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STRATIGRAPHIC DISTRIBUTION OF PLEISTOCENE (IRVINGTONIAN AND RANCHOLABREAN NALMA) FOSSIL REMAINS AT THE CLASSICAL FOSSIL LAKE AREA, LAKE COUNTY, OREGON

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ABSTRACT

Fossil Lake has attracted some of the most famous North American paleontologists for over 140 years. Yet, many of the earlier collections are of limited utility because subtle lithostratigraphic differences were not recognized in the substrate. Not until 1977 was the first step taken to carefully integrate fossil invertebrate and vertebrate remains into a detailed stratigraphic succession of 18 lithic units deposited in nine episodes of rhythmic lake fillings. Once radiometric dates became available, the Fossil Lake area was discovered to include not only late Pleistocene (Rancholabrean North American Land Mammal Age) but also early Irvingtonian NALMA. A major disconformity separates the two ages with approximately 500,000 years of missing section. Therefore, many specimens collected earlier and considered Rancholabrean NALMA are now known to be much older.

As a result, Fossil Lake has been carefully recollected during the last 40 years, and the lithostratigraphy refined. The major contribution herein to the stratigraphic framework beyond previously published works (Martin et al., 2005; Martin, 2014) is the addition of two radiocarbon dates of fossil bone: 30,120 $\pm$ 170 rcbp from Unit 10 and 36,350 $\pm$ 290 rcbp from Unit 9. These dates corroborate the tephra date below in Unit 8 of 47 $\pm$ 2 ka. The compilation of herpetological and mammalian taxon ranges is illustrated on the accompanying range charts that indicate relative taxon abundances and distributional changes over time. Based upon this information, the new collections were analyzed in both lithostratigraphic and temporal frameworks in order to understand their implications for the history and evolution of Fossil Lake.

Each rhythmically deposited package generally consists of transgressive sandstone grading into silty claystone. The basal sandstones contain larger fossils and many terrestrial forms, whereas the claystones are noted for abundant aquatic vertebrates. When the lake clays also contain a large number of terrestrial creatures, a waterhole model explains the biased attritional assemblage.

Based upon range zones and relative taxon abundances, moist, glacially dominated conditions in the early Irvingtonian NALMA altered to the warmer, xeric conditions of the later Rancholabrean NALMA with some fluctuations. The major climatic change is documented in Unit 6 but probably occurred above the major disconformity at the base of Unit 5. Many of the taxa in Unit 5 appear reworked, including many that reflect mesic conditions. Importantly, *Bison* does not occur lower than Unit 5, the base of the Rancholabrean section at Fossil Lake. The following vertebrate taxa were unknown at Fossil Lake prior to our studies: *Scaphiopus*, *Bufo*, *Rana*, Serpentes, cf. *Myotis*, *Mustela*, *Neovison*, *Ursus*, *Brachylagus*, *Neotamias*, *Spermophilus*, *Cynomys*, *Microdipodops*, *Peromyscus*, *Ovis*, *Ovibos*, and *Bison*.

INTRODUCTION

Fossil Lake, a small playa (~16 km^2) in the Fort Rock Basin of south-central Oregon (Figure 1), is the most important Pleistocene vertebrate locality in the Pacific Northwest, and many legendary early geologists and paleontologists have investigated the rocks and fossils of the area. Not surprisingly, the pioneer geologist and paleontologist of Oregon, Thomas Condon, was the first to conduct scientific field investigations (Condon, 1910; McCornack, 1928; Clark, 1989). In 1877, Condon had been summoned to the area by John Whiteaker, the first governor of Oregon, who had visited the site in September, 1876. Most authors (e.g., Condon, 1902, 1910) consider 1876 as the year of discovery; however, Whiteaker may have known about the site in 1875. Tupper (2003) found an editorial written by Whiteaker in the *Eugene City Guard* in which he noted that he had gained possession of proboscidean elements from the Summer Lake area in Lake County. In June, 1877, Whiteaker returned to the area for ranching business and revisited the site consisting of a blowout and two small ephemeral lakes. The fossils had been exposed resulting from sheet wash, wind action, and sand dune migration. He collected two hundred pounds of bones, most of which he gave to Condon, who recognized horse, mammoth, camel, fish, and many types of waterfowl. Horses comprised the most abundant remains, and the area was considered "*Equus* beds" in some early publications. While at the site, Whiteaker, noting the desolation and poor water quality, named the two small lakes in the deflation depression as Fossil Lakes, East and West (Clark, 1989). The bones Whiteaker collected inspired

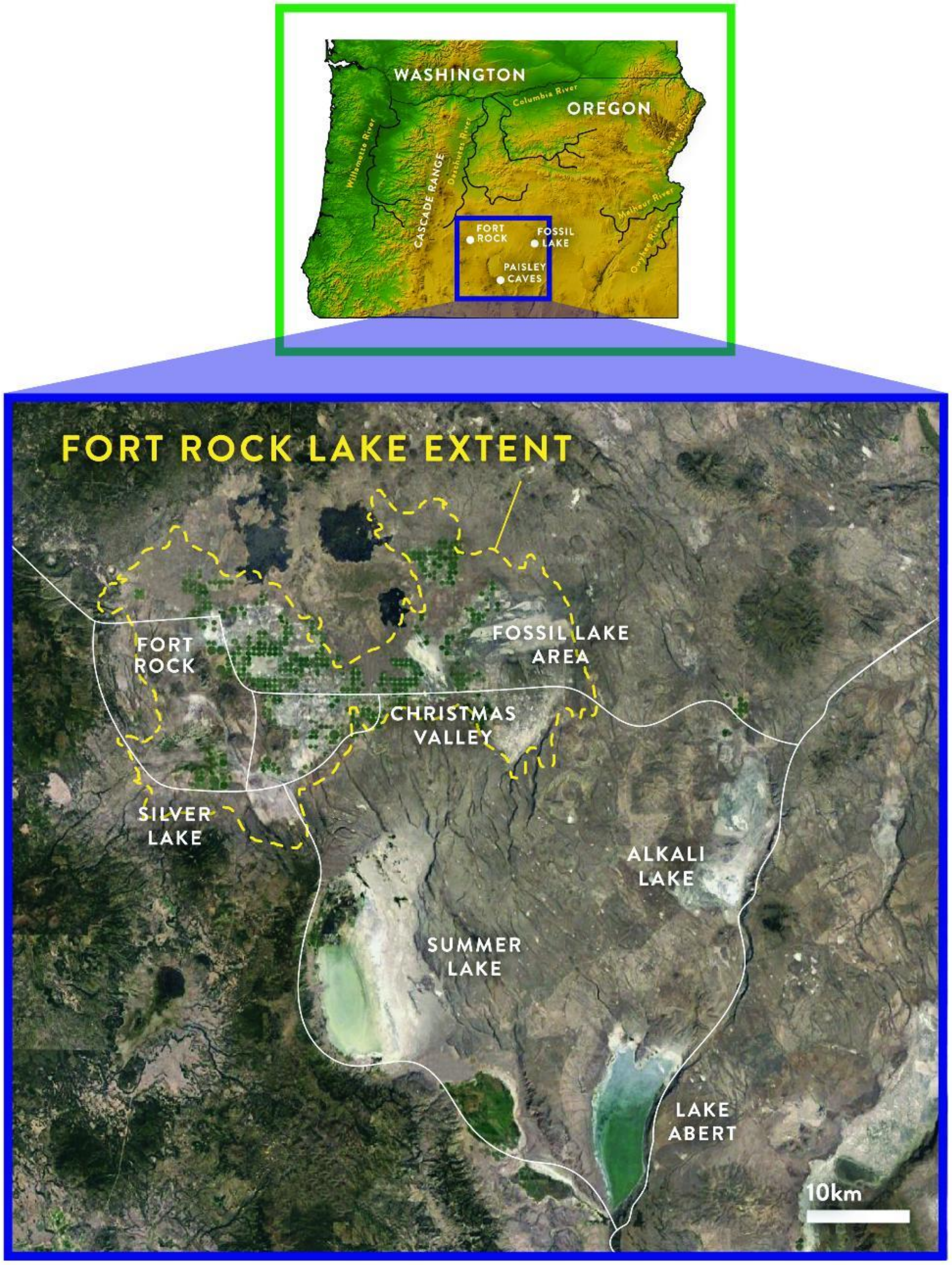

FIGURE 1. Location of the Fossil Lake area in south-central Oregon. The dashed line denotes the extent of pluvial Fort Rock Lake.

Condon, who immediately planned to visit the area, and in early August of 1877, visited the site in the company of John Whiteaker's son, Charles, who was also one of Condon's students. Whiteaker supplied a team of horses, and Charles and George Duncan, postmaster at Silver Lake, guided Condon to the locality (Clark, 1989). Condon found additional vertebrate specimens and noted numerous projectile points among the Pleistocene bones. This importance of this co-occurrence was not lost on Condon, and the eminent paleontologist in Philadelphia, Edward Cope, was contacted.

FIGURE 2. Removal of four fossilized horse (*Equus*) legs from Unit 4 at Fossil Lake, Oregon. Commonly occurring horse remains prompted earlier workers to utilize the term "*Equus* beds" for the area, and the associated legs suggest the individual became mired in the muddy lakebed.

Whether Condon actually contacted Cope or if he encouraged George Duncan to do so is not known, but Cope was contacted, while O.C. Marsh, Cope's adversary who had been sent Tertiary vertebrates for study from Condon previously and had never returned the specimens, was not. Cope was excited about the association of bones and artifacts and immediately contacted Charles Sternberg, a fossil collector from Kansas. Sternberg was in Nebraska, but Cope sent him to Oregon with orders to tell no one where he was going. Sternberg was in Oregon by the end of August, 1877. George Duncan served as guide to the area, which Sternberg claimed to have named as Fossil Lake (Sternberg, 1909); other early authors termed the area the Silver Lake beds or *Equus* beds (Figure 2). Whether Sternberg learned of Whiteaker's name from Duncan or named the site independently, the region has long been termed Fossil Lake, and Fossil Lake, itself, is considered the larger of the two lakes, Whiteaker's Fossil Lake West. For the next few weeks, Sternberg continued collecting vertebrates, and during one of his trips found a Native American lodge. Around the lodge were bleached bones of deer, rabbit, and antelope, none of which were fossilized. Among these Recent bones were points of the variety he had found with the fossilized bones at Fossil Lake. He surmised that the artifacts at Fossil Lake had been deflated down into the fossil levels. In the meantime, however, Cope received Sternberg's initial shipment of specimens and penned a quick note about the association of human artifacts and Pleistocene bones to the American Naturalist (Cope, 1878b). Interestingly, Cope did not credit Sternberg's contributions, an oversight that was probably a relief to Sternberg, who relayed his news invalidating the association too late for Cope's publication. Sternberg described the areas he visited in Oregon in 1881, 1884, and in his autobiography (1909).

