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Errata and Omissions

The Proceedings of the 15th International Congress of Speleology contain either abstracts or full papers of the 500 contributions presented at the Congress. The three volumes of the Proceedings total 2130 pages. The pathway to this mass of material was as follows: Prospective authors submitted an initial abstract to the ICS Science Committee. These abstracts were reviewed by the Committee to ascertain that the subject matter was appropriate for the Congress. The abstracts were then returned to the authors with suggestions and an invitation to prepare a full paper limited to six printed pages. Few papers were rejected, but some were withdrawn so that of 540 initial submissions, 500 were presented at the Congress. The draft papers were sent to the Science Committee who distributed them for review after which they were returned to the authors for such adjustments as the reviewers deemed necessary. The final papers were received by the Science Committee for formal acceptance and were forwarded to the editor. The edited papers were then transmitted to Production Manager for page layout and preparation for the printer.

All of this movement of abstracts and manuscripts was done electronically. In the process of transmittals, various reviews, and editorial handling, a few errors and omissions were created. The lists that follow contain the additions and corrections that have been brought to our attention. We have limited the corrections to matters of fact; small errors in spelling, punctuation, and formatting are not addressed. We apologize to the authors whose papers were mishandled in some manner.

The Editorial Team

Errata

Volume 1, Page 541

Cave Sediments Related to Cretaceous-Tertiary Paleokarst Developed in Eogenetic Carbonate Rocks: Examples from SW Slovenia and NW Croatia by Bojan Otoničar.

The abstract was truncated in printing with only the first few lines appearing in the Proceedings. The full abstract follows.

In the SW Slovenia and NW Croatia a regional paleokarstic surface separates the passive margin shallow-marine carbonate successions of different Cretaceous formations from the Upper Cretaceous to Eocene palustrine and shallow marine limestones of the synorogenic carbonate platform. Thus, the paleokarst corresponds to an uplifted peripheral foreland bulge, when diagenetically immature eugenetic carbonates were subaerially exposed and karstified.
Among the subsurface paleokarstic features vadose and phreatic forms are recognized. For the epikarst, pedogenic features and enlarged root related channels are characteristic. Vadose channels, shafts and pits penetrate up to a few tens of meters below the paleokarstic surface, where they may merge with originally horizontally oriented phreatic cavities. The latter comprise characteristics of caves forming in fresh/brackish water lenses. The phreatic cavities were found in different positions regarding to the paleokarstic surface, the lowest one being some 75 meters below it. Usually only one distinct paleocave level occurs per location, although indistinct levels of spongy porosity and/or irregularly dispersed cavities of different sizes have been noticed locally. The cavities had been subsequently partly reshaped and entirely filled with detrital sediments and flowstones in the upper part of the phreatic, epiphreatic and vadose zones. The internal cave sediments and flowstones may also occur as clasts in deposits (mostly breccias) that fill subsurface paleokarstic cavities and cover the paleokarstic surface. In general, the variety of cave infilling deposits and the amount of surface derived material decrease with the distance from the paleokarstic surface. Below the paleokarstic surface $\delta^{13}$C and $\delta^{18}$O values of cavity deposits usually exhibit good correlation with trend significant for meteoric diagenesis.

Relatively small phreatic cavities of the lowermost part of the paleokarstic profiles are commonly geopetally infilled with laminated mudstone derived from incomplete dissolution of the hostrock overlain by coarse grained blocky calcite of meteoric or mixing meteoric/marine origin. Somewhat larger phreatic caves located shallower below the paleokarstic surface usually exhibit more complicated stratigraphy. Although the lower parts of the caves are still mainly infilled with reddish stained micritic carbonate sediment, different types of flowstone, especially calcite rafts, become more prominent higher in the cave profiles. Gradually in the upper parts of the caves, sediments derived from the paleokarstic surface prevail over autochthonous deposits. Especially channels of the epikarst zone are almost entirely infilled with pedogenically modified material derived directly from the paleokarstic surface. Regardless of their origin, cave deposits had been often intensively modified by pedogenic processes while they were exposed to the paleokarstic surface by denudation. Just prior to marine transgression over the paleokarstic surface some cavities or their parts had been infilled by marine derived microturbidites. It will be shown that especially deposits related to denuded phreatic caves may be of great importance for the study of speleogenetic, geomorphologic and hydrogeologic evolution of a specific karst region.

