present in all (Group I, Table 2). Of the 13 species, *Bursera simaruba* is the most important tree contributing 11% to the total Importance Value for the five forest sites and 5% of the Importance Value for the two ruin sites. Its Importance Value is highest in the westernmost forests. Eleven species were found only in the forest sites (Group II, Table 2); two of these are particularly noteworthy, *Gymnopodium floribundum* and *Caesalpinia gaumeri* having relatively high average Importance Values.

Ten species are present only in the four western forest sites at Calcehtok, Ticul, Tzucacab, and San Mateo; of them, *Guettarda elliptica, Lysiloma bahamense,* and *Neea choriophylla* are most important. Nine species are present only in the three eastern forest sites (Tzucacab, San Mateo, and Othon Blanco); two species of *Coccoloba* (*C. cozumelensis* and *C. spicata*) are the most important of these. The Tzucacab forest is a site of species distribution overlap.

The three eastern forests share eight species with one or both of the ruin sites (Group V, Table 2). Three species, *Manilkara zapota, Cosmocalyx spectabilis,* and *Gymnanthes lucida,* are present at one ruin site (Mirador) and are especially important in the very easternmost forest site (Othon Blanco).

Legumes comprise exactly one-third of the 24 species in the first two groups (Table 2). The western forests have a greater ecological Importance Value in legumes. Four of the ten Group III species (Western Species) are legumes, whereas there is only one, *Pithecellobium albicans,* in all the eastern groups (Groups IV, V, VI). In Group VII, legumes are more important in the western sites. No other distributional pattern is evident for the Group VII species; maybe each should be considered only locally important, or maybe they were present

TABLE 2. Importance Values of 81 of the more common (I.V. ≥1.0 in at least one of the seven sites) woody species (DHB ≥3.0) for five forest and two ruin sites within the north-central Yucatan Peninsula, Mexico. Importance Values were obtained from Appendix I using relativized density, basal area, and frequency data. *Indicates a species likely present at the site but not recorded. CAL = Calcehtok forest; TIC = Ticul forest; TZU = Tzucacab forest; SAN = San Mateo forest; OTH = Othon Blanco forest; MIR = Mirador ruin forest; UIT = Uitizina ruin forest.

	CAL	TIC	TZU	SAN	OTH	MIR	UIT
I. WIDESPREAD SPECIES (13):							
Bursera simaruba	16.00	14.35	11.98	7.30	4.38	5.39	5.22
Thouinia paucidentata	4.58	9.58	2.17	7.26	4.05	6.81	4.64
Bunchosia swartziana	0.65	1.62	0.29	1.96	2.48	0.46	2.51
Spondias mombin	*	1.71	0.35	*	1.01	2.79	1.72
Piscidia piscipula	2.48	5.78	4.28	5.21	1.82	3.30	
Pithecellobium leucospermum	1.04	0.93	0.08	0.43	0.22	0.45	
Semialarium mexicanum	0.95	0.53	1.87	2.17	1.37	0.46	
Eugenia axillaris	0.25	0.62	2.99	0.51	0.24	2.13	
Exostema caribaeum	1.27	2.38	0.74	2.44	0.15	1.04	
Bourreria pulchra	0.71	*	0.36	1.94	0.40	1.29	
Cordia gerascanthus	0.32	*	0.24	1.68	1.07	0.44	
Krugiodendron ferreum	0.49	*	0.17	0.99	1.01	0.47	
Karwinskia humboldtiana		0.90	2.74	*	0.45	*	2.80
II. FOREST-SITE SPECIES (11):							
Gymnopodium floribundum	*	13.94	6.82	0.49	7.07	5.07	
Caesalpinia gaumeri	6.63	8.66	1.71	5.83	3.82		
Lonchocarpus yucatanensis	0.30	2.48	2.37	1.48	2.03		
Acacia gaumeri	1.65	0.76	0.60	1.83	0.11		
Bauhinia divericata	0.25	1.06	0.76	0.76	0.59		
Diphysa carthagenensis	0.41	0.76	0.07	4.81	1.59		
Diospyros cuneata	0.29	*	6.35	0.23	0.32		
Erythroxylum rotundifolium	0.31	*	0.60	3.17	1.28		
Vitex gaumeri	1.17	*	5.82	3.35	0.96		
Lennea sepium	1.15	*	0.10	1.15	0.14		
Jatropha gaumeri	0.13	0.81	*	1.76	0.37		

TABLE 2. (Continued)

	CAL	TIC	TZU	SAN	OTH	MIR	UIT
III. WESTERN FOREST SPECIES (10):							
Guettarda elliptica	3.48	6.34	0.20				
Lysiloma bahamense	7.73	1.03	7.98				
Neea choriophylla	2.27	2.62	3.22				
Cnidoscolus aconitifolius	0.75	1.71	0.15				
Pithecellobium dulce	0.21	2.34	0.22				
Diospyros anisandra	0.74	2.43	0.31				
Alvaradoa amorphoides	1.73	0.81	0.65	0.54			
Mimosa bahamensis	0.67	2.73	0.07	1.20			
Randia gaumeri	1.23	1.63	*	0.85			
Bursera schlechtendalii		0.12	1.40	0.07			
IV. EASTERN FOREST SPECIES (9):							
Pithecellobium albicans		1.62	0.34	0.45	0.44		
Coccoloba cozumelensis			1.28	3.13	1.38		
Coccoloba spicata			2.78	1.76	3.47		
Psidium sartorianum			1.14	0.21	2.64		
Luehea speciosa			1.61	0.52	1.90		
Ardisia escallonioides			0.23	1.13	0.58		
Guettarda gaumeri			0.91	2.20	0.37		
Hampea trilobata			1.99	0.97	0.86		
Malpighia punicifolia			0.19	4.79	*		
V. EASTERN FOREST AND RUIN SPECIES (8):							
Malmea depressa			1.08	1.15	2.33	2.82	1.26
Talisia olivaeformis			0.66	1.33	0.60	1.79	1.86
Drypetes laterifolia			*	0.22	8.12	1.12	1.87
Zuelania guidonia			0.66	0.82	1.36	2.39	
Eugenia buxifolia			2.12	3.92	0.22	1.02	
Nectandra coriacea			0.45		0.33	1.44	
Croton reflexifolius			4.71	1.82	2.42		0.42
Celtis iguanea			0.54	0.54	0.11		3.15

VI. EASTERNMOST FOREST SPECIES (3):							
Manilkara zapota					10.07	1.47	
Cosmocalyx spectabilis					3.21	3.57	
Gymnanthes lucida					11.00	0.44	
VII. MISCELLANEOUS FOREST SPECIES (16):							
Adelia oaxacana	1.06	0.69					
Colubrina reclinata	1.13	2.75					
Sideroxylon foetidissimum	1.09	2.44					
Apoplanesia paniculata	1.49						
Sebastiana adenophora	1.38						
Machaonia lindeniana	7.56			1.47			
Caesalpinia velutina	0.70			1.25	0.49		
Lysiloma latisiliquum				2.35	1.66		
Casearia corymbosa		1.01	0.45				
Colubrina greggii		0.30	1.72				
Acacia riparia		1.58					
Eugenia spp.		1.21					
Cochlospermum vitifolium				1.15		0.13	
Guettarda combsii			1.30		1.54		
Lonchocarpus rugosus			3.36		0.82		
Metopium brownei					3.48		
VIII. RUIN SPECIES (11):							
Brosimum alicastrum		0.77			0.85	35.00	37.47
Croton lundelii						9.75	11.31
Urera baccifera						1.72	9.68
Hybanthus yucatanensis						0.89	3.53
Ficus cotinifolia						2.47	
Ficus spp.						2.94	
Chlorophora tinctoria						1.70	
Capparis indica							4.19
Capparis pachea ssp. *oxysepala*							2.99
Ehretia tinifolia							1.78
Astrocasia tremula					0.24		3.38
TOTAL (maximum 100.00%)	91.43	95.72	86.35	96.69	91.66	98.13	96.91

but unrecorded in some sites because of their rarity or clumped distribution. The two ruin sites have eleven non-leguminous species not usually present at any of the forest sites. *Brosimum alicastrum* was the most important of these ruin-species; at both sites it makes up over 33% of the Importance Value. As stated, *Croton lundelii* and *Urera baccifera* are also important species at the ruin sites.

DISCUSSION

Forests within the northern (above 20°N latitude) Yucatan Peninsula are clearly dry-tropical by the Holdridge (1967) classification. More specifically, the five forest sites are within four different tropical vegetation types described by Miranda (1958), and corroborate quantitatively his height- and deciduousness-based classification system. The Calcehtok and Ticul sites are in the "low-medium deciduous" forest zone of the western and central portions of the state of Yucatán (Figure 1), and have the predicted canopy height of 15 to 20 m. The San Mateo site is a "medium transition" forest with about 25 m canopy height. Adjacent to and east of this zone is Miranda's zone of "tall-medium subdeciduous" forest with a canopy of 25 to 30 m; the Tzucacab site is located within this zone. The Othon Blanco forest is near the western edge of Miranda's "tall subevergreen" forest, which covers the central and southern portions of Quintana Roo.

The increase in canopy height from northwest to southeast across the northern peninsula follows the change in species composition seen across the forest sites as identified by the ordination (Figure 3). These trends in canopy height and species composition mirror annual precipitation patterns for the peninsula presented by García (1965; Figure 1). She gives no precipitation breakdown by wet-dry seasons, but recent official maps prepared by SPP (Secretaría de Programación y Presupuesto) do give isohyets across the peninsula for both seasons from the years 1921 to 1975. Although the five forest sites are in the same isohyet (900 mm) for the wet season (May-Oct), the amount of rain in the dry season(Nov-Apr) differs considerably, from 150 mm in the west (Calcehtok forest region) to more than 300 mm in the east (Othon Blanco forest region), a result of the prevailing westerly winds from the Caribbean Sea. It is likely that during those drier months the difference in precipitation of more than 150 mm affects plant growth and produces the observed gradient in canopy height.

Past quantitative vegetation research in other areas of the peninsula supports this conclusion. Thien et al. (1982) presented data from the dry northwestern region of the peninsula, a forest site around the ruins of Dzibilchaltun (Figure 1) within Miranda's zone of "low deciduous" forest where annual rainfall is less than 700 mm. Here, canopy height ranges from 6 to 8 m. Whigham et al. (1990) described a forest on the east coast of the peninsula near Puerto Morelos, within Miranda's "tall subevergreen" forest zone with a recorded annual precipitation of about 1100 mm, although quite variable. That area has an upper canopy height of 25 m. Rico-Gray et al. (1988) worked in an old-growth forest at San Pedro, in the same area as the San Mateo forest. They recorded an annual precipitation of just under 1000 mm and a canopy height of 20 m.

The T/P (annual mean temperature/annual total precipitation) ratios for those three forests, and for forests reported on here, range from 3.7 (Dzibilchaltun) in the northwest to 2.3 (Othon Blanco) in the southeastern part of the study area, and thus are in the worldwide range for dry tropical forests as described by Murphy and Lugo (1986a). Canopy heights in the Yucatan Peninsula are typical for world dry tropical forest, varying from 8 m (Dzibilchaltun) to 35 m (Othon Blanco), and likewise woody plant Richness (DBH >ca. 2.5 cm), with a range from about 50 species (Dzibilchaltun) to 100 species (Othon Blanco). The broken nature of the canopy is a pronounced characteristic of the more western forests (Calcehtok, Ticul, Tzucacab, San Mateo), and this also was reported for the Dzibilchaltun, San Pedro, and the Puerto Morelos forests.

Over the entire northern Yucatan Peninsula the forests are characterized by several widespread species. *Bursera simaruba*, *Gymnopodium floribundum*, *Piscidia piscipula*, and *Thouinia paucidentata* are usually particularly important. As in the present study, Rico-Gray et al. (1988) and Thien et al. (1982) found the first three species to be common and dominant. There is a species composition difference corresponding to a dry-season precipitation difference of more than 150 mm across the peninsula. In the west, *Casealapinia gaumeri*, *Pithecellobium leucospermum*, *Acacia gaumeri*, *Bunchosia swartziana*, *Diospyros cuneata*, and *Vitex gaumeri* are important species in all the studied forests. The dry-season wetter forests in the eastern and northern region (within Miranda's "tall subevergreen" forest zone) have five species not usually found in the west: *Brosimum alicastrum*, *Drypetes laterifolia*, *Gymnanthes lucida*, *Manilkara zapota*, and *Talisia olivaeformis* (this study and Whigham et al. (1990)). Murphy and Lugo (1986b) reported that *Gymnanthes lucida* was the most common tree in a Puerto Rican dry tropical forest and it has been recognized as an important component of the Antillean flora (Miranda, 1958).

Miranda (1958) identified *Vitex gaumeri* as the "abundant" indicator tree in his "tall to medium subdeciduous" vegetation zone, and an important component of his "medium transition" forest just to the west. From the results of this study, the indicator status for *Vitex* is in doubt. Even though *Vitex gaumeri* has the highest Importance Values at the two sites (Tzucacab and San Mateo, Table 2) within the two vegetation zones just mentioned, it cannot be singled out as anything but a general "forest species." However, this study does corroborate *Manilkara* (*Achras*) *zapota* as an indicator species of the most eastern vegetation zone of "tall subperennial" species: the species was found only at the two sites (Othon Blanco and Mirador ruins) in that zone. Additional quantitative sampling of the peninsula's vegetation needs to be done to confirm other Miranda conclusions.

Could all published accounts of the northern Yucatan forests be describing aberrant vegetation so disrupted by lengthy Maya habitation that little resemblance to a native type exists? Possibly, but this is a worldwide concern in dry-tropical forests (Murphy and Lugo, 1986a). Great care was taken in this study to find the least disturbed sites in the central peninsula, but it is difficult to assess the true age of any of the peninsular forests because of incessant culling practices and coppicing (Rico-Gray and García-Franco, 1992). A few emergent trees scattered among the canopy cover may be a false indication of old age. Still, in this study, all Mayan field assistants were certain that no site had been severely cut for farming during the past 40 years, and, as noted above, some individual plots, even entire forest sites, are more than 100 years old. Miranda (1958) predicted that forest species richness and diversity would not be significantly different in the absence of humans, only that the individual trees would be larger.

Rico-Gray et al. (1988) and Thien et al. (1982) named several species as indicators of the oldest quadrats studied if found in large size and high density. These include *Bursera simaruba, Vitex gaumeri, Caesalpinia gaumeri, Piscidia piscipula,* and *Apoplanesia paniculata.* Along with *Lysiloma bahamense,* these were among the largest trees in the five forest sites analyzed for the present study. It is certain that the forests growing over the ruins were the oldest studied; the Maya viewed them with a special significance and unequivocally stated that little culling had occurred within them for many years.

The San Mateo forest of this study, and the San Pedro forest (Rico-Gray et al., 1988), are less than five km apart. Of the 51 species reported in the San Pedro forest and the 45 species in the San Mateo forest, 25 are common to both, a reflection of tropical diversity; using those 25 species to characterize the forests of this region seemed reasonable, and in total they contributed heavily to the Importance Values: 75% in the San Pedro forest and 66% in the San Mateo forest.

As for many other studies (Bartlett, 1935; Lundell, 1937; Folan et al., 1979; Lambert and Arnason, 1978, 1982), this study clearly shows that the woody vegetation growing on Mayan ruins of the Yucatan Peninsula is different from the vegetation of even adjacent forests (Figure 3). Eleven species are associated with the two ruin sites (Table 2); they contribute 55% of the Mirador site and 75% of the Uitizina site total Importance Values. Of particular significance is *Brosimum alicastrum,* which makes up more than a third of the total Importance Value at each site. It has been thought (Lundell, 1937; Bartlett, 1935), but recently challenged (Lambert and Arnason, 1978, 1982), that *Brosimum alicastrum,* among other species, is more common around ruins because it is a relict from the ancient days of Mayan cultivation. However, such species may be associated with ruins because conditions for growth on rubble are satisfactory (Miranda, 1958) and free from competition from other forest species; i.e., conditions are optimal for growth and reproduction (Lambert and Arnason, 1982). For *Brosimum,* it might be that the bat-dispersal of seeds creates high potential for establishment on ruins, which are bat roosting sites (Peters, 1983).

The Uitizina site is unique. Nine of the 13 widespread species (Table 2) are absent from the site. *Manilkara zapota,* historically a species associated with ruins (Lundell, 1937), is also absent. Oddly, this species is not important at the Mirador site (I.V. = 1.47%). *Talisia olivaeformis* was identified as another ruin-associated species by Lambert and Arnason (1978). In our study, both of the ruin sites, as well as the three most eastern forest sites (Table 2), record it in low Importance.

CONCLUSIONS

This first quantitative study of the north-central Yucatan Peninsula's dry-tropical forests corroborates Miranda's qualitative description of forest types, and clearly documents a change in species composition and height across the peninsula, with these differences likely caused by small and local differences in dry-season rainfall. Certain species (*Bursera simaruba, Thouinia paucidentata, Piscidia piscipula, Gymnopodium floribundum, Caesalpinia gaumeri*) are widespread, quantitatively important, and therefore characteric of the forests in this part of the world.

The average total basal area for all five forest sites (20.2 sq. m per ha) is low, but within the range of 17 to 40 sq. m per ha given by Murphy and Lugo (1986a) for dry-tropical forests. Likewise, the forests studied here fall within parameters from other dry-tropical forests with respect to T/P ratios, Richness, Diversity, canopy height, and structure.

The abandoned Maya ruins of the northern peninsula have a distinct vegetation dominated by *Brosimum alicastrum*, this likely due to the bouldery substrate.

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APPENDIX I.

Species data for five forests and two ruin sites in the north-central Yucatan Peninsula, Mexico. FREQ. = number of plots (10 × 20 m) in which the species was present. STEMS = total number, including coppiced stems, ≥3.0 cm DBH in all plots. DENSITY = stems per ha. AREA = sq. dm per ha. Species with an Importance Value ≥1.0 in at least one of the seven sites are listed. Taxa that could not be positively separated are combined.

	FREQ.	STEMS	DENSITY	AREA		FREQ.	STEMS	DENSITY	AREA
CALCEHTOK FOREST (24 plots sampled)									
Acacia gaumeri Blake	8	5	54.17	21.17	*Adelia oaxacana* (Meull. Arg.) Hemsl.	4	21	43.75	15.26
Alvaradoa amorphoides Liebm.	11	18	37.50	16.74	*Apoplanesia paniculata* Presl	8	17	35.42	22.37
Bauhinia divaricata L.	2	2	4.17	0.35	*Bourreria pulchra* Millsp.	4	9	18.75	8.32
Bunchosia swartziana Griseb.	4	10	20.83	3.12	*Bursera schlechtendalii* Engl.	1	1	2.08	0.30
Bursera simaruba (L.) Sargent	21	163	339.58	669.65	*Caesalpinia gaumeri* Greenm.	13	96	200.00	214.99
Caesalpinia velutina (Br. & Rose) Standl. (or *C. violacea* (Mill.) Standl.)	4	7	14.58	10.21	*Chlorophora tinctoria* (L.) Gaudich.	1	1	2.08	0.65
Cnidoscolus aconitifolius (Mill.) Johnst.	6	6	12.50	1.69	*Colubrina reclinata* (L'Hérit.) Brongn.	7	13	27.08	10.51
Cordia gerascanthus L.	2	3	6.25	4.01	*Diospyros anisandra* Blake	5	10	20.83	2.67
Diospyros cuneata Standl.	2	3	6.25	1.76	*Diphysa carthagenensis* Jacq.	3	4	8.33	1.93
Erythroxylum rotundifolium Lunan	2	2	4.17	4.18	*Eugenia axillaris* (SW.) Willd.	2	2	4.17	0.47
Exostemma carbaeum (Jacq.) R. & S.	8	18	37.50	6.98	*Ficus* spp.	1	5	10.42	2.58
Guettarda elliptica Sw.	14	82	170.83	29.06	*Gymnopodium floribundum* Rolfe	18	436	908.33	222.31
Hybanthus yucatanensis Millsp.	1	2	4.17	0.51	*Jatropha gaumeri* Greenm.	1	1	2.08	0.71
Karwinskia humboldtiana (R.&S.) Zucc.	5	11	22.92	11.16	*Krugiodendron ferreum* (Vahl) de Wil.	3	8	16.67	1.85
Lennea sepium (Jacq.) Walp.	6	25	52.08	22.06	*Lonchocarpus yucatanensis* Pittier	2	3	6.25	2.45
Lysiloma bahamense Benth.	17	73	152.08	287.30	*Machaonia lindeniana* Baill.	15	231	481.25	94.00
Mimosa bahamensis Benth.	3	13	27.08	6.98	*Neea choriophylla* Standl.	11	30	62.50	36.06
Piscidia piscipula (L.) Sargent	10	26	54.17	60.30	*Pithecellobium albicans* (Kunth) Benth.	7	17	35.42	36.68
Pithecellobium dulce (Roxb.) Benth.	1	3	6.25	3.47	*Pithecellobium leucospermum* Brand.	5	11	22.92	20.02
Randia gaumeri Greenm. & Thompson	8	18	37.50	4.82	*Sebastiana adenophora* Pax & Hoffm. (or *S. tikalana* Lundell)	7	25	52.08	11.66
Semialarium mexicanum (Miers) Mennega	5	13	27.08	11.78	*Sideroxylon foetidissimum* Jacq. ssp. *gaumeri* (Pittier) Penn.	6	19	39.58	6.97
Thouinia paucidentata Radlk.	16	91	189.58	74.11	*Vitex gaumeri* Greenm.	6	9	18.75	13.08
TICUL FOREST (9 plots sampled)									
Acacia gaumeri Blake	2	4	22.22	2.85	*Acacia riparia* H.B.K.	3	8	11.11	16.36
Adelia oaxacana (Meull. Arg.) Hemsl.	2	3	16.67	2.26	*Alvaradoa amorphoides* Liebm.	1	3	16.67	14.73

APPENDIX I (Continued)

	FREQ.	STEMS	DENSITY	AREA		FREQ.	STEMS	DENSITY	AREA
Bauhinia divaricata L.	3	5	27.78	3.06	*Brosimum alicastrum* Swartz	2	4	22.22	3.05
Bunchosia swartziana Griseb.	4	9	50.00	7.26	*Bursera schlechtendalii* Engl.	3	7	38.89	11.67
Bursera simaruba (L.) Sargent	9	65	366.67	313.78	*Caesalpinia gaumeri* Greenm.	6	67	372.22	134.77
Casearia corymbosa H.B.K.	3	4	22.22	3.34	*Cnidoscolus aconitifolius* (Mill.) Johnst.	5	7	38.89	5.27
Colubrina greggii S. Wats.	1	1	5.56	0.48	*Colubrina reclinata* (L'Hérit.) Brongn.	4	21	116.67	25.74
Diospyros anisandra Blake	2	29	161.11	16.63	*Diphysa carthagenensis* Jacq.	2	3	16.67	4.46
Eugenia axillaris (Sw.) Willd.	2	2	11.11	1.47	*Eugenia* sp.	3	6	33.33	6.79
Exostema caribaeum (Jacq.) R.&S.	4	18	100.00	18.04	*Guettarda elliptica* Sw.	8	63	350.00	42.85
Gymnopodium floribundum Rolfe	4	72	400.00	77.43	*Jatropha gaumeri* Greenm.	2	4	22.22	4.49
Karwinskia humboldtiana (R.&S.) Zucc.	3	18	100.00	39.25	*Lonchocarpus yucatanensis* Pittier	3	21	116.67	24.50
Lysiloma bahamense Benth.	1	2	11.11	24.62	*Mimosa bahamensis* Benth.	5	21	116.67	16.44
Neea choriophylla Standl.	5	16	88.89	21.71	*Piscidia piscipula* (L.) Sargent	7	16	88.89	116.91
Pithecellobium albicans (Kunth) Benth.	1	1	5.56	1.84	*Pithecellobium dulce* (Roxb.) Benth.	6	12	66.67	10.50
Pithecellobium leucospermum Brand.	3	3	16.67	2.13	*Randia gaumeri* Greenm. & Thompson	4	10	55.56	5.86
Semialarium mexicanum (Miers) Mennaga	1	3	16.67	4.93	*Sideroxylon foetidissimum* Jacq. ssp. *gaumeri* (Pittier) Penn.	5	17	94.44	13.28
Spondias mombin L.	1	1	5.56	50.44	*Thouinia paucidentata* Radlk.	9	87	483.33	105.65
TZUCACAB FOREST (27 plots sampled)									
Acacia gaumeri Blake	5	6	25.93	6.62	*Alvaradoa amorphoides* Liebm.	5	11	20.37	11.48
Ardisia escallonioides Schlecht. & Cham.	3	3	5.56	0.65	*Bauhinia divaricata* L.	9	13	24.07	3.22
Bourreria pulchra Millsp.	3	10	18.52	2.72	*Brosimum alicastrum* Swartz	3	5	9.26	2.57
Bursera schlechtendalii Engl.	1	1	1.85	0.16	*Bursera simaruba* (L.) Sargent	25	310	574.07	339.08
Caesalpinia gaumeri Greenm.	9	56	103.70	23.86	*Casearia corymbosa* H.B.K.	4	10	18.52	4.76
Celtis iguanea (Jacq.) Sargent	2	9	16.67	16.14	*Cnidoscolus aconitifolius* (Mill.) Johnst.	2	2	3.70	0.42
Coccoloba cozumelensis Hemsl.	11	30	55.56	13.20	*Coccoloba spicata* Lundell	20	70	129.53	36.64
Cochlospermum vitifolium (Willd.) Spreng.	10	15	27.78	19.35	*Colubrina greggii* S. Wats.	14	48	88.89	14.72
Cordia gerascanthus L.	3	3	5.56	1.42	*Cosmocalyx spectabilis* Standl.	1	1	1.85	0.44
Croton reflexifolius H.B.K.	22	184	340.74	54.28	*Diospyros anisandra* Blake	4	5	9.26	0.80
Diospyros cuneata Standl.	23	256	474.07	87.75	*Diphysa carthagenensis* Jacq.	1	1	1.85	0.19
Ehretia tinifolia L.	1	2	3.70	0.84	*Erythroxylum rotundifolium* Lunan	4	16	29.63	8.19
Eugenia axillaris (Sw.) Willd.	15	110	203.70	35.90	*Eugenia buxifolia* (Sw.) Willd.	17	62	114.80	16.75

