Late Quaternary Bats From Cebada Cave, Chiquibul Cave System, Belize

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ABSTRACT.—The second occurrence of fossil bats for Central America is reported from Belize. A cranium and articulated atlas of the extinct vampire bat *Desmodus draculae* (Phyllostomidae) were recovered from a corridor of Cebada Cave, a segment of the Chiquibul Cave System. Unlike other bat skeletons found in the cave, the vampire specimen was covered with a thin layer of calcite crystals; although it is probably older than the other bat remains collected in Cebada Cave, it is impossible to determine if it dates to the Pleistocene or Holocene. *Desmodus draculae* was known from four South American sites and one site in the Yucatán Peninsula. The same cave corridor has thousands of other complete bat skeletons, and those collected represent several probable Holocene occurrences. They include at least six phyllostomids (*Tonatia sauro-phila*, *Artibeus lituratus*, *Artibeus* (*Dermanura*) sp., *Carollia subrufa* or *C. brevicauda*, *Sturnira* sp., and *Centurio senex*) and two vespertilionids (*Lasiurus blossevillii* and *Lasiurus ega*). Except for the extinct vampire, the other bat remains belong to extant species in the area.

INTRODUCTION

Cebada Cave is a segment of the Chiquibul Cave System of west-central Belize and eastern Guatemala, where approximately 65 km of large cave passages have been surveyed (Fig. 1). The cave system is a suite of vertically-stacked galleries representing active and abandoned subsurface routes which developed following an ancient underground diversion of the Chiquibul River in Belize (Miller, 1996, 2000).

Bony remains of fossil vertebrates were first recovered from the Chiquibul System by Miller in 1986 (an artiodactyl mandible in the cave of Kabal; Rufus Churcher, pers. comm.). Miller (1989) recorded the skeleton of a juvenile bear of the extinct species *Tremarctos floridanus* collected in Cebada Cave in 1998 (H. Greg McDonald, pers. comm.). Skeletal remains of snakes, bats and recent humans have also been recorded in the system (Krejca et al., 2000). Although bats are ubiquitous in tropical American caves, including Belize, previous biological surveys in Chiquibul caves have concentrated on invertebrates and list only unidentified bats as inhabitants (Reddell

and Veni, 1996). The Cebada Cave bats are the focus of this report.

A single fossil bat, an unstudied specimen of the mormoopid genus *Pteronotus* from the early Pleistocene of El Salvador (Webb and Perrigo, 1984), constitutes the only previous fossil record of bats in Central America. The Cenozoic fossil record of vertebrates in this area is very poor even for the Quaternary, which is typically better represented than earlier periods (Ferrusquía-Villafranca, 1978, 1984; Webb and Perrigo, 1984; Lucas et al., 1997; Webb, 1997).

MATERIALS AND METHODS

The Chiquibul System of caves is the longest in Central America, beginning in the Cayo District of Belize at 490 m and emerging at 190 m in the Petén region of Guatemala. As noted by Miller (1996), the climate is tropical-humid, with mean annual temperatures of 22 °C, rainfall approaching 200 cm/yr, and is covered with a dense rainforest that was lightly logged in the late 1960s and early 1970s. The host rock is a highly brecciated limestone of Cre-

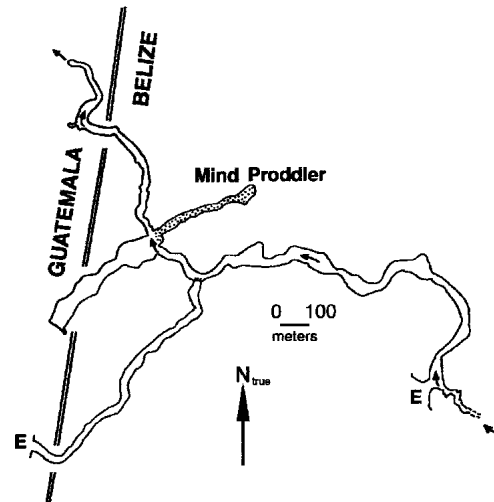FIG. 1. Location of Belize and the Chiquibul Cave System.