**Volume 2, page 650**

**Medical and Governmental Considerations of CO$_2$ and O$_2$ in Volcanic Caves** by William R. Halliday

The final sentence of the first paragraph on page 652 contains incorrect wording. The sentence should read:

“The issue resurfaced when U.S. Geological Survey and National Park Service personnel applied OSHA standards to volunteers in volcanic caves with non-toxic levels of O$_2$ and CO$_2$.”

**Volume 2, page 662**

**Unusual Rheogenic Caves of the 1919 “Postal Rift” Lava Flow, Kilauea Caldera, Hawaii** by William R. Halliday

The first paragraph on page 664 contains several errors and misstatements. The corrected paragraph should read:
“Noxious gas (probably HCl) was encountered only in one tiny cave on the edge of Halemaumau Crater. Presumed sulfate fumes were encountered in numerous caves but were found to be essentially non-toxic. Eye irritation rarely was encountered (Halliday, 2000b). Two types of CO$_2$ monitors previously untested in volcanic caves were required for the last five field trips. They were found to be useless in hyperthermal caves and no significant elevation of CO$_2$ was identified in normothermic examples (Halliday, 2007). In no cave was significantly elevated CO$_2$ identified by changes in normal breathing (Halliday, this volume).”

Volume 2, Page 785

Symposium #11, *Speleogenesis in Regional Geological Evolution and Its Role in Karst Hydrogeology and Geomorphology* was arranged by Alexander Klimchouk and Arthur N. Palmer (not by John Mylroie and Angel Ginés as listed on the title page of the symposium in the Proceedings).

Volume 2, Page 1033

**Uranium Mapping in Speleothems: Occurrence of Diagenesis, Detrital Contamination and Geochemical Consequences**

The correct authors for this paper are: Richard Maire, Guillaume Deves, Ann-Sophie Perroux, Bassam Ghaleb, Benjamin Lans, Thomas Bacquart, Cyril Plaisir, Yves Quinif and Richard Ortega. The names of Bassam Ghaleb and Yves Quinif were omitted in the Proceedings Volume.

Volume 3, Page 1307

**Species Limits, Phylogenetics, and Conservation of Neoleptoneta Spiders in Texas Caves** by Joel Ledford, Pierre Paquin, and Charles Griswold

James Cokendolpher, Museum of Texas, Texas Tech University, Lubbock, Texas was also a co-author for this paper.

Omissions

**The Fossil Bears of Southeast Alaska** by Timothy H. Heaton and Frederick Grady was inadvertently omitted in the final stages of page layout. The reviewed and edited paper follows:
Southeast Alaska is home to brown bears (*Ursus arctos*) and black bears (*U. americanus*) with an unusual distribution. Both species inhabit the mainland, while only black bears inhabit the islands south of Frederick Sound and only brown bears inhabit the islands north of Frederick Sound. Brown bears of the northern islands belong to a distinct lineage and are genetically more similar to polar bears than their mainland counterparts. Bears are among the most common fossils found in caves in the region, and they indicate that both species made greater use of caves as dens when the climate was colder. But no bear fossils are known from the Last Glacial Maximum (LGM), even at On Your Knees Cave where foxes and marine mammals have been recovered across most of this interval. This begs the question of whether bears survived the LGM on coastal refugia or recolonized the islands after the ice retreated. No evidence has been found to settle the question for black bears. Black bears are far more common than brown bears in On Your Knees Cave for the period before the LGM, but they were slower than brown bears in expanding their range across the islands after the ice melted. The evidence for survival in a local refugium is much stronger for brown bears. While they are less common before the LGM, they had a greater distribution than black bears immediately following the LGM, including some of the outermost islands of the archipelago. The lack of brown bear fossils from mainland sites during early postglacial times may indicate that the mainland was not the source of this population. The distinct genetic character of modern island brown bears also suggests that they did not derive from the mainland. Two fossil brown bears from caves of Prince of Wales Island have had successful DNA extractions and match the distinct lineage that now lives only on the northern islands of Southeast Alaska. A refugium for brown bears may have been offshore on the continental shelf which was exposed during the LGM but was flooded by rising sea level in the early postglacial period.