Cope decided to see the site for himself (Osborn, 1931) and contacted Condon in the fall of 1879 about visiting Fossil Lake. With the assistance of a Native American guide, wagon, mules, and horses supplied by the army, Cope visited Crater Lake on his way from Fort Klamath to Silver Lake. A few miles before reaching Silver Lake, the wagon broke down, and ranch hands were subsequently dispensed by George Duncan to retrieve Cope's provisions. While Cope waited, Charles Whiteaker serendipitously arrived at Duncan's ranch and volunteered to take Cope to Fossil Lake. Once at the Lake, Cope was impressed with the number of bones and artifacts and remained convinced of their association (Cope, 1889a). However, Condon (1902) noted in his first book concerning the geology of Oregon that he and Cope were convinced that the artifacts were deflated; the reference to Cope was deleted from his second book (1910). The question of association has remained to the present, especially when Clovis lithics were found among the bones of a juvenile camelid (Minor and Spencer, 1977) at Fossil Lake and when Jenkins et al. (2013) found human evidence at Paisley Caves near Summer Lake (Figure 1) dated approximately 14,300 years before present, which overlaps the uppermost portion of the lithostratigraphic section at Fossil Lake (Martin, 2006, 2014).

As a result of these early expeditions, Cope described many of the specimens in contributions on fish types (Cope 1878a,c and 1883b) and birds and mammals (Cope 1878a, 1883a, 1886, and 1889b). He summarized his work on the geology and paleontology in 1889a,c. Later, R.W. Shufeldt described the birds (1891a,b,c; 1892a,b) and reviewed them again (1913a,b,c). He also reviewed the fossil fish (1913c). Fishes were also investigated by, among others, Jordan (1907), Hubbs and Miller (1948), Taylor (1960), Uyeno (1961), Uyeno and Miller (1963), Miller (1965), Cavender and Miller (1972), Smith (1975), Miller and Smith (1981), and Allison and Bond (1983).

Members of the U.S. Geological Survey, I.C. Russell in 1882 and W. Day in 1883 collected fossils (Russell, 1884, 1905), which repose in the U.S. National Museum, and after the turn of the century, the University of California made collections from the area. Annie Alexander in 1901 (Stein, 2001) and J.C. Merriam in 1904 made trips to the area; the collections repose at the University of California Museum of Paleontology, and relatively little investigation has been undertaken on these specimens with the exception of the birds. Chester Stock and E.L. Furlong made collections from 1923 to 1931. These collections now repose at the Los Angeles County Museum, as do important specimens more recently collected by James Goedert of Washington state. L.H. Miller (1911) published a list of avian fossils described by Shufeldt and included three additional taxa based upon the new collections. Finally, the birds were extensively reviewed by Hildegard Howard (1946, 1964), and additional species were noted by Joseph Jehl (1967).

Other scattered publications during the early twentieth century include those of Waring (1908), who described the geology, agreeing with Russell (1884) that the region was flooded by large Pleistocene lakes, and that of Smith and Young (1926), who first utilized the Fossil Lake Formation for 8 to more than 10 feet (2.4-3 m) of lake silts containing Pleistocene fossils. Condon's daughter, Ellen McCornack (1914) made detailed descriptions of the Fossil Lake area based upon her father's earlier work. Earlier publications concerning the assemblage from Fossil Lake were summarized by O.P. Hay (1927). The significance of the Fossil Lake area was noted by Hay (1927:241) when he stated, "…from the paleontological point of view the most important region in Oregon is found in Lake County, for here have been collected more species of vertebrates than from all other localities in Oregon taken together." Of course, science has progressed since this pronouncement, but Fossil Lake remains one of the most significant sites in the state of Oregon and the nation.

Subsequent publications concerning Fossil Lake include those of Ira Allison of Oregon State University. Allison began investigations in the Fort Rock Basin in 1939, and over the years, published a series of contributions in which he discussed Fossil Lake and described the regional geology (1940, 1941a,b, 1947, 1949, and 1950). His geological investigations were summarized in 1979 and 1982, when he discussed pluvial Fort Rock Lake (Figure 1) and Lake Chewaucan, respectively. Therefore, Allison, in conjunction with Hampton (1964), Walker et al. (1967), and Walker and McHugh (1980), outlined the geology within the area, noting the evolution of the pluvial lakes that appear to have transgressed and regressed repeatedly during the Pleistocene. Allison's major contribution concerning Fossil Lake was published in 1966, in which he summarized the geology and paleontology of the area, including discussions of the invertebrate and vertebrate remains known at the time. He added a later paleontological note concerning the identification and age of the salmonid remains at Fossil Lake (Allison and Bond, 1983). Later works concerning the stratigraphy, geochronology, and paleontology of the Fossil Lake area have principally been those of the author and his colleagues (Martin, 1996; Martin, 2006; Martin, 2010; Martin, 2014; Martin and Kihm, 2003; Martin et al., 2005; Moses and Martin, 2014).

Fossil Lake includes not only vertebrate fossils; invertebrate fossils are also common. Invertebrate fossils can be very abundant, occurring in the thousands of specimens in some lithological units. Most of the invertebrate fossils are freshwater gastropods and ostracods, but a single small species of freshwater pelecypod, *Pisidium variabile*, occurs, as

TABLE 1. Fossil invertebrates from Fossil Lake (modified from Hanley and Ladendorf, 1995).

Gastropoda		
	Planorbidae	
		Planorbella trivolvis
		Helisoma (*Carinifex*) *newberryi*
		Vorticifex effusa
	Lymnaeidae	
		Lymnaea stagnalis
	Valvatidae	
		Valvata virens
Pelecypoda		
	Sphaeriidae	
		Pisidium variabile
	Unionidae	
		Unio sp.

TABLE 2. Fossil fish from Fossil Lake.

Hay (1927)	**Revisions**
Siphateles altarcus (Cope)	*Gila* (*Siphateles*) *altarcus*
Siphateles gibbarcus (Cope)	*Gila* (*Siphateles*) *altarcus*
Notropis angustarca (Cope)	*Gila* (*Siphateles*) *altarcus*
Chamistes oregonus Starks	*Chamistes oregonus*
Chamistes batrachops (Cope)	*Chamistes batrachops*
Chamistes or *Catostomus* sp.	*Catostomus* or *Deltistes*
Oncorhynchus tschawytscha (Walbaum)	*Oncorhynchus mykiss*

well as a fragmentary specimen of *Unio* found recently during mitigation for the Bonneville Power Administration. The gastropods were initially described by Russell (1884) and Cope (1889a); later reviews by Shufeldt (1913c) and Dole (1942) were summarized by Allison (1966). The most recent examination of the freshwater invertebrates was by Hanley and Ladendorf (1995) based upon collections made under the direction of the author and Dr. Allen Kihm. They noted the taxa on Table 1 and described their abundances through the lithostratigraphic section as known at that time.

Because many of the lithological units at Fossil Lake represent lacustrine deposits, abundant fish specimens occur. Cope (1883b) initially described the fish from Fossil Lake, and Jordan (1907) reviewed the fish, adding a salmonid to the assemblage. A revised list (Table 2) of fish from Fossil Lake was provided by Hay (1927). Uyeno (1961), Uyeno and Miller (1963), Miller, (1965), Orr and Orr (1981), Allison and Bond (1983), and Minckley et al., (1986) presented synonymies and revisions shown in Table 2. *Siphateles gibbarcus* was synonymized with *Gila* (*Siphateles*) *altarcus* by Uyeno (1961), and *Notropis angustarca* was also synonymized with *Gila* (*Siphateles*) *altarcus* by Uyeno and Miller (1964). The latter authors also provisionally synonymized *Chasmistes oregonus* with *Chasmistes batrachops*; however, they noted that the two might be successional species. Given the realization that different ages are represented at Fossil Lake (Martin et al., 2005; Martin, 2014), *Chasmistes oregonus* is retained until additional research on the fish collections can be undertaken. Minckley et al. (1986) indicated that *Catostomus* sp. could be either *Catostomus* or *Deltistes.* The large stratigraphically controlled collections of catostomids accumulated by our parties may allow resolution of this question. Finally, the salmonid, *Oncorhynchus tschawytscha* was considered *Salmo* sp. (redband trout) by Allison and Bond (1983), but recent taxonomic revisions indicate that the redband trout should now be considered as *Oncorhynchus mykiss* (See Robins et al., 1991; Gobalet, 2001).

The amphibians from Fossil Lake are yet to be formally described. Expeditions under the direction of the author have recovered mostly frogs and toads. The anurans include *Scaphiopus*, the spade-footed toad; *Bufo*, the typical toad; and *Rana*, the typical frog, with specimens of *Scaphiopus* occurring most abundantly.

Sternberg (1909) mentioned finding "great numbers of the bones and teeth of reptiles, birds, and mammals indiscriminately mingled" during his initial collections. However, reptiles are exceedingly rare at Fossil Lake, and perhaps Sternberg's reptile remains were actually fish elements. No reptiles repose in the collections made by Sternberg or other early collectors. One snake vertebra is reportedly in the University of Oregon collections (W. Orr, per. comm.), one snake vertebra was recovered *in situ* during our expeditions, and a couple more were found in anthill matrix.

Fossil Lake is famous for its bird specimens. One of the factors making Fossil Lake so scientifically important is the diversity and exquisite preservation of birds, including skeletons, partial skeletons, well-preserved isolated elements, and eggshell fragments. As mentioned above, the avian representatives were described initially by Cope and Shufeldt and reviewed by Howard (1946, 1964), Jehl (1967), and Storer (1989). Their updated avian list is Table 3.

In addition to the descriptions by Cope mentioned above, the mammals from Fossil Lake were described by various authors, including Wortman (1898), who described fossil camels; Matthew (1902), who listed and compared the Fossil Lake (Silver Lake) assemblage with the Hay Springs assemblage in Nebraska; Hollister (1911), who described a new species of muskrat (*Fiber oregonus*), now considered a synonym of *Ondatra annectens*; Hay (1921), who named a new species of *Thomomys* (*Thomomys scudderi*); Hay (1927), who included Fossil Lake in

TABLE 3. Fossil birds listed alphabetically from Fossil Lake (Howard, 1946, 1964; Jehl, 1967; Storer, 1989).

