Holocene and Late Pleistocene Bat Fossils (Mammalia: Chiroptera) from Hamilton County, TN, and their Ecological Implications

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Abstract - Chiropteran mandibles from late Pleistocene/Holocene fossil cave localities in Hamilton County were identified in order to examine changes in bat species diversity and population trends over extended periods of time, providing insight into how bats in Southeast Tennessee have responded to major environmental changes over the past 10,000–20,000 years. Generic and species identifications were based on an unpublished key developed by the authors. Measurements of alveolar length (c1–m3) and total length measurements from the symphysis to the condyle were taken for all specimens identified as members of the genus *Myotis* in an attempt to identify species in this genus. The results of this study failed to confirm those of previous univariate morphological studies, suggesting that multivariate morphometric analyses may be needed to establish a means to differentiate among the species in this genus. Diversity data indicated two patterns of species abundance, with *Eptesicus fuscus* (Big Brown Bat) dominating some sites and *Myotis* sp. dominating others. The data suggest, but do not conclusively demonstrate, that a temporal replacement of older *Eptesicus* faunas by younger, *Myotis*-dominated faunas has occurred, connected with post-Pleistocene global warming. In addition, a correspondence between human disturbance and bat populations levels was observed. It is very likely that human disturbance has caused bat populations to become extinct in the caves under study, reinforcing the claim of previous researchers that bat population decline is a recent phenomenon that is tightly linked to human disturbance.

Introduction

The transition between the late Pleistocene Epoch and the early Holocene Epoch is marked by a dramatic change in climate which caused the glacial ice sheets that covered large portions of the continent to gradually retreat (Corgan 1996, Pielou 1991). The warming period at the Pleistocene/Holocene boundary caused major changes in habitat distributions (Pielou 1991). Slowly, the diverse habitats that were common in the Pleistocene were altered as the hypsithermal periods of the early Holocene swept across the continent, with some biogeographical realms shifting northward and others disappearing entirely (Pielou 1991). These ecological changes caused many animal species to change their distribution and many large mammal species to go extinct at this time (Barnosky et al. 2004, Graham et al. 1996, Kurtén and Anderson 1980, Pielou 1991, Schubert et al. 2003). Two major hypotheses exist to explain this extinction pattern: 1) that the climate

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changes at the end of the Wisconsinan glaciation caused the large mammal ex-
tinction, or 2) that prehistoric overkill by humans caused mammal extinctions

Caves play an essential role in our understanding of the Pleistocene Epoch
in North America, as they represent the source of the fossils representing the
largest percentage of known North American Pleistocene faunas (Kurtén and
Anderson 1980, Schubert et al. 2003). They have therefore been critical in al-
lowing paleontologists to document biogeographic and evolutionary patterns
in a great variety of organisms (Corgan 1996, Schubert et al. 2003). Cave de-
posits often preserve Holocene fossils as well, but these are rarely studied by
paleontologists because they do not contain extinct taxa (Schubert et al. 2003).
However, Holocene sites can provide useful information on the evolution
of current ecosystems (Schubert et al. 2003). Tennessee, with its multitude of
caves, provides an excellent environment for exploring fossils from caves in
both the Pleistocene and Holocene (Corgan 1996). Hamilton County contains
a plethora of caves, several of which have been shown to contain Pleistocene
and Holocene fossil remains (Bramblett 1998, Corgan 1996, Gaudin and

Historically, nearly all of our information concerning the vertebrate fauna
of Hamilton County during the Pleistocene and Holocene is based on the
fossils of megafaunal and medium-sized vertebrates unearthed in Lookout
Mountain Cave by Dr. Henry C. Mercer in 1893 (Corgan 1996, Mercer 1894).
Indeed, most of the initial paleontological research on the Pleistocene of North
America focused on extinct mammalian megafauna (Kurtén and Anderson
1980). It was not until the 1920s that the number of mammalian microfaunal
taxa began to increase substantially (Kurtén and Anderson 1980). Due to the
wide biogeographic distribution and broad environmental tolerances of the spe-
cies found in Mercer’s megafaunal sample (Corgan 1996, Mercer 1894), they
are less than ideal indicators of environmental change. Microvertebrates, with
their smaller geographic ranges and narrower ecological niches, could provide
a better understanding of how vertebrate communities responded to environ-
mental changes that occurred during the Pleistocene and Holocene.

Several years ago microfaunal paleontological fieldwork was initiated in
caves at Lookout Mountain, TN (Bramblett 1998; Bramblett and Gaudin 2001;
Gaudin and Bramblett 1999; Gaudin et al. 1998, 1999) and in nearby parts of
Hamilton County (Ooltewah High School, Ooltewah, TN), and a large and di-
verse sample of Pleistocene microvertebrate remains were recovered. Included
in these faunas were over 10,000 skeletal elements from bats, including partial
skulls, mandibles, and isolated postcranial remains (Bramblett and Gaudin
2001, Gaudin and Bramblett 1999). A sample of these bat fossils were identi-
fied (Bramblett and Gaudin 2001, Gaudin and Bramblett 1999), demonstrating
the presence of at least six extant species of bats, most of which are cave-dwell-
ing for at least part of the year: Myotis septentrionalis (Trouessart) (Northern
Long-eared Bat), M. grisescens A.H. Howell (Gray Bat), Perimyotis subflavus
(F. Cuvier) (Tricolored Bat), Corynorhinus rafinesquii Lesson (Rafinesque’s Big-eared Bat), Eptesicus fuscus (Beauvois) (Big Brown Bat), and Lasiurus sp. (L. borealis (Müller) [Eastern Red Bat] or L. seminolus (Rhoads) [Seminole Bat]) (Bramblett and Gaudin 2001, Gaudin and Bramblett 1999). Among these species, C. rafinesquii is currently uncommon and of special concern in parts of its range, and M. grisescens is a federally listed endangered species (Choate et al. 1994, Harvey et al. 1999).