1. Introduction
Our research in southeast Alaska began in 1991 after several bear skeletons were found in El Capitan Cave on Prince of Wales Island by a caving expedition (HEATON and GRADY, 1992, 1993). El Capitan Cave is Alaska’s largest known cave and has passages that flood during storms, but the fossils were found in a quiet upper passage near the surface. One skeleton was complete and undisturbed, suggesting that the bears were denning in the cave, so cavers called this passage the Hibernaculum. It was apparent that the bears accessed the cave by an entrance that had become sealed with soil and logs, and we were able to reopen this entrance to conduct an excavation of the site. Soon cavers discovered skeletons in other caves of the region with similar dimensions, namely horizontal passages 1.5-2.5 meters in diameter. Several natural trap caves with bear fossils were also discovered. Although our research has expanded to include a variety of mammals, birds, and fishes (HEATON and GRADY, 2003), bears have remained a major focus, and our fossil discoveries have contributed to solving the question of whether animals survived the Ice Age in Southeast Alaska.

Most islands of Southeast Alaska are home to bears, but currently there is no more than one species per island. Black bears (*Ursus americanus*) inhabit Prince of Wales Island and most other islands south of Frederick Sound, while brown bears (*Ursus arctos*) inhabit the islands north of Frederick Sound, namely Admiralty, Baranof, and Chichagof (ABC) islands. Both species inhabit the nearby mainland (MACDONALD and COOK, 2007). Prior to the discovery of a fossil record, KLEIN (1965) proposed that this island distribution resulted from a postglacial colonization history: brown bears arriving from the north and black bears from the south. This hypothesis was based on the prevailing assumption that no land animals survived the Last Glacial Maximum (LGM, 24,000-13,000 radiocarbon years B.P.) in Southeast Alaska because of complete ice cover. Although the islands of Southeast Alaska exhibit a nested mammalian fauna suggestive of recent colonization (CONROY et al., 2000), fossil and genetic studies of bears have revealed a much more complex history in the region.

The complete skeleton from El Capitan Cave, as well as portions of several others, were of black bears, distinguished from the living bears on the island only by their large size. Their size seemed especially significant since they appeared to be females based on the lack of bacula and the gracile structure of their skulls. Even more significant was the discovery of even larger bear remains that we identified as brown bear. Finding that Prince of
Wales Island had been home to additional species in early postglacial time conflicted with the simple postglacial colonization model held by KLEIN (1965) and other biologists. In addition to brown bears, we also discovered fossil remains of Arctic fox (*Alopex lagopus*), red fox (*Vulpes vulpes*), and caribou (*Ranifer tarandus*) that no longer inhabit the island. Rather than lacking a fauna at the end of the Ice Age, Prince of Wales Island simply had a different fauna that was adapted to the colder and less forested habitat.

Following this initial discovery we set out to expand our dataset both geographically and chronologically by searching for caves with fossil deposits on different islands and the mainland, in diverse habitats, and of greater antiquity. During the 1990s fossil sites were brought to our attention by cavers exploring the region, often working with the support of Tongass National Forest and guided by forest agendas. After 2000 we began coordinating searches for caves specifically to fill in gaps in our dataset. In spite of limits imposed by limestone distribution and the difficulty of finding sites over 12,000 years old, a long history for both brown and black bears has emerged. During this same period geneticists began DNA studies on living bear populations in Southeast Alaska that complemented our work (HEATON et al., 1996), and we have worked in conjunction with ancient DNA researchers to trace bear lineages back in time. What has emerged is a greatly expanded, but not entirely complete, picture of bear history in Southeast Alaska.

### 2. Postglacial History

The postglacial record of bears in Southeast Alaska is spectacular. Following the discovery of black and brown bears in El Capitan Cave (130 m elevation), additional brown bear skeletons were found in two high elevation caves (over 500 m) on northern Prince of Wales Island: two juveniles in a natural trap called Blowing in the Wind Cave, and parts of 12 individuals in a horizontal tube called Bumper Cave, including skeletons of what appeared to be a mother and her two cubs (Table 1). By contrast, lower elevation caves (below 200 m) on the island, such as Kushtaka and On Your Knees caves (den sites) and Tlacatzinacantli Cave (a natural trap) contained only black bears from the postglacial interval (Table 2). This apparent partitioning of den sites by the two species must be kept in mind when considering other parts of Southeast Alaska where samples from diverse elevations are not available. This does not mean that brown bears were restricted to high elevations because their isotopic signature indicates a stronger marine diet than black bears (HEATON 1995; HEATON and GRADY, 2003).