Aechmophorus occidentalis
Agelaius? or *Euphagus*
**Anabernicula oregonensis*
Anas acuta
Anas carolinensis
Anas cyanoptera
Anas platyrhynchos
Anser albifrons
Aquila chrysaetos
Ardea herodias
Botaurus lentiginosus
Branta bernicla
Branta canadensis
Branta hypisbata?*
*Branta propingua**
Bubo virginianus
Centrocercus urophasianus
Charitonetta albeola
Chen caerulescens
Chen hyperborea
Chen rossii
Childonias nigra
Circus cyaneus
Clangula hyemalis
Colpates cafer
Corvus corax
Cygnus buccinator
**Dendragapus gilli*
**Dendragapus lucasi*
**Dendragapus nanus*
Erolia melanotus
Euphagus cyanocephalus
**Falco oregonus*
*Fulica americana minor**
Haliaeetus leucocephalus
Himantopus mexicanus
**Hypomorphnus sodalis*
Larus californicus
**Larus oregonus*
**Larus robustus*
Limnodromus griseus?
Mareca americana
Melanitta deglandi
Melanitta perspicillata
Mergus merganser
Mergus serrator
Numenius americanus?
Nyroca affinis
Nyroca americana
Nyroca collaris?
Oxyura jamaicensis
Pelecanus erythrorhynchus
Phalacrocorax auritus?
**Phalacrocorax macropus*
Phalaropus lobatus
**Phoenicopterus copei*
**Podiceps parvus*
Podiceps nigricollis
Podilymbus podiceps
Rallus limicola
Recurvirostra americana
Spatula clypeata
**Spizaetus pliogryps*
**Stercorarius shufeldti*
Sterna forsteri
**Sthenelides paloregonus*
Totanus melaleucus
Tympanuchus phasianellus
Xanthocephalus or *Sturnella*
*Stork, species
*Extinct taxa

overviews of Pleistocene paleofaunas; and Stock (1925), who reviewed the ground sloths. The Fossil Lake mammals were reviewed by H.O. Elftman (1931), and this contribution remains the major work concerning the mammals of Fossil Lake. However, Elftman did not study all collections, and the nomenclature of Elftman's publication is dated. Since Elftman's study, works concerning the mammals of Fossil Lake include the designation by Davis (1937) of another new species of *Thomomys* (*Thomomys vetus*); a discussion of large felids by Simpson (1941) and Daggett and Henning (1974); review of the ground sloths by Packard (1952); the notation of the first occurrence of *Cynomys*, the prairie dog, from west of the Rocky Mountains (Martin, 1996); a report of the bighorn sheep, *Ovis canadensis* (Martin, 2014); recognition of only two species of gopher at Fossil Lake, *Thomomys talpoides* and *Thomomys townsendii* (Moses and Martin, 2014); and a comparative discussion of horse phalanges based on older collections (McHorse et al., 2016).

Unfortunately, none of the collections recovered prior to 1977 were stratigraphically controlled; all were essentially bulk samples collected from up to 18 different lithostratigraphic units. As a result, the area was intermittently recollected by parties under the direction of the author over the last 40 years, resulting in thousands of specimens tied to thin lithostratigraphic units that were delineated by Martin et al. (2005), refined by Martin (2014), and presented as the geological section on Figures 3-5. The only additions to the 2014 section on the figures below are two radiocarbon dates: Unit 9 (36,350 $\pm$ 290 rcbp) and Unit 10 (30,120 $\pm$ 170 rcbp). Also, the lateral variation of the upper portion of the section (Units 9-14) from east to west (Martin et al., 2005:144) was discovered to be a condensed section in the west. The ultimate research goal, as presented herein, was to analyze the new collections in both lithostratigraphic and temporal frameworks upon which to superimpose fossil taxa in order to understand their implications for the history and evolution of Fossil Lake.

The essential contributions of this paper are summarized by the accompanying range charts (Figures 3-5). Numerous additions to the Fossil Lake paleofauna are noted principally at a generic level, the operative faunal unit of biostratigraphy. Taxonomic descriptions to species level will be presented in future contributions. Some species are illustrated for genera that contain multiple species such as *Canis*, and families are included where specimen quality was insufficient for generic identity. Moreover, these charts illustrate only specimens collected under the direction of the author that are tied to the lithostratigraphic units delineated in Martin et al. (2005) and Martin (2014). As a result, the paleofaunal charts do not include specimens such as those described by Elftman (1931) and others recovered by earlier collectors because their precise stratigraphic source is unknown. Preservational differences among these older specimens can be unreliable to differentiate lithostratigraphic sources because a single preservational type may occur in multiple strata at Fossil Lake. Rare Earth Element analyses and comparisons, which are still in their infancy, might aid in the differentiation, but such analyses are destructive and expensive for large numbers of specimens.

The taxa discussed herein include amphibians, reptiles, and mammals. Ranges of fish and birds will be presented in later contributions. The fish are relatively conservative with salmonids, cyprinids, and catostomids represented. The salmonids normally occur higher in the Rancholabrean NALMA (North American Land Mammal Age) portion of the section and are characteristic of Unit 17, which appears a high stand of Fort Rock Lake (Allison, 1979) in the Fossil Lake section. The avian specimens are diverse, abundant, and currently being studied by Dr. Jennifer Hargrave at the University of Louisiana Geology Museum, Lafayette. Interestingly, avian eggshell fragments are also abundant, particularly concentrated in Unit 2 and Unit 9.

This contribution reflects systematic stratigraphic collections made since 1989. For two weeks each year, field paleontology classes were conducted under the direction of the author, first at the SD School of Mines and later through the University of Louisiana, Lafayette. These expeditions resulted in many tens of thousands of stratigraphically collected specimens. Those collected early in the studies undoubtedly included specimens that had been eroded and deflated onto lower lithostratigraphic units. Therefore, some mixing of the earliest collections may have occurred. However, subsequent yearly collections from the same local sites and specific strata produced collections with relatively little stratigraphic mixing. During each of the last four years, the author was able to expend six to eight months at Fossil Lake, and as a result, over 100,000 specimens were stratigraphically collected and curated into the public collections at the University of Louisiana Geology Museum. Extreme care was taken to insure these specimens were collected with precise lithostratigraphic provenience.

The culmination of the collection efforts over many years resulted in hundreds of thousands of specimens, most with precise lithostratigraphic association. Nevertheless, erosion and down-section gravitational movement, reworking up-section by aeolian processes, and mixing by biogenic agents (particularly gophers) undoubtedly resulted in some specimens removed from their original position. Therefore, the numbers in each range (Figures 3-5) are qualitative, representing the number of field collections containing a particular taxon from a particular lithostratigraphic unit. These numbers provide a relative degree of taxon abundance in a particular unit: a methodology that is only of utility given the many thousands of specimens collected. Greater precision would be impossible to ascertain given the numerous geological processes that have operated on the fossil specimens over the last 650,000 years at Fossil Lake.

The qualitative numbers were confirmed by general field observations when the collections were recovered. As can be observed in the range charts, mammalian fossils in Unit 1 are moderately abundant, whereas fossils are very abundant in Unit 2 and Unit 4. Overall, the Irvingtonian NALMA portion of the section (Units 1-4) is more prolific than the Rancholabrean portion of the section (Units 5-18). Only Unit 5 of the Rancholabrean section rivals the Irvingtonian units in specimen abundance. Of the remaining Rancholabrean units, fossils in Units 6 through 9 were less abundant. Unit 17 also produced numerous specimens, but most were salmonids, including many skeletons.

The prolific collections from the 18 lithostratigraphic units at Fossil Lake produced many taxa heretofore unknown from the site (Table 4),

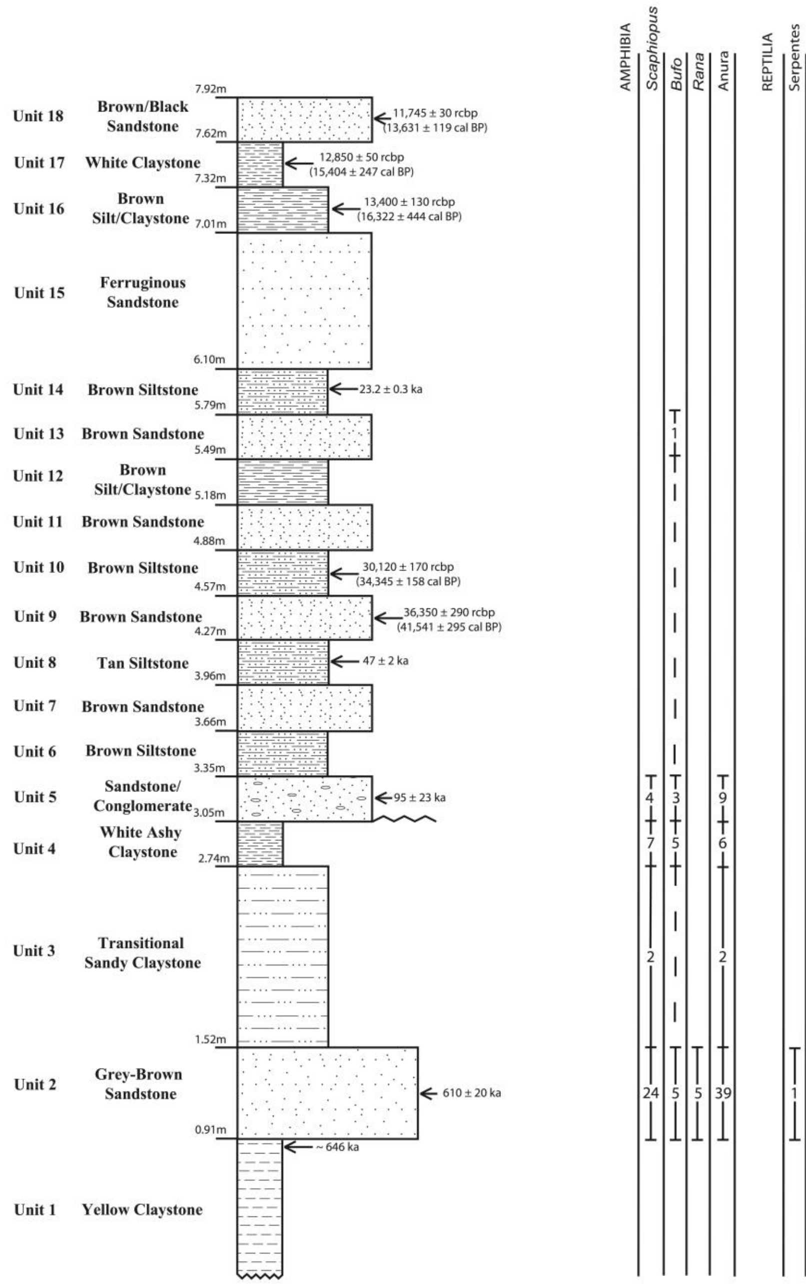

FIGURE 3. Taxon range distribution of lower vertebrates at Fossil Lake. Numbers in the ranges are qualitative based on the numbers of field collections from each lithostratigraphic unit containing a particular taxon. This number provides a relative comparative concept of abundance among units and taxa.