FIG. 2. Plan view of approximately 5 km of the western end of Cebada Cave, including the Mind Proddler. Double line at left marks the surface border between Belize and Guatemala. Arrows indicate the location and direction of flow of the Chiquibul River. Stippling within the Mind Proddler shows the area from which bat remains were collected. E indicates known entryway into the cave.

taceous age upon which a mature karst landscape developed, diverting all surface runoff underground. Passages in the caves may exceed 80 m in width, and those in the river channel of the Cebada Cave segment average 40-50 m in diameter. The latter often have huge silt and mud banks rising steeply 30 m from the river to the walls. The constant 100 % humidity and 22 °C temperatures encourage biological activity, such that the alluvial mud banks are completely covered in worm castings, and are annually re-worked. The floor substrate is variable and may also consist of collapsed bedrock or alluvial deposits of cobbles, gravel, or sand.

The specimens described in this report were collected by Krejca in May, 1999, in a high-level passage corridor known as the Mind Proddler of Cebada Cave (Fig. 2). Higher corridors representing progressively older courses of the cave system are common in the Chiquibul System. The Mind Proddler is located 70 m above current river level, indicating a developmental age of perhaps 700 kyrBP as estimated from dating of speleothem (Miller and Lundberg, 2000). As with other such high cave levels, the original alluvial deposits were veneered with speleothem of calcite flowstone and dripstone (stalagmites and stalactites) as well as evaporite-associated features of gypsum and aragonite. The relative humidity here may be 10-20 % lower than at river level, and except for minor wet-season inputs, the passage is dry and lacks evidence of extant vertebrate or invertebrate fauna. The specimens were collected in the northeastern terminus, which ends at an apparent collapse feature cemented with obscuring calcite deposits. A topographic map and aerial photos of the area show a small valley on the surface above this end of the Mind Proddler; the known location of related passages at this level occur no closer than a kilometer. Active curved stalactites elsewhere in this northeast section imply the presence of long-term airflow; the likely collapse terminus offers a source for wind and a possible former entrance through which animals could have fallen and become trapped. The axis of the Mind Proddler is about 520 m long, averages 30 m wide × 10 m high, and enlarges to 50 m diameter in the collection area. The nearest

physical exits to the cave are 1300 m and 1500 m away from the collection area.

Rough on-site estimates of one bat skeleton per square meter imply an excess of 10 000 bat skeletons occurring on dirt and flowstone on the floor of the Mind Proddler. This figure does not include the more extensive southwest arm of the passage. Many of the bat skeletons seem old and the bones are soft, chalky or powdery, and extremely fragile; but some are fresh enough to have patches of skin and fur (Fig. 3). The specimens without skin and fur probably represent Holocene occurrences. Unlike these bones, one specimen, a cranium of the extinct vampire *Desmodus draculae*, was encrusted with a thin rind of gray and white crystalline calcite covering much of its right side. The thin layer of crystals on the Cebada Cave vampire skull is similar to that on a *D. draculae* skull from Santana Cave near Iporanga, Brazil (Trajano and de Vivo, 1991) and on a specimen from the type locality, Cueva del Guácharo, Venezu-
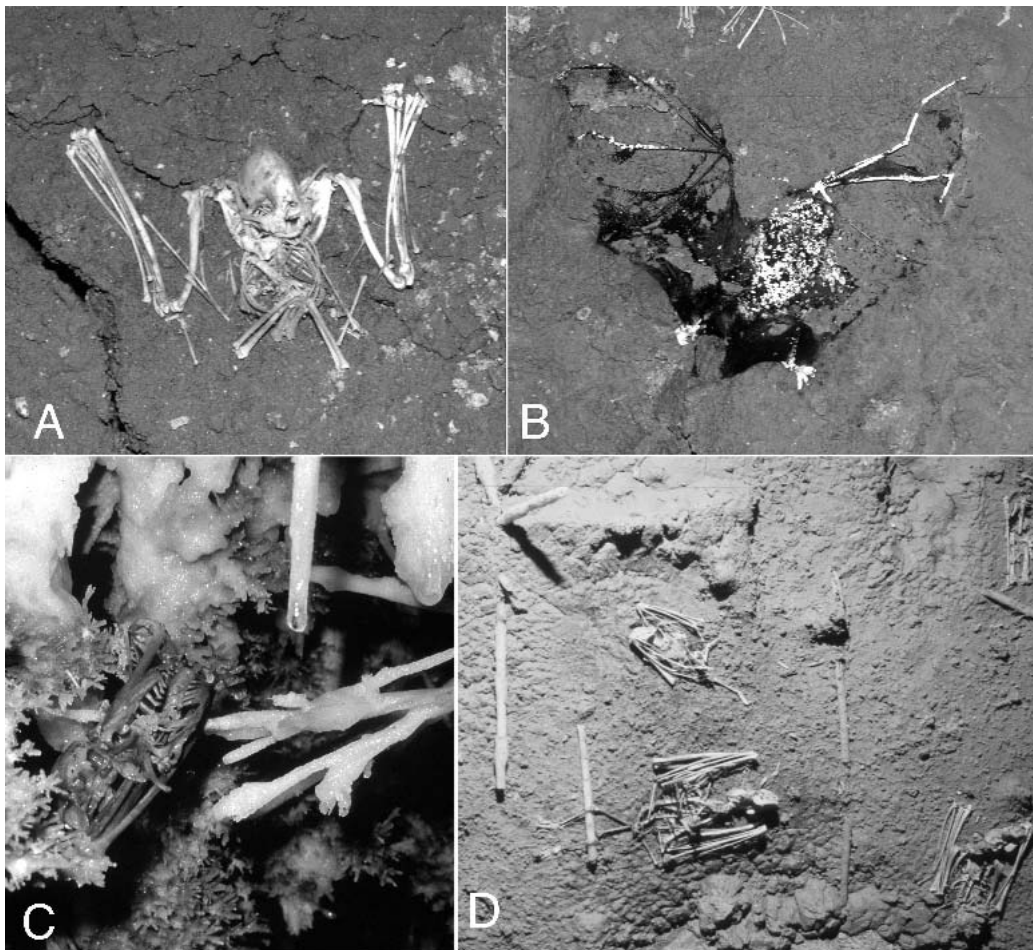