Exostema caribaeum (Jacq.) R.&S.	5	23	42.59	7.69	*Guettarda combsii* Urban	12	32	59.26	9.86
Guettarda elliptica Sw.	2	5	9.26	0.88	*Guettarda gaumeri* Standl.	9	19	35.19	7.25
Gymnopodium floribundum Rolfe	3	15	27.78	6.36	*Hampea trilobata* Standl.	11	43	79.63	41.22
Krugiodendron ferreum (Vahl) Urban	2	3	5.56	0.62	*Lennea sepium* (Jacq.) Walp.	1	2	3.70	0.86
Lonchocarpus rugosus Benth.	21	102	188.89	42.19	*Lonchocarpus yucatanensis* Pittier	15	71	131.48	29.81
Luehea speciosa Willd.	7	48	88.89	29.93	*Lysiloma bahamense* Benth.	19	113	209.26	281.75
Malmea depressa (Baill.) Fries	9	23	42.59	13.18	*Malpighia punicifolia* L.	1	7	12.96	2.24
Mimosa bahamensis Benth.	1	1	1.85	0.15	*Nectandra coriacea* (Sw.) Griseb.	4	8	14.81	5.98
Neea choriophylla Standl.	17	99	183.33	49.22	*Piscidia piscipula* (L.) Sargent	25	104	192.59	76.73
Pithecellobium albicans (Kunth) Benth.	2	5	9.26	14.24	*Pithecellobium dulce* (Roxb.) Benth.	2	6	11.11	1.20
Pithecellobium leucospermum Brand.	1	1	1.85	0.21	*Psidium sartorianum* Nied.	9	33	61.11	9.91
Semialarium mexicanum (Miers) Mennega	17	46	85.19	14.77	*Spondias mombin* L.	3	3	5.56	7.19
Talisia olivaeformis (H.B.K.) Radlk.	7	14	25.93	3.69	*Thouinia paucidentata* Radlk.	15	58	107.41	28.44
Vitex gaumeri Greenm.	17	122	225.93	169.31	*Zuelania guidonia* (Sw.) Britt. & Millsp.	3	10	18.52	18.42
SAN MATEO FOREST (12 plots sampled)									
Acacia gaumeri Blake	4	11	58.33	25.02	*Alvaradoa amorphoides* Liebm.	2	2	8.33	7.13
Ardisia escallonioides Schlecht. & Cham.	4	6	25.00	10.79	*Bauhinia divaricata* L.	3	4	16.67	4.85
Bourreria pulchra Millsp.	6	13	54.17	17.46	*Bunchosia swartziana* Griseb.	7	13	54.17	10.52
Bursera simaruba (L.) Sargent	10	24	100.00	246.44	*Caesalpinia gaumeri* Greenm.	8	18	75.00	200.36
Caesalpinia velutina (B.&R.) Standl. (or *C. violacea* (Mill.) Standl.)	4	7	29.17	14.19	*Celtis iguanea* (Jacq.) Sargent	2	3	12.50	3.93
Coccoloba cozumelensis Hemsl.	7	19	79.17	56.95	*Coccoloba spicata* Lundell	4	9	37.50	36.16
Cordia gerascanthus L.	5	7	29.17	29.69	*Croton reflexifolius* H.B.K.	7	9	37.50	14.77
Diospyros cuneata Standl.	1	1	4.17	1.26	*Diphysa carthagenensis* Jacq.	9	43	179.17	59.80
Drypetes laterifolia (Sw.) Krug. & Urban	1	1	4.17	0.69	*Erythroxylum rotundifolium* Lunan	9	22	91.67	33.08
Eugenia axillaris (Sw.) Willd.	2	3	12.50	2.64	*Eugenia buxifolia* (Sw.) Willd.	9	38	158.33	25.82
Exostema caribaeum (Jacq.) R.&S.	8	14	58.33	25.50	*Guettarda gaumeri* Standl.	6	12	50.00	35.03
Gymnopodium floribundum Rolfe	7	69	287.50	121.67	*Hampea trilobata* Standl.	3	7	29.17	7.32
Jatropha gaumeri Greenm.	5	14	58.33	13.17	*Karwinskia humboldtiana* (R.&S.) Zucc.	1	2	8.33	10.32
Krugiodendron ferreum (Vahl) Urban	4	4	16.67	9.09	*Lennea sepium* (Jacq.) Walp.	4	8	33.33	22.26
Lonchocarpus yucatanensis Pittier	6	7	29.17	10.49	*Luehea speciosa* Willd.	1	3	12.50	11.23
Lysiloma latisiliquum (L.) Benth.	2	3	12.50	103.77	*Machaonia lindeniana* Baill.	3	13	54.17	16.57
Malmea depressa (Baill.) Fries	4	8	33.33	6.16	*Malpighia punicifolia* L.	7	13	179.17	71.78
Mimosa bahamensis Benth.	3	10	41.67	11.06	*Piscidia piscipula* (L.) Sargent	9	21	87.50	118.19
Pithecellobium albicans (Kunth) Benth.	1	2	8.33	10.07	*Pithecellobium leucospermum* Brand.	2	2	8.33	1.31
Psidium sartorianum Nied.	1	1	4.17	0.12	*Randia gaumeri* Greenm. & Thompson	3	5	20.83	6.97

APPENDIX 1 (Continued)

	FREQ.	STEMS	DENSITY	AREA		FREQ.	STEMS	DENSITY	AREA
Semialarium mexicanum (Miers) Mennega	5	12	50.00	41.68	*Talisia olivaeformis* (H.B.K.) Radlk.	2	4	16.67	44.74
Thouinia paucidentata Radlk.	11	52	216.67	150.81	*Vitex gaumeri* Greenm.	6	10	41.67	104.31
Zuelania guidonia (Sw.) Britt. & Millsp.	3	5	20.83	5.04					
OTHON BLANCO FOREST (27 plots sampled)									
Acacia gaumeri Blake	1	1	1.85	0.88	*Ardisia escallonioides* Schlecht. & Cham.	5	6	11.11	2.50
Astrocasia tremula (Griseb.) Webster	2	2	3.70	2.88	*Bauhinia divaricata* L.	5	6	11.11	3.09
Bourreria pulchra Millsp.	3	3	5.56	8.50	*Brosimum alicastrum* Swartz	6	11	20.37	8.61
Bunchosia swartziana Griseb.	12	39	72.22	48.54	*Bursera simaruba* (L.) Sargent	12	23	42.59	275.22
Caesalpinia gaumeri Greenm.	11	26	48.15	220.74	*Caesalpinia velutina* (Britton & Rose) Standl. (or *C. violacea* (Mill.) Standl.)	3	4	7.41	14.57
Celtis iguanaea (Jacq.) Sargent	1	1	1.85	0.16	*Coccoloba cozumelensis* Hemsl.	7	15	27.78	41.55
Coccoloba spicata Lundell	15	40	74.07	119.17	*Cochlospermum vitifolium* (Willd.) Spreng.	1	1	1.85	1.96
Cordia gerascanthus L.	6	10	18.52	32.03	*Cosmocalyx spectabilis* Standl.	17	40	74.07	78.04
Croton reflexifolius H.B.K.	15	32	59.26	37.28	*Diospyros cuneata* Standl.	2	2	3.70	10.74
Diphysa carthagenensis Jacq.	12	17	31.48	18.25	*Drypetes laterifolia* (Sw.) Krug & Urban	24	176	325.93	151.08
Erythroxylum rotundifolium Lunan	9	13	24.07	22.15	*Eugenia axillaris* (Sw.) Willd.	2	2	3.70	2.33
Eugenia buxifolia (Sw.) Willd.	2	2	3.70	0.59	*Exostema caribaeum* (Jacq.) R.&S.	1	2	3.70	1.78
Guettarda combsii Urban	8	11	20.37	60.30	*Guettarda gaumeri* Standl.	3	3	5.56	5.41
Gymnanthes lucida Swartz	21	248	459.26	268.54	*Gymnopodium floribundum* Rolfe	19	88	162.96	120.49
Hampea trilobata Standl.	7	8	14.81	8.88	*Jatropha gaumeri* Greenm.	3	3	5.56	5.65
Krugiodendron ferreum (Vahl) Urban	8	10	18.52	10.58	*Lennea sepium* (Jacq.) Walp.	1	1	1.85	3.32
Lonchocarpus rugosus Benth.	5	6	11.11	25.94	*Lonchocarpus yucatanensis* Pittier	8	24	44.44	74.15
Luehea speciosa Willd.	10	13	24.07	74.43	*Lysiloma latisiliquum* (L.) Benth.	4	4	7.41	120.79
Malmea depressa (Baill.) Fries	15	30	55.56	33.52	*Manilkara zapota* (L.) van Royen	25	144	266.67	416.19
Metopium brownei (Jacq.) Urban	11	16	29.63	213.61	*Nectandra coriacea* (Sw.) Griseb.	3	3	5.56	1.16
Piscidia piscipula (L.) Sargent	8	13	24.07	81.71	*Pithecellobium leucospermum* Brand.	1	1	1.85	10.92
Psidium sartorianum Nied.	8	35	64.81	104.72	*Semialarium mexicanum* (Miers) Mennega	9	15	27.78	25.49
Sideroxylon foetidissimum Jacq. ssp. *gaumeri* (Pittier) Penn.	1	1	1.85	1.40	*Spondias mombin* L.	4	4	7.41	56.98
Talisia olivaeformis (H.B.K.) Radlk.	4	8	14.81	6.99	*Thouinia paucidentata* Radlk.	16	41	75.93	165.44
Vitex gaumeri Greenm.	5	6	11.11	39.29	*Zuelania guidonia* (Sw.) Britt. & Millsp.	8	9	16.67	47.39

MIRADOR RUIN FOREST (12 plots sampled)

Bourreria pulchra Millsp.	2	4	16.67	17.53	*Brosimum alicastrum* Swartz	12	144	600.00	1341.83
Bunchosia swartziana Griseb.	1	1	4.17	1.60	*Bursera simaruba* (L.) Sargent	6	8	33.33	207.96
Chlorophora tinctoria (L.) Gaudich.	2	2	8.33	67.13	*Cordia geriscanthus* L.	1	1	4.17	0.13
Cosmocalyx spectabilis Standl.	5	13	54.17	47.60	*Croton lundellii* Standl.	9	58	241.67	76.48
Diospyros anisandra Blake	1	1	4.17	3.47	*Drypetes laterifolia* (Sw.) Krug & Urban	2	4	16.67	4.29
Eugenia axillaris (Sw.) Willd.	4	7	29.17	7.32	*Eugenia buxifolia* (Sw.) Willd.	2	3	12.50	4.14
Exostema caribaeum (Jacq.) R.&S.	1	4	16.67	24.66	*Ficus cotinifolia* H.B.K.	2	6	25.00	96.55
Ficus spp.	4	4	16.67	96.26	*Gymnanthes lucida* Swartz	1	1	4.17	0.38
Hybanthus yucatanensis Millsp.	2	2	8.33	1.05	*Karwinskia humboldtiana* (R.&S.) Zucc.	2	3	12.50	147.21
Krugiodendron ferreum (Vahl) Urban	1	1	4.17	2.42	*Malmea depressa* (Baill.) Fries	5	9	37.50	19.33
Manilkara zapota (L.) van Royen	3	4	16.67	4.72	*Nectandra coriacea* (Sw.) Griseb.	3	4	16.67	2.45
Piscidia piscipula (L.) Sargent	4	5	20.83	117.06	*Pithecellobium leucospermum* Brand.	1	1	4.17	0.79
Semialarium mexicanum (Miers) Mennega	1	1	4.17	2.15	*Spondias mombin* L.	3	4	16.67	111.74
Talisia olivaeformis (H.B.K.) Radlk.	4	4	16.67	9.59	*Thouinia paucidentata* Radlk.	8	17	70.83	195.82
Urera baccifera (L.) Wedd.	2	9	37.50	12.01	*Zuelania guidonia* (Sw.) Britt. & Millsp.	3	8	33.33	47.25

UITIZINA RUIN FOREST (12 plots sampled)

Astrocasia tremula (Griseb.) Webster	6	14	58.33	13.26	*Brosimum alicastrum* Swartz	12	111	462.50	2066.17
Bunchosia swartziana Griseb.	5	9	37.50	6.06	*Bursera simaruba* (L.) Sargent	5	6	25.00	273.74
Capparis indica (L.) Druce	7	19	79.17	14.73	*Capparis pachea* ssp. *oxysepala* (Radlk.) Iltis	6	9	37.50	21.00
Celtis iguanaea (Jacq.) Sargent	6	10	41.67	26.21	*Croton lundellii* Standl.	12	67	279.17	102.76
Croton reflexifolius H.B.K.	1	1	4.17	0.69	*Drypetes laterifolia* (Sw.) Krug & Urban	4	4	16.67	19.54
Ehretia tinifolia L.	2	3	12.50	76.86	*Hybanthus yucatanensis* Millsp.	7	13	54.17	6.78
Malmea depressa (Baill.) Fries	3	3	12.50	2.08	*Neea choriophylla* Standl.	1	1	4.17	1.08
Spondias mombin L.	3	5	20.83	25.85	*Talisia olivaeformis* (H.B.K.) Radlk.	3	4	16.67	40.80
Thouinia paucidentata Radlk.	6	9	37.50	168.49	*Urera baccifera* (L.) Wedd.	10	58	241.67	90.12

SUMMARY

Numbers in parentheses = percentages based on all species found at each site (Appendix I and II).

SITE	SPECIES	STEMS	AREA	SITE	SPECIES	STEMS	AREA
Calcehtok Forest	41 (69%)	1563 (92%)	2007 (96%)	Ticul Forest	36 (78%)	633 (97%)	1155 (97%)
Tzucacab Forest	54 (58%)	2263 (88%)	1575 (91%)	San Mateo Forest	15 (85%)	584 (97%)	1794 (98%)
Othon Blanco Forest	50 (75%)	1219 (97%)	3087 (95%)	Mirador Ruin Forest	30 (91%)	333 (99%)	2671 (99%)
Uitizina Ruin Forest	18 (78%)	346 (98%)	2956 (99%)				

APPENDIX II

Presence of 68 rarer species (Importance Values <1.0 in all sites) at five forest sites and two ruin sites in the north-central Yucatan Peninsula, Mexico. CAL = Calcehtok forest; TIC = Ticul forest; TZU = Tzucacab forest; SAN = San Mateo forest; OTH = Othon Blanco forest; MIR = Mirador ruin forest; UIT = Uitizina ruin forest.

	CAL	TIC	TZU	SAN	OTH	MIR	UIT
Acacia collinsii Safford	●		●	●			
Acacia dolichostachya Blake						●	●
Acacia pennatula (Schlecht. & Cham.) Benth.	●	●	●				
Adelia barbinervis Schlecht. & Cham.			●				
Agonandra obtusifolia Standl.					●		
Albizia tomentosa (Micheli) Standl.		●	●		●		
Allophyllus cominea (L.) Swartz			●				
Bauhinia ungulata L.			●				
Caesalpinia yacatanensis Greenm.			●				
Callicarpa acuminata H.B.K.			●				
Casearia randioides Lundell	●						
Casimiroa tetrameria Millsp.			●				
Cecropia obtusifolia Bertol.			●				
Cedrela odorata L.					●		
Ceiba aesculifolia (H.B.K.) Britt. & Baker	●	●		●	●		
Chiococca alba (L.) Hitch.			●				
Chrysophyllum mexicanum Brand. ex Standl.			●	●	●		
Coccoloba acopulcensis Standl.							●
Cordia dodecandra DC.					●		
Cornutia pyramidata L.			●				
Cupania glabra Sw.			●		●		
Dalbergia glabra (Mill.) Standl.	●				●		
Diospyros verae-crucis Standl.			●				
Diospyros yatesiana Standl.			●				●
Dipholis salicifolia (L.) A. DC.			●		●		
Duranta erecta L.			●				
Enterolobium cyclocarpum (Jacq.) Griseb.	●						
Erythrina americana Mill.	●	●					
Eugenia laevis var. *gaumeri* (Standl.) McVaugh			●				
Exostema mexicanum Gray			●				
Guazuma ulmifolia Lam.	●	●					
Helicteres baruensis Jacq.	●		●				
Heliocarpus americanus L.			●				
Jacquinia macrocarpa Cav.	●						
Koanophyllon albicaule (Sch. Bip. ex Klatt) K.&R.			●				
Leucaena leucocephala (Lam.) deWit			●				
Malpighia glabra L.			●				
Neomillspaughia emarginata (Gross.) Blake	●		●	●	●		
Nissolia fructicosa Jacq.			●				
Parmentiera aculeata (H.B.K.) Seem.	●						
Phyllostylon rhamnoides (Poisson) Taubert	●						
Piper sempervirens (Trel.) Lundell						●	
Pisonia aculeata L.	●	●					
Platymiscium yucatanum Standl.				●	●		
Plumeria alba L.	●						

Appendix II (Continued)

	CAL	HC	IZU	SAN	OTH	MIR	UH
Plumeria obtusa L.					•		
Pouteria campechiana (H.B.K.) Baehni			•				•
Pouteria unilocularis (Donn. Sm.) Baehni					•		
Pseudobombax ellipticum (H.B.K.) Dugand					•		
Randia longiloba Hemsl.	•						
Randia truncata Greenm. & Thompson	•			•			
Rehdera trinervis (Blake) Moldenke			•				
Sabal mexicana Martius			•		•	•	
Senna atomaria (L.) Irwin & Barneby	•	•	•	•	•		
Senna racemosa (Mill.) Irwin & Barneby				•			
Sideroxylon obtusifolium (R.&S.) Penn.			•				
Simarouba glauca DC.			•				
Spondias purpurea L.	•						
Tabebuia rosea (Bertol.) DC.			•				
Thevetia gaumeri Hemsl.			•				
Trichilia arborea C. DC.			•				
Trichilia glabra L.			•				
Ximenia americana L.			•				
Xylosma flexuosum (H.B.K.) Hemsley			•				
Zanthoxylum caribaeum Lam.	•						
Zemenia frutescens (Mill.) Blake			•				
Unknown No. 1		•					
Unknown No. 2			•				
Totals	20	8	41	8	17	2	1

POPULATION STRUCTURE AND CLONAL GROWTH IN *BROMELIA PINGUIN* L. (BROMELIACEAE) IN DRY FORESTS OF COASTAL VERACRUZ, MEXICO

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Abstract

We studied the distribution, population structure, and clonal growth of *Bromelia pinguin* in two areas (young and old selva) of the tropical deciduous forest at Estación Biológica La Mancha and related those parameters to soil characteristics and seed and seedling predation. *Bromelia pinguin* inhabits both young and old selva, but characteristics of the young selva allow populations of the species to produce more ramets and cover a greater area than do *Bromelia* populations in the old selva. Environmental conditions in both areas are not homogeneous, differing in soil characteristics and the size of canopy gaps. The *Bromelia* population is composed of adult and young individuals that reproduce sexually and asexually by clones. Recruitment is based on clone formation. More than 30% of the ramets in each population were mother plants. The percentage of mother plants in old selva populations was significantly higher than in young selva. This difference suggests that conditions in old selva are more favorable for reproduction. The mean number of stolons in most populations was slightly higher that one, suggesting that maintenance and increase of the populations is through clonal growth.

Introduction

In the tropical deciduous forest of La Mancha Coastal Research Station, Veracruz, Mexico, several factors influence plant distribution and abundance. This community grows on sandy soil of different ages: fossil dunes with a possible Late Glacial age, and recent sand with a possible age of less than a few centuries (see Kellman and Roulet, 1990, for detailed characteristics). Soil characteristics influence plant species distribution and ecological importance values. For example, on the fossil dune, *Bursera simaruba* (L.) Sarg. and *Brosimum alicastrum* Sw. are prominent ("old selva"); in the recent sand, *Enterolobium cyclocarpum* (Jacq.) Griseb., *Cedrela odorata* L., and *Coccoloba barbadensis* Jacq. are prominent ("young selva"; Kellman and Roulet, 1990; Ramírez and García, 1990; Blain and Kellman, 1991). In addition, root proliferation and fine-root biomass are larger in recent sand (Kellman, 1990).

Predation is another factor that influences species distribution and abundance in the tropical deciduous forest at La Mancha. The red land crab (*Gecarcinus lateralis* Frem.) is abundant and consumes seeds and seedlings of several tree species, e.g., *B. alicastrum* and *E. cyclocarpum* (Blain, 1988; Delfosee, 1990),

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including the clonal herb *Bromelia pinguin* L. (García-Franco et al., 1991). Crab predation affects diversity, abundance, and recruitment in those plant species (Delfosee, 1990; García-Franco et al., 1991). Here, we report on a study of the distribution, population structure, and clonal growth of *Bromelia pinguin* at La Mancha Station, and discuss the effect of soil and predation on those parameters, and on population maintenance.

MATERIALS AND METHODS

STUDY SPECIES. *Bromelia pinguin* L. (Bromeliaceae) is a terrestrial plant with indeterminate growth, inhabiting tropical lowland deciduous and dry forests (sea level to 780 m) from Mexico throughout Central America to Venezuela and the Caribbean Islands (Hallwachs, 1983; Smith and Downs, 1979). The species presents serial monocarpy or sympodial dichotomy (plants produce a series of monocarpic axes; Benzing, 1980), and also reproduces by clonal growth. In La Mancha Coastal Research Center, *B. pinguin* forms dense patches or populations (demes) in the tropical deciduous forest. Flowers are present for only a few days, usually in March and April during the dry season. Butterflies and hummingbirds (*Amazilia beryllina* and *Cyranthus latirostris*, Trochilidae) are the main flower visitors. Abundant fruits and seeds are produced each year (García-Franco et al., 1991). However, few genets are recruited because seed and seedling predation by land crabs, *Gecarcinus lateralis*, is very high, sometimes 100% of the seeds and seedlings being eaten (García-Franco et al., 1991). The number of genets in each *Bromelia* population is unknown, but it is possible to distinguish clones based on physical separation. In the present study, we consider each unit (clone) as an individual (sensu Jackson et al., 1985), and the largest plant in each unit as the "mother plant" for the clone.

STUDY SITE. Field work was conducted in lowland tropical deciduous forest at the La Mancha Coastal Research Center (Centro de Investigaciones Costeras La Mancha, CICOLMA) in the state of Veracruz, Mexico (19°36'N, 96°22'W; altitude <100 m). Annual precipitation is 1100-1300 mm, with most rain falling June-September. Mean temperature is 22°-26°C, with a minimum of 10°C and a maximum of 38°C (Moreno-Casasola, 1982). Several types of vegetation are present in the area of the field station: tropical deciduous forest, tropical dry forest, sand dune matorral, and mangrove forest (Novelo, 1978; Moreno-Casasola et al., 1982; Rico-Gray and Lot, 1983). The tropical deciduous forest has a relatively simple structure and composition with tree species such as *Bursera simaruba* (Burseraceae), *Brosimum alicastrum* (Moraceae), *Enterolobium cyclocarpum* (Leguminosae), *Cedrela odorata* (Meliaceae), and *Ficus cotinifolia* H.B.K. (Moraceae). Common shrub species include *Nectandra coriacea* (Sw.) Griseb. (Lauraceae), and *Coccoloba barbadensis* (Polygonaceae) (Ramírez and García, 1990; Blain and Kellman, 1991).

Soils on recent dune (young selva) and fossil dune (old selva) are described by Kellman (1990). Sand particles comprise >95% of the soil at the recent sand study site, but this is reduced to 70-80% on the fossil dune site, where considerable clay formation has occurred. Soil pH is alkaline (7.8-8.5) in recent sand, but approximately neutral (6.9-7.1) in the fossil dune soil. Cation exchange capacity varies from 3 to 12 mmol/100g in recent sand, depending upon organic carbon content, and 20 to 33 mmol/100g in the fossil dune soil (correlated with the clay content there, $r^2=0.05$, $P<0.05$). Total nitrogen in the soil increases throughout the succession, and is closely correlated with organic carbon ($r^2=0.94$, $P<0.05$). Extractable cations are dominated by Ca in the recent sand, and Mg and K are substantially higher in the fossil dune soil. A total element analysis of Ca, Mg, K, Na, and P indicated that soil on the fossil dune has experienced a net loss of Ca, Mg and P during weathering, but no net loss of K and P. (Kellman and Roulet 1990). Soil water infiltration rates on both recent and fossil dune soils are high (Kellman and Roulet, 1990).

POPULATION STRUCTURE. Data were obtained between June 1989 and June 1990. All subpopulations of *Bromelia pinguin* were identified in the old and young selvas of the study area. All individuals in each subpopulation were counted, and listed as either non-reproductive or reproductive. For those that were reproductive, we distinguished asexual reproduction (clonal growth, with stolon presence) or sexual reproduction (presence of fruit or flower). To estimate plant size, we measured the length of five mature leaves (base to tip) from the third leaf verticil.

CLONAL GROWTH. Clonal growth in *Bromelia pinguin* was assessed in 10 of the 16 populations studied; five on young selva, and five on old selva. The subpopulations were selected from a variety of light conditions, slope variations, and types of surrounding vegetation. Clones of *B. pinguin* are so intermixed (tangled) that observations were sometimes difficult to make (see Table 2 for density data).