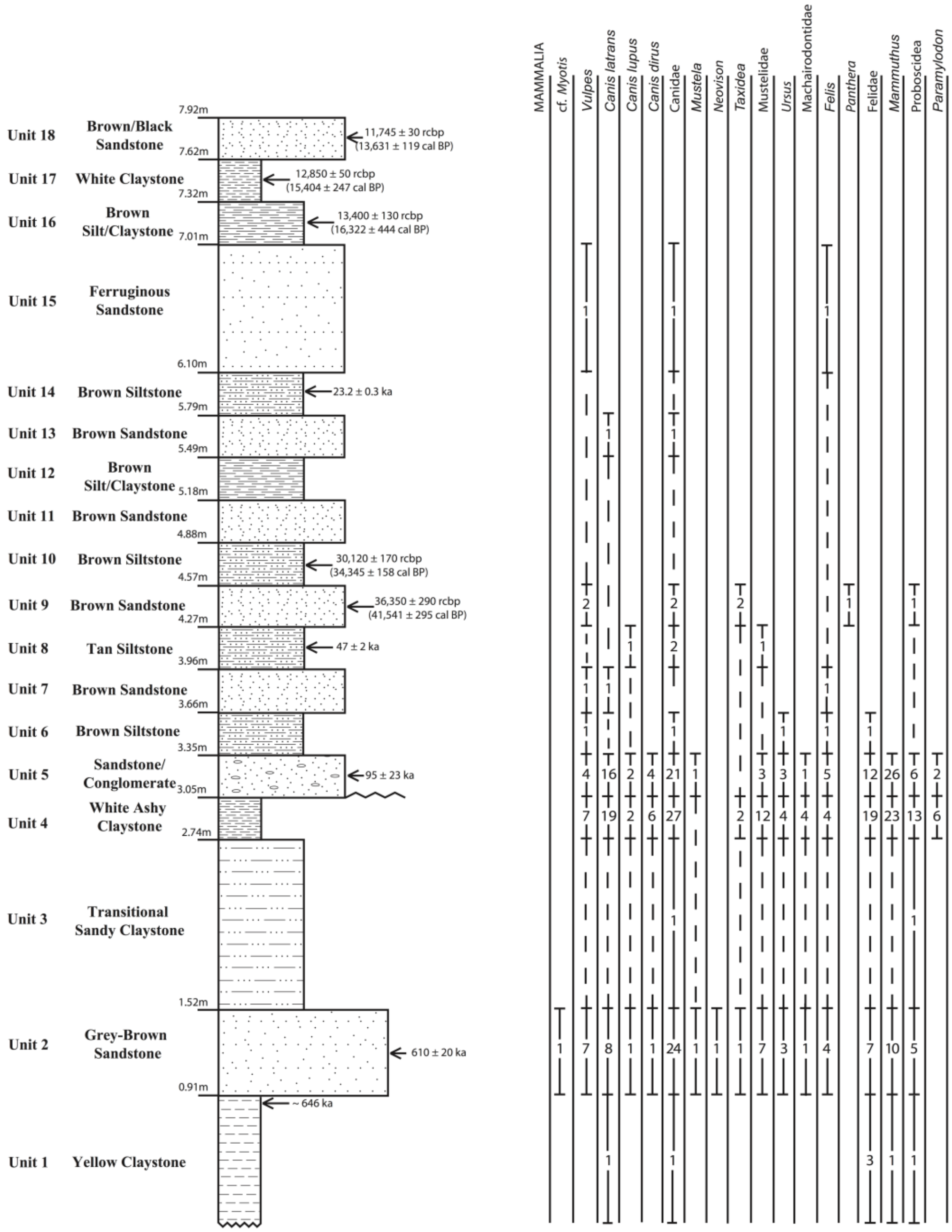

FIGURE 4. Taxon range distribution for Eulipotyphla, Carnivora, Proboscidea, and Pilosa at Fossil Lake.

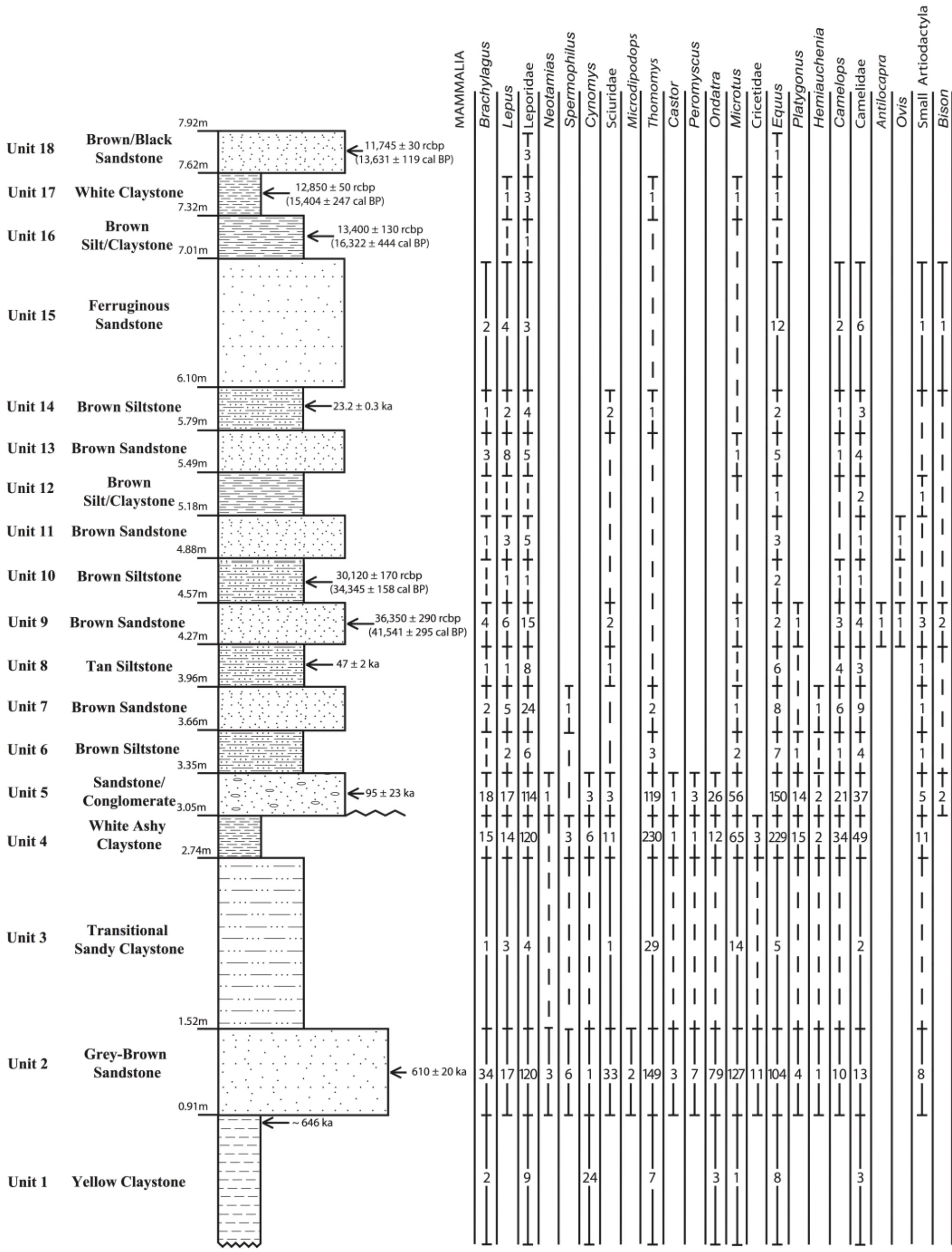

FIGURE 5. Taxon range distribution of Lagomorpha, Rodentia, Perissodactyla, and Artiodactyla at Fossil Lake.

including the first amphibians and reptiles. For the first time at Fossil Lake, fossils were collected with precise lithostratigraphic assignments. The taxon ranges coupled with radiometric dates illustrate relative abundances and distribution of the taxa over time (Figures 3-5).

TABLE 4. Taxa collected from Fossil Lake since 1989 by parties under direction of the author. See Figures 3, 4, and 5.

AMPHIBIA
- Anura
  - *Scaphiopus**
  - *Bufo**
  - *Rana**

REPTILIA
- Serpentes*

MAMMALIA
- Eulipotyphla
  - cf. *Myotis**
- Carnivora
  - *Vulpes*
  - *Canis latrans*
  - *Canis lupus*
  - *Canis dirus*
  - Canidae
  - *Mustela**
  - *Neovison**
  - *Taxidea*
  - Mustelidae
  - *Ursus**
  - Machairodontidae
  - *Felis*
  - *Panthera*
  - Felidae
- Proboscidea
  - *Mammuthus*
- Pilosa
  - *Paramylodon*
- Lagomorpha
  - *Brachylagus**
  - *Lepus*
  - Leporidae
- Rodentia
  - *Neotamias**
  - *Spermophilus**
  - *Cynomys**
  - Sciuridae
  - *Microdipodops**
  - *Thomomys*
  - *Castor*
  - *Peromyscus**
  - *Ondatra*
  - *Microtus*
  - Cricetidae
- Perissodactyla
  - *Equus*
- Artiodactyla
  - *Platygonus*
  - *Hemiauchenia*
  - *Camelops*
  - Camelidae
  - *Antilocapra*
  - *Ovis**
  - Small Artiodactyla
  - *Bison**

*Taxa unknown at Fossil Lake prior to studies by the author and colleagues

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PALEOFAUNAL DISTRIBUTION

The herpetological specimens from Fossil Lake are dominated by anurans, particularly the spade-footed toad, *Scaphiopus*, which occurs in abundance currently at Fossil Lake. *Bufo* and *Rana* are also encountered; the latter being relatively rare. These three taxa had not been previously reported as occurring in the Fossil Lake paleofauna (Table 4). As indicated by the range charts (Figure 3), most anuran occurrences are in the Irvingtonian portion of the section, although Unit 5 also produced significant anurans (Figure 3). Higher in the Rancholabrean portion of the section, a single *Bufo* specimen was preserved in Unit 13. Additional anuran specimens were picked from anthills, but their lithostratigraphic provenience could not be positively ascertained and are not included on the range charts.