FIG. 3. Remains of bats in the Mind Proddler, Cebada Cave. Photographs not to the same scale. A. Skeleton of *Centurio senex* on cave floor. The forearm of this species is usually 42 to 47 mm long. B. Specimen in which portions of the flight membranes (black) and some poorly preserved limb bones remain (white, powdery), but the skull and torso skeleton are absent. C. Partial skeleton of a bat becoming incorporated into speleothems (at left). Note active drips on soda straw and structure at upper right. D. Skeletons of four bats on cave floor with several fallen soda straws. Soda straw beneath the knees of largest bat at lower left is approximately 10 cm long. Photos by J. Krejca.

ela (see photograph in Linares, 1986: p.10). We believe that this rind of crystals on the Cebada Cave vampire skull and its absence on the other Cebada Cave bat skeletons suggests that the extinct vampire skull could date to the Pleistocene. Unfortunately, all bat bones were completely leached of their organic content, as can occur in a few hundred years in the wet, oxidizing conditions of a limestone cave in which active dripstone is forming (T. W. Stafford, pers. comm.). The absence of protein precludes dating the bones by radiocarbon, even using AMS (Stafford et al., 1991). Several bat skeletons visible beneath several millimeters of calcite flowstone were not collected.

Specimens were sent to NJC for study and will be returned to the Ministry of Natural Resources, Forest Department Conservation Division, Belmopan, Belize. The specimens represent at least seven phyllostomids and two vespertilionids. The modern fauna of northern Central America includes about 119 bat species, 70 of which have been confirmed in Belize (McCarthy et al., 1993; McCarthy, 1998, pers. comm.) and about 96 in Guatemala. Many of these species inhabit caves and thus might occur as subfossils or fossils in the Chiquibul system. The specimens have been given temporary catalog numbers prefixed with Ceb. All specimen measurements are in millimeters.

SYSTEMATIC PALEONTOLOGY

Order Chiroptera, Family Phyllostomidae

Desmodus draculae Morgan, Linares, and Ray, 1988

Material.—Ceb329, broken cranium consisting of braincase with articulated atlas, separate right and left pieces of rostrum with maxillary teeth, disarticulated periotic, small fragments. Specimen covered with a coating of calcite crystals (Fig. 4B,E).