Developing stolons were divided into two categories: those with a rosette of leaves (rosette), and those without expanded leaves at their tip (stolons). All stolons were measured monthly between June 1989 and July 1990. For those scored as "stolons," we measured the distance from the base of the leaf of the mother plant to the stolon tip. For those scored as "rosette," we measured the length of five leaves beginning at the base of the rosette. Growth data were pooled to obtain a mean monthly rate of growth, and correlated with precipitation and temperature data recorded during the study. As stolons developed and leaves expanded, they were then classified as rosettes; therefore the number of observations in each category changed during the study. The mean number of stolons per mother plant was obtained from reproductive-stage ramets present in the populations; nine of these with at least ten ramets with clonal growth were compared (Table 2).

RESULTS

DEMOGRAPHIC STRUCTURE. There was a total of 16 populations of *Bromelia pinguin* in the study site, eight in the old selva, and eight in the young selva. The number of individuals per population varied between one and 1096. There were 2235 plants (77.12%) in the young selva subpopulations and 663 plants (22.88%) in the old selva subpopulations (Table 1). Old and young selva subpopulations had the same size-structure pattern; few plants in the smaller classes, higher frequency in the middle classes, and few in the largest size classes (Figures 1 and 2).

Plants could be assigned to three biological stages: non-reproductive (infantiles), clonally reproductive (juveniles), and sexually reproductive (adults).

TABLE 1. Mean leaf size (length in cm, ± s.d., N) of plants of *Bromelia pinguin* representing each of the biological stages determined for each subpopulation. (*=population used in the ANOVA test. 1F=2.84, 2F=3.27, 3F=3.27, 4F=3.59; p<0.001).

Sub-population	All Individuals 1		Infantiles Individuals 2		Juveniles Individuals 3		Adults Individuals 4	
YOUNG SELVA								
1	150.0±50.06	(11)*	120.8±51.17	(6)	185.0±13.23	(5)	185.0±13.2	(5)*
2	120.8±31.17	(5)	120.8±31.17	(5)		(0)		(0)
3	110.3±41.19	(163)*	90.4±36.58	(105)*	146.4±18.13	(58)*	147.2±18.81	(18)*
4	139.9±45.01	(76)*	126.0±45.38	(52)*	161.8±42.52	(23)*	147.8±68.45	(7)*
5	148.5±38.45	(290)*	130.7±37.88	(173)*	175.2±19.53	(97)*	178.8±17.07	(59)*
6	123.1±39.57	(593)*	106.9±37.94	(367)*	149.5±25.40	(201)*	159.4±24.80	(84)*
7	95.0±00.00	(1)	95.0±00.00	(1)		(0)		(0)
8	121.4±33.98	(1096)*	106.6±34.04	(650)*	143.0±19.21	(410)*	144.5±16.16	(116)*
OLD SELVA								
9	135.4±27.81	(42)*	130.5±24.90	(20)*	139.9±30.08	(22)*	151.0±36.47	(3)*
10	129.6±36.43	(388)*	113.9±33.99	(235)*	154.4±24.97	(148)*	148.6±24.51	(31)*
11	138.6±48.02	(163)*	112.0±41.52	(92)*	173.0±31.07	(71)*	174.5±29.20	(13)*
12	132.0±19.62	(6)	133.4±21.59	(5)	125.0±00.00	(1)	125.0±00.00	(1)
13	120.1±34.08	(4)	95.0±00.00	(1)	150.0±00.00	(1)	150.0±00.00	(1)
14	130.4±27.98	(46)*	114.7±29.73	(22)*	144.7±16.94	(19)*	146.0±17.79	(9)*
15	137.3±12.45	(2)	137.3±12.45	(2)		(0)		(0)
16	105.9±41.82	(12)*	89.6±45.93	(7)*	119.9±14.94	(4)	125.0±25.94	(4)*
TOTAL	126.8±38.65	(2898)	110.4±37.26	(1745)	151.4±25.65	(1060)	156.0±25.80	(351)

TABLE 2. Number of mother plants and number of stolons produced in populations of *Bromelia pinguin* with more than 10 clones. Area occupied, and density of plants and stolons of populations with similar total number of plants (*ANOVA F=8.66, $F_{0.001\ (8,1040)}$=3.27;Tukey test $_{q0.001,\ 1040,\ 9}$=5.903).

Sub-population	Total Mother Plants	Mother Plants with Stolons (%)	Stolons per Mother Plant $\overline{x}$±s.d.	Area (sq. m)	Plant Density (Plants per sq.m)	Stolon Density (Stolons per sq. m)
YOUNG SELVA						
13	1096	410 (37.0)	1.185±0.48	1849.91	0.59	0.22
6	586	201 (34.3)	1.149±0.39	939.85	0.62	0.21
5	290	97 (33.5)	1.072±0.26	638.30	0.45	0.15
3	163	58 (35.6)	1.224±0.49	223.56	0.73	0.26
4	72	23 (31.9)	1.174±0.39	128.92	0.56	0.18
OLD SELVA						
10	388	148 (38.5)	1.169±0.47	512.48	0.75	0.29
11*	163*	71 (43.6)*	1.690±0.89	128.01	1.27	0.55
14	46	19 (41.3)	1.053±0.23	36.16	1.27	0.53
9	42	22 (52.4)	1.136±0.35	33.26	1.26	0.66

Infantiles were present in the smaller leaf-size classes (89.6-137.3 cm), adults were present in the intermediate leaf-size classes (125.0-185.0 cm), and juveniles were present over a wider range of leaf-size classes (119.9-185.0 cm) (Figures 1 and 2; Table 1). The young and old selva subpopulations were significantly different in mean size of all individuals and in mean size within the biological stages (One Way ANOVA, $p<0.001$; Table 1). Mean leaf size of all individuals in young selva populations (Kruskal-Wallis, H=125.65 $p<0.05$) were significantly different, and old selva populations (Kruskal-Wallis, H=9.52 $p<0.05$) were also significantly different.

Individuals with sexual reproduction can be separated into two subgroups: those with sexual reproduction as well as clonal growth, and those with only sexual reproduction. Mean leaf size and inflorescence size of individuals with only sexual reproduction were smaller than for individuals with both sexual and clonal reproduction (t-Student; t=6.19 d.f.=73, and t=4.23 d.f.=73, $p<0.05$, respectively).

Mean size of individuals within populations in young selva was significantly different (One Way ANOVA, F=41.15, $p<0.05$). On the contrary, there was no difference in mean size of individuals in old selva (One Way ANOVA, F=2.15, $p>0.05$). Mean size of individuals for each biological stage surveyed (infant, juvenile, adult) for populations in young selva was significantly different (One Way ANOVA, F=29.25, F=32.19, and F=13.46, $p<0.05$, respectively). In old selva, the mean size of individuals was significantly different only for juveniles and adults (One Way ANOVA, F=13.20, F=3.60, $p<0.05$, respectively), and not among infants (F=1.5, $p>0.05$).

Subpopulations with similar total numbers of individuals in young and in old selvas were compared. For example, young selva population number 5 had a larger mean size for all individuals, juveniles, matures, and adults than did old selva population number 10 (t-Student; t=6.93, d.f.=289; t=3.69, d.f.=172; t=4.62, d.f.=29; and t=9.30, d.f.=96, p<0.05; respectively). On the other hand, sizes of individuals in old selva population number 11 were larger then in young selva population number 3 (t-Student; t=5.79, d.f.=162; t=4.18 d.f.=91; t=2.52, d.f.=12; t=4.82, d.f.=57; p<0.05; in the same order).

CLONAL GROWTH. Individuals of *Bromelia pinguin* produce ramets before flowering, usually by the time they reach a mean leaf length of 151.4 (±25.65) cm (n=1060). Clonal growth starts in the axillary buds of basal rosette leaves nearest to the ground. The stolons, which are covered by bracts, grow plagiotropically or diagonally upwards over the mother plant. The first leaves are produced when the stolons reach a mean length of 78.2 (±18.33) cm (n=35). Mother plants can abort stolon development at any time prior to stolon leaf production (five cases were observed). Abortion is evidently not related to insect attack or disease. Mother plants can produce new stolons at a later time.

Stem production and growth occur throughout the year but more frequently during the rainy season, when water availability and temperature are higher. Stolons grow faster during this period because of higher precipitation (Figure 2) (r=0.48, p<0.05; Spearman rank correlation coefficient). There was no statistical correlation with temperature. Growth of rosettes was significantly correlated with temperature (r=0.54, p<0.05) and with precipitation (r=0.47, p<0.05).

Rosettes grow rapidly and can produce roots when a mean size of 102.17 (±14.76) cm (n=28) is attained. Such clones can produce new stolons before they flower, such that at times as many as three generations of clones are interconnected, corresponding to the "guerrilla" type of reproduction (Lovett-Doust, 1981). The size of the rosettes that produce new stolons (117.6 (±5.73) cm, n=106) is very similar to the size of juveniles within the whole population at the study site (Table 1).

Mother plants of *Bromelia pinguin* produce one to five clones during their lifetime, but 1.20 (±0.49) is the average number of stolons per adult (n=1060). However, mother plants of subpopulation 11 produced a higher number of stolons per adult ramet (Table 2). Two pairs of populations with similar numbers of individuals were compared. Populations 9 (n=42) and 14 (n=46) were not different in mean number of stolons (p>0.1; Table 2), but populations 3 and 11, with equal numbers of individuals (163), were significantly different in the number of stolons produced (p<0.001; Table 2).

DISCUSSION

Bromelia pinguin inhabits old and young areas of deciduous forest in the study site, but the young selva populations have many more ramets and cover a greater area than do populations in old selva (Figures 1 and 2; Tables 1 and 2). Environmental conditions in young and old areas are not homogeneous. Bromeliad populations in young selva differ significantly in mean size when all plants are pooled or when categorized by life stages. In contrast, pooled individuals from populations in old selva differ significantly in size only when compared by life stages. Individuals in one area of the forest were larger than individuals in other areas, without a clear dominance pattern between areas. This suggests that soil characteristics and size of canopy gaps could be a factor determining ramet development within populations.

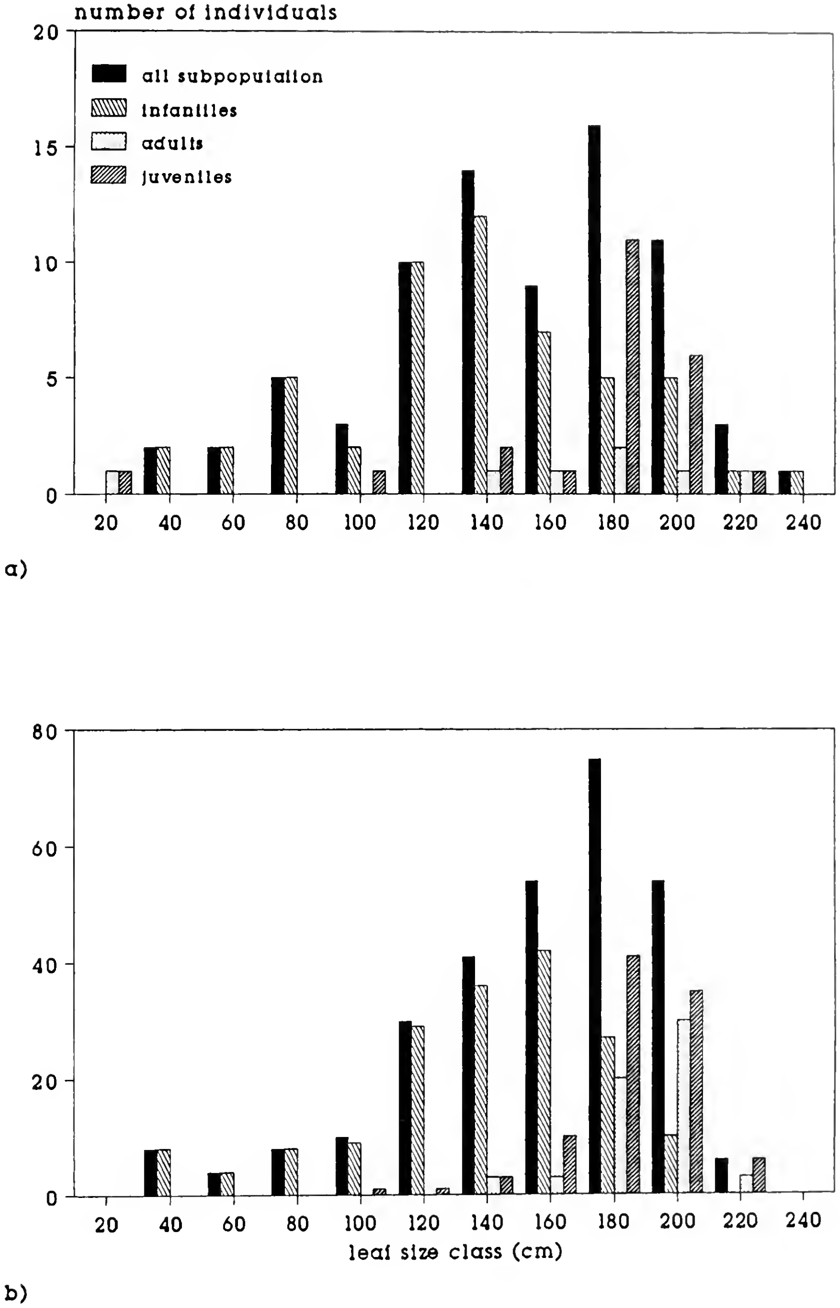

Figure 1. Leaf size class distribution for individuals of *Bromelia pinguin* from two populations in young selva at La Mancha Station, Mexico. Data from Table 1: a = population number 4; b = population number 5.

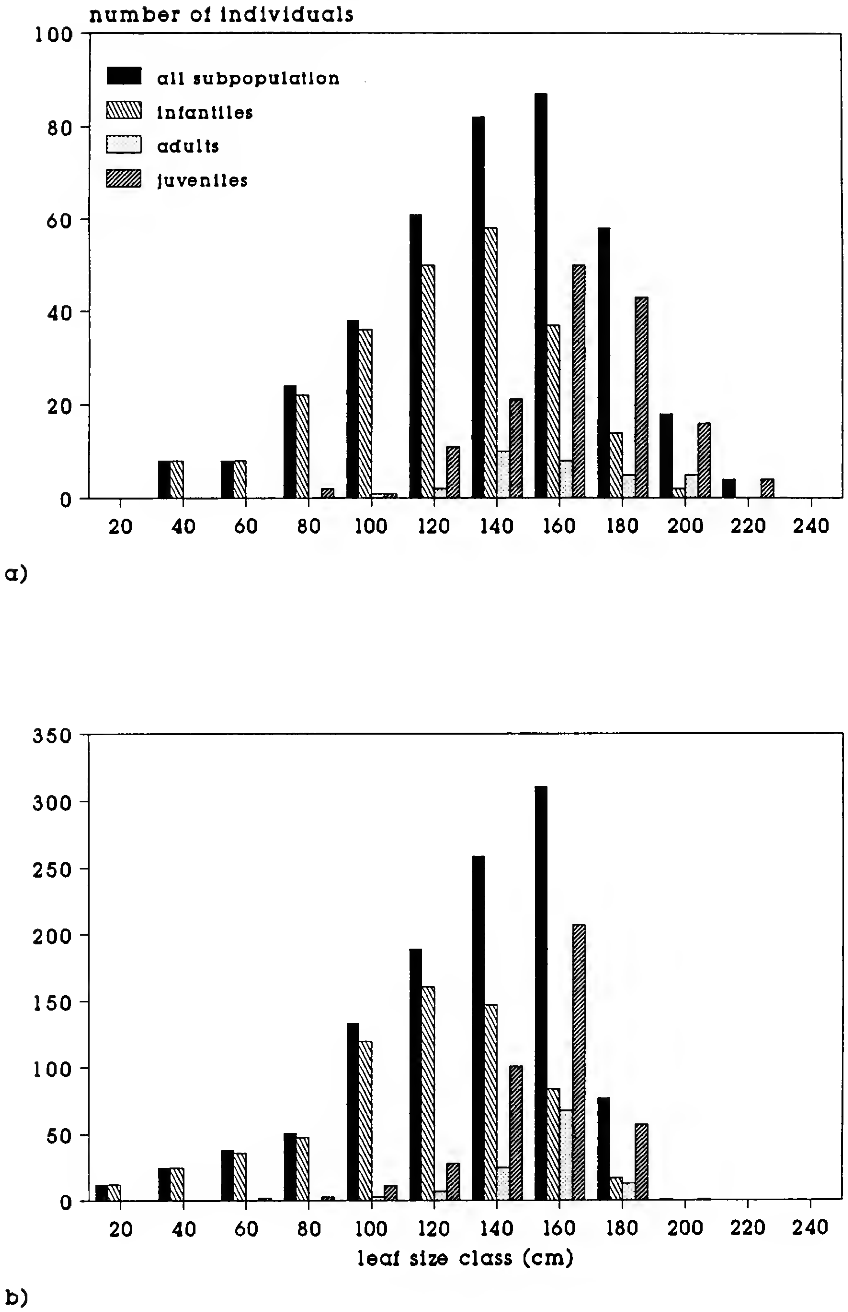

Figure 2. Leaf size class distribution for individuals of *Bromelia pinguin* from two populations in old selva at La Mancha Station, Mexico. Data from Table 1: a = population number 10; b = population number 13.

Each *Bromelia pinguin* population is formed by adult and young individuals that reproduce both sexually and asexually (by clones). High seed and seedling predation means that recruitment is based on clone formation (García-Franco et al., 1991). More than 30% of the ramets in each population were mother plants (Table 2). Nevertheless, the percent of mother plants in old selva populations was significantly higher than in young selva (t-Student; t=3.41, $p<0.05$, percent values transformed to arcsin; Sokal and Rohlf, 1969). This difference suggests that conditions in old selva are more favorable for clonal reproduction. The mean number of stolons in most populations is slightly higher that one, suggesting that replacement is only of the mother plant.

There is strong seasonality in availability of water and nutrients in the study site (Kellman and Roulet, 1990; Blain and Kellman, 1991). Biomass increases during the rainy season (Kellman, 1990); humidity strongly affects clonal growth of rosettes and stolons. Clonal growth during wetter periods allows each ramet to cover a greater area with increasing light reception. Integration (a physical and physiological interdependence among the ramets of a clone, sensu Jackson et al., 1985) can be particularly beneficial in environments where resources are scarce or are distributed over space and time, such as on sand dunes or rocks (Grime, 1979). Integration may well inhibit the establishment of other plant species within populations, such as in colonies of the terrestrial bromeliad *Achmea magdalenae* (André) André ex Baker (Brokaw, 1983).

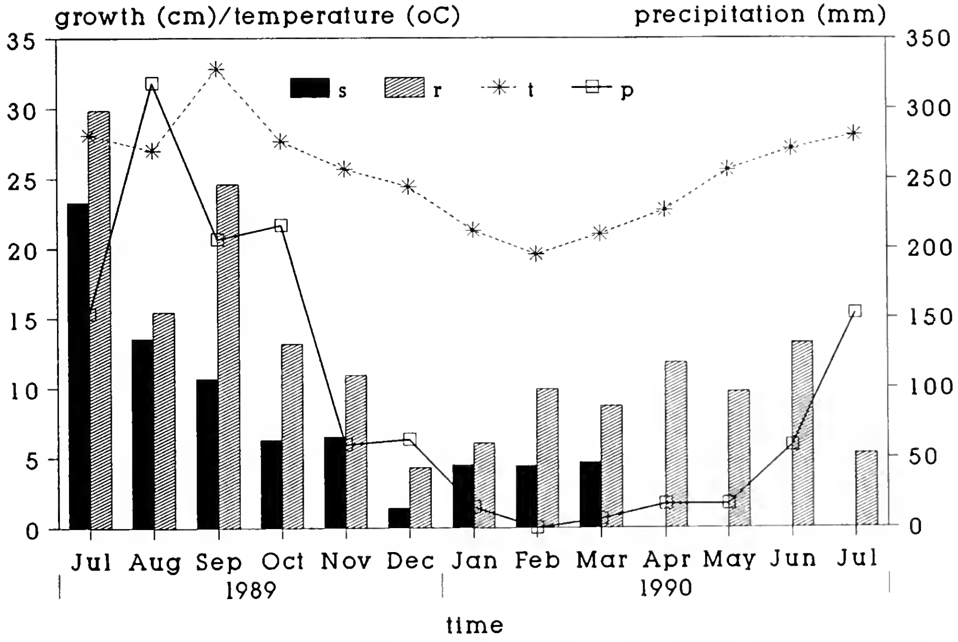

Figure 3. Growth of *Bromelia pinguin* at La Mancha Station, Mexico, relative to monthly temperature and precipitation. r=growth of rosettes in cm. s=growth in length of stolons in cm. t=temperature. p=precipitation.

Individuals of *Bromelia pinguin* usually begin reproduction by clonal growth and reproduce sexually after or during stolon development. Some individuals reproduce sexually before producing stolons, and our data suggest that individuals reproducing both clonally and sexually are more vigorous, larger, and produce larger inflorescences. Clonal structure apparently benefits these plants by making more resources available for sexual reproduction.

Vegetative reproduction can be advantageous for plants inhabiting environments of great stress, or when ramets outlive seedlings (Fenner, 1985). The abundance of crabs and their effects on seed predation and dispersal can influence the structure of plant communities (Louda and Zedler, 1985; O'Dowd and Lake, 1990). Also, selective seedling herbivory has been shown to occur (O'Dowd and Lake 1990). Seed predation, mainly by *Gecarcinus lateralis*, affects diversity and abundance of species such as *Brosimum alicastrum*, *Enterolobium cyclocarpum*, and *Cedrela odorata* in deciduous forest at our study site (Blain, 1988; Delfosee, 1990; García-Franco et al., 1991). The similarity in the structure of *Bromelia pinguin* populations suggests that they likewise may be subject to the same seed and seedling predation pressures at La Mancha.

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THE CYCLOPOID COPEPOD (CRUSTACEA) FAUNA OF NON-PLANKTONIC CONTINENTAL HABITATS IN LOUISIANA AND MISSISSIPPI

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ABSTRACT

Cyclopoid copepod crustaceans were collected in benthic and littoral samples from spatially limited mosquito-breeding habitats including a canal, small perennial and ephemeral ponds, sloughs, swales, rice fields, ditches, puddles, cemetery pits, and old tires in southern Louisiana, principally in greater New Orleans, and in Mississippi. The local fauna is relatively diverse, with 25 species in this collection and a total of 34 recorded from the region. An unexpectedly large neotropical faunal component included *Apocyclops panamensis, Diacyclops bernardi, Mesocyclops longisetus, Mesocyclops reidae, Thermocyclops inversus*, and *Thermocyclops tenuis.* The known ranges of *D. bernardi, M. reidae*, and *T. inversus* are extended to the United States. *Metacyclops cushae,* described from New Orleans, closely resembles neotropical species. *Mesocyclops ruttneri*, newly recorded from the United States, may have been introduced from tropical East Asia.

INTRODUCTION

During 1989-91, cyclopoid copepods (Crustacea) were collected from mosquito breeding sites in southern Louisiana and northwestern Mississippi as part of a search for copepod species that would be potentially useful for biological control of larvae of *Aedes albopictus* (Skuse) (Marten, 1989, 1990a-c). We list the species collected and compare the species richness of the Louisiana-Mississippi assemblage with cyclopoid faunas of other regions of North America, especially the south-central United States. We discuss the known geographical distributions and habitats of species of particular interest.

MATERIALS AND METHODS

Copepods were collected throughout the year at ca. 200 sites in the New Orleans-Slidell area (southeastern Louisiana). Habitats included canals, *Spartina* marshes, permanent and ephemeral ponds, ephemeral pools, and ditches. Sev-

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eral hundred discarded tires and 40 tree holes were also sampled. Copepods were collected from 32 rice fields in Jefferson Davis Parish (southwestern Louisiana) and 10 rice fields in the vicinity of Cleveland (northwestern Mississippi).

The copepods were collected with a standard dipper used to collect mosquito larvae. The dipper consisted of a 400 ml plastic cup at the end of a one-meter wooden pole. Copepods were also collected from canals and ponds by dragging a plankton net parallel to the shore. They were collected from tires by removing the water with a hand-held plastic cup, and from tree holes by sucking out the water with a turkey baster. Water dipped from each site was passed through a 200 µm Nitex net to strain out copepods. The contents of the net were suspended in a small amount of water, and copepods were removed with a Pasteur pipette and fixed and preserved in 70% ethanol. For species determination, specimens were mounted temporarily in glycerin or lactic acid media, or permanently in commercial polyvinyl lactophenol medium with a little chlorazol black E added, and examined using a Wild M20 compound microscope. Representative specimens were deposited in the National Museum of Natural History, Smithsonian Institution; the remaining material is in the collection of GGM.

RESULTS

Species inventory and nomenclature.