Reptiles are hereby recorded from Fossil Lake for the first time (Figure 3; Table 4). A single snake vertebra was collected *in situ* from Unit 2, and a couple other vertebrae were collected from anthill matrix secured at Fossil Lake. Although the exact unit of origin of these latter specimens cannot be surely determined, the ants appeared to have sampled the Irvingtonian portion of the section. Therefore, no reptiles have yet been recovered from the Rancholabrean portion of the section and a total of only three snake vertebrae were discovered overall; no turtles or lizards have been found among the huge samples of specimens recovered from Fossil Lake. The paucity of reptilian taxa from Fossil Lake is not an artifact of collection bias. In addition to repeated extensive crawling at most sites, over 1.5 tons (1360 kg) of anthill and screened matrix was picked for small vertebrates. No amphibians or reptiles have yet been formally described, although a manuscript is in preparation.

Of the mammals, only a single eulipotyphlan specimen, a bat humerus, was recovered from Unit 2, another addition to the Fossil Lake paleofauna (Figure 4; Table 4). This humerus compares most favorably with that of *Myotis* according to Dr. Nick Czaplewski, University of Oklahoma, Sam Noble Museum. Bat specimens are normally relatively rare in waterlain deposits, although some excellent specimens occur in lacustrine deposits such as the Eocene German Messel (Habersetzer et al., 1992) and Wyoming Green River shales (Jepsen, 1966). This occurrence in Unit 2 appears to have been deposited along appearsto have bee deposited along the lake margin as the result of wave action. Shrews and moles might also be expected in these marginal lacustrine deposits, but none were positively identified during the decades of surface collection and from picked matrix samples.

Canids and felids were the most commonly observed carnivores at Fossil Lake. Fox and coyote specimens were particularly prolific, especially in Units 4 and 5, but ranged through much of the lithostratigraphic section. For example, *Canis latrans* was recovered from Unit 1, where carnivores are normally rare, and *Vulpes* was discovered relatively high in the section from Unit 15. Specimens designated as Canidae on Figure 4 are principally in the fox-coyote size range. Larger canids, *Canis lupus* and *Canis dirus*, are represented at Fossil Lake in fewer numbers and with shorter vertical ranges (Figure 4) based on known specimens. *Canis lupus* has a slightly longer range at Fossil Lake extending from Unit 2 to Unit 8, whereas *Canis dirus* was not found above Unit 5. Although reworking of *Canis dirus* specimens from Unit 4 into Unit 5 is a possibility, two of the jaws retained teeth that were unlikely to have survived erosion and redeposition.

Smaller carnivores within the Mustelidae are typically rare at Fossil Lake (Figure 4). Weasel, mink, and badger were documented low in the section from Unit 2 to Unit 5, although *Taxidea* elements were found higher in Unit 9. The occurrences of *Mustela* and *Neovison* represent new records at Fossil Lake (Table 4). Bears are also rare in the Fossil Lake area, and all appear to represent *Ursus*; no positive evidence of *Arctodus* was identified in these collections. The range of *Ursus* at Fossil Lake extends from Unit 2 to Unit 6 (Figure 4). The single specimen derived from Unit 6 is a partial skeleton of a juvenile that will be fully described in a later contribution.

Of the cats (Figure 4), a felid of similar size or slightly smaller than *Felis concolor* predominates. This taxon has a long range at Fossil Lake from Unit 2 to Unit 15, but is most commonly found in Units 2, 4, and 5. Another record (See Elftman, 1931) at Fossil Lake of the North American lion, *Panthera atrox*, was collected from Unit 9. This specimen compares favorably in size with the African lion, suggesting assignment to *Panthera atrox* rather than to the jaguar, *Panthera onca*. Simpson (1941) questioned, and reiterated by Daggett and Henning (1974), the assignment of *Felis* sp. major (Elftman, 1931) to *Panthera atrox,* believing its slightly smaller size could indicate *Panthera onca.* This controversy will be discussed further in a separate contribution. Also, a few fragmentary specimens provisionally assigned as machairodontids were distributed from Unit 2 to Unit 5, essentially derived from the Irvingtonian portion of the section.

All known proboscidean specimens from Fossil Lake represent *Mammuthus columbi*; no mastodon specimens have been identified to date. Moreover, most larger specimens such as tusks, teeth, and long bones were derived from Unit 4. Most of the more complete sloth specimens have also been found in Unit 4, mirroring the proboscidean occurrences. The known range of the sloth (*Paramylodon*) at Fossil Lake is only from Unit 4 to Unit 5 (Figure 4).

Throughout the Fossil Lake section, leporids are one of the dominant taxa, and members of the family have been recovered from every exposed lithostratigraphic unit (Figure 5). *Brachylagus*, the pygmy jackrabbit, was identified at Fossil Lake for the first time (Table 4). This small leporid is found in sagebrush-covered plains, is absent from country without sagebrush (Bailey, 1936), and its local biostratigraphic range extends from Unit 1 through Unit 15, whereas that of *Lepus* extends from Unit 2 through Unit 17. At a familial level, leporids occur in every lithostratigraphic unit (Figure 5). Among these specimens are probably leporid genera as yet unrecognized. Leporids are most common in Units 2, 4 and 5, which are the most fossiliferous units in the Fossil Lake section.

Rodents are relatively common at Fossil Lake (Figure 5), dominated principally by *Thomomys* and *Microtus*; sciurid, heteromyid, castorid, and cricetid specimens are less abundant. The occurrences of *Neotamias*, spermophilines, *Microdipodops*, and *Peromyscus* represent newly discovered taxa at Fossil Lake (Table 4). Within the Sciuridae, the chipmunk, *Neotamias*, is recorded from lower in the section in Unit 2 and Unit 5. Small spermophilines were found only in Units 2, 4, and 5, although postcrania of an appropriate size to be assigned to small ground squirrels were found as high as Unit 14 (Figure 5). One of the most interesting sciurid occurrences at Fossil Lake is that of the prairie dog, *Cynomys* (Martin, 1996), which now occurs principally east of the Rocky

Mountains. The range distribution is also unusual in that *Cynomys* is the most abundant mammalian taxon in Unit 1, where partial skeletons have been recovered. The range extends into Unit 2 up to Units 4 and 5 (Figure 5). Those specimens from Unit 5 are more poorly preserved than those below and may have been reworked.

Geomyoids include the heteromyid, *Microdipodops pallidus*, and the geomyids, *Thomomys talpoides* and *Thomomys townsendii* (Moses and Martin, 2014). The heteromyid, a new addition to the paleofauna, is restricted to Unit 2, based upon positive identifications; however, isolated incisors suggest the taxon may occur higher into Units 4 and 5 (Figure 5). *Thomomys* represents the most abundant rodent taxon at Fossil Lake, and numerous skeletons have been found in Units 2, 4, and 5, although most skeletons (>90%) were derived from Unit 4. Specimens of *Thomomys* occur in Unit 1 and extend into Unit 17 (Figure 5); however, as noted in Moses and Martin (2014), the species distribution is somewhat disjunct vertically. *Thomomys talpoides*, which currently survives at Fossil Lake, appears in Unit 1, but in Unit 2 through Unit 4 and into Unit 5, most specimens represent *Thomomys townsendii*, which occurs today just to the east. *Thomomys talpoides* dominates the Rancholabrean portion of the Fossil Lake section above Unit 5. Moses and Martin (2014) correlated the appearance, relative disappearance, and reappearance of *Thomomys talpoides* with warmer and drier environmental conditions as discussed below.

The beaver, *Castor*, has another interesting distribution, or perhaps its lack thereof. Only five occurrences of *Castor* have been documented in the extensive collections accumulated from Fossil Lake. Of these, the beaver appears in Unit 2, where three specimens were collected, and one each was derived from Unit 4 and Unit 5 (Figure 5). The paucity of this riparian-adapted rodent and its limited distribution no higher than Unit 5 can reflect both habitat preferences and environmental conditions as noted in the distributional analysis below.

The cricetid rodents include *Peromyscus*, *Ondatra*, and *Microtus* (Figure 5). The latter genus is the second only to *Thomomys* in abundance among rodents at Fossil Lake, has a similar range from Unit 1 to Unit 17, and also mirroring the range of the gophers, *Microtus* occurs most commonly in Units 2, 4, and 5. At the other end of the spectrum is *Peromyscus*, the most rare of the cricetids at Fossil Lake, with only eleven positively identified specimens and three possible incisors occurring in Units 2 through 4 and 5. The small size of these specimens might suggest the rarity could be the result of collection bias. However, even after the picking of 1.5 tons (1360 kg) of matrix, the numbers did not significantly change. *Peromyscus* is definitely rare at Fossil Lake. In contrast, the muskrat, *Ondatra*, adapted to a lacustrine environment, is much more abundant (Figure 5) and ranges from Unit 1 to Unit 5, with the greatest concentration in Unit 2. Interestingly, this lacustrine-adapted rodent is not found in any of the lacustrine clays higher than Unit 5 in the Rancholabrean portion of the section.

The ungulates at Fossil Lake include the horse and a spectrum of artiodactyls ranging from peccaries to *Bison.* Horses were the most abundant ungulate encountered at Fossil Lake and were found in every lithostratigraphic unit exposed at Fossil Lake (Figure 5). The greatest abundance is in Unit 4, where partial skeletons were most common, although another skeleton was found on the upper contact of Unit 15. The position of bones in stacks of this skeleton is suggestive of human activity rather than natural taphonomic processes, but concrete evidence is wanting, owing principally to the weathered state of the osteological elements and lack of associated human artifacts. Overall, the greatest concentrations of *Equus* elements are in Units 2, 4, and 5 (Figure 5).