Although a small population of P. subflavus persists in Ooltewah High School Cave, we found no evidence that bat colonies are currently dwelling in any of the Lookout Mountain caves in which fossils were discovered (Bramblett 1998). The presence of extensive bat colonies in these caves in the Pleistocene and Holocene, and their absence today, raises intriguing questions regarding the causes of their disappearance. Obvious human disturbance is evident at all our Lookout Mountain Cave localities. These disturbances range from a railroad track that runs through one entrance to guided tours at another entrance. Human perturbation is thought to be a major contributor to declines in cave bat populations by disturbing hibernation or nursery sites (Tuttle 1979).

Tuttle (1979) used the size and color of stains from bat guano (or other bodily secretions) on the ceilings of caves as an indicator of the size of historical bat populations roosting in the caves. The estimates of current population size were obtained by taking the number of square meters covered by new guano and multiplying it by the mean clustering density of 1828/m² (Tuttle 1975, 1976, 1979). Historic colony size was calculated from the area covered by old guano deposits or the area of staining on the cave roof (Tuttle 1979). Tuttle’s work suggested that M. grisescens, a species of bat found among the fossil bats from the Lookout Mountain caves, had recently experienced a dramatic population decline (Tuttle 1979). We note that this inference depends on the assumption of roost fidelity, i.e., that colonies roost in the same part of the cave ceiling each year (Tuttle 1979). Though Tuttle may have observed roost fidelity during the six years of his study (Tuttle 1979), it is possible that over centuries or millennia the bats slowly migrated across the cave ceiling, using different parts as roosting areas. If the latter were true, Tuttle’s (1979) inferences about the long-term population trends in this species might need to be reconsidered.

Paleontology may offer an alternative method for examining long-term population trends by providing data over a longer time frame than guano stains will allow. Furthermore, paleontological studies offer an independent source of data via the preservation of actual remains. Because most bat species from the Pleistocene and Holocene of North America are still extant (Kurtén and Anderson 1980), comparison of information on the known taxonomic diversity and ecological characteristics of the modern bat fauna (Barbour and Davis 1969; Best and Jennings 1997; Caceres and Barclay 2000; Choate et al. 1994; Decher and Choate 1995; Fujita and Kunz 1984; Harvey 1992; Harvey et al. 1999; Jones 1977; Kunz and Martin 1982; Kurta and Baker 1990; Shump and Shump 1982a, b) to paleontological cave assemblages has the potential to yield
insight into a number of interesting questions. For example, such comparisons can give us insight into how changes in biogeographic distributions and population levels over time are correlated with environmental changes. The goal of the present study is to use paleontology as a tool to contribute to our knowledge of the historical ecology of bats. We identified chiropteran mandibles from known fossil localities in order to examine changes in population and species diversity over extended periods of time. This information in turn should provide insight into how bats in Southeast Tennessee have responded to major environmental changes, including climate change, habitat change, and human disturbance over the past 10,000–20,000 years.

Methods

Chiropteran mandibles were identified based on a taxonomic key for lower jaws of Holocene bats from the southeastern United States prepared by three of us (T.J. Gaudin, J.L. Bramblett, and A.N. Miller) (see Supplemental Appendix 1, available online at http://www.eaglehill.us/SENAonline/suppl-files/s10-4-882-Gaudin-s1, and, for BioOne subscribers, at http://dx.doi.org/10.1656/S882.s1). This key allowed for identifications of most specimens to the species level. However, only one species (Myotis septentrionalis) within the genus Myotis was distinguishable using meristic characteristics. A quantitative method for determining species identifications within the genus Myotis was used by Guilday et al. (1977) to identify specimens belonging to the species Myotis grisescens and Myotis leibii (Audubon and Bachman) (Eastern Small-footed Bat). Their method involved measuring alveolar length between alveolus of the lower canine and the last lower molar (c1 to m3). These measurements were plotted on a histogram, revealing distinct peaks associated with the smallest (M. leibii) and the largest (M. grisescens) species of Myotis (Guilday et al. 1977). We repeated Guilday et al.’s (1977) measurements for all specimens identified as members of the genus Myotis. Total mandibular lengths from the symphysis to the condyle were also taken on all Myotis specimens for purposes of comparison. All measurements were obtained using Mitutoyo® dial calipers, and recorded to the nearest 0.01 mm. The measurement data were then used to construct histograms using Microsoft Excel®. No current method can be used to unambiguously identify skeletal remains of the other southeastern US species of Myotis to the species level (M. sodalis Miller and Allen [Indiana Bat], M. austroriparius [Rhoads] [Southeastern Bat], and M. lucifugus [LeConte] [Little Brown Bat]). Therefore, we were unable to distinguish these species in this study.

Taxonomic identifications and provenance of over 900 unidentified fossil bat mandibles from four localities were recorded in a database at the University of Tennessee at Chattanooga Natural History Museum. Two of the localities lie in separate portions of Lookout Mountain Cave (herein designated as RR, RF) (Barr 1961, Corgan 1996). Another unnamed locality was designated Cave Without Name (CWN) by Gaudin et al. (1998, 1999). All of these localities lie at the north
end of Lookout Mountain near Chattanooga, TN. The final locality is Ooltewah High School Cave (OHS) in Ooltewah, TN (Table 1). After all bat fossils were identified and cataloged, the diversity at specific recovery sites within each cave locality was determined using pie charts created in Microsoft Excel®. Minimum number of individuals (MNI) (based on right mandibles) were initially calculated in order to estimate population sizes for the various bat species at each site (Benton et al. 1994). However, total number of elements ultimately was used because MNI yielded sample sizes that were too small for analysis.

The total number of elements for each species at a given site was then used to calculate heterogeneity and evenness measures from each site using Simpson’s measure of evenness (Simpson 1949), Camargo’s index of evenness (Carmargo 1993), and Smith and Wilson’s index of evenness (Smith and Wilson 1996) using the computer program Methods® (Krebs 2000). The Methods® program was also used to generate Euclidean distances, a Bray-Curtis metric (Bray and Curtis 1957), a Canberra metric (Lance and Williams 1967), and percent similarities (Renkonen 1938) for each locality except OHS cave. These latter tests require data from at least three sites. Unfortunately, OHS cave did not have enough sites to run these analyses. Evenness measurements should indicate the degree to which relative abundances of individuals among the different species are comparable (Krebs 2000). Euclidean distance, Bray-Curtis metric, Canberra metric, and percent similarity give information about the degree of relative similarity among the sites at a given locality with regards to species composition. Several sites were omitted from analysis for the Euclidean distance, Bray-Curtis metric, Canberra metric, and percent similarity measures from both the RF (site 5) and RR (sites 7 and 8) localities. The small number of species recovered from these sites interfered with the function of the pertinent equations.