The collections contained a total of 25 cyclopoid species (Table 1). Identification of most species was straightforward, but explanation is necessary for some of the names employed in this article. We use the old name *Eucyclops elegans* for the American species that is frequently identified as the European *Eucyclops speratus* (Lilljeborg, 1901), and have listed records of *E. speratus* by other authors as *E. elegans* in Table 1. The systematics of *Megacyclops* is presently confused; specimens from New Orleans, reported as "*Megacyclops viridis* species group" by Marten (1990b) were eventually identified as *M. latipes* according to unpublished criteria developed by A. A. Weaver (in litt. to JWR, 1993). Most of the specimens of *Mesocyclops longisetus* were congruent with *M. longisetus* subspecies *curvatus* Dussart, 1987. *Mesocyclops ruttneri* was identified with some difficulty because of its resemblance to several Caribbean species, and is redescribed elsewhere (Reid, 1993). *Metacyclops cushae* was earlier listed as *M. denticulatus* by Marten (1989). *Microcyclops rubellus* (Lilljeborg, 1901) is considered by Reid (1992) and other authors as a separate species rather than a subspecies of *Microcyclops varicans* (G. O. Sars, 1863). The species of *Tropocyclops* encountered in this study fit the current diagnoses of *T. prasinus* sens. str. or *T. extensus*, as presented by Dussart and Fernando (1990) and Reid (1991), but not that of the commonly reported *T. prasinus mexicanus* (Kiefer, 1938).

Species reported from several other general collections in the region are listed in Table 1 under their currently recognized generic names. In the case of the very old records listed by Penn (1947), the species are listed under our best guess as to the taxa meant: *Cyclops brevispinosus* Herrick, 1884, is possibly a synonym of *Acanthocyclops vernalis*; *Cyclops serrulatus* Fischer, 1851, is a synonym of *E. agilis*; and *Cyclops fluviatilis* Herrick, 1882, is a synonym of *Tropocyclops prasinus. Diacyclops navus* was reported by Nasci et al. (1987) as *Thermocyclops dybowskii* (Lovén, 1890); this record was corrected by Reid et al. (1989).

TABLE 1. Copepoda Cyclopoida species records from five surveys in the south-central United States. Locales are as follows: present report, southern Louisiana and northwestern Mississippi; Penn (1947), New Orleans; Nasci et al. (1987), southwestern Louisiana; Harris (1978), northern Mississippi; Binford (1978), southern Louisiana.

	Present Study	Penn (1947)	Nasci et al. (1987)	Harris (1978)	Binford (1978)
COSMOPOLITAN SPECIES					
Ectocyclops rubescens Brady, 1904	•	•	•		
Eucyclops agilis (Koch, 1838)	•	•	•	•	
Paracyclops chiltoni (Thomson, 1883)	•				
Paracyclops fimbriatus (Fischer, 1853)				•	
Macrocyclops albidus (Jurine, 1820)	•		•	•	•
Macrocyclops fuscus (Jurine, 1820)				•	
NORTH AMERICAN OR CIRCUMBOREAL SPECIES					
Halicyclops sp.			•		
Eucyclops agilis montanus (Brady, 1878)				•	
Eucyclops prionophorus Kiefer, 1931	•			•	
Eucyclops elegans (Herrick, 1884)	•		•	•	•
Megacyclops latipes (Lowndes, 1927)	•		•		
Megacyclops viridis (Jurine, 1820)		•			
Orthocyclops modestus (Herrick, 1883)	•				
Paracyclops poppei (Rehberg, 1880)	•		•	•	
Tropocyclops extensus (Kiefer, 1931)	•				
Tropocyclops prasinus (Fischer, 1860)	•	•	•	•	•
Tropocyclops prasinus mexicanus Kiefer, 1938				•	
Acanthocyclops exilis (Coker, 1934)			•		
Acanthocyclops venustoides (Coker, 1934)			•		
Acanthocyclops vernalis (Fischer, 1853) s.l.	•	•?	•	•	•
Diacyclops crassicaudis var. *brachycercus* (Kiefer, 1929)	•			•	
Diacyclops navus (Herrick, 1882)	•		•		
Diacyclops thomasi (S.A. Forbes, 1882)			•	•	•
Mesocyclops edax (S.A. Forbes, 1891)	•			•	•
Metacyclops cushae Reid, 1991	•				
Microcyclops rubellus (Lilljeborg, 1901)	•		•	•	
NORTH AND SOUTH AMERICAN SPECIES					
Homocyclops ater (Herrick, 1882)	•	•	•	•	
NEOTROPICAL SPECIES					
Apocyclops panamensis (Marsh, 1913)	•		•		
Diacyclops bernardi (Petkovski, 1986)	•				
Mesocyclops longisetus (Thiébaud, 1914) s.l.	•				
Mesocyclops reidae Petkovski, 1986	•				
Thermocyclops inversus Kiefer, 1936	•				•
Thermocyclops tenuis (Marsh, 1909)	•			•	
ASIAN SPECIES [?]					
Mesocyclops ruttneri Kiefer, 1981	•				
SPECIES TOTAL	25	6	16	17	7

Species-habitat relationships.

Large permanent water bodies (canals, golf course ponds) in the New Orleans-Slidell area contained *Acanthocyclops vernalis, Eucyclops agilis, Eucyclops elegans, Homocyclops ater, Macrocyclops albidus, Mesocyclops ruttneri, Microcyclops rubellus,* and *Tropocyclops prasinus.* Nine species were common in the New Orleans-Slidell area in marshes, roadside ditches, temporary ponds, and temporary pools holding water for extended periods: *Acanthocyclops vernalis, Diacyclops navus, Ectocyclops rubescens, Eucyclops agilis, Eucyclops elegans, Macrocyclops albidus, M. rubellus, Thermocyclops inversus,* and *Tropocyclops extensus.* In addition to these, pools in wooded areas contained *Megacyclops latipes* and *Orthocyclops modestus.* Only one tree hole contained copepods, and they were *Paracyclops poppei.* Discarded tires in wooded areas contained some of the same species found in the surrounding woods, namely *A. vernalis, D. navus, E. rubescens, E. agilis, M. albidus, P. poppei,* and *O. modestus. Eucyclops elegans, P. chiltoni,* and *T. prasinus* were each collected from a single tire, and a single specimen of *M. ruttneri* was collected from a marsh.

In the New Orleans-Slidell area, pools and small depressions (swales) holding water only for short periods of time contained *Acanthocyclops vernalis, Diacyclops navus, Metacyclops cushae, Microcyclops rubellus,* and *Thermocyclops tenuis.* These species often appeared as soon as there was water. *Diacyclops crassicaudis* var. *brachycercus* and *Diacyclops bernardi* were also collected, but each was found in only one swale. *Apocyclops panamensis* was found in a freshwater swale that was sometimes flooded with brackish water. The Louisiana rice fields contained *Acanthocyclops vernalis, Ectocyclops rubescens, Eucyclops elegans, Macrocyclops albidus, Mesocyclops ruttneri, Mesocyclops reidae, Microcyclops rubellus, Paracyclops chiltoni, Paracyclops poppei, Thermocyclops inversus, T. tenuis,* and *Tropocyclops extensus.* The Mississippi rice fields contained *A. vernalis, Diacyclops crassicaudis* var. *brachycercus, Eucyclops agilis, E. elegans, Macrocyclops albidus, Mesocyclops ruttneri, M. reidae, Microcyclops rubellus,* and *Tropocyclops extensus.* Either *Acanthocyclops vernalis* or *Mesocyclops ruttneri* occurred in almost every field that was sampled in Louisiana and Mississippi, but never together.

DISCUSSION

These collections, although limited primarily to small bodies of standing or very slowly flowing water, revealed a species-rich cyclopoid fauna (Table 1). Previous studies in the region collected many fewer species on average. Only six species were recorded previously from New Orleans proper (Penn, 1947). Binford (1978) collected seven species of cyclopoids during monthly samples over a one-year period in the Atchafalaya River and associated swamps in south-central Louisiana. Harris (1978) listed 17 species from collections in northern Mississippi made over a one-year period from a wide variety of lentic and lotic habitats. Nasci et al. (1987) recorded 16 species from similar mosquito-breeding habitats in southwestern Louisiana.

The fauna of ephemeral pools reported here is like that occurring in similar waters elsewhere. Nasci et al. (1987) reported that *Acanthocyclops vernalis* was almost constantly present in three woodland ponds in southwestern Louisiana. In those ponds, two of which frequently dried, *Diacyclops navus* was collected less often but also persisted through the year. Nasci et al. (1987) reported a total of

6-11 species from each pond. In New Orleans, similar woodland ponds contained a total of 11 species, most of these the same that were recorded by Nasci et al. (1987). Taylor and Mahoney (1990) reported an analogous association of *Acanthocyclops vernalis* and *Diacyclops haueri* Kiefer, 1931, in an ephemeral bay lake in South Carolina, which supported an assemblage of nine cyclopoid species.

Some 96 species of cyclopoid copepods of the family Cyclopidae are presently recorded from North America north of Mexico. Usually, about one-fourth of this number inhabit any particular region. The 34 copepod taxa now reported from Louisiana and Mississippi constitute the most species-rich assemblage so far recorded from North America. Although such comparisons are not well founded because the few intensive investigations of regional cyclopoid copepod faunas on this continent differed in their objectives and collecting techniques, a review of some other local totals provides perspective. One of the most comprehensive faunistic studies in the United States is the eight-year survey reported by Bunting (1973) for Tennessee, in which 22 species were recorded from 653 samples from 476 localities including a wide variety of habitats. The copepod fauna of North Carolina is almost equally well known, thanks to the investigations of Yeatman (summarized in 1944) and subsequent workers. From North Carolina there are 27 species recorded to date (Adams et al., 1992). Smith and Fernando (1978) reported 25 species from lacustrine and non-lacustrine habitats in southern Ontario. In tropical regions of comparable extent, cyclopoid copepod species diversity may be slightly higher. For instance, from Cuba, 35 species and subspecies of cyclopids have been reported, although several records need to be substantiated (Reid, 1990). The 25 species recorded in our collections is a higher total than would be expected from the limited types of habitats sampled. Even though the local list may be slightly inflated because of taxonomic problems, the area total of 34 taxa is surprising.

Characterization of the geographical distribution of the cyclopoid species collected in Louisiana and Mississippi (Table 1) reveals that the relatively high number of species is due mainly to a significant neotropical component. Southern Louisiana lies within the northern ranges of six neotropical species, three of these documented from the United States for the first time in this study. A seventh, previously undescribed species with neotropical affinities (*Metacyclops cushae*) was discovered in New Orleans, and an eighth, probably introduced species (*Mesocyclops ruttneri*) is recorded for the first time in the Americas.

Apocyclops panamensis is a common inhabitant of brackish coastal lagoons and ponds around the Gulf and Caribbean, and has been recorded from the mid-Atlantic coast of the United States, south as far as the northern coast of South America (Reid, 1990). *Mesocyclops longisetus* occurs commonly from southern South America to the Antilles and Mexico, and sporadically in the southern conterminous United States, where the New Orleans find is only the third confirmed record, the others being from Texas and Florida (reviewed by Reid, 1993). The subspecies *M. longisetus curvatus* may be distributed through Central America, the Antilles, and southern North America, with the nominate species restricted to continental South America (Dussart, 1987).

Mesocyclops reidae, an Antillean and Central American species, is common in small bodies of water in Honduras (Marten and Reid, unpublished). The record from Mississippi rice fields extends its known range significantly northward from tropical Mexico (Reid, 1990, 1993).

Thermocyclops tenuis extends throughout the lowland neotropics, with sporadic records in the southwestern and south-central United States. Many records of this species are from ephemeral waters (Reid, 1989).

The record of *Thermocyclops inversus* was previously reported briefly by Reid (1989). This species is common in southern Mexico, Central America, and Cuba, with a few records from Brazil, but was unknown north of the Tropic of Cancer until the New Orleans find. The Louisiana record thus represents a northward range extension of about 900 km. *Thermocyclops inversus* is a common plankter in large Central American lakes, but has also been recorded from reservoirs, ponds, wells, and caves (Reid, 1989).

The find of *Diacyclops bernardi* represents an equally surprising northward range extension. It is known elsewhere only from San Andrés Island off Nicaragua, and from Yucatán, Mexico (Reid, 1993). The species was collected from brackish water (salinity up to 30 ‰) in a dug well and a shallow cave on San Andrés, and in Mexico from a coastal pond.

Metacyclops cushae, described from New Orleans, resembles an Argentinian species, *M. denticulatus* Dussart and Frutos, 1986, and is most likely neotropical in origin. This is the first confirmed published report of a species of *Metacyclops* in North America, although the genus is widespread in tropical and temperate regions of other continents including Europe and Asia (Reid, 1991). *Metacyclops cushae* was found at only three localities in greater New Orleans, two grassy sloughs and one ditch, all containing water only seasonally.

The eighth species of probable tropical origin is *Mesocyclops ruttneri*, which is newly recorded for North America in this study. *Mesocyclops ruttneri* was originally described from a greenhouse in Austria, now destroyed; no wild populations are known to exist in Europe (Kiefer, 1981). Specimens of *M. ruttneri* were recently identified by Reid (1993) in samples from wild populations in China, Thailand, and Viet Nam, and the species is morphologically similar to several Asian congeners. It seems likely that *M. ruttneri* was introduced from Asia into both Austria and the southern United States. Specimens of *M. ruttneri* were collected in abundance from a permanent pond-like canal in New Orleans, and in rice fields in Louisiana and Mississippi. The species is obviously well established in the region.

This study confirms the supposition of Reid (1992) that the neotropical cyclopoid copepod faunal component in the southern United States is more significant than previously estimated. However, most of the cyclopoids of neotropical affinities present in southern Louisiana and Mississippi may be near the northern limit of their ranges. Most have been collected only sporadically, and are probably existing alongside rather than directly competing with members of the North American fauna. The only suggestion of competition in the available collection data is the apparent mutual exclusion of *Acanthocyclops vernalis* and *Mesocyclops ruttneri* in rice fields.

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TULANE STUDIES IN ZOOLOGY AND BOTANY

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LIFE HISTORY OF THE YAZOO DARTER (PERCIDAE: *ETHEOSTOMA RANEYI*), A SPECIES ENDEMIC TO NORTH-CENTRAL MISSISSIPPI

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LEAF-MINER DEFENSES IN *BROMELIA PINGUIN* L. (BROMELIACEAE) IN VERACRUZ, MEXICO

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OBSERVATIONS ON SOME FUNGI FROM LOUISIANA AND MISSISSIPPI IN COMPARISON WITH THOSE OF MEXICO

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SOME REALLOCATIONS OF TYPE LOCALITIES OF REPTILES AND AMPHIBIANS DESCRIBED FROM THE MAJOR STEPHEN H. LONG EXPEDITION TO THE ROCKY MOUNTAINS, WITH COMMENTS ON SOME OF THE STATEMENTS MADE IN THE ACCOUNT WRITTEN BY EDWIN JAMES

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LIFE HISTORY OF THE YAZOO DARTER (PERCIDAE: *ETHEOSTOMA RANEYI*), A SPECIES ENDEMIC TO NORTH-CENTRAL MISSISSIPPI

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Abstract

The Yazoo darter, *Etheostoma raneyi*, is restricted to tributaries of the Little Tallahatchie and Yocona Rivers (Yazoo River drainage) in north-central Mississippi. The species inhabits small, clear streams, many of which are spring-fed, and have a variety of substrate types including silt, clay, sand and gravel. In Morris Creek, a second-order stream in Lafayette County, Mississippi, *E. raneyi* was found in a diversity of microhabitats. *Etheostoma raneyi* is short-lived, with very few individuals living more than two years. Yazoo darters are sexually dimorphic, with males larger and more brightly colored than females. Both sexes become reproductively mature during the first year of life. The sex ratio of the Morris Creek population is female-biased. Like other members of subgenus *Nanostoma*, Yazoo darters use the egg-attaching spawning strategy. Batch fecundity of Yazoo darters is 52, and the average diameter of ova in this size class is 1.05 mm. Based on gonadal condition, the spawning season lasts from March to June. Yazoo darters are the most abundant fish in Morris Creek.

Introduction

Etheostoma raneyi is one of eight species of subgenus *Nanostoma* (snubnose darters) described since 1991, bringing the number of described species to 20. Additional species await scientific description. Snubnose darters are relatively short-lived, small, sexually dichromatic fishes that use the egg-attaching spawning strategy (Page, 1983). Most species inhabit flowing pools and riffles of small streams (Suttkus and Etnier, 1991). At least three species of subgenus *Nanostoma* are considered imperiled (Williams et al., 1989), due in part to their limited distributions. The restricted range and lack of life-history information for many species of subgenus *Nanostoma* have concerned conservationists. The objective of this study is to provide life history information necessary for protection of the Yazoo darter and to compare with life histories of other species of *Nanostoma*.

Most snubnose darters occur in southern tributaries to the Ohio River, Gulf Coastal drainages east of the Mississippi River, and lower Mississippi tributaries (Suttkus and Etnier, 1991). Many are endemic to single drainages or have limited geographical distributions (Boschung et al., 1992). The Yazoo darter (*Etheostoma raneyi* Suttkus and Bart) is endemic to small streams of the upper Yazoo River drainage, Mississippi (Figure 1). Suttkus et al. (1994) reported the species from 15 sites (five in the Yocona River and ten in the Little Tallahatchie), while

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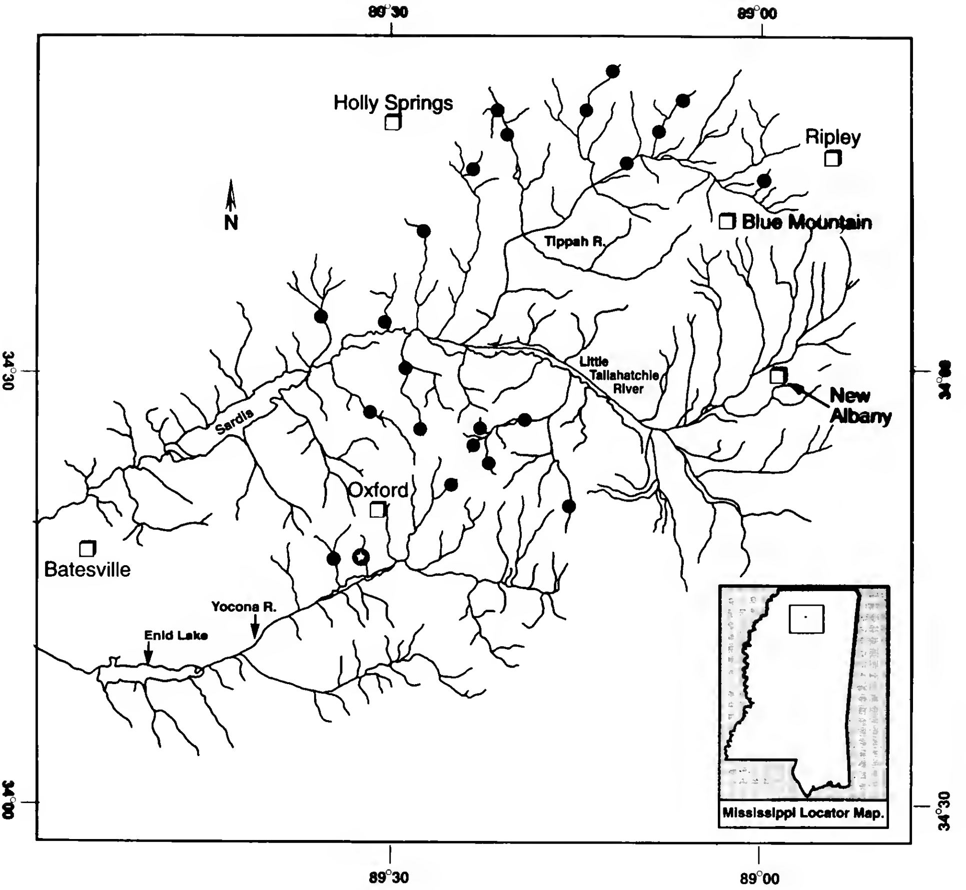

Figure 1. Distribution of *Etheostoma raneyi*. Study site is indicated by a star (modified from Thompson and Muncy, 1985).

in an unpublished status report Thompson and Muncy (1985) reported the Yazoo darter from 23 sites. Six sites listed by Suttkus et al. (1994) were not cited by Thompson and Muncy (1985), suggesting that the species may be found present at 29 sites.

STUDY SITE

Morris Creek is a clear, second-order stream that drains forested and agricultural lands for approximately 6.5 km before draining into the Yocona River. The study area is 3.2 km northeast of Taylor, Mississippi (T9S, R3W, sec. 16, 19 and 20) (Figure 1). At the study site the stream averages 3 m in width and has pool, riffle, and run habitats, and abundant woody debris. Substrates include clay, silty sand, coarse sand, gravel, and cobble. A narrow riparian zone is present, but much of the surrounding land is used for row crops or pasture. Yazoo darters used for spawning observations were collected from two streams: Lee Creek and an unnamed tributary to Bay Springs Branch, both of the Little Tallahatchie drainage, Lafayette County, Mississippi. The tributary to Bay Springs Branch is within the University of Mississippi Biological Field Station (T7S, R2W, sec. 34); its average width is approximately 1.5 m, and the dominant substrate is sand. Woody debris and submerged aquatic vegetation (primarily *Sparganium*) are common. Lee Creek (T7S, R3W, sec. 1) averages 3 m in width and substrates include clay, silty sand, coarse sand, gravel, and cobble. Woody debris is common, and much of the surrounding land is forested.

MATERIALS AND METHODS

Yazoo darters were collected monthly from March 1993 to May 1994; two samples per month were made March-May 1994. All sampling was done using a three-meter-long minnow seine, and an effort was made to sample a wide variety of microhabitats. A general description of habitat type (run, riffle, pool, or undercut bank) was made for all seine hauls. At every location where a Yazoo darter was collected, the following habitat variables were measured: water depth and velocity (average of three measurements of each), substrate composition (percent composition by particle size, estimated by the modified Wentworth scale outlined in Ross et al., 1990), stream width, percent canopy cover, and the percent and make-up of instream cover. The identity and abundance of other species of fishes collected was recorded for all seine hauls. Exceptions are for species of *Fundulus* and *Erimyzon* that were not identified to species in the field. For the purpose of Table 1, species of *Lepomis* and *Micropterus* were lumped. Specimens of Yazoo darters were preserved in 5% buffered formalin; other fishes were released.

Homogeneity of distribution of darters among the five habitat types was evaluated using R × C G-tests of independence (Sokal and Rohlf, 1981). The relationship between darter density and habitat type was further explored using principal components analysis (PCA) with Varimax rotation, using the SYSTAT software package (Wilkinson, 1990). A scree test indicated the number of meaningful components. Standardized factor scores for all combinations of components were plotted and numbers of darters were overlaid on the factor score plots. This two-step procedure does not assume linearity between abundance of fishes and environmental variables and is appropriate for these data (Ross et al., 1987; Ross et al., 1990).

Sex, standard length (SL), and age of preserved darters were determined in the laboratory. Standard length was measured to the nearest 0.1 mm using dial calipers. Age was determined to the nearest month by counting scale annuli. April was used as month zero, since it is near the middle of the spawning season. Scales for age analysis were removed above the lateral line and near the tip of the depressed pectoral fin.

Seasonal changes in gonad mass for both sexes were quantified using gonadosomatic index (GSI). Gonads and eviscerated specimens were dried at 55°C for 24 hours and weighed to the nearest 0.001 gm. Gonadosomatic index was calculated by dividing gonad mass by adjusted somatic mass (mass of eviscerated specimen) and multiplying by 1000. The reproductive condition of males was classified as latent or mature by examination of testes. Latent testes were tiny strands of clear tissue; mature testes were enlarged and opaque. The reproductive condition of females was determined by examination of ovaries and their classification into one of six developmental stages according to Heins and Baker (1993): latent (LA), early maturing (EM), late maturing (LM), mature (MA), ripening (MR), or ripe (RE). Five ova were counted and measured in each of the

TABLE 1. Relative abundance of occurrence of fishes in Morris Creek, Lafayette County, Mississippi, 1993-1994 (n=12 samples). Fishes were identified in the field and released; fishes in the genera *Lepomis*, *Micropterus*, *Fundulus* and *Erimyzon* are lumped for the purpose of this table (see text for explanation).

Etheostoma raneyi	.207	*Semotilus atromaculatus*	.036
Cyprinella camura	.168	*Erimyzon* spp.	.021
Percina sciera	.102	*Etheostoma whipplei*	.018
Fundulus spp.	.168	*Micropterus* spp.	.012
Noturus phaeus	.079	*Hypentelium nigricans*	.010
Pimephales notatus	.073	*Etheostoma proeliare*	.010
Notropis rafinesquei	.057	*Etheostoma parvipinne*	.003
Etheostoma lynceum	.040	*Etheostoma nigrum*	.002
Lepomis spp.	.040	*Pimephales vigilax*	.001
		Etheostoma swaini	<.001

three largest size classes for 43 females from seven samples taken during the breeding season (March-June 1993; March-May 1994). These size classes were distinct, and separated by at least 0.30 mm of diameter. The diameter of each ovum was expressed as an average of the smallest and largest diameters to account for irregularity in shape (as typical for many darter species, the eggs were concave in shape). Measurements were made using a dissecting microscope and ocular micrometer. Reproductive data were analyzed using the SYSTAT software package (Wilkinson, 1990).

Spawning mode was determined by observation of breeding activities in aquaria. Reproductively active males (identified by bright spawning coloration) and females (identified by distended abdomens containing ripe eggs) were collected from a tributary to Bay Springs Branch (1993 and 1994) and Lee Creek (1995) and transported to the laboratory. Animals were placed in 84 or 840 liter aquaria and maintained at 19-21°C. Aquaria contained the following substrates known to be used for spawning by other darter species: logs, plants and boulders (used by egg-attachers); gravel and sand substrate (used by egg-buriers); and cavities (used by egg-clumpers and egg-clusterers) (Page, 1985). Study animals were collected on 17 April 1993 (6 females, 3 males), 10 March 1994 (5 females, 4 males), and 25 March 1995 (2 females, 2 males); spawning usually occurred within two days of capture. Observations were made several times a day for 10 days following introduction into the aquaria. Observation periods were from 15 minutes to 2 hours. Spawning events were recorded with an 8 mm video camera. A total of seven spawning pairs were observed. The spawning description is based on the observations and from reviewing video tapes of spawning episodes. Five eggs from each spawning event were measured to the nearest 0.01 mm with a dissecting microscope and ocular micrometer.