Discussion.—The vampire skull is damaged, with large holes in the left side of the braincase. The rostrum is broken away from the braincase but pieces are preserved which hold most of the calcite-encrusted
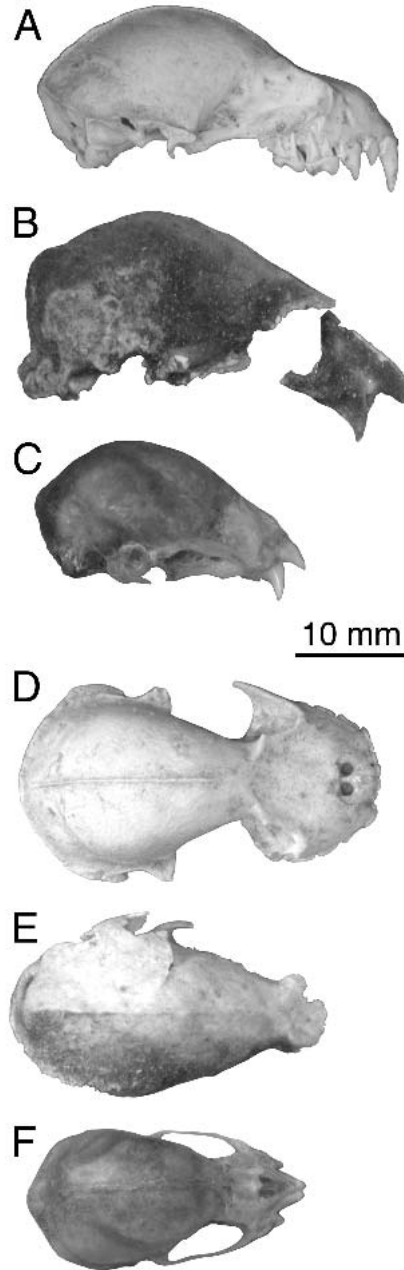

FIG. 4. Bat crania in lateral views (A-C) and dorsal views (D-F). A, D. *Artibeus lituratus* (Ceb249). B. *Desmodus draculae* braincase and associated rostrum fragment with upper incisor and canine, plus articulated axis vertebra encrusted with calcite (Ceb329). E. *Desmodus draculae* braincase and articulated axis (Ceb329); note dark calcite crystals covering most of right side. C, F. *Desmodus rotundus* modern cranium for size comparison.

upper teeth. The auditory bullae are preserved in situ. The left periotic is separated from the skull and its semicircular canals are broken off. The calcite-encrusted left malleus and incus are preserved. Measurements of the Chiquibul cranium are very similar to those of other *D. draculae* crania from South America (summarized in Czaplewski and Cartelle, 1998: table 6) and no qualitative differences occur. The measurements of the Chiquibul specimen reported here are slightly greater than the real dimensions of the skull because of the presence of the calcite coating: interorbital constriction, 6.35; zygomatic breadth, 16.48; mastoid breadth, 15.75; breadth of braincase, 15.82; distance from interorbital constriction to lambdoid crest, 21.5; basioccipital constriction, 3.39; dorsal margin of foramen magnum to top of lambdoid crest, (broken; estimated at) 6.3; anterior edge of foramen magnum to postpalatal spine, (broken; estimated at) 15.0; breadth across paroccipital processes, 12.33; width across external edges of occipital condyles, 8.68; alveolar length of maxillary toothrow, 5.06; alveolar length of I1, left 3.90, right 4.34; transverse width of I1, left 1.30, right 1.40; alveolar length of C1, left 2.70, right 2.82; transverse width of C1, left 1.12, right 1.23; crown height of C1, left 3.75, right 3.80; width of cochlea measured across second half-turn, 2.70; distance from ventral edge of fenestra cochleae to anterior apex of cochlea, 3.40; greatest diameter of fenestra cochleae, 1.10; least diameter of fenestra cochleae, 0.85.

Desmodus draculae is known from six sites: an open site in northern Argentina (Pardiñas and Tonni, 2000), three caves in Brazil (Trajano and de Vivo, 1991; Cartelle and Abuhid, 1994; Czaplewski and Cartelle, 1998), a cave (the type locality for the species) in Venezuela (Morgan et al., 1988), and a cave in the Yucatán Peninsula in Mexico (Arroyo-Cabrales and Ray, 1997). The last site, Gruta de Loltún, Yucatán, is just 400 km N of the Chiquibul cave system and is the nearest known locality of occurrence of the large vampire (identified as *D. cf. draculae* by two humerus fragments from Loltún; Arroyo-Cabrales and Ray, 1997). No specimen of *D. draculae* has been di-

rectly dated radiometrically; most are considered to date to the late Pleistocene by association with other extinct species of mammals in the cave sites. The Argentinian specimen, an isolated upper canine from an open site near Centinela del Mar, Buenos Aires province, is considered to be late Holocene by firm stratigraphic correlation and faunal association (Pardiñas and Tonni, 2000).

Tonatia saurophila Koopman and Williams, 1951

Material.—Ceb500 associated dentaries and cranium lacking most of braincase; Ceb341 right M2; Ceb336 right M3; Ceb330 left dentary with m1; Ceb331 right dentary with m1-m3; Ceb334 right p4; Ceb335 left p4; Ceb337 left m1; Ceb340 left m3.