Table 1. Cave locality information.

<table>
<thead>
<tr>
<th>Cave</th>
<th>Elevation</th>
<th>Latitude and longitude</th>
<th>Site</th>
<th>Site age (YPB)</th>
<th>Sediment type</th>
<th>Sample size (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>CWN</td>
<td>660’</td>
<td>35.024°N, 85.342°W</td>
<td>1</td>
<td>14,459 ± 786</td>
<td>Yellow sand</td>
<td>26</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2</td>
<td>14,459 ± 786</td>
<td>Yellow sand</td>
<td>13</td>
</tr>
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<td></td>
<td></td>
<td></td>
<td>4</td>
<td>14,459 ± 786</td>
<td>Yellow sand</td>
<td>32</td>
</tr>
<tr>
<td>RF</td>
<td>660’</td>
<td>35.021°N, 85.338°W</td>
<td>1</td>
<td>14,811 ± 682</td>
<td>Orange clay</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2</td>
<td>14,811 ± 682</td>
<td>Orange clay</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>4</td>
<td>14,811 ± 682</td>
<td>Orange clay</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>5</td>
<td>14,811 ± 682</td>
<td>Orange clay</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>6</td>
<td>25,458 ± 2100</td>
<td>Orange clay</td>
<td>21</td>
</tr>
<tr>
<td>RR</td>
<td>700’</td>
<td>35.021°N, 85.338°W</td>
<td>1</td>
<td>16,148 ± 483</td>
<td>Orange clay</td>
<td>614</td>
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<td></td>
<td></td>
<td></td>
<td>2</td>
<td>Unknown</td>
<td>Dark silty clay</td>
<td>86</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>3</td>
<td>&gt;10,000</td>
<td>Orange clay</td>
<td>20</td>
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<td>5</td>
<td>&lt;500</td>
<td>Orange clay</td>
<td>18</td>
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<td></td>
<td></td>
<td>7</td>
<td>Unknown</td>
<td>Dark silty clay</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>8</td>
<td>Unknown</td>
<td>Dark silty clay</td>
<td>4</td>
</tr>
<tr>
<td>OHS</td>
<td>800’</td>
<td>35.095°N, 85.066°W</td>
<td>1</td>
<td>&lt;10,000</td>
<td>Brown sandy silt</td>
<td>4</td>
</tr>
</tbody>
</table>
Ages of sites within each locality were determined by radiocarbon dating and faunal analysis. AMS Radiocarbon dating was performed by Rafter Radiocarbon Laboratory (Lower Hutt, New Zealand). Elements used for the radiocarbon analysis were selected from Pleistocene species, where possible, in an attempt to approximate the maximum ages for each site. Dates were obtained for three sites in RR: RR1 at \( \approx 16,000 \) ybp, based on radiocarbon dating \((16,148 \pm 483 \) ybp, date based on dermal scute from the extinct *Dasypus bellus* (Simpson) [Beautiful Armadillo], sample ID number R 24720/1); RR3 at >10,000 ybp, based on the presence of *D. bellus* (Kurtén and Anderson 1980); and RR5 at <500 ybp, based on the presence of *Mus musculus* L. (House Mouse). The site at the OHS cave locality was dated at <10,000 ybp based on the presence of *Blarina carolinensis* (Bachman) (Southern Short-tailed Shrew), which, according to Klippel and Parmalee (1982), likely arrived in middle Tennessee in the Holocene. Radiometric dates were obtained for two sites in RF: RF1 at \( \approx 15,000 \) ybp \((14,811 \pm 682 \) ybp, date obtained from molar of extinct peccary *Mylohyus* sp., R 24888/2); and RF6 at \( \approx 25,500 \) ybp \((25,458 \pm 2100 \) ybp, date obtained from radius of *Marmota monax* L. (Woodchuck), R 24888/3). However, sites RF1–5 were part of the same streambed, and fossils at all five localities are recovered only in the upper few centimeters of sediment. We therefore believe that all five sites can be treated as effectively contemporaneous. Similarly, a radiometric date was obtained for only one site in CWN (CWN1 dated at 14,459 ± 786 ybp, date obtained from upper molar of *Mylohyus* sp., R 24888/1), but because CWN2 and CWN4 were part of the same streambed, with fossils found only in the upper few centimeters of sediment, they too were treated as contemporaneous. Note the deposits from the RR (16,000 ybp to <500 ybp) and RF (25,500 ybp to 15,000) localities likely exhibit a relatively small temporal overlap, and that both encompass a broad range in time, from 10 to 15 thousand years (Table 1).

**Results**

A total of 909 bat mandibles were identified from the four cave localities. The most common genus within the sample was *Myotis*, with 439 elements. The most common species identified was *Eptesicus fuscus*, with 268 elements. Other taxa that occurred in smaller numbers included species within the genus *Corynorhinus* (68 elements: *C. sp.*, 42 elements; cf. *C. sp.*, 20 elements; *C. rafinesquii*, 6 elements), *Perimyotis subflavus* (29 elements), and *Lasiurus borealis* or *L. seminolus* (6 elements; cf. *L. borealis* or *L. seminolus*, 1 element). A portion of the sample was unidentifiable at the genus or species level (97 elements).

Of those 439 specimens belonging to the genus *Myotis*, 309 elements were sufficiently preserved to obtain mandibular measurements. Total mandibular lengths (symphysis to condyle) for this sample ranged from 9.38 mm to 11.60 mm (Fig. 1). Alveolar length (c1 to m3) ranged from 4.72 mm to 7.50 mm (Fig. 2). The histograms created based on these measurements show several distinct peaks (Figs. 1, 2). For total mandibular length, six peaks are noted at 9.4
mm, 9.7–9.8 mm, 10.1 mm, 10.4 mm, 11.1 mm, and 11.4 mm (Fig. 1). A total of five peaks are present among the alveolar length data. These occur at 5.0 mm, 5.5 mm, 5.7–5.8 mm, 6.2 mm, and 6.5 mm respectively (Fig. 2).