RESULTS

Etheostoma raneyi was the most abundant fish in Morris Creek (Table 1). Other common fishes included bluntface shiner (*Cyprinella camura*), dusky darter (*Percina sciera*), topminnows (*Fundulus notatus* and *Fundulus olivaceous*), brown madtom (*Noturus phaeus*), and bluntnose minnow (*Pimephales notatus*). Other species of *Etheostoma* present in the stream included redfin darter (*Etheostoma whipplei*), cypress darter (*Etheostoma proeliare*), goldstripe darter (*Etheostoma parvipinne*), johnny darter (*Etheostoma nigrum*), brighteye darter (*Etheostoma lynceum*), and gulf darter (*Etheostoma swaini*) (Table 1).

TABLE 2. Occurrence of Yazoo darters (*Etheostoma raneyi*) among five habitat types in Morris Creek, Lafayette County, Mississippi. Data were pooled from 10 sample dates, 1993-1994.

HABITAT	NUMBER OF SAMPLES	NUMBER OF DARTERS	PERCENT WITH DARTERS
Run	52	23	44%
Swift riffle	74	30	41%
Moderate riffle	105	46	44%
Undercut bank	100	47	47%
Pool	55	37	67%

HABITAT. *Etheostoma raneyi* was a habitat generalist. Yazoo darters were evenly distributed among runs, swift riffles, moderate riffles, and undercut banks, but were slightly more common in pools (Table 2). Overall comparison of all five habitat types showed a significant association between habitat and darter occurrence ($G=11.00$, $p<0.03$, 4 df). However, when pools were dropped from the analysis, the result became nonsignificant ($G=0.73$, $p<0.87$, 3 df). Principal components analysis of habitats associated with darter occurrence showed that darters were found in a wide range of habitat configurations (Figure 2). Similar overlays of darter density were made for all other combinations of factor plots, but no relationships were demonstrated. Three components explained 64% of the total variance (Table 3). Principal component I (factor I) ordinated darter occurrences along a gradient from deep sites with fine substrates and low velocity to shallow sites with coarse substrates and high velocity. Principal component II (factor II) ordinated occurrences along a gradient of sites with low instream cover and a high percentage of canopy cover to sites with high instream cover and a low percentage of canopy cover, while component III described an inverse relationship between stream width and water velocity.

DEMOGRAPHICS. Age and sex composition of the *E. raneyi* population in Morris Creek is shown in Table 4. Sex ratios were significantly female-biased in the age one class, and for the total sample. The oldest female was 45.5 mm SL and 34 months of age; the oldest male was 52.6 mm SL and 33 months of age. Mean length of males was longer (SL) (36.4 mm, SD=6.1) than females (34.5, SD=5.2) ($t=3.3$; $p<0.001$) in the total sample.

GROWTH. Growth of *E. raneyi* was rapid during the first months of life, declined between four and ten months of age, and leveled off after ten months (Figure 3). Standard length (mm) was positively correlated with age (months) for 129 males ($SL=19.484+18.388*\log X$, $r=0.7$, $p<0.01$) and 199 females ($SL=17.346+17.366*\log X$, $r=0.8$, $p<0.01$). By seven to nine months of age, mean length of males was greater than that of females (samples were lumped for these three months due to sample size) ($t=6.5$, $p<0.001$; mean SL males=39.46 mm, $n=19$; females=33.01 mm, $n=17$), suggesting that males grow faster than females do.

GONADAL DEVELOPMENT. All females >30 mm SL (8 months of age and older) and all males >34 mm SL (8 months of age and older) were reproductively mature in March of 1993 and 1994. Males developed intense breeding coloration (described by Suttkus et al., 1994) and mature testes in December (Figure 4). Some males had mature testes throughout the spring and early summer, but the testes of all males were latent by July. This prolonged period of reproductive readiness is supported by the gonadosomatic index (GSI) for males, which

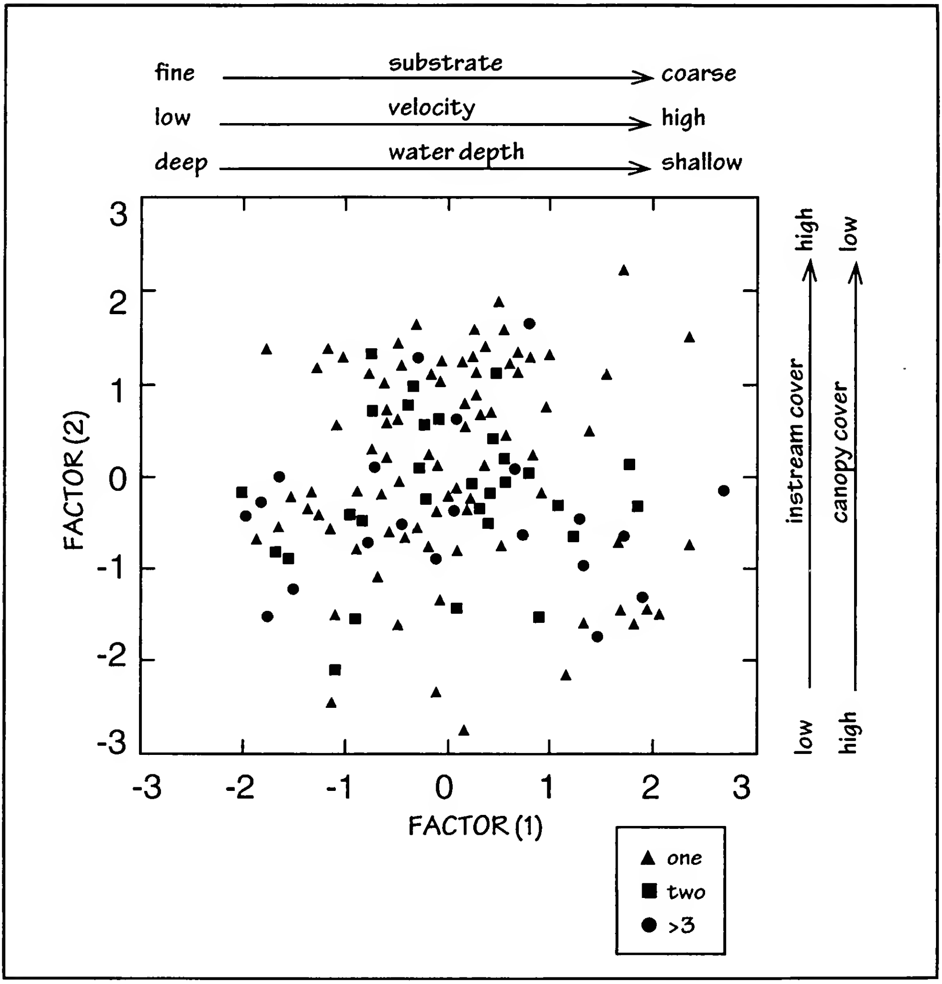

Figure 2. Overlay of numbers of *Etheostoma raneyi* samples on plot of standardized factor scores for Factor 1 and Factor 2.

increases during late winter, peaks in early spring, and declines in the summer (Figure 5).

Ovaries of females begin maturation in late fall, and some individuals have ripe ovaries by early spring (Figure 6). All ovaries are latent by July, similar to the pattern seen in males. The GSI for females also closely follows the pattern of development in males (Figure 5); the values of GSI are much higher in females than in males, illustrating the higher investment by females in ova.

Standard length was positively correlated with the GSI of males (r^2=0.183, $p<0.006$; GSI=5.455+3.074 SL) and of females (r^2=0.127, $p<0.002$; GSI=-1.351+0.238 SL) (Figure 7). There was also a relationship between SL and somatic weight for females (r^2=0.942, $p<0.001$; somatic weight=-0.441+0.017 SL),

TABLE 3. Variable loadings > 0.4 (loading value of 0.398 was retained) on three principal component axes, after varimax rotation. Percent variance explained by each component is given in parentheses.

	PRINCIPAL COMPONENT		
VARIABLE	I (26.0%)	II (19.0%)	III (18.5%)
Substrate	0.727		
Velocity	0.698		0.398
Depth	-0.665		
Cover		0.773	
Canopy		-0.694	
Width			-0.933

and for males ($r^2=0.942$, $p<0.001$; somatic weight=-0.666+0.023 SL) and males and females had virtually identical relationships between these variables (Figure 8).

By June, the number of ova in all size classes decreases (Figure 9). Peak numbers were seen in early spring, corresponding to peak GSI values and percentages of ripe ovarian stages. The mean number and diameter of ova in the three largest size classes for 43 females sampled during the breeding season are, from largest to smallest: 52 (SD=20), 1.05 mm (SD=0.11); 80 (SD=35), 0.74 mm (SD=1.10); 303 (SD=129), 0.38 mm (SD=0.03). Both the number and diameter of ova increased with standard length ($r^2=0.480$, $p<0.001$; number=64.732+3.243 SL; $r^2=0.376$, $p<0.001$; diameter=0.524+0.014 SL) (Figure 10).

SPAWNING BEHAVIOR. Male Yazoo darters are nonterritorial, but display aggression toward conspecific males when a male engaged in courtship or spawning is approached by another male. Males react by chasing the intruder, or performing stationary lateral displays with erect fins. No elaborate courtship displays were observed in this species. Prior to spawning, males typically pursue females as they move about the substrate selecting a spawning site. When a female is receptive, the male mounts her back with his caudal peduncle to her side. The pair then vibrate as the female attaches an egg to the spawning substrate. Eggs are usually attached singly to the substrate. Of the 29 episodes observed, 18 (62%) eggs were attached to a submerged log, 6 (21%) to plants or plant roots, 3 (10%) to the gravel substrate, and 2 (7%) to large rocks. The average diameter of five eggs removed from an aquarium was 1.28 mm. Typically, a single pair spawned numerous times in succession, but not all mountings

TABLE 4. Age and sex composition of Yazoo darters from Morris Creek, Lafayette County, Mississippi, 1992-1993.

	AGE GROUP				
	0	1+	2+	3+	TOTAL
Male	71	49	8	1	129
Female	82	106	11	0	199
Total	153	155	19	1	328
χ^2	0.79, p=0.3	20.90, p<0.001	0.47, p=0.49		14.94, p<0.001
Sex ratio (female:male)	1.2:1	2.2:1	1.1:1		1.5:1

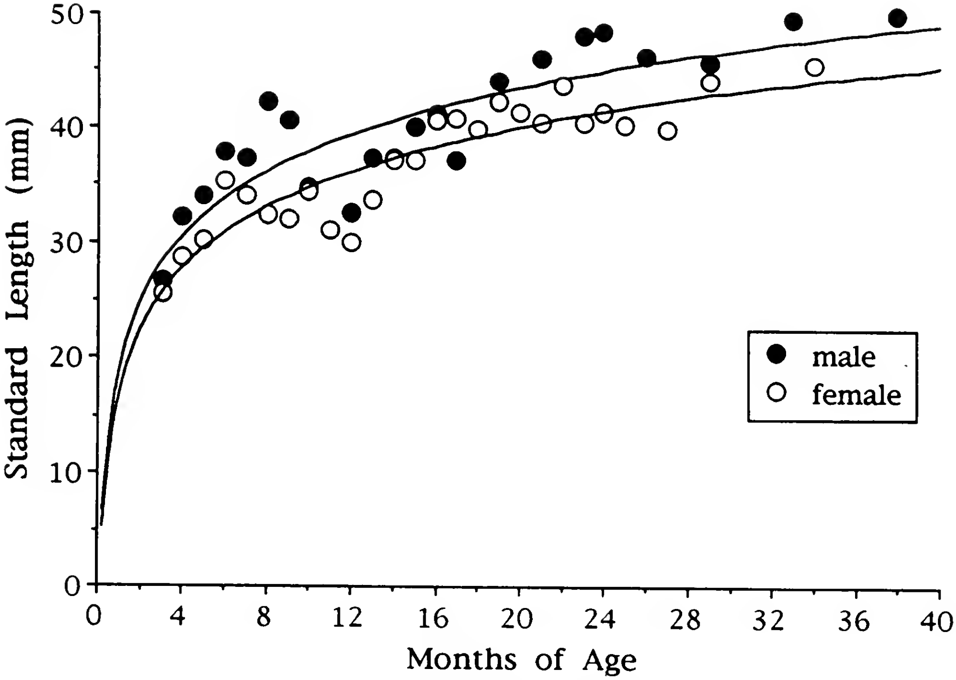

Figure 3. Growth curves for males and females of *Etheostoma raneyi*. Points represent sample means.

resulted in the release of an egg. Males and females were promiscuous, and no parental care was provided to the eggs.

DISCUSSION

The Yazoo darter (*Etheostoma raneyi*) is one of 20 described species of snubnose darters, subgenus *Nanostoma* (Page, 1981). Typical habitat of most adults of subgenus *Nanostoma* was described by Page and Mayden (1981) as clean pools with moderate current and bedrock, cobble or gravel substrate. Exceptions among upland *Nanostoma* species are *Etheostoma etnieri*, which prefers riffles and runs (Bouchard, 1977), *Etheostoma zonale*, which inhabits rocky, vegetated riffles (Page and Mayden, 1981), and *Etheostoma coosae*, which occurs in all stream mesohabitats (riffles, runs, pools) over gravel or cobble substrate (O'Neil, 1981). Habitat descriptions of *Nanostoma* species found in lowland streams reflect the physical characteristics of these streams, which usually have sand and gravel substrates and low to moderate gradients. *Etheostoma zonistium*, a lowland species, occurs predominantly in stream margin habitat with sand or sand and gravel substrate, and is found less frequently in run and riffle habitat (Carney and Burr, 1989). *Etheostoma pyrrhogaster* is found in stream margin, pool, run and riffle habitat over sand substrate (Carney and Burr, 1989). *Etheostoma raneyi* is also found in lowland streams, and like *E. coosae* (O'Neil, 1981) and *E. pyrrhogaster*, is found in all habitats. Our analysis showed that *E. raneyi* individuals were evenly distributed among runs, swift riffles, moderate riffles and undercut banks, but were slightly more common in pools. However, higher darter density

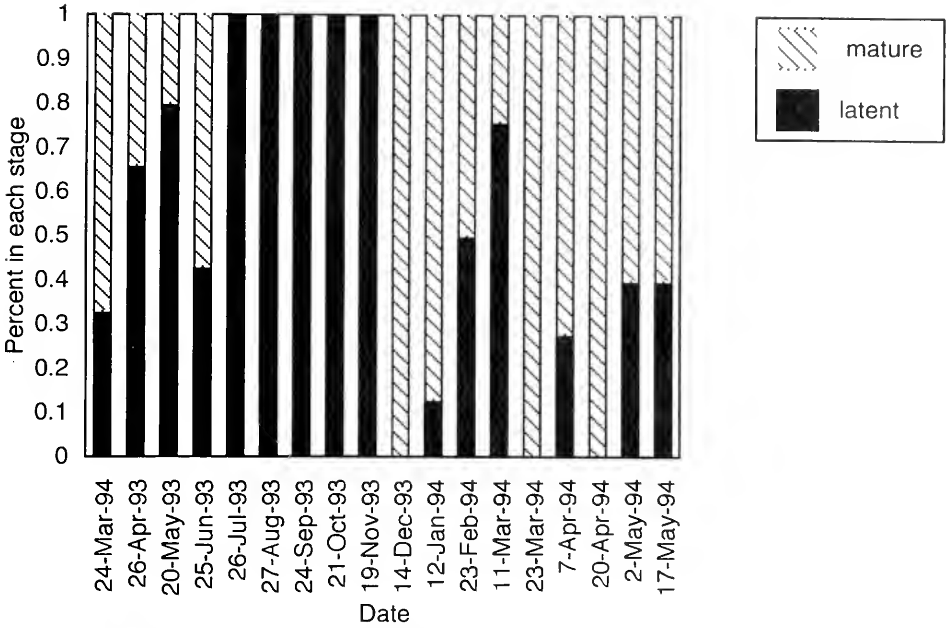

Figure 4. Monthly changes in testicular development of *Etheostoma raneyi* males.

in any particular habitat was not demonstrated by the overlay of darter density on plots of PCA factor scores. *Etheostoma raneyi* was the most common species in Morris Creek, and was found in most seine samples that had fishes. Similarly, Carney and Burr (1989) found that *E. zonistium* was the most common species found in West Fork Clarks River, Kentucky.

Like other species in the snubnose group, Yazoo darters are short-lived, with very few individuals surviving more than two years (33-34 months). Some individuals of *E. zonistium*, *E. pyrrhogaster* and *E. coosae* live more than two years (Carney and Burr, 1989; O'Neil, 1981), while the maximum life span of *E. simoterum* is just 18 months (Page and Mayden, 1981). The longest life span reported for a *Nanostoma* species is for *E. zonale*, with individuals that survive more than three years (Lachner et al., 1950).

The sex ratio of *E. raneyi* is female-biased for age group one, and for the total sample. Female bias has been reported for components of populations of *E. coosae* (O'Neil, 1981), *E. simoterum* (Page and Mayden, 1981), and *E. zonistium* (Carney and Burr, 1989), and may be caused by differential mortality in the brightly colored males (Carney and Burr, 1989).

As reflected by higher GSI, female *E. raneyi* invest more than males do in gonadal tissue. This is typical of most fishes (Moyle and Cech, 1988), and suggests that females invest more in reproduction. However, male investment in reproduction could be manifested not only in gonadal tissue, but in sexually selected traits as well. In many species, larger males have a reproductive advantage over smaller males, due to intrasexual competition for females or female choice for larger males. This size difference could be manifested in greater length (SL) of males or in greater somatic weight. In *E. raneyi*, males do not invest more than females in somatic weight, but achieve longer lengths (SL), as

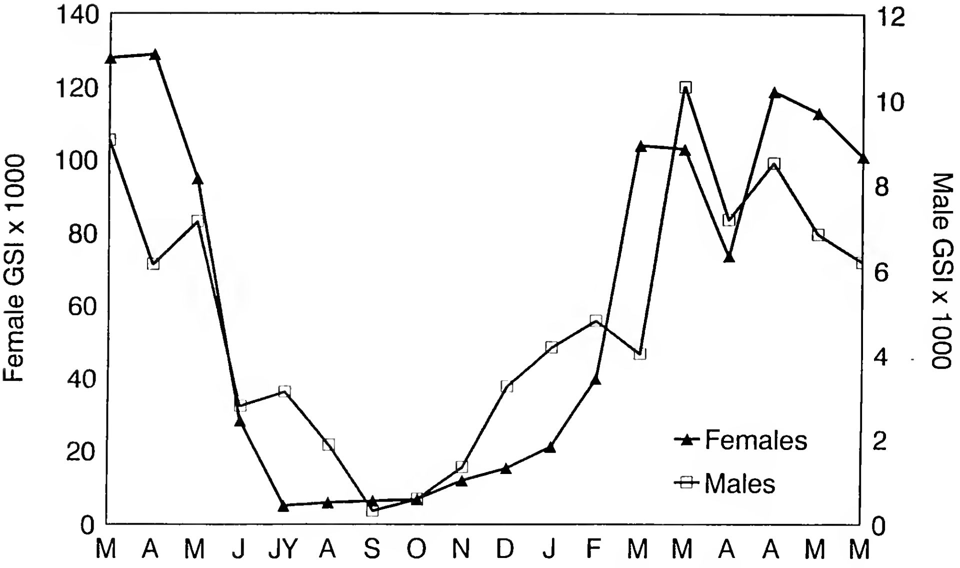

Figure 5. Monthly changes in mean gonadosomatic index of *Etheostoma raneyi* males and females.

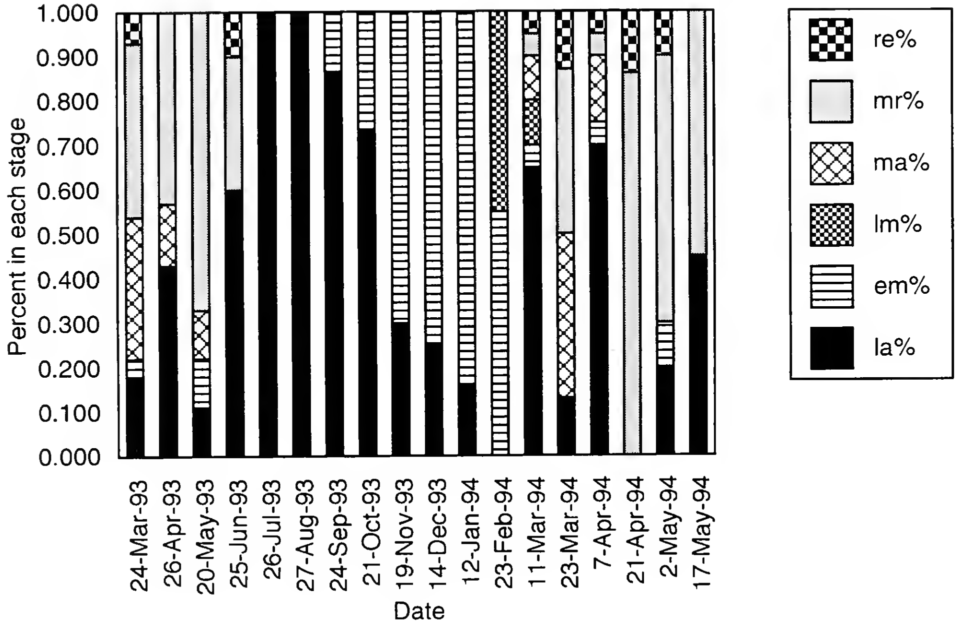

Figure 6. Monthly changes in ovarian development of *Etheostoma raneyi* females. Ovarian stages are latent (la), early maturing (em), late maturing (lm), mature (ma), and ripe (re).

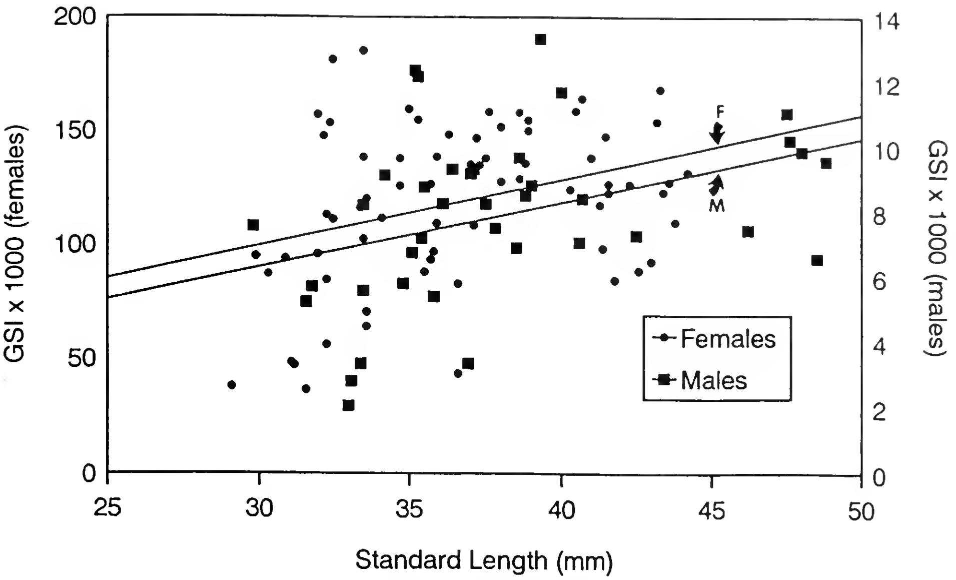

Figure 7. Relationship between standard length (SL) and gonadosomatic index (GSI) for *Etheostoma raneyi* males and females.

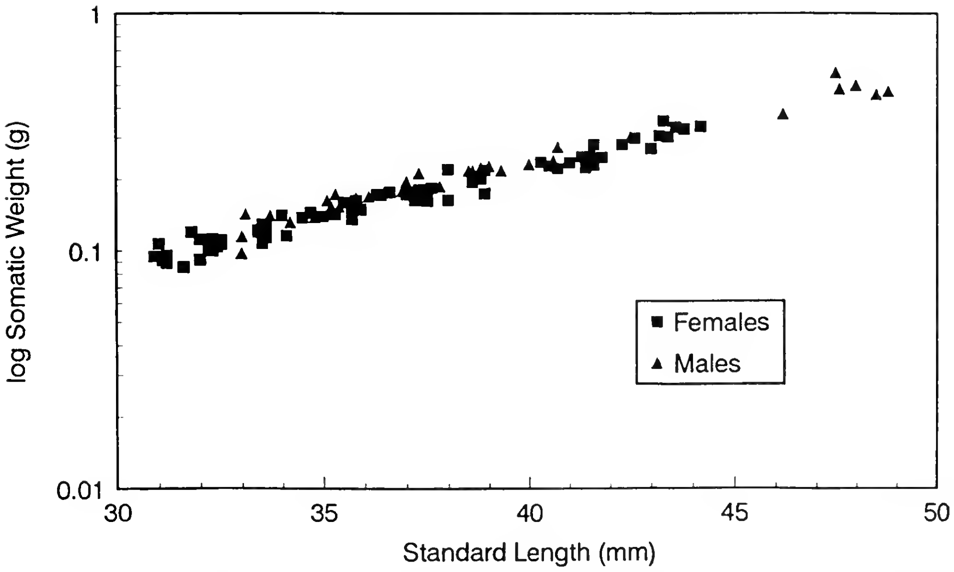

Figure 8. Relationship between standard length (SL) and somatic weight for *Etheostoma raneyi* males and females.