**Table 1. List of radiocarbon dated brown bear (*Ursus arctos*) fossils from caves of Southeast Alaska in order of age.**

<table>
<thead>
<tr>
<th>Laboratory #</th>
<th>Age (years B.P.)</th>
<th>δ¹³C</th>
<th>Site</th>
<th>Island</th>
<th>Sample</th>
</tr>
</thead>
<tbody>
<tr>
<td>AA-15224</td>
<td>7,205 ± 65</td>
<td>-17.9</td>
<td>Bumper Cave</td>
<td>POW</td>
<td>Dentary</td>
</tr>
<tr>
<td>AA-56996</td>
<td>9,590 ± 95</td>
<td>-20.5</td>
<td>Deer Bone Cave</td>
<td>Coronation</td>
<td>Radius</td>
</tr>
<tr>
<td>AA-07794</td>
<td>9,760 ± 75</td>
<td>-18.0</td>
<td>El Capitan Cave</td>
<td>POW</td>
<td>Humerus</td>
</tr>
<tr>
<td>AA-10451</td>
<td>9,995 ± 95</td>
<td>-18.5</td>
<td>Blowing in the Wind Cave</td>
<td>POW</td>
<td>Ribs</td>
</tr>
<tr>
<td>AA-52223</td>
<td>10,700 ± 100</td>
<td>-17.1</td>
<td>Enigma Cave</td>
<td>Dall</td>
<td>Humerus</td>
</tr>
<tr>
<td>AA-15225</td>
<td>10,970 ± 85</td>
<td>-19.5</td>
<td>Bumper Cave</td>
<td>POW</td>
<td>Molar</td>
</tr>
<tr>
<td>AA-15223</td>
<td>11,225 ± 110</td>
<td>-16.8</td>
<td>Bumper Cave</td>
<td>POW</td>
<td>Humerus</td>
</tr>
<tr>
<td>AA-52221</td>
<td>11,600 ± 100</td>
<td>-14.6</td>
<td>Enigma Cave</td>
<td>Dall</td>
<td>Dentary</td>
</tr>
<tr>
<td>AA-44450</td>
<td>11,630 ± 120</td>
<td>-18.2</td>
<td>Colander Cave</td>
<td>Coronation</td>
<td>Humerus</td>
</tr>
<tr>
<td>AA-15222</td>
<td>11,640 ± 80</td>
<td>-17.8</td>
<td>Bumper Cave</td>
<td>POW</td>
<td>Rib</td>
</tr>
<tr>
<td>AA-15226</td>
<td>11,715 ± 120</td>
<td>-16.0</td>
<td>Enigma Cave</td>
<td>Dall</td>
<td>Humerus</td>
</tr>
<tr>
<td>AA-32122</td>
<td>11,910 ± 140</td>
<td>-18.1</td>
<td>El Capitan Cave</td>
<td>POW</td>
<td>Rib2</td>
</tr>
<tr>
<td>AA-52222</td>
<td>11,930 ± 120</td>
<td>-14.6</td>
<td>Enigma Cave</td>
<td>Dall</td>
<td>Skull</td>
</tr>
<tr>
<td>AA-10445</td>
<td>12,295 ± 120</td>
<td>-18.3</td>
<td>El Capitan Cave</td>
<td>POW</td>
<td>Pelvis</td>
</tr>
<tr>
<td>AA-33783</td>
<td>26,820 ± 700</td>
<td>-16.3</td>
<td>On Your Knees Cave</td>
<td>POW</td>
<td>Astragalus</td>
</tr>
<tr>
<td>AA-52219</td>
<td>29,040 ± 600</td>
<td>-16.3</td>
<td>On Your Knees Cave</td>
<td>POW</td>
<td>Rib</td>
</tr>
<tr>
<td>AA-52220</td>
<td>29,590 ± 980</td>
<td>-17.7</td>
<td>On Your Knees Cave</td>
<td>POW</td>
<td>M2/</td>
</tr>
<tr>
<td>AA-33792</td>
<td>31,700 ± 1900</td>
<td>-16.2</td>
<td>On Your Knees Cave</td>
<td>POW</td>
<td>Molar</td>
</tr>
<tr>
<td>AA-52218</td>
<td>31,900 ± 1,300</td>
<td>-19.6</td>
<td>On Your Knees Cave</td>
<td>POW</td>
<td>Claw</td>
</tr>
<tr>
<td>AA-52207</td>
<td>33,300 ± 1,500</td>
<td>-17.0</td>
<td>On Your Knees Cave</td>
<td>POW</td>
<td>Phalanx 1</td>
</tr>
<tr>
<td>AA-15227</td>
<td>35,365 ± 800</td>
<td>-15.9</td>
<td>On Your Knees Cave</td>
<td>POW</td>
<td>Femur</td>
</tr>
<tr>
<td>AA-52215</td>
<td>38,800 ± 3,000</td>
<td>-10.0</td>
<td>On Your Knees Cave</td>
<td>POW</td>
<td>Phalanx 2</td>
</tr>
<tr>
<td>Laboratory #</td>
<td>Age (years B.P.)</td>
<td>δ¹³C</td>
<td>Site</td>
<td>Island</td>
<td>Sample</td>
</tr>
<tr>
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<td>------------------</td>
<td>------</td>
<td>------</td>
<td>--------</td>
<td>--------</td>
</tr>
<tr>
<td>CAMS-27263</td>
<td>2,790 ± 60</td>
<td>-23.2</td>
<td>Kushtaka Cave</td>
<td>POW</td>
<td>Artifact</td>
</tr>
<tr>
<td>AA-57000</td>
<td>3,425 ± 50</td>
<td>-12.5</td>
<td>Lawyers Cave</td>
<td>Mainland</td>
<td>Humerus</td>
</tr>
<tr>
<td>CAMS-31068</td>
<td>3,960 ± 50</td>
<td>-20.7</td>
<td>On Your Knees Cave</td>
<td>POW</td>
<td>Dentary</td>
</tr>
<tr>
<td>AA-36637</td>
<td>4,847 ± 58</td>
<td>-21.2</td>
<td>Hole 52 Cave</td>
<td>Mainland</td>
<td>Skeletal</td>
</tr>
<tr>
<td>SR-5265</td>
<td>6,290 ± 50</td>
<td>-21.4</td>
<td>Kushtaka Cave</td>
<td>Mainland</td>
<td>Skull</td>
</tr>
<tr>
<td>AA-10447</td>
<td>6,415 ± 130</td>
<td>-21.1</td>
<td>El Capitan Cave</td>
<td>POW</td>
<td>Skull</td>
</tr>
<tr>
<td>CAMS-24967</td>
<td>8,630 ± 60</td>
<td>-21.4</td>
<td>Kushtaka Cave</td>
<td>POW</td>
<td>Femur</td>
</tr>