Because *Myotis septentrionalis* was the only species in this genus that could be identified with a meristic (i.e., size-independent) characteristic, species-level variation in total mandibular and alveolar length measures was examined separately. *M. septentrionalis* exhibited broad variation in both measurements, overlapping much of the range of the total data sample, with mandibular lengths ranging from 10.3–11.4 mm (mode of 10.9 mm), and alveolar lengths (c1–m3) ranging from 5.5–6.9 mm (mode of 6.5 mm). When *M. septentrionalis* was removed from the total sample (Figs. 3, 4), the peak at 11.4 mm in the total mandibular length data was eliminated, whereas the other five original peaks remained intact (Fig. 3). For the alveolar length data, removal of *M. septentrionalis* left all peaks intact, but resulted in a decrease in the magnitude of the peaks at 5.5 mm, 6.2 mm, and 6.5 mm (Fig. 4).

The total number of individuals, site diversity, and site age are summarized in Tables 1 and 2. Charts illustrating the abundance of species recovered at each

![Figure 1](image1.png)

**Figure 1.** Histogram showing distribution of mandibular lengths (measured from symphysis to the condyle) among all *Myotis* specimens measured in the present study (*n* = 120).

![Figure 2](image2.png)

**Figure 2.** Histogram showing distribution of alveolar lengths (measured from c1 to m3) among all *Myotis* specimens measured in the present study (*n* = 309).
site (Figs. 5–8) appear to fall into two categories. Half the sites are dominated by *Eptesicus fuscus*, with *E. fuscus* comprising at least 50% of the total number of recovered specimens (Figs. 5, 6). These *E. fuscus*-dominated sites include all the sites at the Cave without name (CWN) locality and the Ruby Falls entrance to Lookout Mountain Cave (RF) locality. The remaining bat faunas are dominated by members of the genus *Myotis* (Figs. 7–9). Faunas where *Myotis* comprised

Table 2. Summary of similarity metrics at each locality. BC = Bray-Curtis metric, CM = Canberra metric, ED = Euclidean distance, and PS = percent similarity.

<table>
<thead>
<tr>
<th>Locality</th>
<th>Sites</th>
<th>BC</th>
<th>CM</th>
<th>ED</th>
<th>PS</th>
</tr>
</thead>
<tbody>
<tr>
<td>CWN</td>
<td>1 vs. 2</td>
<td>0.46</td>
<td>0.15</td>
<td>4.55</td>
<td>69.2</td>
</tr>
<tr>
<td></td>
<td>1 vs. 4</td>
<td>0.86</td>
<td>0.91</td>
<td>1.93</td>
<td>95.0</td>
</tr>
<tr>
<td></td>
<td>2 vs. 4</td>
<td>0.40</td>
<td>0.21</td>
<td>6.31</td>
<td>69.2</td>
</tr>
<tr>
<td>RF</td>
<td>1 vs. 2</td>
<td>0.51</td>
<td>0.31</td>
<td>6.81</td>
<td>80.0</td>
</tr>
<tr>
<td></td>
<td>1 vs. 4</td>
<td>0.33</td>
<td>0.42</td>
<td>7.35</td>
<td>92.0</td>
</tr>
<tr>
<td></td>
<td>1 vs. 6</td>
<td>0.83</td>
<td>0.57</td>
<td>2.45</td>
<td>76.8</td>
</tr>
<tr>
<td></td>
<td>2 vs. 4</td>
<td>0.67</td>
<td>0.57</td>
<td>1.50</td>
<td>80.0</td>
</tr>
<tr>
<td></td>
<td>2 vs. 6</td>
<td>0.45</td>
<td>0.49</td>
<td>7.09</td>
<td>64.8</td>
</tr>
<tr>
<td></td>
<td>4 vs. 6</td>
<td>0.38</td>
<td>0.83</td>
<td>8.00</td>
<td>84.8</td>
</tr>
<tr>
<td>RR 15</td>
<td>1 vs. 2</td>
<td>0.23</td>
<td>0.21</td>
<td>81.83</td>
<td>68.3</td>
</tr>
<tr>
<td></td>
<td>1 vs. 3</td>
<td>0.06</td>
<td>0.13</td>
<td>94.82</td>
<td>77.3</td>
</tr>
<tr>
<td></td>
<td>1 vs. 4</td>
<td>0.04</td>
<td>0.13</td>
<td>96.59</td>
<td>59.8</td>
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<td>1 vs. 5</td>
<td>0.06</td>
<td>0.14</td>
<td>95.30</td>
<td>57.0</td>
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<tr>
<td></td>
<td>2 vs. 3</td>
<td>0.38</td>
<td>0.43</td>
<td>14.93</td>
<td>79.4</td>
</tr>
<tr>
<td></td>
<td>2 vs. 4</td>
<td>0.24</td>
<td>0.41</td>
<td>16.60</td>
<td>64.0</td>
</tr>
<tr>
<td></td>
<td>2 vs. 5</td>
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<td>0.46</td>
<td>15.09</td>
<td>73.6</td>
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<td></td>
<td>3 vs. 4</td>
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<td>0.63</td>
<td>2.41</td>
<td>65.0</td>
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<td></td>
<td>3 vs. 5</td>
<td>0.68</td>
<td>0.61</td>
<td>2.10</td>
<td>65.0</td>
</tr>
<tr>
<td></td>
<td>4 vs. 5</td>
<td>0.80</td>
<td>0.94</td>
<td>1.61</td>
<td>86.1</td>
</tr>
</tbody>
</table>

Figure 3. Histogram showing distribution of mandibular lengths (measured from symphysis to the condyle) among all *Myotis* specimens, except *M. septentrionalis*, measured in the present study (n = 101).
at least 50% of recovered specimens are found at all the sites from the railroad entrance to Lookout Mountain Cave (RR) and the Ooltewah High School Cave locality (OHS). Among all the sites excavated, RR1 had the largest number of

Figure 4. Histogram showing distribution of alveolar lengths (measured from c1 to m3) among all *Myotis* specimens, except *M. septentrionalis*, measured in the present study \((n = 258)\).