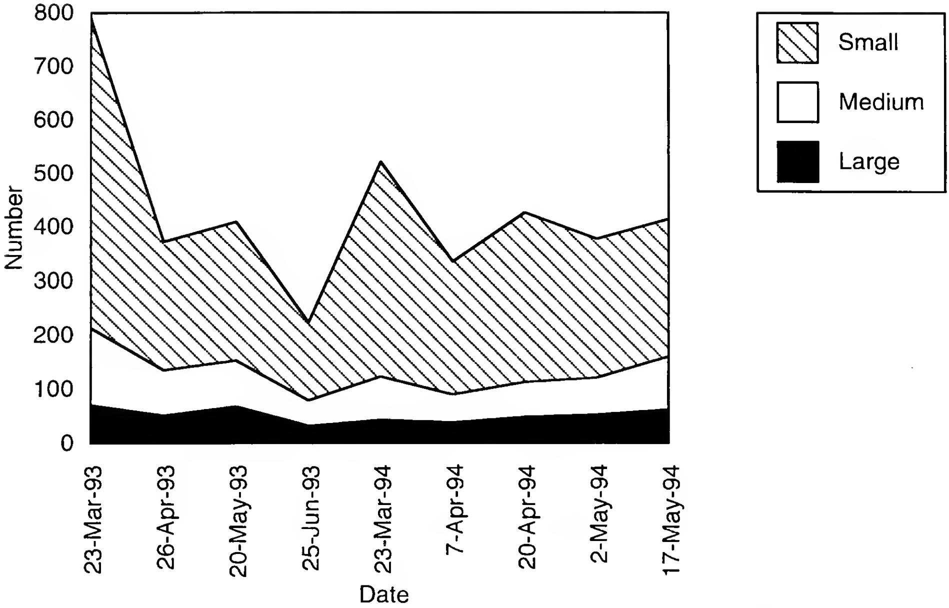

Figure 9. Changes in the number of ova in the three largest size classes of *Etheostoma raneyi* females during the 1993 and 1994 breeding seasons.

in other *Nanostoma* species (Page and Mayden, 1981; Carney and Burr, 1989). If males expend more energy than females do on courtship and aggression during the breeding season, males would be predicted to lose more somatic weight during that time. This is not suggested by our data, but our samples were lumped over the duration of the breeding season, and may not reveal such subtle relationships. Males also invest in bright breeding colors that are undoubtedly the result of sexual selection, although this has yet to be tested for darters. Bright colors may be responsible for differential mortality in males due to predation, and this could also be viewed as a cost of reproduction. More research on reproductive investment in darters is needed before an apparent differential investment by the sexes is understood.

The spawning period for *E. raneyi* is from March through June. A relatively long spawning season is also found in *E. pyrrhogaster* and *E. zonistium* (Carney and Burr, 1989), and in *E. rafinesquei* (Weddle and Burr, 1991). April has been reported as the peak spawning season for *E. barrenense* and *E. rafinesquei* (Stiles, 1974; Page and Burr, 1982), *E. coosae* (O'Neil, 1981), and *E. simoterum* (Page and Mayden, 1981).

Comparing the fecundity and diameter of ova for fishes is difficult, due to differences in methodology among studies. The mean number of ova in the largest size class, or batch fecundity, of female *E. raneyi* was 52 (n=43 females), and the mean diameter of these ova was 1.05 mm. The mean batch fecundity of *E. rafinesquei* is 48.3 (Weddle and Burr, 1991).

Etheostoma raneyi shares the egg-attaching spawning strategy with all other species of *Nanostoma* for which spawning behavior is known (Page, 1985; Keevin et al., 1989). These species exhibit no parental care, and deposit eggs in small

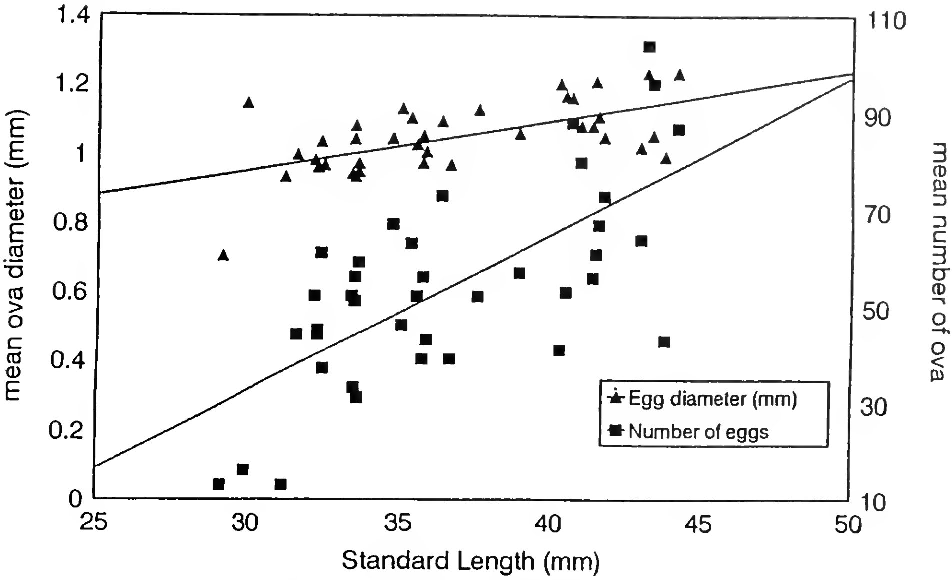

Figure 10. Relationship between number and diameter of ova and standard length (SL) of *Etheostoma raneyi* females.

numbers. Male *E. raneyi* did not maintain territories associated with particular spawning substrates, but were aggressive to other males. Such moving territories were also observed in *E. barrenense* and *E. rafinesquei* (Stiles, 1974), *E. simoterum* (Page and Mayden, 1981), *E. flavum* (Keevin et al., 1989), and apparently *E. pyrrhogaster* and *E. zonistium* (Carney and Burr, 1989). Page (1983) proposed that the egg-attaching strategy provided some protection from egg predation. This tendency to place the eggs in several places probably precludes economic defensibility of any given spawning substrate and, as a result, territoriality is not seen in these species.

Although *E. raneyi* has a limited distribution, within its range it can be the most common species, and does not appear to be in danger of extinction. However, individual populations of *E. raneyi* should be carefully monitored, because the small streams that are typical habitat for the species are often targeted for habitat alteration, or are degraded by poor land use. For a species with a limited distribution, the loss of several populations and resulting fragmentation of the species' range could quickly lead to imperilment. With *E. raneyi*, monitoring and habitat protection could alleviate retroactive recovery efforts currently needed for other species of subgenus *Nanostoma*.

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LEAF-MINER DEFENSES IN *BROMELIA PINGUIN* L. (BROMELIACEAE) IN VERACRUZ, MEXICO

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Abstract

Leaf-miners are present on leaves of all adult sexually reproducing individuals of *Bromelia pinguin* (Bromeliaceae), but not on leaves of vegetatively reproducing or immature individuals; thus, we hypothesized that there should be differences in defenses between them. No differences were found when we compared metabolic contents, humidity, and nitrogen of mined and unmined leaves, but found significant differences in ash, fiber and lipid contents. Mined leaves had more fiber and lipids and less ash than unmined leaves, but differences may exist only during a short period of time and were not detected by our research. The leaf-miner *Melanagromiza* sp. (Diptera: Agromizidae) attacks leaves with the highest fiber contents. Cited research is on trees and their seedlings, but results could differ in large clonal plants where metabolites move between ramets. The response of leaf-miners could be to a combined series of factors other than food quality or the amount or type of defenses, such as a plant-herbivore-parasitoid complex.

Introduction

Plants cover most of the Earth's surface, and even though subject to varying degrees of herbivory by a diversity of organisms, they are not eliminated because, among other things, they ensure their own defense (Crawley, 1983; Howe and Westley, 1988; Thompson, 1982; Weis and Berenbaum, 1989). Plant defenses include mechanical protection on the surface of the plant, complex polymers or silica crystals that reduce plant digestibility, and plant toxins that kill or repell herbivores at very low concentrations (Coley and Aide, 1991; Howe and Westley, 1988; Rico-Gray, 1989). There are large differences among plant species in both the amount and type of anti-herbivore defense toxins in their leaves (Coley, 1988). Defenses against herbivory should be allocated in direct proportion to the tissue or plant part that confers the greatest fitness to the individual plant (Dirzo, 1984). Plant defenses change with time (e.g., leaves toughen as they mature, and sometimes potent toxins in young leaves are replaced by lignified or silicified tissues in older leaves and twigs), and virtually all plants and plant shoots become less palatable as they mature (Dirzo, 1984; Howe and West-

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ley, 1988). In general, young leaves are more vulnerable to herbivores than are mature leaves (Coley and Aide, 1991), and leaf-miners have been found to be more abundant on seedlings in comparison with mature plants of the same species (Godfray, 1985).

In a tropical dry forest on the coast of Veracruz, Mexico, the leaf-miner *Melanagromiza* sp. (Diptera: Agromizidae) was present on leaves of all adult, sexually reproducing individuals of *Bromelia pinguin* L. (Bromeliaceae), whereas, leaves of vegetatively reproducing or immature individuals did not have leaf-miner tunnels. *Bromelia pinguin* is monocarpic, dying slowly after fruiting, usually leaving a living offshoot (García-Franco and Rico-Gray, 1995). We hypothesized that there should be differences in defenses between dying, sexually reproducing individuals, and younger, non-sexually reproducing individuals. Plants of *B. pinguin* present many features considered to be protection against herbivores. The straplike leaves are highly fibrous, they have hard pointed tips, with sharp hooked thorns on their margins, and thick cuticles (García-Franco and Rico-Gray, 1995; Hallwachs, 1983). Leaves of *B. pinguin* also have flavonoids (penduletine, cirsimaritine, casticine), ferulic acid, diterpenoids derivated from filoctadone (3-oxofilocladan-16-ol, filocladan-16α-diol, 3-oxopimar-15ene-7β, 8β-diol), sterols (estigmasterol, β-sitosterol, β-D-glucositosterol), and β-D-glucopiranose (Chávez-Gallardo, 1993, and references therein). Despite this range of defenses, the plants are subject to attack by different organisms (Table 1); in particular a leaf-miner, the larva of a fly, *Melanagromiza* species.

STUDY SITE

Field work was conducted in a lowland tropical deciduous forest at Centro de Investigaciones Costeras La Mancha (CICOLMA) on the coast of the state of Veracruz, Mexico (19° 36' N, 96° 22' W; altitude <50 m). Annual precipitation varies greatly (1100-1700 mm), but most falls between June and September, and mean temperature is 22°-26°C (minimum 10°C, maximum 38°C; García-Franco and Rico-Gray, 1995). *Bromelia pinguin* inhabits the sandy understory of the tropical dry and deciduous forests, which have a relatively simple structure and composition, with tree species such as *Bursera simaruba* (L.) Sarg. (Burseraceae), *Brosimum alicastrum* Swartz (Moraceae), *Enterolobium cyclocarpum* (Jacq.) Griseb. (Leguminosae), *Cedrela odorata* L. (Meliaceae), *Ficus cotinifolia* Kunth (Moraceae), and shrub species such as *Nectandra coriacea* (Sw.) Griseb. (Lauraceae), and *Coccoloba barbadensis* Jacq. (Polygonaceae) (Blain, 1988; Blain and Kellman, 1991).

TABLE 1. Herbivores observed on *Bromelia pinguin* and the plant structure affected at La Mancha, Veracruz, Mexico during the period of April 1989-March 1991.

Leaf:	(larva) *Melanagromiza* sp. (Diptera:Agromyzidae) (larva) *Mandura quinquemaculata* (Lepidoptera:Sphingidae) (adult) *Gecarcinus lateralis* (Decapoda:Brachyura)
Spike:	(ant-tended) Membracidae (Homoptera)
Fruit:	(larva) Drosophilidae, Sarcophagidae (Diptera) (larva) Lepidoptera
Seed:	(adult) *Gecarcinus lateralis*
Seedling:	(adult) *Gecarcinus lateralis*

Materials and Methods

Bromelia pinguin is a terrestrial plant in dry habitats from Mexico to Venezuela and on the Caribbean Islands, from sea level to 780 m elevation (Hallwachs, 1983; Smith and Downs, 1979). Serial monocarpy or sympodial dichotomy (Benzing, 1980), sexual reproduction, and clonal growth are present in its life cycle. In CICOLMA it forms dense patches or subpopulations (demes) on sandy soils in deciduous forest. Flowers are present for a few days during the dry season (March-April). Butterflies and hummingbirds (*Amazilia beryllina*, *Cyranthus latirostris*: Trochilidae) are the main flower visitors (García-Franco and Rico-Gray, 1995). Although a high fruit set with abundant seeds is produced every year, seed and seedling predation by red land crabs (*Gecarcinus lateralis* Frem.) is so high that few genets are recruited (García-Franco et al., 1991).

Plant material was collected between August and September of 1989, air dried and sent to the laboratories (5 kg dry weight each of mined and unmined leaves to each laboratory). Collections were made just after peak rainfall, to avoid possible differences due to environmental stress. In general, herbivores use plants because either they are rich in nutrients (e.g., nitrogen, humidity content) or poor in defenses (physical or chemical); thus two types of analyses were needed. Ash, humidity, fiber, lipids, and nitrogen analyses were conducted at the Departamento de Química y Biología, Universidad de las Américas. Determinations were made in duplicate according to the methods in Horwitz (1980) with an error margin of 0.1-2.0%. Metabolic contents (MeOH extract), to test for allelochemicals, were analyzed with chromatography (HPLC) and visible UV light spectrum at the Departamento de Farmacía, Facultad de Química, U.N.A.M. (Chávez-Gallardo, 1993). Insects were collected throughout the study period (April 1989-March 1991).

Results

No differences in metabolic contents were found when mined and unmined leaves were compared (Figure 1). We did not find significant differences when humidity (ANOVA, $F_{(1,2)}=1.22$, $p>0.384$) and nitrogen (ANOVA, $F_{(1,2)}=9.9$, $p>0.088$) contents were compared between mined and unmined leaves (Figure 2). On the other hand, we found significant differences in the percent of ash (ANOVA, $F_{(1,2)}=54.366$, $p<0.018$), fiber (ANOVA, $F_{(1,2)}=16.341$, $p<0.05$), and lipid (ANOVA, $F_{(1,2)}=133.031$, $p<0.007$) contents, between mined and unmined leaves. Mined leaves had more fiber and lipids, and less ash than did unmined leaves (Figure 2).

Discussion

Leaf-miners attack leaves on old and decaying *Bromelia pinguin* plants: the toughest leaves, the ones with the highest fiber content. We found no differences in nitrogen or water content, or in secondary compounds, between leaves in young and old plants, unless the higher lipid contents of older leaves is attractive to miners.

Coley (1987) found that in *Cecropia*, herbivores show significant preference for leaves from larger plants, suggesting that leaf defenses decrease with plant size or age. Cooke et al. (1984) demonstrated that young leaves of several tree species have more toxins and less nutritive value than do mature leaves. How-

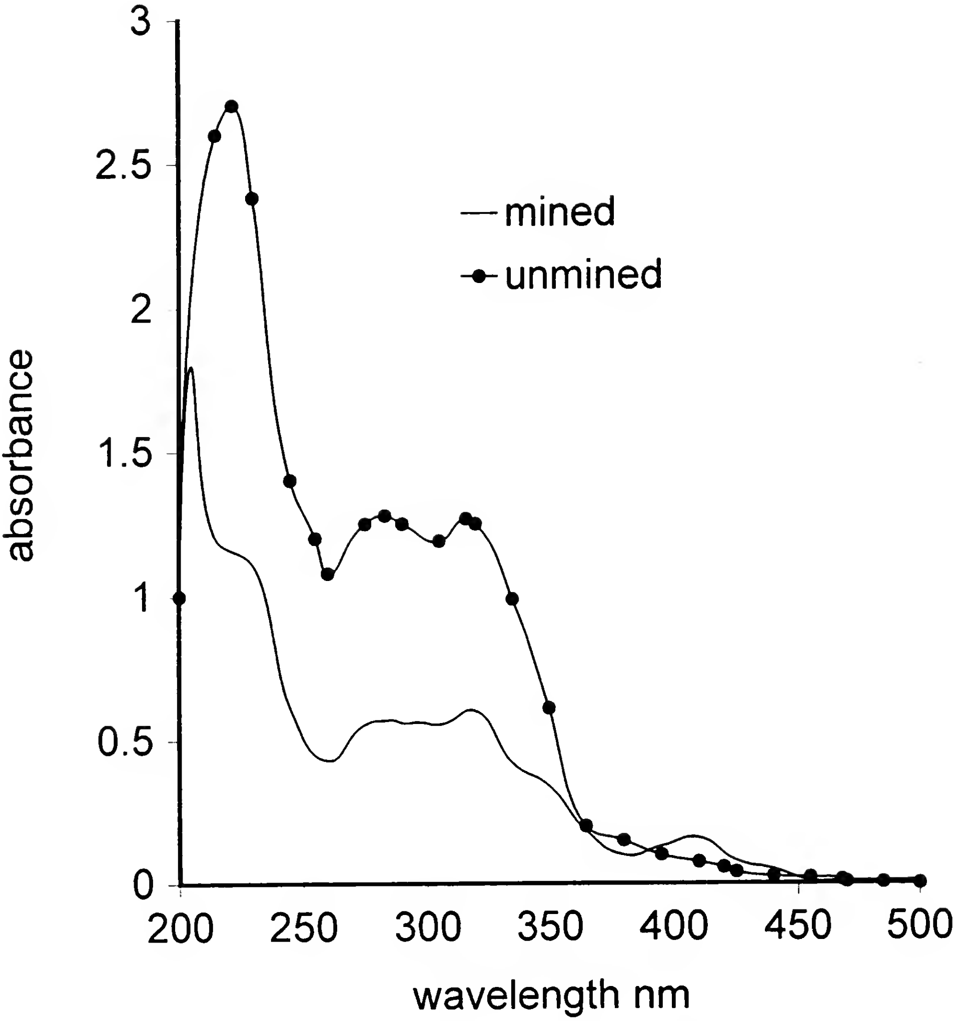

Figure 1. Ultraviolet spectra of the methanolic extract of *Bromelia pinguin* for mined and unmined leaves.

ever, the response of leaf-miners could also be to a combination of factors other than food quality or the amount or type of defenses.

Flowering and fruiting by *B. pinguin* may act as a mating cue for adults of the *Melanagromyza* fly. Female flies oviposit on the leaves of decaying plants, whereas their offspring develop during the warm-humid portion of the year. The mating time and ovipositing behavior of adult *Melanagromyza* flies could be a response to an absence of predators or parasitoids. Instead of a direct response to plant phenology, *Melanagromyza* flies might be influenced by a plant-herbivore-parasitoid complex (Price et al., 1980, 1986), or fly behavior may be influenced by wasp activity patterns (Thompson, 1994).

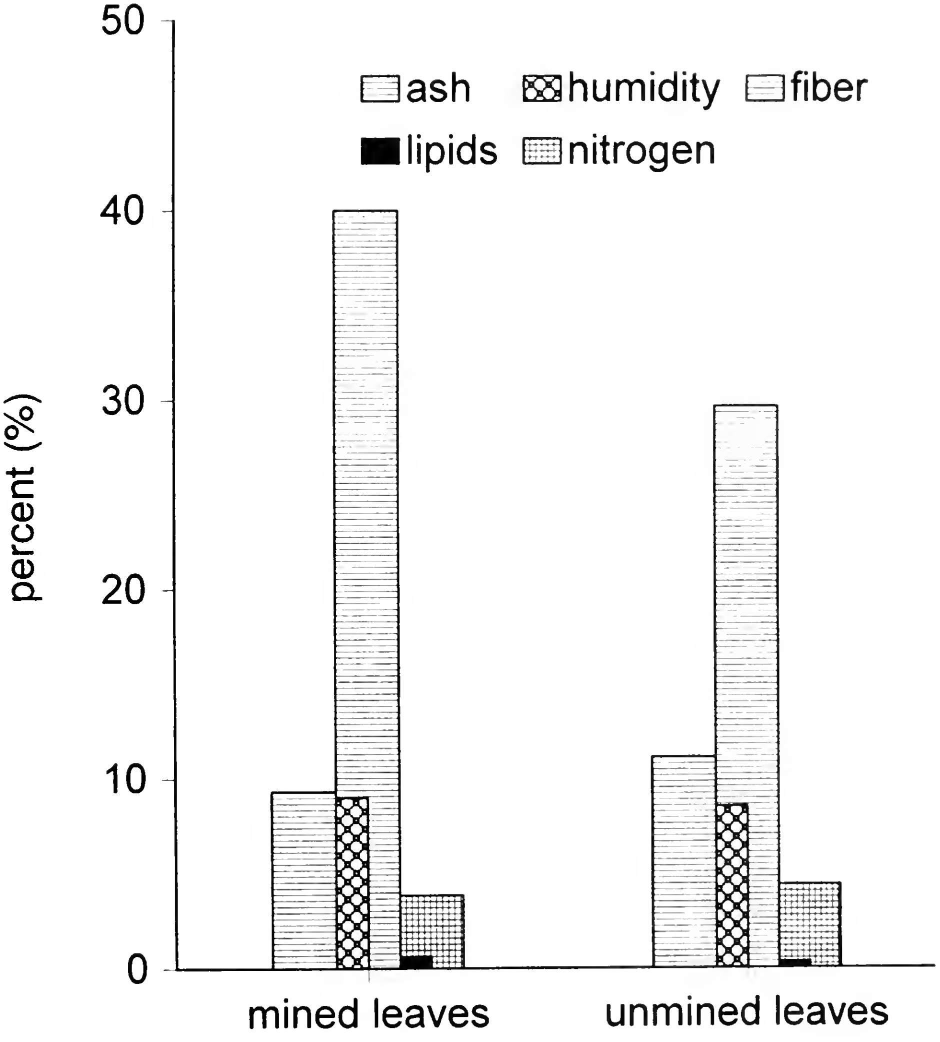

Figure 2. Percent contents of ash, water, fiber, lipids, and nitrogen for mined and unmined leaves of *Bromelia pinguin*.

In certain situations, a heavy attack by leaf-miners could be considered beneficial because it increases the chance of leaf abscision and elimination of miners (Simberloff and Stiling, 1987). The effect of leaf-miners on *B. pinguin* should be negligible because the attack is on dying leaves whose main compounds already should have been relocated to offshoots, fruits, and seeds (Jackson et al., 1985). Leaf-miners were only found in decaying individuals, but mined and unmined leaves did not differ in secondary metabolites.

The question remains: Why are only the decaying individuals attacked? The response of a plant to attack from herbivores or pathogens depends in part on its condition, and in part on its inherited ability to relocate resources. If serious stress diverts energy from chemical defense, plants or even parts of plants weakened by shade, disease, poor soil, or recurrent defoliation may be vulnerable to herbivory (Howe and Westley, 1988). In our example, old plants ("mother plants") could be weakened as a result of relocation of metabolic products to offshoots ("daughters") and fruits (Cook, 1985; Pitelka and Ashmun, 1985). Finally, much work has been done on the effect of certain metabolic products (e.g., tannins) and nitrogen levels on insect growth and food preferences, with conflicting results (Cooke et al., 1984). Although our results do not show major differences between mined and unmined plants, differences may exist during a short period of time, but were not detected by our research. Also, cited research is on trees and their seedlings, and results could differ in large clonal plants, where metabolites move between ramets.

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OBSERVATIONS ON SOME FUNGI FROM LOUISIANA AND MISSISSIPPI IN COMPARISON WITH THOSE OF MEXICO

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Abstract

Forty species of fungi (2 Ascomycotina, 37 Basidiomycotina, and 1 lichen) were collected during several field trips carried out in Louisiana and Mississippi. The discussion of these species emphasizes their distribution in Mexico, mainly in mesophytic forests, a type of vegetation with strong similarities to the eastern deciduous forests of the U.S.A. *Psilocybe pseudobullacea* is recorded from the U.S.A. for the first time, and *P. tampanensis* and *P. cubensis* are new records from Mississippi or Louisiana.

Introduction

Many species of fungi found in the eastern U.S.A. also occur in the tropics, subtropics, and high mountains of Mexico (Sharp, 1948; Welden and Lemke, 1961; Guzmán, 1973). During a summer foray organized by the Gulf States Mycological Society (12-19 June 1995) in Mississippi, and some independent trips in Louisiana, several fungi were found that are common to both countries. These are discussed.

Fungi Considered

Table 1 shows the forty species discussed here, of which twenty were gathered by the author and deposited in the herbarium of the Institute of Ecology (XAL) at Xalapa, Veracruz, Mexico. These fungi were found in five localities (Table 2). Two of these are covered by forests, two are deposits of sugarcane bagasse, and the fifth consists of the gardens and streets of New Orleans.

Observations on the Species

One of the two ascomycetes (Table 1) was *Hypomyces lactifluorum*. It is a common parasite of russulaceous fungi and distorts the basidiocarp and gives it a reddish orange color. The parasite is common in *Quercus*, *Pinus-Quercus*, and mesophytic forests of Mexico, and also occurs in the deciduous forests of eastern North America. This host-parasite combination is edible and quite common in Mexico where it is sold in markets under the name of "enchilado" or "hongo enchilado" (i.e., hot mushroom), because of its somewhat spicy taste. *Xylaria magnoliae* grows only on the fallen fruits of *Magnolia*, a tree common both to the deciduous forests of eastern U.S.A. and the mesophytic forests of Mexico. San Martin-González and Rogers (1989) reported this species from Mexico on fruits of *M. schiedeana* Schl. *Xylaria magnoliae* is closely similar to *X. persicaria* (Schwein.:

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TABLE 1. Species of fungi considered. The numbers indicate the localities (Table 2). An asterisk indicates specimens deposited at XAL Herbarium.