<tr>
<td>AA-18451R</td>
<td>9,330 ± 155</td>
<td>-23.9</td>
<td>Kushtaka Cave</td>
<td>POW</td>
<td>Femur</td>
</tr>
<tr>
<td>AA-32118</td>
<td>10,020 ± 110</td>
<td>-22.2</td>
<td>Tlacatzinacantli Cave</td>
<td>POW</td>
<td>Femur</td>
</tr>
<tr>
<td>AA-36641</td>
<td>10,080 ± 120</td>
<td>-21.6</td>
<td>Hole 52 Cave</td>
<td>Mainland</td>
<td>Phalanx</td>
</tr>
<tr>
<td>AA-33780</td>
<td>10,090 ± 160</td>
<td>-21.2</td>
<td>On Your Knees Cave</td>
<td>POW</td>
<td>Phalanx</td>
</tr>
<tr>
<td>CAMS-42381</td>
<td>10,300 ± 50</td>
<td>-20.7</td>
<td>On Your Knees Cave</td>
<td>POW</td>
<td>Articul</td>
</tr>
<tr>
<td>AA-36636</td>
<td>10,350 ± 100</td>
<td>-18.9</td>
<td>Hole 52 Cave</td>
<td>Mainland</td>
<td>Skull</td>
</tr>
<tr>
<td>AA-36640</td>
<td>10,420 ± 110</td>
<td>-21.6</td>
<td>Hole 52 Cave</td>
<td>Mainland</td>
<td>Skull</td>
</tr>
<tr>
<td>AA-07793</td>
<td>10,745 ± 75</td>
<td>-21.1</td>
<td>El Capitan Cave</td>
<td>POW</td>
<td>Humerus</td>
</tr>
<tr>
<td>AA-32120</td>
<td>10,860 ± 120</td>
<td>-21.8</td>
<td>Tlacatzinacantli Cave</td>
<td>POW</td>
<td>Skull</td>
</tr>
<tr>
<td>AA-32117</td>
<td>10,870 ± 120</td>
<td>-21.8</td>
<td>Tlacatzinacantli Cave</td>
<td>POW</td>
<td>Skull</td>
</tr>
<tr>
<td>AA-36638</td>
<td>10,930 ± 140</td>
<td>-19.8</td>
<td>Hole 52 Cave</td>
<td>Mainland</td>
<td>Skull</td>
</tr>
<tr>
<td>AA-32119</td>
<td>10,970 ± 120</td>
<td>-22.4</td>
<td>Tlacatzinacantli Cave</td>
<td>POW</td>
<td>Fragment</td>
</tr>
<tr>
<td>AA-33202</td>
<td>11,460 ± 130</td>
<td>-19.9</td>
<td>Hole 52 Cave</td>
<td>Mainland</td>
<td>Canine</td>
</tr>
<tr>
<td>AA-10446</td>
<td>11,540 ± 110</td>
<td>-20.0</td>
<td>El Capitan Cave</td>
<td>POW</td>
<td>Skull</td>
</tr>
<tr>
<td>AA-10448</td>
<td>11,565 ± 115</td>
<td>-18.7</td>
<td>El Capitan Cave</td>
<td>POW</td>
<td>Skull</td>
</tr>
<tr>
<td>AA-10599</td>
<td>28,695 ± 360</td>
<td>-20.7</td>
<td>On Your Knees Cave</td>
<td>POW</td>
<td>Calcaneum</td>
</tr>
<tr>
<td>AA-21570</td>
<td>29,820 ± 400</td>
<td>-20.8</td>
<td>On Your Knees Cave</td>
<td>POW</td>
<td>Vertebra</td>
</tr>
<tr>
<td>AA-33781</td>
<td>36,770 ± 2300</td>
<td>-18.6</td>
<td>On Your Knees Cave</td>
<td>POW</td>
<td>Femur</td>
</tr>
<tr>
<td>AA-33194</td>
<td>38,400 ± 3000</td>
<td>-18.4</td>
<td>On Your Knees Cave</td>
<td>POW</td>
<td>Humerus</td>
</tr>
<tr>
<td>AA-33198</td>
<td>39,000 ± 3100</td>
<td>-19.5</td>
<td>On Your Knees Cave</td>
<td>POW</td>
<td>Rib</td>
</tr>
<tr>
<td>AA-16831</td>
<td>41,600 ± 1500</td>
<td>-20.7</td>
<td>On Your Knees Cave</td>
<td>POW</td>
<td>Tibia</td>
</tr>
<tr>
<td>AA-36653</td>
<td>25,000 +</td>
<td>-22.0</td>
<td>On Your Knees Cave</td>
<td>POW</td>
<td>Premolar</td>
</tr>
<tr>
<td>AA-36655</td>
<td>27,000 +</td>
<td>-18.2</td>
<td>On Your Knees Cave</td>
<td>POW</td>
<td>Baculum</td>
</tr>
<tr>
<td>AA-33196</td>
<td>38,500 +</td>
<td>-19.4</td>
<td>On Your Knees Cave</td>
<td>POW</td>
<td>Scapula</td>
</tr>
<tr>
<td>AA-52206</td>
<td>38,500 +</td>
<td>-20.8</td>
<td>On Your Knees Cave</td>
<td>POW</td>
<td>Metapodial</td>
</tr>
<tr>
<td>AA-52204</td>
<td>39,100 +</td>
<td>-20.2</td>
<td>On Your Knees Cave</td>
<td>POW</td>
<td>Canine</td>
</tr>
<tr>
<td>AA-33200</td>
<td>39,400 +</td>
<td>-19.3</td>
<td>On Your Knees Cave</td>
<td>POW</td>
<td>Canine</td>
</tr>
<tr>
<td>AA-33195</td>
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<td>POW</td>
<td>Humerus</td>
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<tr>
<td>AA-33199</td>
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<td>-19.9</td>
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<td>POW</td>
<td>Canine</td>
</tr>
<tr>
<td>AA-44448</td>
<td>41,000 +</td>
<td>-21.7</td>
<td>On Your Knees Cave</td>
<td>POW</td>
<td>Molar</td>
</tr>
<tr>
<td>SR-5110</td>
<td>43,050 +</td>
<td>- On Your Knees Cave</td>
<td>POW</td>
<td>Vertebra</td>
<td></td>
</tr>
<tr>
<td>SR-5111</td>
<td>44,940 +</td>
<td>- On Your Knees Cave</td>
<td>POW</td>
<td>Skull</td>
<td></td>
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</table>