Figure 5. Species diversity based on total number of individuals recovered per species at each of the various sites within the Cave without Name (CWN) locality: a. Site 1, b. Site 2, and c. Site 4.
individuals, the highest level of species diversity, and included all species of Chiroptera found within the total sample (Fig. 7a, Table 1).

Information on the similarity among sites (excluding OHS) obtained using Euclidean distance (ED), Bray-Curtis metric (BC), Canberra metric (CM) and percent similarity (PS) indicate varying degrees of similarity (Table 2). Among the sites within CWN, sites 1 and 4 appear to be the most similar, with a 95% similarity. Sites 1 and 4 also have BC and CM values that approach 1, and a markedly smaller ED than other site-by-site comparisons. This similarity can also be observed by comparing the species list for these sites (Fig. 5).

Strong PS are seen throughout all sites in RF, with the lowest being ≈65% for site RF2 versus RF6. Site RF6 exhibits a stronger PS value when compared with site RF4 (≈85%) than it does when compared to site RF2, which is similar in age to site RF4 (Table 1). The ED values for site RF6 are relatively high when compared with sites RF2 and RF4 (7.09 and 8.00, respectively), but markedly lower.

Figure 6. Species diversity based on total number of individuals recovered per species at each of the various sites within the Lookout Mountain Cave, Ruby Falls (RF) locality: a. Site 1, b. Site 2, c. Site 4, and d. Site 6.

Figure 7 (opposite page). Species diversity based on total number of individuals recovered per species at each of the various sites within the Lookout Mountain Cave, Railroad entrance (RR) locality: a. Site 1 and b. Site 2.
when compared with site RF1 (2.45). Some inconsistencies can be noted when comparing results across indices. CM seemed to indicate that site RF4 and RF6 are the most similar. Values from BC showed sites RF1 and RF6 as most similar, whereas PS indicated sites RF1 and RF4 are most similar. Sites RF2 and RF4 had the smallest ED values.

Figure 8. Species diversity based on total number of individuals recovered per species at each of the various sites within the Lookout Mountain Cave, Railroad entrance (RR) locality: a. Site 3, b. Site 4, c. Site 5, and d. Site 8.

Figure 9. Species diversity based on total number of individuals recovered per species at each of the various sites within the Ooltewah High School Cave (OHS) locality.
The railroad entrance to Lookout Mountain sites also exhibited fairly high PS values (57% or greater). ED, CM, and BE indicate similarity among all sites except site RR1, although PS values for site RR1 are well within the range of the other site-by-site comparisons. The most similar sites appear to be RR4 and RR5, with the smallest ED (1.61), BC and CM values very close to 1, and a very high PS (86.1%). This observation is reinforced by a comparison of species abundance patterns for those sites (Fig. 8b, c).

Information on the heterogeneity and evenness within each locality was obtained using Smith and Wilson’s index (SW), Carmago’s index (C), and Simpson’s measure of evenness (S) (Table 3). These indices indicated that most localities had a moderate level of biodiversity. High levels of biodiversity were noted using SW, C, and S for RR1 (SW = 0.204, C = 0.379, S = 0.390) and RR2 (SW = 0.316, C = 0.292, S = 0.241). Results from SW also indicated that RF6 (SW = 0.267, C = 0.548, S = 0.55) had high levels of biodiversity, whereas the other indices indicated average levels of biodiversity at this site. Relatively low biodiversity was evident using SW, C, and S for RF4 (SW = 0.924, C = 0.833, S = 0.9) and OHS1 (SW = 0.813, C = 0.75, S = 0.8). The value of 1.0 for RR8 using SW, C, and S reflected the fact that sample size for all species were equal at this site.

### Discussion

Although, as noted previously, only *Myotis septentrionalis* could be distinguished from other *Myotis* species based on meristic characters, we were able to recognize some *Myotis grisescens* and *M. leibii* specimens based on morphological measurements. However, the size distribution within our sample differs dramatically from that of Guilday et al. (1977). Guilday et al.

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### Table 3. Summary of heterogeneity and evenness at each site.

<table>
<thead>
<tr>
<th>Sites</th>
<th>S</th>
<th>C</th>
<th>SW</th>
</tr>
</thead>
<tbody>
<tr>
<td>CWN1</td>
<td>0.691</td>
<td>0.590</td>
<td>0.569</td>
</tr>
<tr>
<td>CWN2</td>
<td>0.494</td>
<td>0.577</td>
<td>0.696</td>
</tr>
<tr>
<td>CWN4</td>
<td>0.603</td>
<td>0.563</td>
<td>0.341</td>
</tr>
<tr>
<td>RF1</td>
<td>0.590</td>
<td>0.573</td>
<td>0.566</td>
</tr>
<tr>
<td>RF4</td>
<td>0.900</td>
<td>0.833</td>
<td>0.924</td>
</tr>
<tr>
<td>RF5</td>
<td>0.667</td>
<td>0.667</td>
<td>0.743</td>
</tr>
<tr>
<td>RF6</td>
<td>0.550</td>
<td>0.548</td>
<td>0.267</td>
</tr>
<tr>
<td>RR1</td>
<td>0.390</td>
<td>0.379</td>
<td>0.204</td>
</tr>
<tr>
<td>RR2</td>
<td>0.241</td>
<td>0.292</td>
<td>0.316</td>
</tr>
<tr>
<td>RR3</td>
<td>0.476</td>
<td>0.500</td>
<td>0.515</td>
</tr>
<tr>
<td>RR4</td>
<td>0.600</td>
<td>0.600</td>
<td>0.680</td>
</tr>
<tr>
<td>RR5</td>
<td>0.476</td>
<td>0.511</td>
<td>0.576</td>
</tr>
<tr>
<td>RR8</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
</tr>
<tr>
<td>OHS1</td>
<td>0.800</td>
<td>0.750</td>
<td>0.813</td>
</tr>
</tbody>
</table>
(1977) identified any specimen with an alveolar length of 5.5 mm or less as pertaining to *M. leibii* and any specimen with an alveolar length of 6.6 mm or greater as belonging to *M. grisescens* (Guilday et al. 1977). In contrast, in our study, the lower alveolar peak occurred at 5.0 mm, and no clear upper alveolar length peak was present, except for a peak at 6.5 mm (Fig. 2) that fell within the range of *M. septentrionalis* (5.5–6.9 mm) and therefore could not be attributed to *M. grisescens*. When the total length data were examined, a clear upper peak could not be seen once *M. septentrionalis* was removed from the histogram (Fig. 4). Nevertheless, we were able to assign specimens above the range for total mandibular length in *M. septentrionalis* (11.5 mm or greater) to *M. grisescens*. Specimens occurring at or below the lower peaks in both total mandibular length (9.5 mm or less) and alveolar length (5.0 mm or less) were assigned to *M. leibii*.