ASCOMYCOTINA

Hypomyces lactifluorum (Schwein.: Fr.) Tul. (1)
**Xylaria magnoliae* J. D. Rogers (1)

BASIDIOMYCOTINA

Amanita hemibapha (Berk. & Broome) Sacc. (1)
Amanita rubescens (Pers.: Fr.) S. F. Gray (1)
Amanita vaginata (Bull.: Fr.) Vittad. (1)
Boletus edulis Bull.: Fr. (1)
Boletus pinophilus Pilát & Dermek (1)
Calvatia cyathiformis (Bosc) Morgan (1)
Calostoma cinnabarina Desv. (1)
**Cantharellus confluens* (Berk. & M. A. Curtis) Petersen (1)
**Cantharellus lateritius* (Berk.) Singer (1)
**Chlorophyllum molydites* (Meyer: Fr.) Mass. (3,4,5)
**Conocybe lactea* (Lange) Métrod (1)
**Craterellus odoratus* (Schwein.) Fr. (1)
Cymatoderma caperatum (Berk. & Mont.) Reid (2)
Ganoderma curtisii (Berk.) Murrill (1)
Hydnopolyporus fimbriatus (Fr.) Reid (1)
Lactarius hygrophoroides Berk. & Curt. (1)
Lentinus boryanus (Berk. & Mont.) Singer (1)
**Lepiota americana* (Peck) Peck (3,4)
**Microporellus obovatus* (Juhng.) Ryvarden (1)
**Panaeolus antillarum* (Fr.) Dennis (1)
**Perenniporia phloiphila* Gilb. & Blackwell (5)
**Pleurotus pulmonarius* (Fr.) Quél. (2)
**Pluteus cervinus* (Schaeff.: Fr.) Kumm. (1,4)
**Psilocybe cubensis* (Earle) Singer (1)
**Psilocybe pseudobullacea* (Petch) Pegler (3)
**Psilocybe tampanensis* Guzmán & Pollock (1)
Pycnoporus sanguineus (L.: Fr.) Murrill (1)
Russula brevipes Peck (1)
Russula flavida Frost & Peck (1)
**Russula virescens* (Schaeff. ex Zanted) Fr. (1)
Schizophyllum commune Fr. (1)
Sparassis spathulata (Schwein.: Fr.) Fr. (1)
**Stereum frustulatum* var. *subpileatum* (Berk. & M. A. Curtis) Welden (2)
**Stereum fasciatum* (Schwein.) Fr. (2)
Trichaptum biformis (Fr.) Ryvarden (1)
**Volvariella volvacea* (Bull.: Fr.) Singer (4)
**Xerula chrysopepla* (Berk. & M. A. Curtis) Singer (1)

LICHENS

**Chiodecton sanguineum* (Sw.) Vain.

Fr.) Berk. & M. A. Curtis, a fungus found exclusively on fallen fruits of *Liquidambar*, another common tree of the above-mentioned U.S.A. forests.

Among the basidiomycetes observed were species of *Cymatoderma*, *Sparassis*, and *Stereum* of the thelephoraceous fungi, *Cantharellus* and *Craterellus* among the

TABLE 2. Localities where fungi were observed.

1. Old River Wild Life Management Area, Pearl River County, Mississippi. Subdeciduous forest with *Quercus*, *Carya*, *Magnolia*, *Pinus*, and meadows.

2. Jean Lafitte National Historical Park, Barataria Unit, Jeffersson Parish, Louisiana. Swampy forest with *Taxodium*, *Acer*, *Celtis*, *Quercus*.

3. Donaldsonville region, Ascension Parish, Louisiana. Sugarcane bagasse.

4. Near Brusly, West Baton Rouge Parish, Louisiana. Sugarcane bagasse.

5. New Orleans, Orleans Parish, Louisiana. Streets and parks.

chanterelles, and *Ganoderma*, *Hydnopolyporus*, *Pycnoporus*, *Perenniporia*, and *Trichaptum* of the polyporaceous fungi.

Cantharellus lateritius and *C. confluens* are closely related. Corner (1966) considered *C. confluens* conspecific with *C. odoratus*, citing clamp connections on the hyphae of both. Petersen (1979a) wrote about *C. lateritius* and *C. confluens*: "The colors of pileus and stipe (in *C. confluens*) are brighter than those of *C. lateritius*, and with virtually no pinkish component. Microscopic characters vary little in the two taxa." At first (1979b) Petersen reported *C. lateritius* as *C. odoratus* and *C. confluens* as *C. lateritius*. In his color plate II, figures 5-8, he shows one fungus (the true *C. confluens*) with a more orange pileus and a white to yellow hymenium as compared with the other (the true *C. lateritius*), which is paler or more pinkish in both parts. *Cantharellus confluens* was described from Orizaba, Veracruz, Mexico (Berkeley, 1867) as *Craterellus confluens* Berkeley & M. A. Curtis. It was next reported by Guzmán and Sampieri (1984) as *C. odoratus* from the region of Huatusco, Veracruz. This fungus is very frequent in both regions and is the most important edible mushroom in the Huatusco market, where it is known as "hongo de encino" (i.e., oak mushroom). It is so popular and excellent in taste among edible species that it won first place among mushroom dishes prepared during a Mushroom Exposition at Xalapa in 1983 (Guzmán and Sampieri, 1984). This fungus is known today in Córdoba and Xalapa regions as "hongo de Huatusco" (i.e., Huatusco's mushroom), because every year it is present in the dishes at the mushroom fairs of Córdoba. Petersen (1979a) states that *Cantharellus lateritius* "is by far the most common cantharelloid fungus with suppressed hymenial folds in eastern North America." It is a tropical element in the eastern U.S.A. versus *C. confluens*, which appears to be a rare species. One of the collections of *C. odoratus* reported by Guzmán and Sampieri (1984) from the Cofre de Perote region (Veracruz State) in a color plate (Figure 4) is really *C. cibarius*; this is also an important edible mushroom quite frequent in *Pinus-Quercus* forests of Mexico. *Cantharellus cibarius* is exported to the U.S.A. and Europe.

Cymatoderma caperatum is a tropical element in the eastern U.S.A. and is quite common in southern Louisiana and Mississippi during warm, wet periods. *Sparassis spathulata* is unknown in Mexico, but *S. crispa* Wolf: Fr. and *S. radicata* Weir are more or less common in the *Pinus-Quercus* forests of the country. *Stereum frustulatum* var. *subpileatum* Welden and *S. fasciatum* (*S. ostrea* (Blume & Nees: Fr.) Fr.) are common in the same *Pinus-Quercus* and mesophytic forests of Mexico. Among the polypores, *Ganoderma curtisii*, *Hydnopolyporus fimbriatus*, *Microporellus obovatus*, and *Trichaptum biformis* are of frequent occurrence in *Pinus-Quercus* and mesophytic forests of Mexico. *Perenniporia phloiphila,* found on the bark of *Quercus virginiana* Mill. in New Orleans, is unknown in Mexico. *Pycnoporus sanguineus* is sometimes considered conspecific with *P. cinnabarina* (Jacq.: Fr.) Karst. (Cunningham, 1995; Castillo and Guzmán, 1970). I have examined several collections from the eastern U.S.A., mainly from Michigan, and compared them with several from Mexico, Colombia, and Brazil and could not find any difference between them in either macroscopic or microscopic features. This fungus, with *Schizophyllum commune,* is a very common species in the eastern U.S.A. but in Mexico they grow only in the tropical and subtropical (mesophytic) vegetation; they are absent from *Pinus-Quercus* forests except in some sites that border on the tropics. These two species, *Pycnoporus sanguineus* and *Schizophyllum commune,* may be used as ecological indicators from tropical sites with a strong human influence (Guzmán, 1994).

Among the agarics (Table 1), all are more or less common in pine-oak forests or mesophytic forests of Mexico, or both, except *Chlorophyllum molybdites,* which is typical of meadows and gardens of tropical regions. *Lepiota americana,* frequent in the sugarcane bagasse of sites 3 and 4, seems rare in Mexico (Guzmán and Guzmán-Davalos, 1992). *Panaeolus antillarum,* also known as *P. solidipes* (Peck) Sacc., *P. campanulatus* (L.: Fr.) Quél., or *P. phalaenarum* (Fr.) Quél. sensu Kühner & Romagnesi, is not an uncommon meadow mushroom on cow or horse dung in all the world's tropical and subtropical regions, including the eastern U.S.A. *Volvariella volvacea* occurs in all tropical regions of the world but is rare in the eastern U.S.A. and in the mesophytic forests of Mexico. *Xerula chrysopepla* is a widespread mushroom growing from the tropics to the cold coniferous forests, although rare in the latter and in deciduous and mesophytic forests.

The three species of *Psilocybe* represent new records for Mississippi and Louisiana. *Psilocybe tampanesis* was known previously only from the type locality: SE of Badon, near Tampa, Florida, and is based on one specimen (Guzmán and Pollock, 1978; Guzmán, 1983). The Mississippi material, also one specimen, was collected in a meadow of sandy soil, a habitat similar to that of the type collection. However, the Mississippi specimen has a conic-subumbonate pileus versus a convex and slightly umbilicate pileus in the type, a feature not considered significant enough to separate the Mississippi specimen into another species. More specimens are needed from the two localities to properly evaluate this feature. The spores and cheilocystidia, as well as the paucity of pleurocystidia, agree in both collections. Spores from the Mississippi material are 9.5-10.5 (-11) × 6.5-7 (-8) × 6-6.5 (-9) µm, and are subrhombic and thick-walled. The pleurocystidia are rare, 12-16 (-17.5) × (5-) 5.5-6.5 (-9) µm, vesiculose-acuminate or lageniform, and cheilocystidia are (14.5-) 16-25.5 (-32) × 4-6.5 (-7) µm and lageniform. *Psilocybe pseudobullacea* was known only from eastern Africa, Sri Lanka, New Guinea, Ecuador, Venezuela, and Mexico (Guzmán, 1983), where it grows on dung or sugarcane bagasse. The Louisiana specimens, one collection with several basidiomes on sugarcane bagasse, agree well with my previous description (Guzmán, 1983). This is the first record for the U.S.A. The spores are (8.5-) 9.5-11 × (6-) 6.5-7 × 6-7 µm, the cheilocystidia (12-) 13.5-25 × 5.5-8 µm; the pleurocystidia are absent. The fungus does not show a bluing reaction, and consequently it does not have hallucinogenic properties. Finally, *P. cubensis* is a subtropical fimicolous fungus widely distributed throughout the world, but has not been reported formally from the Mississippi region. The single specimen collected has spores (12-) 13-16 (-17.5) µm long, which agree well with those reported earlier (Guzmán, 1983). It is interesting to note that the hallucinogenic *P. caerulescens* Murrill, described from Montgomery, Alabama in 1923 has not been collected elsewhere in the U.S.A. It is a common species in Mexico and has been reported from Panama and Venezuela (Guzmán, 1983) and from Martinique in the Caribbean zone (Pegler, 1983b).

Pleurotus pulmonarius, also known as *P. ostreatus* var. *florida* Eger (Guzmán et al., 1994), seems to be of frequent occurrence in the eastern U.S.A. and in southern Europe, but unknown in Mexico. By means of a spore print from the Louisiana collection, this species is now being cultured at Xalapa in an attempt to obtain fructifications and for crossing with other strains, especially the Florida strain. *Lentinus boryanus*, also known as *L. dentosa* (Fr.) Murrill, is a common edible fungus in subtropical Latin America, where it grows on stumps. It is closely related to the Japanese shi'itake *L. edodes* (Berk.) Singer. Both species are treated by Pegler (1983a) as members of the genus *Lentinula* (Tribe Collybiae). *Amanita hemibapha* is recognized in eastern U.S.A. under the name *A. caesarea* var. *americana* (Scop.) J.-E. Gilbert, and is confused with *A. arkansana* Rosen. *Amanita hemibapha* is edible and is commonly sold in the markets of southeastern Mexico under the names "tecomate" and "yullo" because of a similarity in the reddish orange color of the pileus to a wild cucurbitaceous fruit called by those names.

Calostoma cinnabarina and *Calvatia cyanthiformis* are often found in the subtropics of Mexico, the former in mesophytic forests and the latter in the meadows and grasslands of those forests. *Calvatia* is a popular edible mushroom called "hongo bola" (i.e., ball mushroom). Spores from old basidiomes are used frequently to heal wounds. *Chiodecton sanguineum*, also known as *Cryptotheca rubrocinata* (Ehrenb.) Thor, is, with its conspicuous reddish margin, the only lichen treated here. It occurs so regularly in Mexican mesophytic forests that it can be used as an ecological indicator for climax conditions of subtropical humid forests in Mexico (Guzmán, 1994).

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SOME REALLOCATIONS OF TYPE LOCALITIES OF REPTILES AND AMPHIBIANS DESCRIBED FROM THE MAJOR STEPHEN H. LONG EXPEDITION TO THE ROCKY MOUNTAINS, WITH COMMENTS ON SOME OF THE STATEMENTS MADE IN THE ACCOUNT WRITTEN BY EDWIN JAMES

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Abstract

The Stephen H. Long Expedition to the Rocky Mountains was the first expedition to the West that had trained biologists in its party. In this paper that section of the expedition from Council Bluff to the Rockies and return to Cape Girardeau is reviewed, and various type localities and dates of collection of type specimens are corrected or elaborated. These include *Elaphe obsoleta, Coluber constrictor flaviventris, Thamnophis proximus, Thamnophis sirtalis parietalis, Sistrurus catenatus tergeminus, Masticophis flagellum testaceus, Cnemidophorus tessellatus, Bufo cognatus, Crotaphytus collaris,* and *Scincella lateralis.* Comments on the genus *Bipes* and horned lizards, genus *Phrynosoma* are included.

Introduction

The Major Stephen H. Long expedition from Pittsburgh to the Rocky Mountains in 1819-1820 was a milestone in the early exploration of the American West. For the first time actual scientists were made part of an expedition, these being Thomas Say, zoologist, William Baldwin, botanist, Augustus E. Jessup, geologist, and Titian Ramsay Peale, an artist and taxidermist as "assistant naturalist." Baldwin, unfortunately, became ill and left the expedition at Franklin, Missouri Territory (Missouri did not become a state until 1821), and Jessup resigned in the fall of 1819. They were replaced in June 1820, at Council Bluff (site of Omaha, Nebraska and Council Bluffs, Iowa) by Edwin James, a physician, botanist, and geologist. To allow the reader an appreciation of the problems posed by the account of the expedition, a brief history seems in order.

Stroud (1992) suggested that "Although Say, as senior scientist, most likely should have assumed the task of compiling his writings with those of Long, Baldwin, and James, James took over instead. Probably Say was too involved with writing *American Entomology* and editing and writing for the Journal of the Academy of Natural Sciences. Nevertheless he was much occupied with editing the expedition's account." Furthermore, "James had apparently very much wanted the job of writing the expedition's account, most likely because he was virtually penniless at the time. But he told his brother that he felt 'wholly incompetent to it. It has been as you know a matter of my own seeking and if I shall hereafter be thought to have failed in it, on my own head be the mischief.'" Stroud (op. cit.) also says that James indicated he would probably be "able to shift a part of the responsibility from myself by the proper construction of the title," which he did:

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the title page states that the account is "compiled from the notes of Major Long, Mr. T. Say, and other gentlemen of the party."

The account of the expedition was published in two places, one (James, 1823) was published by Carey and Lea in Philadelphia, and with some differences, a little later (1823) in London by Longman, Hurst, Rees, Orme, and Brown (persons citing one or the other should note the minor differences in the titles). The London edition contains on page 36 a statement referring to the Philadelphia edition, thus the Philadelphia edition is the earlier printing. Although both accounts are dated 1823, the Philadelphia edition, at least, actually had an 1822 printing of an Atlas (I have not seen the Atlas, which contains four pages of text plus plates and figures) and, in fact, the 1823 account had a claim of propriety registered with the Chief of the Eastern District of Pennsylvania in 1822 (Thwaites, 1905). Another account, much abbreviated and with little of the natural history, was written by Captain J. R. Bell (Bell's official report apparently was lost or suppressed by the War Department but by a fluke his diary was discovered by Harlin M. Fuller, in 1932, whose college roommate had mentioned an old diary passed on within his family). Bell's account has important value for dates because he noted some event, no matter how trivial, for each day of the expedition. Fuller used the diary as the basis for a master's degree at Stanford University and later, with Leroy R. Hafen, published an edited version (Fuller and Hafen, 1957). Goodman and Lawson (1995) also mention that Bell's dates are more reliable than some in James' account. And herein begins some of the problem with the account.

Returning from Colorado, the party divided into two groups, one led by Long, with James in accompaniment, to find the headwaters of the Red River, but which mistakenly followed the Canadian River, and another group with Bell and Say to follow the Arkansas River downstream to Fort Belle (Fort Smith), Arkansas Territory. Say's manuscripts and descriptions of species were stolen on the night of August 30, 1820, by three deserting soldiers who took the horses that carried Say's saddlebags. At that time the party was located about ten miles south of Tulsa, Oklahoma, near the Arkansas River. Where Say's notes made subsequent to the August 30 theft might be is unknown. To complicate matters, the collected specimens were placed in the Charles Willson Peale Museum in Philadelphia, a precedent set earlier by Thomas Jefferson, who ordered that specimens from the Lewis and Clark Expedition be deposited there. The Peale Museum went bankrupt in 1843 and six years later the museum items were bought at auction by P. T. Barnum and Moses Kimball (Stroud, 1992). Barnum's material was destroyed by fire in 1851, but most of the Kimball part eventually went to the Museum of Comparative Zoology at Harvard; Jose Rosado of that Museum says (in litt.) that they have no specimens identifiable with the Long Expedition. The lost Barnum holdings probably included the types of species described by Say. The account written by James thus is partially done from memory because of the theft of Say's notes. Yet the detailed descriptions in the account, e.g., scale counts of snakes, suggest that the specimens Say collected had tags with data on them. Stroud (1992) says "Baldwin recounted that Mr. Peale has painted most of Say's fishes and amphibia," but this was before they left Pittsburgh. Stroud (op. cit.) also says "It was fortunate that Say had such a good memory—probably trained by the numerous literary quotations he had once committed to it—for he was able to reconstruct most of the information stolen with his saddlebags. Luckily he still had the notes he had taken up to and including his stay at Engineer Cantonment" (campsite used in winter of 1819-1820).

In Thwaites (1905, vol. 17), Long is quoted as saying that "Most of the collections made on the expedition have arrived at Philadelphia and are in good preservation . . ." Long's account is mainly a report on the topography and Indians (he was attached to the Topographical Engineers of the army); but Long mentions mammals and a casual reference to abundance of reptiles and says that Say's specimens were shipped from New Orleans. Long also reports that, "The sketches executed by Mr. Peale amounted to one hundred and twenty-two. Of these, twenty-one only were finished; the residue being merely outlines of quadrupeds, birds, insects, &c." Dates are sometimes different, but Bell's diary apparently has the accurate dating because he had made an entry for every day of the trip.

Chittenden (1902, vol. 2, p. 578) says of the itinerary, "It would scarcely be possible to find in any narrative of Western History so careless an itinerary, and in a scientific report like that of Dr. James it is inexcusable." Typically, when an animal was obtained by Say he immediately would take notes on its appearance. However, where descriptions of new species are presented by James, they may not necessarily be at the point in the chronological account where the animal was taken. James, in fact, bitterly commented about Major Long, whom he apparently disliked; in a letter to his brother from Cape Girardeau, he stated that Long allowed him neither time to examine and collect, nor means to transport plants or minerals. "We were hurried through the country as if our sole object had been, as it had been expressed in the orders which we received at starting 'to bring the expedition to as speedy a termination as possible'" (Stroud, 1992: 123). One must suppose that Long pushed as rapidly on the entire expedition, thus descriptions may have been delayed until adequate time allowed for a presentation, or that details from memory could not be made in clear association with dates or places.

For the present writing I have mostly used the microcard version of the Philadelphia edition of James' account, and in place of the London edition I have used the version of Thwaites (1905). My interest in the Long expedition resulted from the publication of Goodman and Lawson (1995), which, though primarily concerned with the botany of the trip, has proved most fruitful in establishing the probable routes taken and dates of encampment. The text of James' account is difficult to follow because one is not sure whose notes are being utilized, even though the writing styles are different. The Philadelphia edition is more complete, and also has an index. Goodman and Lawson deal only with the trip from Council Bluff, and emphasize the botany, nothing of the animals, but they do give dates, maps, and photographs to verify the illustrations made by the expedition artist Samuel Seymour. I do not deal with that part of the expedition from Pittsburgh to St. Louis, only with the St. Louis area, the trek westward, and the return to Cape Girardeau, Missouri, an area visited previously during the St. Louis stopover.

TYPE LOCALITIES

Elaphe obsoleta

This is the first herpetological species described from the trek westward from St. Louis. Dowling (1952) gives the statement "on the Missouri River from the vicinity of Isle au Vache to Council Bluff," this from the Philadelphia account.

Dowling then says, "Cow Island is near Leavenworth County, Kansas, and is somewhat more than 100 miles downriver from Council Bluffs, Iowa. At present it appears unnecessary to restrict the type locality further. Should this be necessary at some later date, it could reasonably be restricted to the vicinity of Cow Island, where Say carried on his investigations for some time." Schmidt (1953) gives the type locality as "Isle au Vache to Council Bluffs on the Missouri River; rest. to Council Bluffs on the Missouri River." Stejneger and Barbour (1943) say for *Elaphe obsoleta obsoleta*, "Isle au Vache [sic] (the "sic" is S. and B.'s wording) to Council Bluffs on the Missouri River."

On pages 139-140 (vol. 1) of James (1823) in the Philadelphia edition, which is an account of the area around Isle au Vache, James reported (obviously from Say's notes) "We have seen at Bellefontain [an old military post near St. Louis], as well as at several other points on this river, a pretty species of sparrow, which is altogether new to us;* and several specimens of a serpent have occurred, which has considerable affinity with the pine snake of the Southern States or bull snake of Bartram [Bartram, 1791].*" The terms pine snake and bull snake would refer to genus *Pituophis.* The asterisks indicate descriptions at the bottoms of pages 139 and 140. On page 139 the description of the sparrow *Fringilla grammacea* Say begins and states "Shot at Bellefontain on the Missouri," and on page 140, footnote 163 refers to the description of *Coluber obsoletus.* At this point the account is referring to animals seen at Bellefontain. The actual description is of a black snake of "anterior half with a series of dull-red large circles, formed upon the skin between the scales on the side," and the animal is said to resemble *Coluber constrictor* "but the scales are decidedly smaller, and the number of its plates and scales approach it still more closely to that uncertain species *C. ovivorus*" [*C. ovivorus* Merrem 1820: 134, but the spelling there is *ouiourus* and a footnote indicates Linn S.N. I, p. 385]. I think the reference is to Tomus I of the 12th edition of Linnaeus' *Systema Naturae* where *ovivorus* appears on page 385. The reference also says "C.N. 203+73" [the ventral scute count of *ouiourus* is much below that of *obsoleta* but would fit *Elaphe vulpina,* whose range currently reaches just north of St. Louis north of the Missouri River, and the subcaudal count of 73 exceeds the 71 maximum reported by Powell (1990) for *Elaphe obsoletus*]. "It is not an uncommon species on the Missouri from the vicinity of Isle au Vache to Council Bluff." That the sparrow was described much later than it was collected is a clear indication that descriptions are not necessarily associated with point of collection, and, of course, might also be an indication that *Coluber obsoletus* was taken from Bellefontain. The statement "It is not an uncommon species. . . ." sounds like an afterthought and makes Bellefontain seem a logical type locality.

What was Say seeing at Bellefontain? Terms such as pine snake and bull snake would apply to blotched specimens, hence possibly *Elaphe guttata emoryi* at the edge of its currently known range, or juvenile *Elaphe obsoleta. Lampropeltis c. calligaster* and *Elaphe vulpina* are ruled out because their highest ventral counts are below the minimum count for *E. obsoleta.* Anderson's (1965) map shows the northern range of *E. guttatta* as being a little south of Bellefontain. Bartram's (1791) pine snake, however, would be the Florida variety, whose blotches are obscure on the anterior half of the body but the Floridian version of *Pituophis melanoleucus* does not occur anywhere near St. Louis, and *P. m. sayi,* the species that does occur near St. Louis, is vastly different in pattern.

At this point I must accept the "Isle au Vache" type locality, but the puzzle is what Say was seeing at Bellefontain where they stayed for several days. That some degree of blotching was evident in the *Elaphe* at Isle au Vache could be a confirmation of what Say saw at Bellefontain and assumably Say would have captured some of the snakes seen at Bellefontain.