Discussion.—In the skull with associated dentaries, all tooth loci are represented except for the lower incisor and canine. *Tonatia* species were recently separated into *Tonatia* and *Lophostoma* by Lee et al. (2002). The Cebada Cave specimens represent a large species of *Tonatia*, larger than *Lophostoma evotis* and much larger than *L. brasiliense*, but about the size of *T. saurophila* and *L. silvicola*; the latter species can be distinguished from one another by the breadth of their postorbital constriction and by a small foramen in the anterior of the palate (Williams et al., 1995). The postorbital constriction in the Cebada Cave cranium measures 5.84, matching that of *T. saurophila* and exceeding that of *L. silvicola*. The Cebada Cave skull has a small anteromedial foramen between the upper incisors and the incisive foramina which is filled with a tiny growth of calcite. The presence of the anteromedial foramen also identifies this bat as *T. saurophila* and differentiates it osteologically from *L. silvicola*. *Tonatia saurophila* was described as an extinct species based on fossils from Jamaica (Koopman and Williams, 1951), its only previously reported fossil record (Morgan, 2001), but it lives in southern Belize and surrounding areas at present (McCarthy, 1982, 1987).

Carollia subrufa (Hahn, 1905) or C. brevicauda (Schinz, 1821)

Material.—Ceb349 left C1; Ceb333 left P3; Ceb352 right M1; Ceb353 left M1; Ceb354 right M2; Ceb305 left dentary with p4-m2; Ceb306 right dentary fragment with p4-m2; Ceb297 left c1; Ceb316 right c1; Ceb360 left p3; Ceb301 right p3.

Discussion.—Direct comparisons of the isolated teeth and dentary fragments of *Carollia* from Cebada Cave show that these specimens are medium-sized among Central American *Carollia* species. Of the two dentaries preserved (Ceb305 and 306), the dentary depth as measured behind the last lower molar (Pine, 1972) is 2.3 and 2.3, respectively; mandibular tooth row length of Ceb305 is 8.2 (Ceb306 is broken and cannot be measured). These measurements put the Cebada specimens above the size range of the smallest Central American species *C. castanea*, below that of the large *C. perspicillata*, and within the ranges of the two medium-sized species, *C. subrufa* and *C. brevicauda*. The upper molars of the Cebada Cave *Carollia* are more narrowed lingually than in *C. perspicillata*. The lateral profile of the m1 shows discrete cusps, unlike those in *C. castanea* (Pine, 1972). The Cebada specimens belong to *C. subrufa* or *C. brevicauda* but there are no distinguishing features in the fragments that can separate these two species. Only *C. brevicauda* and *C. perspicillata* occur in the modern fauna of Belize; *C. subrufa* occurs at present mainly on the Pacific slope of northern Central America. In northern Central America *C. subrufa* is restricted to dry zones (McCarthy, pers. comm).

Artibeus lituratus (Olfers, 1818)

Material.—Ceb244 cranium; Ceb245 cranium; Ceb246 cranium and mandible; Ceb247 partial cranium and mandible; Ceb248 cranium and mandible; Ceb249 cranium and mandible (Fig. 4A, D); Ceb213 right half of rostrum; Ceb243 cranium fragment; Ceb214 rostral fragment; Ceb215 rostral fragment; Ceb216 rostrum; Ceb217 right half of rostrum; Ceb251 numerous periotic bones; Ceb260 miscellaneous post-cranial elements; Ceb118-138, Ceb176 P3s; Ceb75, Ceb86, Ceb88-95, Ceb97-98, Ceb175, Ceb183, Ceb359, P4s; Ceb1-5, Ceb10, Ceb13-14, Ceb16, Ceb208, Ceb212, Ceb219 M1s; Ceb38-53, Ceb55, Ceb58 M2s; Ceb221-222, Ceb227-228, Ceb232-241 mandible fragments; Ceb223-226, Ceb229-231, edentulous mandible fragments; Ceb99-104, Ceb108-109, Ceb111-114, Ceb116, Ceb186-207 canines; Ceb179-182, Ceb277-280, Ceb283-289, Ceb291-292 p3s; Ceb74, Ceb76-85, Ceb184-185, Ceb220 p4s; Ceb20, Ceb22, Ceb24-32, Ceb34-36, Ceb218, m1s; Ceb15, Ceb18-19, Ceb62-71, Ceb73 m2s; Ceb7, Ceb12, Ceb21, Ceb33, Ceb37, Ceb56-57, Ceb106, Ceb139-174, Ceb242, Ceb251-253, Ceb255-267, Ceb281, Ceb293, Ceb295, Ceb313, Ceb347, Ceb350-351, Ceb355, Ceb361-362 miscellaneous isolated teeth and fragments.