Although differences in the age or the mode of formation of the deposits may exist between the present study and that of Guilday et al. (1977), it is not readily apparent how these differences would translate into differences in the distribution of measurements found in both studies. The range in locality age (<500 ybp to 25,500 ybp) is much greater in our study than in that of Guilday et al. (1977). Guilday et al. (1977) estimate that the Clark’s Cave deposit is somewhere between 20,000 and 11,000 ybp. Thus, their fauna may be older than some of our remains. Therefore, it is conceivable that the relevant species of *Myotis* have changed size over time, as is known to occur in other mammalian lineages, which often become smaller in the warming post-Pleistocene climate (Kurtén and Anderson 1980). This hypothesis would explain the apparent reduction in the size of *M. leibii* mandibles, but would not account for the lack of a clear upper peak for *M. grisescens* in our analysis. It is also possible that both analyses have erred in assuming that Holocene species represent a reasonable proxy for Pleistocene diversity. It is certainly possible that different *Myotis* species, either extinct varieties or Recent species with a different modern geographic distribution, inhabited these areas at various times in the Pleistocene, skewing the measurement distribution of one or both analyses. Whatever the cause, taken together, the results of the two studies imply that simple length measures may not be sufficient even for identification of the largest and the smallest *Myotis* species. Moreover, neither we nor Guilday et al. (1977) were able to distinguish between the medium-size *Myotis* species from the southeast [*M. austroriparius*, *M. sodalis*, and *M. lucifugus*]. It seems clear that multivariate morphological studies are needed to establish a means to differentiate among the species in this genus. Such multivariate analyses are beyond the scope of this study.

Community-level numeric analysis seems to suggest close similarity among sites within CWN (Table 2). This similarity makes sense considering that sites in CWN occur within a single dry streambed. The fact that sites CWN1 and CWN4 are physically the two most distant sites at the locality but are ecologically the most similar seems to confirm that all sites at this locality are uniform in age and composition, and may once have been part of a
larger metapopulation. Interestingly, similar intra-site homogeneity is evident for RF, even though there appears to be a 10,000-year age difference between RF1–4 and RF6. Some RF sites appear to be more similar to RF6 than other RF sites of similar age, and all sites are dominated by *Eptesicus fuscus*. Therefore, based on this sample, site age does not appear to have a strong effect on species composition for RF sites. The RR locality also exhibits substantial similarity among sites for some, but not all, measurements. Though species composition among sites was similar (Figs. 7 and 8), ED, CM, and BC indicated a sizable difference between site 1 and the other sites (Table 2). This difference may be due to the large sample size from site 1 (614 elements) when compared to other sites (4–86 elements). The large sample sizes of RR1 and RR2 may also help explain the higher level of biodiversity noted for both localities using SW, C, and S. Similarly, the relatively small sample size (4–6 elements) of RF4, RR8, and OHS1 likely explains the low levels of diversity seen using SW, C, and S for these localities.

The variation in the abundance of particular bat genera and species among localities is apparent from the species distributions pie charts shown in Figures 5–9. These figures indicate that *E. fuscus* dominates sites within CWN and RF, whereas *Myotis* sp. dominates sites at RR and OHS. The reason for this difference in abundance is not clear. RF and RR are both part of the same cave system and share similar external environments, indicating that external environments probably do not play a role in the pattern of dominance observed. Cave size also does not seem to be a factor in determining species abundance. RF and RR are part of a single large cave system, but have distinctly different species abundance patterns. OHS and CWN are relatively small caves, but are also dominated by different species.

Habitat preference of extant bat species might help explain species distributions within our sample. Some bat species, like *Myotis grisescens*, roost only in caves (Barbour and Davis 1969, Choate et al. 1994, Harvey 1992, Harvey et al. 1999). Other species like *M. leibii, E. fuscus,* and *Perimyotis subflavus,* occur in a wider range of habitats that include abandoned mines, man-made structures, rock crevices, trees, etc. (Barbour and Davis 1969, Choate et al. 1994, Harvey 1992, Harvey et al. 1999). Although one species, *L. seminolus,* will occasionally roost in caves, and individuals of several other species of southeastern *Lasiurus* are sometimes found in and around cave entrances, the preferred roosting habitat for most southeastern *Lasiurus* are trees (Barbour and Davis 1969, Choate et al. 1994, Harvey 1992, Harvey et al. 1999), which almost certainly explains why *Lasiurus* sp. represents only a small portion of the sample. Interestingly, exclusively cave-dwelling species do not make up a majority of our sample. However, with the exception of *Lasiurus,* there is no clear correlation between habitat preferences and the pattern of species abundance in our sample. In fact, *Myotis* sp. and *E. fuscus* were found to dominate cave localities that appear to conflict with their general habitat preferences. Many species of *Myotis* prefer cool but not freezing winter hibernacula, and tend to be more abundant in
deeper portions of the caves they inhabit (Barbour and Davis 1969, Best and Jennings 1997, Choate et al. 1994, Decher and Choate 1995, Harvey 1992, Harvey et al. 1999)—M. leibii is an exception to this generalization, but this rare, cold-tolerant species apparently represents only a small portion of our sample. On the other hand, E. fuscus is very cold tolerant and prefers cooler, even freezing hibernacula (Barbour and Davis 1969, Choate et al. 1994, Harvey 1992, Harvey et al. 1999). It is therefore often found near the entrances of caves. Yet in our own sample, Myotis were prevalent from the front of the Lookout Mountain cave system (RR locality), whereas E. fuscus were abundant at the back of the same cave system (RF locality).