Artiodactyls at Fossil Lake include peccary, camel, pronghorn, bighorn sheep, bison, and muskox. The latter taxon is represented by a specimen collected during Colonel William Day's survey in 1883 that went unnoticed in the U.S. National Museum collections until our investigations. The precise provenience of the juvenile left distal metatarsal of *Ovibos* is unknown and, therefore, is not recorded on Figure 5. The occurrence is mentioned here only for completeness of the paleofauna. In the well-documented collections, *Platygonus* is relatively rare and extends from Unit 2 to Unit 9 (Figure 5), indicating survival of peccaries to approximately 40 ka at Fossil Lake. The greatest concentrations of peccary specimens were found in Unit 4 and Unit 5. Camels are more abundant, including *Camelops* (Figure 6) and a smaller taxon, *Hemiauchenia*, represented by many specimens on Figure 5 listed as Camelidae. Camels were found from Unit 1 through Unit 15, and their greatest abundances were predictably in Units 2, 4, and 5; Unit 4 produced the most complete specimens including some jaws with teeth. *Ovis* and *Antilocapra* are illustrated as rare on Figure 5, based upon specimens positively identified to generic level. Bighorn sheep specimens occur in Unit 9 and Unit 11, respectfully (Martin, 2014); a single pronghorn

FIGURE 6. Dentary with dentition of *Camelops* collected from Unit 4 at Fossil Lake.

specimen was derived from Unit 11. However, many of the specimens listed as Small Artiodactyla (Figure 5) probably represent these two taxa, greatly extending the range of these two ungulates. Bison are relatively rare at Fossil Lake; only five specimens have been collected during our surveys, the first mention of specimens of this important taxon occurring at Fossil Lake was in Martin et al. (2005). Interestingly, all documented specimens occur above the disconformity at the base of Unit 5 (Figure 5) that separates the early Irvingtonian from the late Rancholabrean NALMA. This distribution of *Bison* corresponds with the radiometric dates derived from the Fossil Lake section (Martin, 2014, this contribution). Precise stratigraphic collecting is imperative, particularly at Fossil Lake where the lithostratigraphy is subtle. Most previous collectors assumed that the entire Fossil Lake area was late Pleistocene, equivalent to the Rancholabrea assemblages (see Kurten and Anderson, 1980), and therefore, collected bulk samples with little regard for source lithology. Important collections in repositories across the country are mixed and have lost much of their scientific utility. As Figures 3 to 5 indicate, two of the three most prolific fossil-producing units are actually Irvingtonian rather than Rancholabrean NALMA; therefore, mixing of two ages in the early collections is probable. Fossil Lake provides a cautionary note concerning scientific fossil collection from areas with significant vertical extent: 1) fossils must be intimately tied to their stratigraphic level. Determination of the lithostratigraphic succession normally requires several years to completely unravel and correlate stratigraphic sections over a significant lateral area, and 2) large samples (in the thousands where possible) should be collected over many years to fully appreciate the complexities of a fossiliferous area.

ANALYSIS OF PALEOFAUNAL DISTRIBUTION

Based upon the lithology of the fossiliferous units and the range zones of genera recovered from Fossil Lake outlined above, interpretations and conclusions may be offered. Nine rhythmically bedded packages exposed at Fossil Lake have been interpreted as waxing and waning sedimentary packages deposited in Pleistocene lakes (Martin et al., 2005). Each rhythmite consists of basal sand, occasionally with minor gravel, grading upward into a silty to sandy claystone. The lower sands represent the transgressive phase of the rhythmite, and the upper clay represents the lacustrine event. The lithological textures and paleoenvironments represented by the lithostratigraphic units that comprise the rhythmites provide important keys for interpretations. First, the coarser basal units, such as Unit 2 and Unit 5 are of adequate grain size to host larger fossil remains. Not surprisingly, these two units are exceedingly fossiliferous (Figures 3-5, 7). Secondly, the very fine-grained lacustrine clays normally produce fish remains, including skeletons, particularly in Unit 4 and Unit 17. Generally, the lower sandstone portion of each package was characterized by greater numbers of disarticulated terrestrial vertebrates, whereas the upper claystone was less fossiliferous and dominated by aquatic vertebrates. Therefore, grain sizes (texture) and depositional environments dictated to a great extent the number and types of fossils illustrated on Figures 3-5.

Unit 1, a yellowish claystone, represents an upper lacustrine unit of a rhythmite and is characterized by cypriniform fish. However, as noted on Figures 4 and 5, terrestrial vertebrates were also collected. Interestingly, two of the most common mammals, *Cynomys* and *Thomomys*, and to a lesser extent the leporids, exist in burrows and their remains may have been intruded into the unit prior to deposition of Unit 2. A thick tephra (Martin et al., 2005), the Rye Patch Dam tephra (~646 ka), lies suprajacent to the area where the prairie dogs, gophers, and lagomorphs were found. The volcanic event may explain the demise of the creatures in their burrows and account for their excellent preservation. The muskrat, *Ondatra*, was an inhabitant of the lake environment; the other mammals

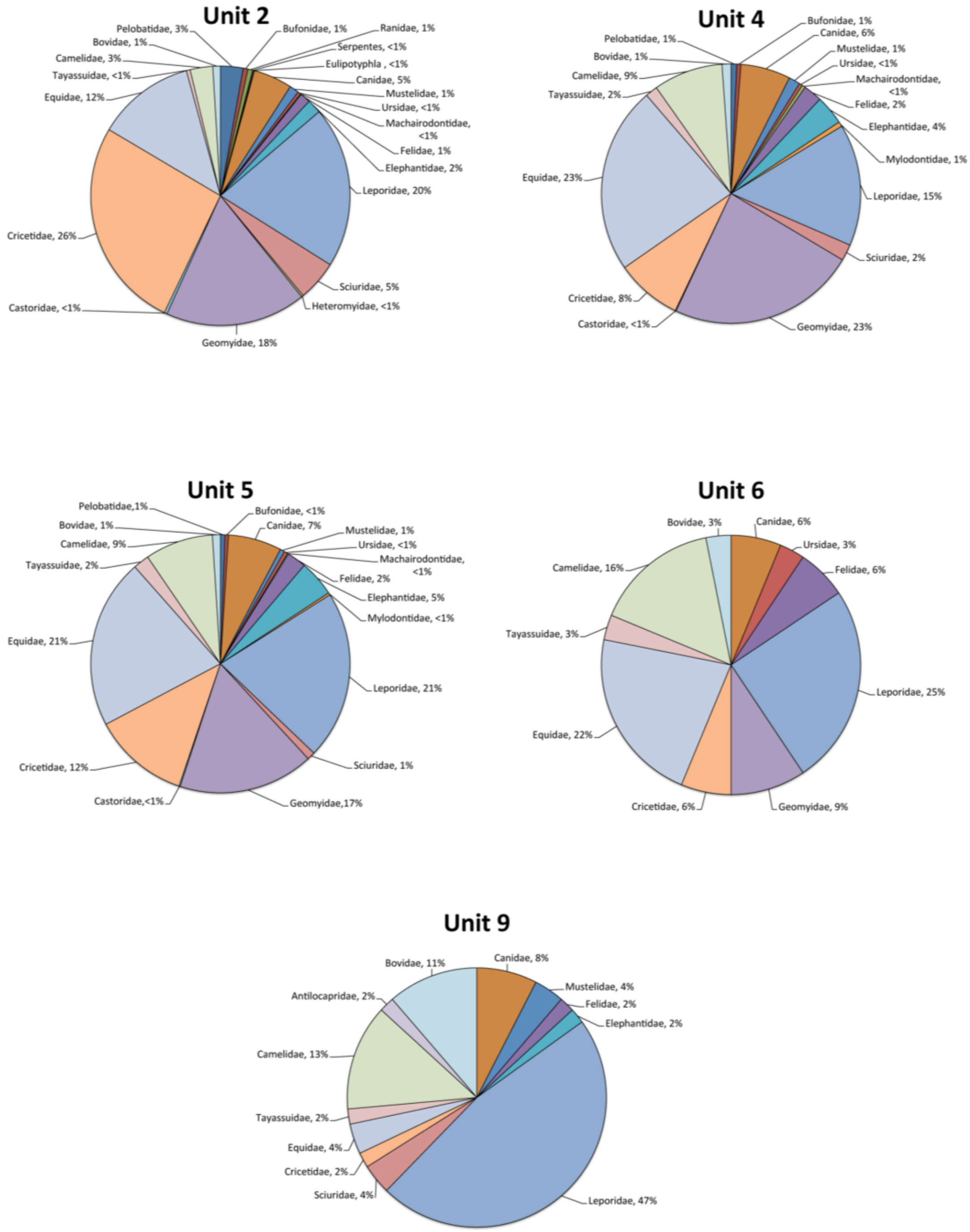

FIGURE 7. Comparison of Fossil Lake taxa at a familial level from Units 2, 4, 5, 6, and 9.

from Unit 1 shown on Figures 4 and 5 seemingly existed in the proximity of the lake, and their remains were washed into the lake and preserved in the lacustrine settings. Some elements of these mammals exhibited abrasion, and all were isolated; no associated skeletons were observed, as was typically the case with the prairie dog and some gopher remains.

Unit 2 is one of the three most fossiliferous units in the exposed Fossil Lake section (Figures 3-5) and hosts a tephra compositionally most similar to the Dibekulewe viritic tuff radiometrically dated at ~610 ka (Martin et al., 2005). This unit consists of a thin, iron-stained unconsolidated sandstone with a sharp lower contact that represents the base of the transgressive cycle of the successive rhythmite. Unit 2 is probably somewhat time transgressive, representing the reworking of previously deposited sediments, as well as the influx of coarser materials that were subjected to the energy of shoreline migration. Nearly every creature that existed at Fossil Lake is represented in Unit 2 and provides a clear picture of the paleofauna at Fossil Lake during the early Irvingtonian NALMA. Thousands of elements of catostomids and cyprinids occur, with only one incomplete specimen of associated elements. The fish carcasses appear to have disarticulated and been deposited in the wave-dominated, shoreline environment. Numerous isolated bird specimens, principally of waterfowl, and thousands of eggshell fragments occur in Unit 2, suggesting nesting along the lake margin. Similar disarticulation occurs with the amphibian and mammalian specimens illustrated on Figures 3-5; no articulated skeletons were encountered in tens of thousands of specimens collected, and the only associated partial skeletal material was that of a chipmunk and a gopher. Abrasion of many elements, particularly of the smaller taxa, is minimal, owing to the paucity of gravel-sized clasts in the depositional system.