Table 2. List of radiocarbon dated black bear (*Ursus americanus*) fossils from caves of Southeast Alaska in order of age.
Several postglacial deposits have also been found on the mainland near the town of Wrangell and on two of the outermost islands of the Archipelago: Coronation and Dall Islands (HEATON and GRADY, 2003). Today only black bears inhabit Dall Island while no bears inhabit Coronation Island (MACDONALD and COOK, 2007). Three early postglacial cave deposits have turned up six individuals, all of which match brown bear (Table 1). Deer Bone Cave is a den cave while Colander Cave is a natural trap, and Enigma Cave is larger and more complex with bear skeletons both in horizontal den passages and at the bottom of pits. All these caves are at 200 m elevation or lower. By contrast, two postglacial cave deposits on the mainland, a den site called Lawyers Cave and a complex cave with horizontal passages and pits called Hole 52, contain only black bear remains (Table 2). Brown bears may have denned at higher elevation, but no such sites are known. The remarkable conclusion from these sites is that the two bear species had nearly the opposite distribution in the early postglacial period than they do today. Currently both species inhabit the mainland while only black bears inhabit the southern islands of Southeast Alaska. Shortly after the Ice Age only brown bears inhabited the outer islands, both species occupied the large Prince of Wales Island, and only black bears are documented from the mainland.