Discussion.—This is the most abundant species in the material from Cebada Cave. The specimens include several crania, a few of which have associated dentaries. The most complete available skulls and dentaries appear to represent one species, *A. lituratus*, but other large species of *Artibeus* may be represented among the numerous isolated teeth and bone fragments.

The Cebada Cave crania are very large (Table 1) and bear prominent postorbital processes and a distinct beading along the dorsal edge of the orbit. These features distinguish *A. lituratus* from *A. jamaicensis* (Davis, 1970). M3 is absent and the postorbital constriction is at or anterior to the posterior edge of the hard palate when viewed dorsally; this distinguishes *A. lituratus* (including *A. intermedius*; Marques-Aguiar, 1994) from the other large species of *Artibeus*: *A. obscurus, A. amplus,* and *A. jamaicensis* (Lim and Wilson, 1993). *Artibeus obscurus* and *A. amplus* are presently restricted to South America. The preorbital process is relatively well developed and the angular process of the dentary is broad; these features also confirm that the Cebada bats belong to *A. lituratus*, one of the most distinctive species of large *Artibeus* (Marques-Aguiar, 1994). The crania of the Cebada specimens are larger than in *A. jamaicensis*, the other large species of *Artibeus* found in Central America in historic times.

TABLE 1. Measurements (mm) of crania of *Artibeus lituratus* from Cebada Cave, Belize. Dashes indicate broken specimen where no measurement is possible.

Measurement	Specimen number (Ceb)					
	244	245	246	247	248	249
Greatest length of skull	31.00	33.35	31.60	—	—	32.35
Condylobasal length	27.95	—	28.10	—	—	28.45
Postorbital constriction	6.05	6.85	6.65	6.50	6.65	6.70
Breadth of braincase	14.10	—	14.40	—	—	14.00
Mastoid breadth	17.50	—	17.70	—	—	17.70
Length of maxillary toothrow	10.40	11.45	11.40	10.00	—	11.20
Length of palate	14.60	15.45	14.50	13.00	—	14.90
Breadth across M2s	13.80	13.70	15.10	13.05	—	14.35

Artibeus lituratus is known in the fossil state from caves near Lagoa Santa, Minas Gerais, Brazil. Winge (1893) listed *Artobius* [sic] *perspicillatus* from deposits in a cave known as Lapa da Escrivania, near Lagoa Santa; these specimens were collected during the nineteenth century without provenance data and represent mixed Pleistocene and Holocene occurrences. Paula Couto (1946) considered this taxon to be equivalent to *Artibeus ?jamaicensis lituratus* (= *A. ?lituratus*), but the Lagoa Santa specimens should be re-examined due to the difficulty in distinguishing many members of this genus. *Artibeus lituratus* is common today throughout Central America.

Artibeus (Dermanura) Gervais, 1856 sp.

Material.—Ceb298 left C1; Ceb296 right C1; Ceb273 left P3; Ceb275 left P3; Ceb358 left P4; Ceb307 mandible with right p3; Ceb110 left c1; Ceb105 right c1; Ceb282 left p3; Ceb290 left p3; Ceb96 right p4; Ceb177 right p4; Ceb363 left p4; Ceb11 right m1; Ceb23 left m1; Ceb72 left m2; Ceb294 left m2; Ceb60 right m2.

Discussion.—These specimens clearly belong to one or more of the small fruit-eating bats of the subgenus *Dermanura* (Van Den Bussche et al., 1998) known in Central America: *A. (D.) azteca, A. (D.) tolteca, A. (D.) phaeotis*, or *A. (D.) watsoni*. The only available mandible fragment (Ceb307) has no alveolus for an m3; mandibular tooth row length for this specimen is 6.8. The Cebada Cave mandible is smaller than that

of *A. azteca* based on measurements of the mandibular toothrow (Davis, 1969). *Artibeus azteca* lives in highland habitats in Guatemala and elsewhere but not in Belize (McCarthy, pers. comm.). Mandibular tooth row measurements have not been published for the other species.