Because Unit 2 contains such a complete sample of the Irvingtonian paleofauna, numerous first appearances of taxa from Fossil Lake are recorded on Figures 3-5. All of the herpetological taxa appear in Unit 2 (Figures 3, 7), dominated by *Scaphiopus*, the spade-footed toad, that currently exists at Fossil Lake in some abundance. The fossil specimens could indicate a relatively dry environment of deposition, but another possibility is that the sandy substrate is particularly preferred by these burrowing anurans. Conversely, the frog, *Rana*, is the least abundant amphibian, and based upon our collections, is confined to Unit 2 (Figure 3). The relative rarity of frogs could also indicate drier conditions or could be a response to the cold Pleistocene conditions of the time. This surely explains the lack of reptilian taxa. Only a few small snake vertebrae occur (Figure 3), and no turtles or lizards. As explained above, collecting bias does not play a part in explaining the paucity of reptiles at Fossil Lake; therefore, extremely cold winters likely explains the reptile absences.

The mammals that appear in Unit 2 are numerous (Figures 4 and 5), and some also provide clues about the environment of deposition at the time. Although the bat, cf. *Myotis*, is rare and could be found in many paleoenvironments, its occurrence is not surprising along the lakeshore, where these bats congregate to hunt insects and drink. The carnivore numbers are dominated by *Canis latrans* and a felid near the size of *Felis concolor*. *Vulpes* is also relatively abundant, but mustelids, ursids, and large cats are comparatively rare. As mentioned above, leporids, *Thomomys*, and *Microtus* become abundant in Unit 2; *Ondatra*, a pond-dweller, is likewise common, more common than elsewhere in the section. In contrast, *Castor*, a taxon most at home near moving water, is rare; only three specimens were found in Unit 2. This discrepancy is very suggestive that the populations from Unit 2 are near lacustrine rather than near riparian paleoenvironments, even though this unit represents one of the coarsest units in the exposed section and may exhibit minor cross bedding. All of the fossil sciurids are relatively uncommon at Fossil Lake compared to their great local abundance today. Only one occurrence of *Cynomys* was noted in Unit 2, a great difference from their abundance in Unit 1. Chipmunks and small ground squirrels are also uncommon in Unit 2 but occur here in greater numbers than elsewhere in the section. They, along with *Microdipodops*, *Castor*, and *Peromyscus*, may have existed more distal to the lakeshore environment. Horses far exceed any other ungulate in numbers of specimens (Figure 5) and individuals, and *Hemiauchenia* and *Camelops* make their first appearance here in the exposed Fossil Lake section. The unconsolidated rounded sandy nature of Unit 2 coupled with the habits of the creatures discovered in the unit suggest a lakeshore deposit, probably the result of wave action with minor additions of gully/riparian sediments derived from around this internally drained basin.

Unit 3 and Unit 4 may be considered together and regarded as the lacustrine portion of the rhythmite that was initiated by Unit 2 (Martin et al., 2005). Unit 2 grades into the tan sandy claystone of Unit 3, which may vary in thickness from essentially absent to over a meter. Sand content decreases up-section until a distinctive white claystone (Unit 4) with reworked tephra caps this rhythmite. Unit 4 represents one of the most fossiliferous units in the Fossil Lake section and also lies below a major disconformity that separates the early Irvingtonian section from the late Rancholabrean units. The fine clay and devitrification of volcanic ash resulted in extraordinary preservation. Fish skeletons and bird elements are common, many represented by partial skeletons. Anurans occur, but in relatively fewer numbers than Unit 2. Mammals are common, including many partial skeletons. Some individuals of heavier taxa appear to have been mired, and only partially articulated legs remain (e.g., Figures 2, 8). The proximal elements of these legs may be broken away or eroded, suggesting the bodies were not buried with the legs, may have been scavenged, and were removed prior to deposition of Unit 5. Although carnivores are relatively uncommon, they may be well preserved when encountered. Only coyotes and cougar-sized felids appear in any abundance, and mustelid postcrania are slightly more abundant than in Unit 2. Of course, carnivores are overall rare, as would be expected by comparison with living population numbers. Mammoth remains are more abundant in this unit than any other at Fossil Lake. Enamel plate thicknesses and plate counts on molars collected (Figure 9) confirmed the identification of the Fossil Lake mammoth as *Mammuthus columbi*. Sloth elements are also more abundant in this unit than any other at Fossil Lake. These two large creatures were likely candidates to be mired in the white mud. Likewise, horses and the giant camel, *Camelops* (Figure 8), were found in relative abundance. *Equus*, in particular, is the most abundant large taxon in Unit 4 (Figure 5), with more specimens collected here than from any other unit sampled at Fossil Lake and a preponderance of their bones was found occurring at high angles to the horizontal bedding plane. The abundance of mammalian specimens including so many skeletons, begs the question of how did these creatures become entombed in these lacustrine sediments. Mired skeletons provide some evidence that the water was shallow and subaerial exposure may have occurred periodically. The “quicksand-like mud” (Allison, 1966) trapped some creatures, and others expired around the waterhole and their bones were scattered, trampled and scavenged, as typically occurs around African waterholes today (Behrensmeyer and Dechant-Bosz, 1980). In fact, these authors considered the primary burial process in a swamp or lake habitat to be trampling. As a result, bones often occur at very high angles, and seldom were bones found flat lying in Unit 4, even those of birds and small to medium-sized mammals. Smaller mammals are normally more rare than larger taxa in Unit 4 at Fossil Lake, another taphonomic characteristic of such waterhole habitats (Behrensmeyer and Dechant-Bosz, 1980). The notable exceptions are some smaller leporids and *Thomomys*, which commonly are associated with burrows; many skeletons of *Thomomys* were collected from Unit 4 that appear to have been preserved in burrows (Figure 10). Therefore, some members of the assemblage from Unit 4 may have been intruded before deposition of Unit 5. The time difference between burrowed and non-burrowed specimens does not appear significant because the isolated specimens found *in situ* are identical to those found in burrows. Therefore, based upon mired skeletons, bones occurring at high angles, scavenged elements, and high percentage of larger taxa, a biased attritional assemblage that accumulated around a watering hole appears to explain the vertebrate occurrences in Unit 4 with an overprint of small, burrowing mammals.

The major disconformity below Unit 5 is significant because of the great amount of time represented at the unconformity and the degradational effect on units below. Radiometric dates indicate that medial and late Irvingtonian, as well as early Rancholabrean NALMA sediments, were either not deposited and/or were degraded during this missing time interval. In any event, a hiatus of approximately 500,000 years occurs between Units 4 and 5. Although Unit 5 rests directly on Unit 4 in most areas of exposure at Fossil Lake, some differential erosion occurred, and Unit 5 is apparently time transgressive. Specimens eroded during the degradation of Unit 4 and other previously deposited and eroded units might have been concentrated by the waxing of the rhythmite whose base is Unit 5. Nearly every taxon occurring in Unit 4 is also found in Unit 5, but many fewer are found higher than Unit 5 as illustrated in Figure 7, taxa presented at a familial level. Therefore, at least some of the taxa represented in Unit 5 may have been reworked from Unit 4 or below. Those taxa whose ranges end within Unit 5 are more likely to have been reworked; conversely, those taxa in Unit 5 whose ranges extend beyond Unit 5 and have been found elsewhere in the region may not have been reworked. For example, reworking of carnivore specimens seems possible because similar numbers of occurrences are in

FIGURE 8. Horse leg found at relatively high angle in Unit 4.

both Units 4 and 5, but most taxa exhibit a rapid decline in numbers higher in the section. Therefore, some reworking may have occurred. Suspected machairodontids have no recorded occurrences above Unit 5, nor do sloths (Figures 4, 7). All the specimens of these taxa in Unit 5 are fragmentary and may have been reworked. Proboscidean specimens do not occur in Unit 6 but persisted much later in the area and occur in Unit 9. Another example may be *Cynomys*, whose greatest abundance is documented in Unit 1. No specimens have been found higher than Unit 5, and no prairie dogs have been recorded from anywhere else in the Pacific Northwest. Therefore, the occurrences in Unit 5 above the disconformity may have been the result of reworking. The rodents *Thomomys* and *Microtus* are very abundant in Unit 5, and they were also exceedingly abundant in Unit 4 (Figure 5). However, above Unit 5 numbers of specimens drop significantly (Figure 7), suggesting some of the specimens occurring in Unit 5 may have been reworked. Specimens of *Castor*, *Peromyscus*, and *Ondatra* are unknown above Unit 5 at Fossil Lake. The single occurrence of *Castor* in Unit 5 is suspected to have been the result of reworking; however, those of *Peromyscus* and *Ondatra* are more questionable because more occurrences of these two taxa occur in Unit 5 than Unit 4. Of course, concentration of specimens in the coarser unit above the major disconformity may account for this discrepancy. Horses, peccaries, and camels have similar numbers between Units 4 and 5, and once again plummet above Unit 5 (Figure 5). Overall, the abundance of occurrences in Unit 5 may well be the result of reworking from Unit 4; however, some creatures certainly were deposited directly in Unit 5 such as *Canis dirus*, leporids, *Thomomys*, *Microtus*, horses, and camels, among others. Specimens of these taxa were well preserved, including partial skeletons, and some consisting of jaws with intact dentitions. Another taxon occurrence that appears the result of direct deposition in Unit 5 is that of *Bison*, a taxon that does not appear lower in the section (Figure 5).

The Rancholabrean units above Unit 5 are somewhat easier to interpret (Figures 3-5). The lower sandstone portions of the rhythmites are normally more fossiliferous than the upper portions, fewer cases of reworking are apparent, and the content of the paleoassemblages normally differs from those Irvingtonian units below. Unit 6, the upper lacustrine portion of the rhythmite with Unit 5, exhibits a striking change in the number of taxa and their occurrences (Figures 4, 5 and 7). Partial skeletons of a leporid and ursid were collected, carnivores are very rare, no proboscidean or sloth specimens were found, and leporids and *Equus* occur in some abundance along with a few gophers and camels. Overall, the assemblage in Unit 6 is very depauperate compared to that in Unit 5 (Figures 4, 5 and 7), and those taxa present are dominated by leporids, horses, and camels. Only a few specimens of gopher and vole might be considered to represent taxa adapted to exist near water, but these taxa are also found under much more severe conditions. In fact, the distribution of species of *Thomomys* suggests a switch from more mesic conditions represented by *Thomomys townsendii*, which prefers deep, moist, valley-bottom soils and normally does not extend into dry sagebrush areas (Bailey, 1936), in Units 2-4 to more xeric conditions from Unit 5 to Recent times represented by *Thomomys talpoides* (Moses and Martin, 2014), which is common on sagebrush plains in open, arid country (Bailey, 1936). Overall, a discernible change appears from an overall assemblage indicating more mesic conditions to one suggesting a much drier paleoenvironment (Figure 7). This paleoenvironmental shift may have occurred at the onset of Unit 6, but a more plausible explanation is that many of the taxa suggestive of mesic conditions in Unit 5 were actually reworked from below a major unconformity.