Discovering the postglacial history of bears in the northern islands of Southeast Alaska, where only brown bears live today, has been hampered by a paucity of limestone and a lack of any fossil discovery. Since brown bears thrived in the southern islands in early postglacial times, there is no reason to doubt their presence farther north. Whether black bears ever colonized the northern islands remains a mystery. To the south of Alaska a pattern similar to Prince of Wales Island has been documented by Canadian investigators. Haida Gwaii (Queen Charlotte Islands) and Vancouver Island are currently home only to black bears. Fossil black bears have been found dating back to 10,000 years B.P. on Haida Gwaii (RAMSEY et al., 2004; FEDJE et al., 2004) and from about 9,800 to 12,000 years B.P. on Vancouver Island (NAGORSEN et al., 1995; NAGORSEN and KEDDIE, 2000). Brown bears from Haida Gwaii have been found dating from 10,000 to 14,500 years B.P., showing that they once were widespread on coastal islands.

Another remarkable pattern visible in Tables 1 and 2 is the sheer number of early postglacial bears. With the exception of the sealed hibernaculum of El Capitan Cave, all of these sites remain open for potential denning today. Yet far more specimens of both black and brown bears date between 9,000 and 12,000 years B.P. than date to the 9,000 years since then. Most of these remains were exposed on the cave floors (not fully buried) so were not selected for dating based on their potential antiquity. Either bears were more numerous in early postglacial times or they were denning in caves much more regularly. The fact that natural trap caves (at least a third of the sites) show this same pattern suggests a high bear population. None of the other species we have studied show this distinct chronological pattern. Perhaps the early successional stages of forest development following the melting of the glaciers provided a high density of berries and other edible foods preferred by bears for the herbivorous part of their diet. Since climax forests are lacking in such foods, modern bears are attracted to forest clear-cuts, shorelines, and other disturbed areas where such plants grow.

3. Ice Age History
The single site in Southeast Alaska that has produced an extensive Ice Age record (prior to 13,000 radiocarbon years B.P.) is On Your Knees Cave. It is a small cave on the northern tip of Prince of Wales Island discovered during a logging survey and had only a few bones initially exposed. The significance of the site was only recognized when a partial brown bear femur was radiocarbon dated to 35,365 years B.P. (Table 1). Excavation began in 1996 and continued until 2004. An extensive record of mammals, birds, and fish was discovered covering at least the last 45,000 years (HEATON and GRADY, 2003) plus an extensive archaeological record including the oldest human remains from Alaska or Canada (DIXON et al., 1997). Devil’s Canopy Cave on Prince of Wales Island is the only other site where we obtained an Ice Age radiocarbon date (on marmot), but extensive excavation produced only a few rodent and insectivore remains. Our extensive efforts to find an Ice Age site on the outer islands of Southeast Alaska have so far been unsuccessful.