Coluber constrictor flaviventris, Thamnophis sirtalis parietalis, Thamnophis proximus

The expedition spent the winter of 1819-1820 near present-day Omaha, Nebraska, and Council Bluffs, Iowa. The winter quarters (James vol. 1, p. 146 of the Philadelphia edition) "was on the west bank of the Missouri, about a half mile above Fort Lisa, five miles below Council Bluff, and three miles above the mouth of Boyer's River." The site, called Engineer Cantonment, was about 100 yards northwest of a limestone quarry. Sometime between December 12 and December 30, 1819 (both the Philadelphia and London editions describe events of December 12, but without any other accounting; the next date shown is December 30, so the exact date cannot be determined), laborers at the quarry opened fissures in which a number of snakes were hibernating. Included were three kinds considered to be new species: *Coluber parietalis* (*Thamnophis sirtalis parietalis*), *C. flaviventris* (*C. constrictor flaviventris*) and *C. proximus* (*Thamnophis proximus*). Setting the site of Engineer Cantonment as the type locality seems easy enough. The latest statements of type locality are, for *Thamnophis sirtalis parietalis*, "Stone quarry on west side of Missouri River three miles above mouth of Boyer's River, Washington County, Nebraska . . . collected by Thomas Say 1819" (Rossman, 1980); for *Coluber constrictor flaviventris* Wilson (1978) says, "west bank of the Missouri . . . three miles above the mouth of Boyer's River; restated by Rossman (1963: 109) as 'approximately 3 miles ENE Fort Calhoun, Washington County, Nebraska'." Wilson adds, "collected by T. Say on 12 December 1819." Wilson's literature citation for the James account says Peary and Lea (sic), an obvious error for Carey and Lea. For *Thamnophis proximus*, Rossman (1970) gives "*Coluber proximus* Say 1823: 339 . . . Stone quarry on west side of the Missouri River, 3 miles above the mouth of Boyer's River," restated as "approximately 3 miles ENE Fort Calhoun, Washington County, Nebraska" by Rossman (1963: 109). Rossman (1963) actually says, "The specimen was collected in Nebraska at a stone quarry on the west side of the Missouri River, 3 miles above the mouth of Boyer's River (Iowa) by Long's expedition to the Rocky Mountains in 1819 or 1820. The type locality lies approximately 3 miles ENE Fort Calhoun, Washington County, Nebraska." Rossman (1963) also indicated that Smith and Taylor (1945) listed the holotype as lost, but it was probably deposited in the Academy of Natural Sciences of Philadelphia, though this is not a certainty (H. M. Smith, personal communication to Rossman). As stated above, we know that the expedition's specimens were to be deposited in the Charles Willson Peale Museum.

Goodman and Lawson (1995, p. 3, footnote 4), say that the mouth of Boyer River once entered the Missouri about 3/4 mile below the Washington-Douglas county line but has now been shifted via modern feats of engineering upstream five miles. Thus, to allow for the original Boyer River situation, the type locality for all three species described from the quarry, and with respect to the map and statements on page five of Goodman and Lawson, I hereby restate the type localities as about five miles south of Ft. Calhoun, Section 28, T17N, R13E in Washington County, Nebraska.

Sistrurus catenatus tergeminus

According to Minton (1983), the type locality of *Sistrurus catenatus tergeminus*, described by Say as *Crotalus tergeminus*, is "indefinite; restricted to Winfield, Cowley County, Kansas [Smith and Taylor, 1950]. No holotype designated." In my estimate, this assessment is erroneous. Grant that Cowley County is well within the range of that subspecies, but the expedition account of August 17, perhaps August 18, 1820, contains no mention of rattlesnakes. The actual description that appears on page 499 (vol. 1) of the Philadelphia edition is for the date of July 4, 1820, when the party was in Adams County, Colorado. Stejneger and Barbour (1939) did not recognize *S. c. tergeminus*. Schmidt (1953) says, "Locality not stated; designated as headwaters of Arkansas River." Gloyd (1940) says "Type locality indefinite; no type specimens designated," and Klauber (1956) says, "Type locality: between the Mississippi River and the Rocky Mountains; type specimen: none designated. Type locality subsequently restricted to Winfield, Cowley County, Kansas, by Smith and Taylor . . ." But many references to *Crotalus tergeminus* appear at earlier dates in the text, and such a clear statement of encounters with it is given that I believe I can give a more specific locality.

In volume one, page 344 of the Philadelphia edition appears the following: "On the 12th [April 1820] Lt. Graham, Lt. Talcott of Camp Missouri, Mr. Seymour and I, accompanied by a soldier, departed in our small row boat, for the purpose of ascending Boyer Creek [Boyer River], and ascertaining the point at which that stream discharges from the Bluffs." James, we must note, did not arrive at the Council Bluff winter encampment until June, and he remarks in a footnote (p. 200) that succeeding notes, especially about the Omawhaws [Omaha Indians], and the last chapter of volume one and the first five chapters of volume two were from Say's notes; the statement of the trip up the Boyer starts off chapter six, but clearly the "and I" refers to Say. The writing style, the lack of specificity about plants, and the detailing of animals clearly constitute Say's writing style. The account says for April 14: "We saw numbers of the smaller species of rattle snake, [p. 375, lists reptiles seen at Engineer Cantonment, the campsite of the winter of 1819-1820, or at other indicated places on their journey. That list includes *Crotalus horridus*, a much larger species and *C. durissus* (probably a misnomer for some specimens of *C. horridus*)] which had, no doubt, but lately left their winter dwelling." On April 17 they returned to their tent where a soldier had killed three rattlesnakes while pitching the tent (the tent was erected April 15 and the party had to put blankets on their backs to travel because of the bluffs on the river). The opportunity was ripe for securing and preserving specimens; thus, a possible type locality is along the Boyer River in Crawford or Harrison County, Iowa, most likely Harrison County because the account suggests that they did not get too far upriver. But as I will show below, a more likely type locality is in Colorado.

In Nebraska today, the range of *Sistrurus catenatus tergeminus* is restricted to a small section of the extreme southeastern part of the state (Filmore, Lancaster counties, and Gage and Nemaha counties in 1891 according to Hudson, 1942). The James account gives several other references to the species in Nebraska and also associates them with prairie dog towns. As indicated below, I am surprised that they did not indicate that they were encountering or also encountered the prairie rattlesnake, *Crotalus viridis*, which usually is the rattlesnake associated with prairie dog towns. To further back up the expedition's report that *Sistrurus* occurred in prairie dog towns is the statement at the top of volume two, page 48 of the Philadelphia edition; it reads, "We also captured a rattlesnake*, which like the *tergeminus*, we have found to inhabit a barren soil, and to frequent the villages of the Arctomys of the prairie [= prairie dog], but its range appeared to us confined chiefly to the vicinity of the Rocky Mountains . . ." The asterisk refers to the description of *Crotalus confluentus* [*C. viridis*] on page 48. Admittedly the failure to encounter *C. viridis* in Nebraska is puzzling, but perhaps that is because all of Say's notes covering that region were lost with the stolen saddlebags and the account from memory may not have been as good as one would like. What few prairie dogs (*Cynomys ludovicianus*) remain in Nebraska occur relatively far east, but do not overlap the current range of *Sistrurus catenatus tergeminus*. As late as 1900 a prairie dog colony was located near Fontanelle in Washington County, about 25 miles northwest of Omaha and the records show also that the prairie dog reached Jefferson County (Jones, 1964). But Nebraska is a heavily agricultural state and the transition of prairie to farmland may perhaps have eliminated *Sistrurus* from the bulk of the state. This is not an easy conclusion to reach because *Sistrurus catenatus* has survived agricultural activity in Illinois, Kansas, and Oklahoma.

On June 28 (vol. one, p. 485 of the Philadelphia edition), when the party was near Sterling, Logan County, Colorado, the account says, "About some sandy ridges, which we passed in the middle of the day, several miliary rattle snakes were seen, two of which were killed. These had been occasionally met with all along the Platte, but were by no means numerous." The term "miliary" is reference to *Sistrurus miliarius*, the pigmy rattlesnake of the southeastern states. On July 4 (vol. one, pp. 499-500 of the Philadelphia edition), at which time the party was somewhere between Platteville, Weld County, Colorado and just south of Brighton, Adams County, the account reads: "Rattle snakes of a particular species* [the * indicates the description of *Crotalus tergeminus* on p. 499] are sometimes seen in these villages [prairie dog villages]. They are found between the Mississippi and the Rocky Mountains, and appear to prefer unproductive soil, where their sluggish gait may not be retarded by the opposing obstacles of grass and weeds. Whilst exploring Boyer Creek, of the Missouri, in the spring of 1820, our party met with six or eight of them during one day's march on the prairie, and on our subsequent journey to the Rocky Mountains we several times encountered equal or even greater numbers, in the same space of time. This is the species of serpent which travellers have observed to frequent the villages of the prairie dogs, and to which they have attributed the unnatural habit of voluntary domiciliation with that interesting animal. . . . From the disparity in the number of plates and scales, and the greater size of the vertebral spots in this species than in the *C. miliarius* we have been induced to consider this a distinct species. Specimens are in the Philadelphia museum." Because they were still referring to "miliary rattlesnake" on June 28, and the July 4 description seems to be applied to snakes seen at that time, I believe that this is the most appropriate association of a date, place, and description to define the type locality of *Crotalus tergeminus*, notwithstanding the fact that opportunity to collect the snakes occurred first on the Boyer Creek trek in Iowa and that the locality is north of present-day distribution.

Masticophis flagellum testaceus

Mention of this snake is made in different places in the two versions of James' account and differ somewhat. The Philadelphia edition mentions the discovery and description (vol. one, p. 48), the description immediately following that of *Crotalus confluentus*, whereas the London edition, as seen in Thwaites' presentation, reports *Coluber testaceus* in volume three, page 236 (p. 39 of Thwaites), and *Crotalus confluentus* appears on page 40 of Thwaites. From the reading of the James account, one might glean that this snake was taken on July 17, possibly July 18, but Bell, who was exacting in covering every day no matter how trivial a report, says clearly that hunters caught a large red snake on July 16. Wilson (1973) gives the type locality as "headwaters of the Arkansas near the Rocky Mountains = junction of Turkey Creek with the Arkansas River, 12 miles W Pueblo, Pueblo County, Colorado. Holotype lost." Other than the minor date detail, this seems adequately accurate when compared with the different accounts that mention the place where the species was discovered. I note that Wilson (1973) erroneously lists Carey and Lea as Peary and Lea as the publisher and fails to indicate that the type locality, as relating to Pueblo, was more specifically defined by Maslin (1953). A casual sketch of a snake's head made by Titian Ramsay Peale on 16 July 1820, which appears to be that of a *Masticophis flagellum*, is in the collection of Peale's drawings at the American Philosophical Society.

Cnemidophorus tesselatus

In the Philadelphia account by James this species is described as "Genus Ameiva. *A. Tesselata* Say. Tessellated Lizard." The London edition, published slightly later, says "Genus Ameiva—*A. tessellata*, Say Tesselated lizard." The holotype is lost.

Price (1986) cited the Philadelphia account; he indicates that literature up to 1949 used either spelling and also that Burt (1931) treated *C. tigris* and *C. grahamii* as junior synonyms of "*testellatus*" (Burt had emended the name to "*tessellatus*" based on the adjectival spelling and justified by article 39 of the International Code of Zoological Nomenclature). Whether the Philadelphia edition has a typographical error probably is a moot question, and article 32 of the International Code of Zoological Nomenclature (1985) probably would allow the single "l" spelling to prevail. Price (op. cit.) says that "*tesselatus* is derived from *tessella* (L., "little square stone")." Checklists, e.g., Stejneger and Barbour (1943) or Schmidt (1953) use "*tessellatus*," obviously considering the single "l" to be an error.

The entire matter of the nomenclature takes on a new perspective in a paper by Walker et al. (in press). What has been called *Cnemidophorus tesselatus* involves both diploid and parthenogenetic lizards, and Walker et al. show that the original type locality today apparently has no lizards that match the type description; hence they establish a neotype and new type locality for *tesselatus* and give the population at the original type locality a new name.

James' account is not clear on where the lizard was collected. Various authors have discussed the type locality, (Smith and Burger, 1949; Smith and Taylor, 1950; Maslin, 1950; Milstead, 1953) the problem being the names of creeks encountered en route, but the restriction of the type locality to Pueblo, Colorado by Maslin (1959) seems reasonable in terms of the general area through which they were passing. Maslin ascertained that the type locality should be restricted to "the junction of Fountain Creek and the Arkansas River, Pueblo Co., Colorado." Goodman and Lawson (1995) confirm the identity of the creek.

Bufo cognatus

Krupa (1990) gives the type locality as "The alluvial fans of the [Arkansas] River" in Prowers County, Colorado. The actual statement (James, vol. two, p.

190, Philadelphia edition) is "The alluvial margins of the river are gradually dilating as we descend . . ." The date of collection is July 29, 1820, and likely the specimen was taken around the camp in the evening because heavy rain had fallen on the 28th. From Bell's account of July 29 (Fuller and Hafen, pp. 204-205) the party apparently was a few miles west of Holly, Prowers County, which I here define as the type locality: Approximately 3 miles west of Holly, Prowers County, Colorado. Various checklists (e.g., Schmidt, 1953) have defined it as Powers County, but the correct name is Prowers County, the name used by Maslin (1959), Smith (1934), and Stejneger and Barbour (1943), among others.

Crotaphytus collaris

This species, described as *Agama collaris* in volume two, page 252 of the Philadelphia version of James, is mentioned in the September 5, 1820, narrative: "A beautiful species of lizard, (agama) is occasionally met with in this territory." Axtell (1989) discussed the type locality, which is an enigma. Axtell pointed out that James indicated (p. 251) that the party [the Bell party that followed the Arkansas River] had arrived at Mr. Glen's trading house near the Verdigris River about a mile above its confluence with the Arkansas. Stejneger (1890, p. 103) expressed the first opinion on the type locality: "The type of Say's *Agama collaris* came from the Verdigris River, near its junction with the Neosho River, Creek Nation, Indian Territory." Stejneger gave no explanation for his restriction. Stejneger and Barbour (1917, 1923, 1933, 1939, 1943) gave the restricted locality as "Verdigris River near its union with the Arkansas River, Oklahoma." Axtell goes on to say that most workers have accepted that type locality, or changed it only slightly, but Webb (1970) gives the type locality as "near Colonel Hugh Glenn's [both the London edition of James' account and Bell's account spelled it Glenn] Trading Post on the east bank of the Verdigris River about two miles above its confluence with the Arkansas River." According to Webb, this site is in Wagoner County, Oklahoma, about four miles ENE of Ft. Gibson (Muskogee County) near the Muskogee-Wagoner County Line. Note, however, that Ft. Gibson is east of the Grand River (= Neosho River) and the site indicated by Webb would be in either Cherokee or Muskogee County. More correctly he should have said WNW of Fort Gibson.

Axtell (1989) states that he visited the vicinity of Webb's inferred type locality, where the Verdigris has an exposed bluff where Glenn's Trading Post might have been, but no one living in the vicinity remembered anything about the post or its location. At the nearby town of Okay, Oklahoma, the science teacher and other residents Axtell questioned knew the lizard by the Oklahoma vernacular name of "mountain boomer," but agreed that they had not seen or heard of them in the vicinity of Okay. Axtell thus chose not to accept Webb's version because of the still unanswered site questions (personal communication) and provisionally accepted the Stejneger and Barbour (1917) type locality. I contacted Webb, who said that he well-remembered discussing the matter with Dr. A. O. Weese, an ecologist at the University of Oklahoma, who had edited the journal for that part of the expedition chronicled by Titian Ramsay Peale and suggested the type locality that Webb used, but that so far as Webb knew, substantiating information has not been published. In any case, I note that Webb (1970) showed records for *Crotaphytus collaris* in both Wagoner and Muskogee counties. The Bell party arrived at the trading post at 10 A.M. and left that morning, hardly time enough for Say to have done any collecting, and their subsequent trek was through low country, hardly a suitable habitat for *Crotaphytus.*

However, as noted for September 3 and 4, the account tells of passing rocky-topped hills. The map shown in Fuller and Hafen (1957), apparently constructed by the Bell party, shows the campsites. When the latitudes and longitudes of the map are compared with those of a modern-day map, the campsites of September 3 and 4 are NW of Muskogee, Oklahoma, or perhaps at Muskogee. Both sites are south of the Arkansas River, and definitely not along the Verdigris River. Although the map coordinates shown by Bell are inaccurate, the account is clear in relation to the Verdigris River. In July, 1996, I searched around Tullahassee and Porter, Wagoner County, areas just west of Okay, areas that I suspect may have been the type locality; I can verify that suitable habitat for *Crotaphytus* exists west of Okay.

The crux of the type locality problem, I believe, lies in how one reads the statement "A beautiful species of lizard (agama), is occasionally met with in this territory." My feeling is that the term "territory" really refers to the fact that Oklahoma, at that time, was part of Arkansas Territory. That the lizard was met with occasionally does not mean that it was necessarily seen and captured near Okay. I believe that I can infer that the lizard was likely taken in some of the rugged terrain west of Okay, possibly even as far northwest as Tulsa. But because the party reached the summit of the hills that divide the drainages of the Arkansas and Verdigris, and with the large hills near the Grand (Neosho) River in sight, I would guess that the lizard was secured perhaps somewhere southwest or northwest of Tullahassee, Wagoner County, Oklahoma on 4 September, 1820. In view of the ambiguities associated with the narrative, the Stejneger and Barbour (1917) statement seems the best that can be said, except that I would add that the type locality should read, "Verdegris River . . . Oklahoma, probably in Wagoner County."

Scincella lateralis

In volume two, page 324 of the Philadelphia account (no mention of the species is given in the London account presented by Thwaites, 1905) this species was described as *Scincus lateralis.* Brooks (1975) gives for the type locality "banks of the Mississippi River below Cape Girardeau [Cape Girardeau County] (the brackets are those of Brooks) Missouri." Brooks then goes on to say: "Holotype, U.S. Natl. Mus. 3152, collected by S. W. Woodhouse (not examined by author)."

The expedition had been to Cape Girardeau on the way west; they returned to Cape Girardeau October 10, 1820, and James (Philadelphia edition, p. 324) says "about November 1, 1820 Mssrs. Say, Graham, and Seymour had so far recovered their health, as to venture on a voyage to New Orleans, on their way home." Each of those men had apparently contracted malaria. "They left Cape Girardeau in a small boat, which they exchanged at the mouth of the Ohio River for passage on a steam boat [*Riverboat Yankee* (Stroud, 1992: 124)] about to descend. Mr. Peale, who had escaped the prevailing sickness, accompanied them. On his way down the Mississippi, Mr. Say observed the new animal described in the subjoined note.*" A footnote follows, continuing onto page 325, in which *Scincus lateralis* is described. The account (p. 325) says of *Scincus lateralis*: "occurred during our passage down the Mississippi to New Orleans, and proved to be specifically identical with specimens which I formerly collected in Florida and East Georgia." No mention is made of Woodhouse or of any landings on the banks of the Mississippi. Furthermore Samuel W. Woodhouse was born in 1821, after the expedition was completed, and could not have collected the skink. Also, we must recall that specimens collected by the expedition were to be deposited in the Charles Willson Peale Museum in Philadelphia, not in Washington.

Stejneger and Barbour (1917, 1923) called the animal *Leiolopisma laterale* (Say), but later (1939) called it *Leiolopisma unicolor* (Harlan). That change, Stejneger (1934) explained, was because *Scincus lateralis* Say was preoccupied, having been used by Daudin (1803). Lonnberg (1896) showed that the specimen was actually a Mediterranean species, *Gongylus occulatus* (Forskäl, 1775), and that the available name for the North American species was *Scincus unicolor* Harlan (1827). The publication date for Harlan's name was corrected by Stejneger and Barbour (1939) to 1825, but they used the name *Leiolopisma unicolor*, giving the type locality as "Southern states." Schmidt (1953), however, gives the credit to Say, 1823, in Long's expedition and as volume two, page 324, with the site as "Banks of the Mississippi below Cape Girardeau, Missouri." I contacted Dr. George Zug at the U.S. National Museum of National History, who said that Doris (Doris Cochran, 1961) listed USNM 3152 as a type, but that she had listed a fair number of specimens that are *not* types. Further, he said, her specimen locality data far exceed those in the catalog. The catalog entry is "*Plestiodon* Arkansas River Dr. Woodhouse 21 1." Zug said, "reidentified, pencil entry in Doris' handwriting: Mo added to locality, also in pencil by Doris to note date when specimen was entered in the catalog." Zug thinks the specimen unlikely the type, although we have no way of tracking its origin beyond the original catalog entry. Thus the original version in James' account must stand, and the type locality should read "Likely just below Cape Girardeau, Cape Girardeau County, Missouri" with credit given to Say, 1823. I searched a number of habitats that seemed suitable for *Scincella* just below Cape Girardeau in July, 1996, but did not encounter the species.

MISCELLANEOUS COMMENTARY

One of the most remarkable things mentioned in the Long Expedition account appears in volume one, page 484 of the Philadelphia version for June 27, 1820. At that time, the party apparently was in what we now know as Logan County, Colorado, between Crook and Sterling (Goodman and Lawson, 1994) near the Platte River: "We observed in repeated instances, several individuals of a singular genus of reptiles (Chirotes. Cuv.) which, in form, resemble short serpents, but are more closely allied to the lizards, but being furnished with two feet. They were so active that it was not without some difficulty that we succeeded in obtaining a specimen. Of this (as was our uniform custom, when any apparently new animal was presented) we immediately drew out a description. But as the specimen was unfortunately lost, and the description formed part of the zoological notes and observations, which were carried off by our deserters, we are reduced to the necessity of merely indicating the probability of the existence of the *Chirotes lumbricoides* of naturalists, within the territory of the United States." Modern nomenclature would place *Chirotes* in the genus *Bipes*, a lizard genus known only from western Mexico and Baja California. A justification of this remarkable observation was suggested by Campbell (1980). Support for the validity of the observation was presented by Dundee (1980), who was told by a farm boy in the western Nebraska sandhills, and apparently familiar with all of the lizards on his home area, that two-legged lizards were occasionally found there, especially when digging post holes or pulling up old fence posts. But Gans and Papenfuss (1980), who worked extensively with amphisbaenians, to which group *Bipes* belongs, report that all species they have encountered were rather sluggish and easily caught and doubted very much that the Long party had encountered such an animal. Supplemental to the Long Expedition account are Taylor's (1938) remarks strongly suggesting that *Bipes* might occur in Arizona.

But how do we explain the observation? Say was noted for being meticulous in his observations and the statement "We encountered" suggests that indeed other members of the party saw the animal. Clearly some very intensive collecting in the Logan County area and the Nebraska sandhills is needed to try to verify the expedition's narrative. Campbell (1980) did suggest that possibly the species may have been relict in the Nebraska-Colorado area and perhaps close to extinction. Even if the original notes had not been stolen, the lack of a voucher specimen would still place the observation in doubt.

A remarkable oversight of the Long Expedition seems to me to be Say's failure to describe a species of *Phrynosoma*; a horned lizard certainly is an animal not easily forgotten and the party obviously saw *Phrynosoma* because, on several occasions, the account refers to orbicular lizards, the term used in those days for horned lizards. On or about July 15, 1820, probably near Fountain Creek, perhaps two miles south of Fountain, El Paso County, Colorado (Philadelphia edition, vol. 2, p. 35) the account says, "Orbicular lizards were found about this camp, and had been once or twice noticed near the base of the mountain." In the Philadelphia edition (vol. two, p. 51) is the statement, "We had proceeded eight or ten miles from our camp. . . . Here the barren cedar ridges are succeeded by still more desolate plains, with scarce a green, or living thing upon them, except here and there a tuft of grass, an orbicular lizard, basking on the scorching sand. . . ." This was July 19, probably close to Pueblo, Colorado. Earlier, on August 6, 1819, Say and a party journeyed westward up the Kansas River (Kaw River) and in the Philadelphia edition (vol. one, p. 138) the account says: "In ascending the Konzas river [Kansas River], one hundred, or one hundred and twenty miles from the Missouri, you discover numerous indications, both in the soil, and its animal and vegetable productions of an approach of that Great Sandy Desert, which stretches eastward from the base of the Rocky Mountains. You meet there with the orbicular lizard or 'horned frog', an inhabitant of the arid plains of New Mexico." James' and Long's party, on August 1, 1820, after the parties had split, were on Ute Creek east of Yates in Harding County, New Mexico and volume two, pages 89-90 of the Philadelphia edition say, "Several rattlesnakes were seen and many orbicular lizards. These are evidently of two distinct species, differing from each other in the length of the spines and position of the nostrils. Scarce any two of either species are precisely similar in colour, but the markings are permanent. Both species possess in a slight degree, the power of varying the shades of colour. We could find no conspicuous difference marking the different sexes in the species with long spines; the other we have not have sufficient opportunity to examine." Judging by today's horned lizard distribution, they most likely were seeing *Phrynosoma cornutum* and *P. douglassi*.

From so many mentions of orbicular lizard, one would think that surely Say would have described at least one, possibly two species, the latter if James' and Long's party had collected specimens. Coues (1895, vol. 2, p. 431) says that Zebulon M. Pike wrote in his journal for October 24, 1806: "and strange as it may appear, I have seen the wishtonwish, the rattlesnake, the horn frog [*Phrynosoma douglasi*, with which the prairie abounds . . .] (The brackets are by Coues)." Coues is wrong about *Phrynosoma douglasi* (sic) because on October 24 Pike was between Larned and Great Bend, Kansas; *douglassi* does not occur in Kansas, only *P. cornutum*. Say quite likely had seen the paper by Barton (1806), who associated a specimen taken by the Lewis and Clark Expedition with *Lacerta orbicularis* (Linnaeus, 1758). Price (1990) has pointed out that *L. orbicularis* is a senior synonym of *Phrynosoma orbiculare*, and that Barton (1806) called his specimen "Lacerta *Tapajaxin*," but deferred a full description to another paper. That paper (Barton, 1809) is a description of a salamander, *Ambystoma maculatum*. Thus Barton's name L. *Tapajaxin* is a nomen nudum for *Phrynosoma cornutum*, and credit for *P. cornutum* goes to Harlan (1825). Most likely Say thought that the orbicular lizards encountered were a species that Barton had already described. Had the two different forms mentioned by the Long and James party in New Mexico come into Say's hands, quite likely Say would have described at least one horned lizard.

All in all, a reader of the Long Expedition can only curse the deserters who fled with Say's saddlebags; otherwise an accurate zoological account would have been a significant contribution from the expedition team.

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