Centurio senex Gray, 1842

Material.—Ceb344 fragmentary skull and mandible; Ceb276 right half of rostrum with broken teeth; Ceb209 left maxilla with I2-M2; Ceb210 right maxilla with I2, P4-M1; Ceb254 right maxilla with C1-P4; Ceb211 left maxilla with P4-M1; Ceb115 right C1; Ceb268 left P3; Ceb357 left P3; Ceb270 right P3; Ceb6 left M1; Ceb17 left M1; Ceb9 right M1; Ceb8 right M1 fragment; Ceb54 right M2; Ceb61 right M2; Ceb345 edentulous mandible; Ceb332 edentulous right dentary fragment; Ceb346 edentulous mandible fragment; Ceb348 mandible with right and left c1s and p3s, and left p4-m2; Ceb339 right p3; Ceb356 left p3; Ceb271 left p4; Ceb272 left p4; Ceb269 right p4; Ceb59 left m2.

Discussion.—Although most specimens are broken and poorly preserved, they are clearly identifiable as *C. senex*. Previous reports of this species as a fossil include a cranium reported as a subfossil in owl pellets from Infierno (near Gómez Farías), Tamaulipas, Mexico, by Koopman and Martin (1959), and two mandibles reported from a layer above the deepest layer in which archeological remains were found,

in Gruta de Loltún, Yucatán, Mexico, by Arroyo-Cabrales and Alvarez (1990). The species is found today throughout Central America in a variety of habitats where it may be locally abundant, but normally it frequents foliage rather than caves (Rick, 1968; McCarthy, 1982, 1987).

Sturnira Gray, 1842 sp.

Material.—Ceb178 left P4; Ceb300 left P4; Ceb299 left M1; Ceb274 right P3; Ceb302 right maxilla fragment with M1-M3; Ceb303 mandible with right p3-m2 lacking ascending rami; Ceb304 left dentary fragment with m1-m3 lacking ascending ramus; Ceb308 mandible with all lower teeth, encrusted with calcite, lacking ascending rami; Ceb107 left c1; Ceb338 left p4.

Discussion.—Length of mandibular tooth row in two of the Cebada Cave specimens is 7.36 for specimen Ceb303 and 7.48 (right side) and 7.32 (left side) for Ceb308. Few measurements are available for the four species of *Sturnira* (*S. lilium, S. ludovici, S. luisi*, and *S. mordax*) known in the modern fauna of Central America. Comparing with measurements provided by Arroyo-Cabrales and Alvarez (1990), Davis (1980), and Owen (1987), the Cebada specimens are slightly smaller than *Sturnira luisi* but within the range of *S. lilium, S. ludovici*, and *S. mordax*. The Cebada specimens lack a protolophid on m1, indicating they do not belong to *S. ludovici* but instead to one of the other two species.

Sturnira lilium is presently widespread throughout Central America including Belize, while the range of *Sturnira mordax* encompasses only mountainous parts of Costa Rica and western Panama and does not include Belize. *Sturnira mordax* has no fossil record while *S. lilium* is known as a fossil in late Pleistocene-Holocene cave deposits in Lapa da Escrivania, Brazil (Winge, 1893; but those specimens should be revisited given changes in the systematics of *Sturnira*), and in Gruta de Loltún, Yucatán, Mexico (Arroyo-Cabrales and Alvarez, 1990).

Family Vespertilionidae

Lasiurus blossevillii Lesson and Garnot, 1826

Material.—Ceb328 skull, dentaries, atlas; Ceb367 left half of rostrum with C1-M3; Ceb364 right half of rostrum with I1-C1 and P4-M1 (P3 socket is empty); Ceb342 right M1 or M2; Ceb326 right dentary fragment with c1-m2; Ceb366 left dentary fragment with c1-m3.

Discussion.—The specimens have a tiny P3 typical of members of the subgenus *Lasiurus* s. str. and unlike the yellow bats of the subgenus *Dasypterus*. The p4 is two-rooted in the two available dentaries. Size is slightly smaller than in comparative specimens of *L. borealis* from eastern North America and is similar to *L. blossevillii* from the southwestern United States. The latter species is known as a fossil in the early Pliocene of Arizona, USA (Czaplewski, 1993) and from late Pleistocene and Holocene cave deposits in Lapa da Escrivania near Lagoa Santa, Brazil, (Winge, 1893; Cartelle, 1994). The species presently occurs throughout Central America and normally roosts in the foliage of broadleaf trees. Remains of this and other *Lasiurus* species have been found in caves on several occasions (Myers, 1960).

Lasiurus ega (Gervais, 1856)

Material.—Ceb365 left maxilla fragment with P4-M1; Ceb315 right I1; Ceb317 left C1; Ceb319 right C1; Ceb309 right P4; Ceb323 left M1; Ceb322 right M1 or M2; Ceb324 right M1 or M2; Ceb343 right M3; Ceb325 right dentary with p4-m3; Ceb327 edentulous left dentary; Ceb320 left c1; Ceb318 right c1; Ceb314 left p3; Ceb321 right p3; Ceb312 left m1 or m2; Ceb311 left m1 or m2; Ceb310 left m3.