For a single site, On Your Knees Cave provides a superb record of animals during the LGM and the preceding interstadial. As can be seen in Tables 1 and 2 many bone dates are beyond the radiocarbon limit, but uranium dates on speleothem fragments date back to 185,800 ± 2,800 years B.P. (DORALE et al., 2003). Both black and brown bears were present and probably used the cave as a den from at least 41,000 years B.P. until the approach of the LGM (Tables 1 and 2). We have not dated enough samples to be certain exactly when their use of the cave ceased, but no bear remains have been dated to the glacial maximum itself. A sample of 25 ringed seal (Phoca hispida) specimens were radiocarbon dated from 24,150 ± 490 to 13,690 ± 240 years B.P., which is the very interval that the
bears (and caribou) are missing. Arctic and red foxes, other marine mammals, and sea birds also date to the LGM, so the cave was available and used as a den (by foxes) during that interval. One ringed seal humerus has bite marks that match bear canines, but it could be a polar bear (*Ursus maritimus*) kill that was scavenged by foxes.

Black bear fossils outnumber brown bear fossils in On Your Knees Cave by a ratio of about 10:1. This is not evident in Tables 1 and 2 because we selected specimens of both species for dating. This difference could represent a greater abundance of black bears or a partitioning of den sites by elevation like we see during the postglacial period. Other elements of the fauna suggest that conditions during the interstadial were similar to the early postglacial interval before a climax forest was established.

4. Genetics
TALBOT and SHIELDS (1996) found that brown bears of Admiralty, Baranof, and Chichagof (ABC) islands (Southeast Alaskan islands north of Frederick Sound) are distinct from all other populations based on mitochondrial DNA and are more closely related to polar bears than to their mainland counterparts. Using nuclear microsatellite variations PAETKAU et al. (1998) confirmed this result for females but detected some exchange of males with the local mainland population. LEONARD et al. (2000) discovered a fossil from Yukon Territory matching the ABC bears and dating to \(36,500 \pm 1,150\) years B.P., so this clade had a wider distribution before the LGM. Nevertheless, the current restricted range of this clade suggests that the islands of Southeast Alaska acted as a refugium for this population during the glacial maximum (HEATON et al., 1996). Further support for this hypothesis comes from early postglacial fossils of Prince of Wales Island and Haida Gwaii. After several failed attempts at extracting ancient DNA, BARNES et al. (2002) reported that a brown bear fossil from Blowing in the Wind Cave (AA-10451 on Table 1) belongs to the ABC clade. Further work by Sarah Bray (personal communication) also linked a bear from Bumper Cave (AA-16553 on Table 1) and ones from Haida Gwaii to the ABC clade.

STONE and COOK (2000) found that black bears from the southern islands of Southeast Alaska belong to a mitochondrial lineage that is also found on the islands and coastal mainland of British Columbia and down the coast to northern California. Several other mammal species have distinct coastal lineages with a similar range, but it remains unclear whether the source of these lineages was south of Cordilleran glaciers or on coastal refugia, possibly in Southeast Alaska (COOK et al., 2001, 2006).

5. Conclusions
The absence of a fossil record of bears from the LGM leaves open the question of whether they survived the glacial expansion in Southeast Alaska on coastal refugia or recolonized afterward. Cave faunas document that both brown and black bears were present during the preceding interstadial and reappeared in great numbers soon after the ice melted. Genetic evidence for a distinct coastal lineage, where refugial isolation is the simplest explanation, is strong for brown bears but more equivocal for black bears. Both bears are refugial species in the sense that they were adversely affected by glaciation and struggled to survive under unfavorable climatic conditions. By contrast, other carnivores such as ringed seals, Arctic foxes, and likely polar bears flourished and expanded their ranges during the LGM. The extent to which the Arctic and refugium faunas competed with one another is unknown, but their interactions could have been a factor in the temporary loss of black and brown bears from On Your Knees Cave.

What we learn from postglacial bears is that the species were able to move about freely and colonize territory that was favorable for them, rather than being restricted by barriers and competition. Solving the full puzzle of bear history in Southeast Alaska will require finding additional faunas of similar antiquity to On Your Knees Cave, as a single site cannot document the movements of species. During the LGM the expanding glaciers pushed mammal populations westward, while falling sea level opened up new habitat to the west and changed the configuration of the coastal corridor. The possibility that populations of bears and other mammals found suitable refugia to survive the LGM in Southeast Alaska is very possible.

References