Colony size may also contribute to the observed pattern in species abundances. Several bat species present in our sample are characterized by large colony sizes of 100 to over 1000 individuals. This pattern is typical for M. grisescens, M. lucifugus, M. sodalis, and E. fuscus (Barbour and Davis 1969, Choate et al. 1994, Decher and Choate 1995, Harvey 1992, Harvey et al. 1999, Kurta and Baker 1990). It is perhaps not surprising then that these two genera, Myotis and Eptesicus, dominate the overall sample, although it does not explain why particular faunas are dominated by one genus or the other. Our remains also incorporate species (Corynorhinus sp., Lasiurus sp., Perimyotis subflavus, M. septentrionalis, and M. leibii) that roost singly or in small colonies less than 100 individuals (Barbour and Davis 1969; Best and Jennings 1997; Caceres and Barclay 2000; Choate et al. 1994; Fujita and Kunz 1984; Harvey 1992; Harvey et al. 1999; Kunz and Martin 1982; Shump and Shump 1982a, b). One might expect these taxa to dominate the small samples obtained from smaller caves because small caves cannot accommodate large colonies. However, this was not the case in our study. One small cave system, CWN, was dominated by E. fuscus remains, whereas the other small cave system, OHS, yielded mostly remains from Myotis sp., although none of the OHS Myotis specimens could be identified to species.

M. septentrionalis represents a sizable portion of the sample from the Lookout Mountain cave system (RR and RF), yet it has colonies of no more than 100 individuals (Barbour and Davis 1969, Caceres and Barclay 2000, Choate et al. 1994, Harvey 1992, Harvey et al. 1999). The prevalence of M. septentrionalis may be an indication that several of these cave sites preserve a mixed-age assemblage. The large sample of M. septentrionalis elements is likely the result of the accumulation of elements over a long period of time. Although the sites themselves do not provide detailed stratigraphic information, time averaging of M. septentrionalis specimens could be demonstrated through AMS radiocarbon dating of multiple specimens, but this is expensive and is beyond the scope of this study.

It is possible that the differential pattern of species abundance at different sites can be explained as the result of temporal changes associated with overall climate change in the area. Most of the E. fuscus-dominated localities (CWN1, 2, and 4 and RF1, 2, 4, and 6) are similar in age, having been dated
to an age of about 14,000 ybp (14,811 ± 682 ybp [RF1, 2, and 4] and 14,459 ± 786 ybp [CWN sites]). However, site RF6, which is also *E. fuscus* dominated, is ≈10,000 years older (25,458 ± 2100 ybp) than the other sites. The age range for *Myotis*-dominated sites (RR and OSH) is even more substantial. Within two RR localities alone, there are sites radiocarbon dated to >16,000 ybp (16, 148 ± 483 ybp [RR1]) and sites dated faunally to <500 ybp (RR5). The OHS cave was faunally dated to <10,000 ybp. The *Eptesicus*-dominated faunas are by and large older than the *Myotis*-dominated faunas. Moreover, the oldest site, RF6, has the highest percentage representation of *E. fuscus* of any of our sites (20/21 specimens), although the sample size is modest. The youngest site (RR5) has the highest proportion of *Myotis* remains (14/18 specimens), and the other post-Pleistocene site (OHS1) is 75% *Myotis* (3/4 specimens), although the sample sizes at both sites are small. In the Pleistocene sites from the RR locality, *Myotis* comprises closer to 50% of the respective faunas (e.g., 11/20 specimens at RR3, 303/614 at RR1). It is tempting to interpret this pattern as a temporal replacement of *E. fuscus* by species in the genus *Myotis*. Furthermore, this temporal change would be consistent with changes in climate that are occurring simultaneously. The substantial climatic warming that has occurred since the mid-Pleistocene (Pielou 1991) could be construed as favoring the less-cold-tolerant species of *Myotis* over the more-cold-tolerant *E. fuscus*. However, it is important to note that the *Myotis*-dominated faunas overlap the *E. fuscus*-dominated faunas by at least two thousand years, and that only four sites in the study have been carbon dated. Therefore, at this point, we cannot conclude with certainty that the patterns of species abundance are created by temporal changes in climate.

While global warming might explain faunal changes in the distant past, and may be inferred as a continuing source of faunal change in the near future, it has been suggested that recent changes in bat species diversity and abundance are attributable to human-related disturbances. The results of our study would seem to reinforce this conclusion. Our fossils provide evidence that the Lookout Mountain cave system supported large bat populations for over 25,000 years. Bat remains are recovered from deposits formed as recently as <500 ybp (RR5), indicating that the disappearance of bats from this system is a very recent phenomenon. It is known that as human population levels rapidly increased in the area over the past 500 years, human disturbance of the caves has increased. In the Lookout Mountain cave system, these disturbances include saltpeter mining, the building of a railroad tunnel through the RR locality, and even the use of the RF locality as a tourist site. These data therefore strongly implicate anthropogenic disturbance as a major source of bat disappearance in the Lookout Mountain cave system. Thus, these results reinforce Tuttle’s (1979) claim, based on different lines of evidence (guano stains), that bat population decline in southeast Tennessee is a recent phenomenon that is tightly linked to human disturbance. It also reemphasizes the need to decrease human disturbance in order to prevent further declines in extant bat abundance and diversity.
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Literature Cited


Supplement: Key to Holocene Bat Species of the Southeastern U.S. Based on Lower Jaw Morphology

The following institutional abbreviations are used in the illustrations: MDT = Mammal collection, Southern Adventist University, Collegedale, TN; UGAMNH = University of Georgia, Museum of Natural History, Athens, GA; UTCM = Mammal collection, University of Tennessee at Chattanooga Natural History Museum. All scale bars represent 5mm, except for the illustrations of single teeth (Figures 2 & 8), which represent 1mm.