Discussion.—The specimens belong to a bat much larger than *L. blossevillii* and much smaller than *L. intermedius*. Specimen Ceb365, a maxilla fragment with P4-M1, lacks an alveolus for a P3, indicating a member of the subgenus *Dasypterus*. Specimen Ceb327, an edentulous ramus, has an alveolar formula indicating a two-rooted

p4. The mandibular tooth row length in two specimens (Ceb327 and 325) is 6.43 and 6.56, respectively. This species has been reported twice as a fossil: from Grutas de Loltún, Mexico, in a bed at the Pleistocene-Holocene boundary and in Holocene beds above it (Arroyo-Cabrales and Alvarez, 1990) and from the late Pleistocene or Holocene of Lapa da Escrivania near Lagoa Santa, Brazil (Winge, 1893; Cartelle, 1994). *Lasiurus ega* presently occurs throughout Belize and other parts of Central America, where it typically roosts in tree foliage; its occurrence in Cebada Cave suggests that, like other species of *Lasiurus*, it sometimes enters caves, becomes disoriented or is unable to exit and perishes.

DISCUSSION

Given the thousands of bat skeletons observed in Cebada Cave, there are probably many additional species not documented here. The skeletons likely represent a relatively long span of time, hundreds or thousands of years, but until the bones are radiometrically dated it will not be possible to determine their precise age.

Few species of bats became extinct in the Neotropics during the Quaternary (Morgan, 1999). The only extinct bat in the Cebada Cave is the large vampire, *Desmodus draculae*. This species has been reported from a few localities in South America but no specimen has been directly dated. These records are typically assumed to date to the late Pleistocene because the species is extinct, but some indirect dates on materials associated with extinct vampire bones are relatively young. The record of *D. draculae* from Argentina is from sediments containing a fauna indicating the late Holocene and is associated with radiometric dates of about 300 years ago (Pardiñas and Tonni, 2000). This record may be unusually late because it is from a coastal area. Coastal records of the extinct North American vampire *D. stocki* from the Channel Islands, California, are also much later than continental records of the species. This is presumably because the large mammals that provided them with blood went extinct on the mainland, while on the coast and islands, sea lions and seals, on which modern vampires (*D. rotundus*) feed continued to exist (Guthrie, 1980). The other Cebada Cave bats, by virtue of their lack of a calcite rime, probably date to the Holocene. The Cebada Cave *D. draculae,* with its thin covering of calcite, may not date to the Pleistocene. Local calcite deposition within a cave can vary greatly in the amount deposited, depending on conditions, and the amount of calcite is at best only a rough indicator of age. Some archeological artifacts in Belizean caves illustrate this phenomenon; for example, in the Actun Kabal section of the Chiquibul Cave System, a one-meter-tall stalagmite formed on one pottery bowl situated under a water drip, whereas another vessel immediately adjacent to it has almost no calcite deposition (McNatt, 1996: fig. 1). Nevertheless, in the absence of radiometric dates, we tentatively consider the Cebada Cave *D. draculae* to represent a Pleistocene occurrence of the species.

The absence of the extant vampire, *D. rotundus*, from Cebada is interesting in light of the presence of *D. draculae*. As has been suggested by Morgan et al. (1988), Arroyo-Cabrales and Ray (1997), and Czaplewski and Peachey, in press), *D. draculae, D. stocki*, and *D. rotundus* may represent clinal temporal and/or geographic variants of a single species lineage. However, the two radiometric dates associated with *D. draculae* at coastal sites mentioned above place it in the late Holocene (Guthrie, 1980; Pardiñas and Tonni, 2000) whereas the species has also been found in caves in South America in association with extinct Pleistocene megafauna (Cartelle and Abuhid, 1994; Czaplewski and Cartelle, 1998). Remains of *D. draculae* and *D. rotundus* were found at Toca da Boa Vista, Brazil, but not in association (Cartelle and Abuhid, 1994). Moreover, in a different Brazilian cave (Gruta dos Brejões), a *D. rotundus* cranium was found adhering to the underside of a dung bolus attributed to the extinct sloth *Nothrotherium maquinense*. The dung was dated to 12 200 ± 120 radiocarbon yrBP (Czaplewski and Cartelle, 1998). Thus, minimal evidence argues for contempora-

neity and against *D. draculae* being a chronospecific antecedent of *D. rotundus*.

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