1. Dental formula 2-1-2-3 .......... *Eumops glaucinus*, Wagner’s Mastiff Bat (Family Molossidae)
1’. Dental formula 3-1-2-3 or 3-1-3-3 ................................................................. 2

2. Dental formula 3-1-2-3 ................................................................. 3
2’. Dental formula 3-1-3-3 ................................................................. 9

3. Mandible length greater than 13mm ................................................................. 4
3’. Mandible length less than 13mm ................................................................. 6

4. Coronoid process much taller than canine; width of p2 approximately equal to anteroposterior length; greatest mandibular length typically more than 14.5mm ................................................................. *Eptesicus fuscus*, Big Brown Bat (Figure 1a & b)
4’. Coronoid process approximately same height as canine; p2 triangular or rectangular, with width greater than anteroposterior length; greatest mandibular length typically less than 14.5mm ........................................................................................................ 5 (Figure 1c & d)

Figure 1. a, Mandible of *Eptesicus fuscus* (UTCM 312) in occlusal view. b, Mandible of *Eptesicus fuscus* (UTCM 312) in left lateral view. c, Mandible of *Lasiurus cinereus* (UTCM 246) in left lateral view. d, Mandible of *Lasiurus cinereus* (UTCM 246) in occlusal view.
5. p2 rectangular, with width greater than anteroposterior length; m3 with well developed talonid

\[\text{Lasiurus cinereus}, \text{ Hoary Bat (Figures 1c \\& d, 2)}\]

5’. p2 triangular, with apex directed labially; m3 with strongly reduced talonid

\[\text{Lasiurus intermedius}, \text{ Northern Yellow Bat (Figure 2)}\]

Figure 2. Upper image - Left m3 of \textit{Lasiurus cinereus} (UTCM 246) in occlusal view; lower image - Left m3 of \textit{Lasiurus intermedius} (UGAMNH 15131) in occlusal view.

6. Coronoid process small, triangular, posterior edge displaced anteriorly from mandibular condyle; posterior notch separating mandibular condyle and angle absent

\[\text{Tadarida brasiliensis}, \text{ Brasilian Free-Tailed Bat (Family Molossidae) (Figure 3a)}\]

6’. Coronoid process well developed posterior edge contacts mandibular condyle; posterior notch separating mandibular condyle and angle present

Figure 3. \textbf{a}, Mandible of \textit{Tadarida brasiliensis} (UGAMNH 2883) in left lateral view. \textbf{b}, Mandible of \textit{Perimyotis subflavus} (UTCM 246) in left lateral view.

7. Posterior margin of coronoid process nearly horizontal; small diastema separates i2 from i3 and i3 from canine

\[\text{Perimyotis subflavus}, \text{ Eastern Pipistrelle (Figure 3b)}\]

7’. Posterior margin of coronoid process directed anterodorsally; no diastema between i2, i3 and canine
8. Wide mandibular symphysis, incisors do not broadly overlap; width of i2 and i3 nearly equal to width of i1; p2 square, width approximately equal to anteroposterior length ..........................................................*Nycticeius humeralis*, Evening Bat (Figure 4a)

8’. Mandibular symphysis narrower, incisors broadly overlap; width of i1 much greater than width of i2 and i3; p2 rectangular, width much greater than anteroposterior length ..........................................................*Lasiurus borealis*, Red Bat or *Lasiurus seminolus*, Seminole Bat (Figure 4b)

Figure 4. a, Mandible of *Nycticeius humeralis* (UGAMNH 3041) in occlusal view. b, Mandible of *Lasiurus borealis* (UTCM 534) in occlusal view.

9. Lingual cingulum on molar trigonids absent, leaving distinct indentations between the paraconid and metaconid of each tooth; talonid broad mesiodistally, breadth nearly equal labiolingual width; m1 paracristid curved with paraconid elevated and displaced anteriorly; angular process directed laterally or posterolaterally; mandibular foramen typically exposed laterally ..........................................................10 (Figures 5a &c, 6a)

9’. Lingual cingulum on molar trigonids present, no indentations between the paraconid and metaconid of each tooth; talonid narrow; m1 paracristid nearly straight, with low paraconid close to metaconid; angular process directed posteriorly and only slightly laterally; mandibular foramen never exposed laterally ..........................................................11 (Figures 5b & e, 6b)

Figure 5. a, Mandible of *Corynorhinus rafinesquii* (UGAMNH 1626) in occlusal view. b, Mandible of *Myotis grisescens* (UTCM 79) in occlusal view. c, Upper image - Right m1 of *Myotis grisescens* (UTCM 79) in occlusal view; lower image - Right m1 of *Corynorhinus rafinesquii* (UGAMNH 1626) in occlusal view.
10. Mandibular angle directed laterally; p1 and p2 transversely oval.......................... Corynorhinus rafinesquii, Rafinesque’s Big-Eared Bat
10’. Mandibular angle directed posterolaterally; p1 and p2 round ......................... Corynorhinus townsendii, Townsend’s Big-Eared Bat

11. Incisors subequal; main cusp of p3 with lingual crest directed medially creating a distinct lingual bulge on the tooth .............................................

............................................. Lasionycteris noctivagans, Silver-Haired Bat (Figure 7)
11’. i3 distinctly larger than i1 and i2; main cusp of p3 with lingual crest directed posteriorly, lingual bulge absent............................................. 12

Figure 7. Mandible of Lasionycteris noctivagans
(UGAMNH 2784) in occlusal view.

12. Mandibular length greater than or equal to 11.5mm ................. Myotis grisescens, Gray Bat
12’. Mandibular length less than 11.4mm, alveolar length less than 6.6 mm............... 13

13. Alveolar length (c1-m3) less than or equal to 5.0 mm............................... Myotis leibii, Eastern Small-Footed Bat
13’. Mandibular length less than 11.5mm, alveolar length greater than 5.0 mm............... 14
14. p3 rectangular, anteroposterior length much greater than width, with distinct lingual indentation; middle labial cusp of I3 small, not extended labially; mandibular length often greater than 11mm..............................*Myotis septentrionalis*, Northern Long-Eared Bat (Figure 2f)

14’. p3 square, anteroposterior length approximately equal to width, lacking distinct lingual indentation; middle labial cusp of I3 large, extended labially; mandibular length rarely greater than 11mm..............................*Myotis lucifugus*, Little Brown Bat, or *Myotis austroriparius*, Southeastern Bat, or *Myotis sodalis*, Indiana Bat (Figure 2g)

Figure 8. a, Left p3 of *Myotis septentrionalis* (MDT 175) in occlusal view. b, Left p3 of *Myotis grisescens* (UTCM 349) in occlusal view.