A taxon that may contradict this overall pattern is *Brachylagus*, which exclusively prefers sagebrush country. *Brachylagus* ranges essentially throughout the section and has concentrations in Units 2-4, the units suspected of being deposited under mesic conditions.

FIGURE 9. Molar of *Mammuthus columbi*, University of Louisiana Geology Museum (ULGM V4882) found in Unit 4 at Fossil Lake.

Perhaps local conditions were not so severe as to prohibit the growth of sagebrush, which currently occurs in areas with severe winters, or perhaps some smaller postcranial elements regarded as *Brachylagus* may represent a small species of *Sylvilagus*, a taxon that is also likely represented by some occurrences in the Leporidae on Figure 4.

The remaining lithostratigraphic units (Figures 3-5) are overall less fossiliferous and characterized by foxes, coyotes, cougar-sized cats, numerous leporids, ground squirrels, gophers, voles, horses, and camels (Figure 7). The last known appearance of a peccary is in Unit 9, and specimens of the American lion, pronghorn, and bighorn sheep appear at the same level (Figures 4 and 5). This unit may contain specimens

FIGURE 10. Fossil gopher skeleton (*Thomomys*) from Fossil Lake found in a burrow in Unit 4.

reworked from Unit 8. Many ranges in the Rancholabrean portion of the section will change with additional collections, particularly those of the carnivore and artiodactyl genera. Overall, the taxa preserved in the collections from Units 6 to 18 appear to represent xeric conditions more similar to those of today compared to the colder, somewhat more mesic conditions of the early Irvingtonian NALMA portion of the Fossil Lake section.

The rhythmite capped by Unit 17, a white claystone near the top of the preserved lithostratigraphic section, is an exception compared to other Rancholabrean rhythmites. The lower sand unit, Unit 15, appears to contain principally windblown sands with large cross beds, some of very high-angle, festoon-like cross beds. This unit indicates that sand dunes common in the area today minimally had developed prior to 16,322 $\pm$ 444 cal BP (Figures 3-5), and a horse skeleton occurring on the upper surface of Unit 15 indicates subaerial exposure. Higher in the section (Unit 16), these sands were reworked by flooding initiated during the formation of the lake represented by the white claystone (Unit 17). Unit 17 is characterized by numerous salmonid skeletons (*Oncorhynchus mykiss*) occurring with no cypriniforms, although cypriniforms occur in the overlying sand of Unit 18. The abundance and exclusive occurrence of salmonids in Units 17 suggests cooler waters, either as the result of a climatic shift, deeper waters, or both. The return of cypriniforms in the overlying unit suggests a climatic shift had to have been relatively short-lived, so deeper water appears a likely explanation for the abundance of salmonids.

According to radiocarbon dates of salmonid bones, the deep lake appears to have existed between approximately 15,100 to 16,700 cal BP (Figures 3-5), occurring between the dates of 14,500 cal BP (Jenkins et al., 2013) for a lacustrine high stand at Paisley Caves to the south in the Summer Lake Valley and the postulated date of 18,000 cal BP (Friedel, 1994) for the highest water level in pluvial Fort Rock Lake. Therefore, the Fossil Lake section (Units 16 and 17) appears to reflect an important high stand of Fort Rock Lake.

CONCLUSIONS

Fossil remains have been recovered from the Fossil Lake area for over 140 years but were never placed into a detailed stratigraphic context. Unfortunately, for many years, the area was considered to be of one age, so all specimens were essentially considered as bulk samples. In 1977, the first stratigraphically collected samples, and a rudimentary lithostratigraphic framework was recognized and later refined (Martin et al., 2005; Martin, 2014; this contribution). Collections derived over the last 40 years resulted in hundreds of thousands of specimens tied to 18 exposed lithostratigraphic units. The ultimate goals of this undertaking were to analyze the new collections in both lithostratigraphic and temporal frameworks upon which to superimpose fossil occurrences in order to understand their implications for the history and evolution of Fossil Lake. Nine rhythmically bedded sedimentary packages that are comprised of these 18 lithological units are interpreted as the result of the waxing and waning of episodic Pleistocene lakes (Martin et al., 2005). Each rhythmite consists of a transgressive basal sandstone grading into an overlying argillaceous to fine-grained, sandy claystone. The basal sandstones typically contain larger fossils and contain many terrestrial vertebrates as exemplified by Unit 2, whereas the claystones are normally less fossiliferous and dominated by aquatic vertebrates, particularly fish as demonstrated by the abundant salmonid skeletons in Unit 17. However, Unit 4, a white claystone, contradicts this pattern by containing numerous terrestrial mammals. Many of these creatures appear to have been mired in the lacustrine muds, many isolated bones were found at high angles, and some elements exhibit evidence of scavenging, suggesting a shallow watering hole scenario. Therefore, a biased attritional accumulation model where creatures with similar behaviors, habits, or lifestyles cause them to be deposited together may well explain the diversity of vertebrates in this unit.

A major disconformity that occurs below Unit 5 is significant because evidence of the medial and late Irvingtonian NALMA, as well as early Rancholabrean NALMA sediments, are missing between early Irvingtonian and late Rancholabrean deposits. Unit 5 usually rests directly on Unit 4 but some differential erosion occurred. Ninety-one percent of taxa found in Unit 4 persist in Unit 5; however, only 41 percent persist into Unit 6. Therefore, some taxa from Unit 5 were probably reworked from Unit 4 or below. Those taxa whose ranges end within Unit 5 may be suspect to having been reworked. However, some taxa from Unit 5 were not reworked, such as *Canis dirus*, leporids, spermophilines, *Thomomys*, *Microtus*, horses, and camels, among others. Representatives of these taxa were well preserved, not abraded, included partial skeletons, and some consisted of jaws with teeth. Another occurrence in Unit 5 resulting from direct deposition is that of *Bison*, a taxon that does not appear lower in the Irvingtonian section.

Fewer specimens were derived from the rhythmites composed of Units 7 to 18, the basal sandstones appear more fossiliferous than the overlying claystones, and their paleofaunal assemblages appear to represent xeric conditions more similar to those of today. Within this interval, two additional radiocarbon dates were obtained (Figures 3-5). From Unit 10, fossil bone produced a date of (30,120 ± 170 rcbp) and from Unit 9, bone produced the date of (36,350 ± 290 rcbp). These dates appear to corroborate the tephra date derived from the subjacent unit, Unit 8, which was geochemically correlated with the Marble Bluff bed (Mount St. Helens set C) and dated at 47 ± 2 ka (Martin et al., 2005). One rhythmite appears unusual compared to the other Rancholabrean rhythmites. Units 15 through 17 document an arid, windblown landscape flooded by a lake dominated by salmonid skeletons. Typical arid conditions of the Rancholabrean rhythmites occur above and below, suggesting the salmonids were able to survive in a deeper lake. The radiometric dates suggest a high stand approximately between 15,100 to 16,700 cal BP, which lies between previously suggested dates (Freidel, 1994; Jenkins et al., 2013) and may more accurately reflect a high stand of Fort Rock Lake in the Fossil Lake area.

The accompanying range charts (Figures 3-5) illustrate specimens principally at the generic level collected by our field parties. These collections produced numerous taxa heretofore unknown from Fossil Lake (Table 4) and provide statistically significant samples for many taxa whose systematic descriptions will appear elsewhere. The local taxon ranges at Fossil Lake (Figures 3-5) illustrate relative abundances and distributional changes over time.

Amphibians are recorded from Fossil Lake for the first time (Figure 3; Table 4). *Scaphiopus*, the spade-footed toad, is the most abundant anuran at Fossil Lake, and its abundance may signify a relatively dry depositional environment or the preference of a sandy substrate for burrowing. *Bufo* is relatively common, and one specimen has been found as high as Unit 14; otherwise, the occurrences of *Bufo* and *Scaphiopus* are concentrated in Units 2-5. On the other hand, *Rana* is relatively rare, occurring only in Unit 2. Rarity of frogs could also indicate drier conditions or could be a response to the colder Pleistocene conditions of the time. This hypothesis also explains the distribution of reptiles that are reported for the first time from Fossil Lake. Only a few snake vertebrae occur among the hundreds of thousands of specimens collected, and no turtles or lizards were discovered, suggesting an unfavorable climate.

Other striking absences within this exceedingly large sample size are shrews and moles; only one bat element represents the eulipotyphlan groups. Canids, particularly fox and coyote, are abundant throughout the section, but larger canids, *Canis lupus* and *Canis dirus*, are more rare with more restricted ranges (Figure 4). A few records of weasel, mink, and badger occur low in the section from Unit 2 to Unit 5, although *Taxidea* also occurs higher in Unit 9. The records of *Mustela* and *Neovison* represent newly discovered taxa in the Fossil Lake paleofauna (Table 4). *Ursus* is the only bear recognized in these collections, extending from Unit 2 to Unit 6. A felid similar in size to *Felis concolor* appears to be the most abundant cat, and along with the coyote, are the most abundant carnivores. Another record of *Panthera atrox* was discovered in Unit 9, and a few fragmentary machairodontid specimens were distributed from Unit 2 to Unit 5 (Figure 4). If the single occurrence in Unit 5 were reworked, the range of the machairodontids would be essentially Irvingtonian at Fossil Lake.

Mammuthus columbi is the only proboscidean currently recognized at Fossil Lake, and most of the better preserved specimens were found in Unit 4. Here, at least one specimen appears to have been mired and perished (Allison, 1966). Most well-preserved ground sloth specimens have also been found in Unit 4, suggesting a natural trapping mechanism for these large herbivores.

Leporids are very abundant at Fossil Lake, particularly *Brachylagus* (a new addition to the paleoassemblages) and *Lepus*. The only rodents that were found in such abundances were *Thomomys* and *Microtus*, although *Ondatra*, which prefers ponded water, exhibits a surge in numbers from Unit 2 to Unit 5, and *Cynomys* is most abundant in Unit 1. Two of the most abundant rodents, *Cynomys* and *Thomomys*, were often discovered in burrows (Figure 10); perhaps explaining their abundance compared other rodents. Chipmunks, small spermophilines, *Microdipodops*, *Castor*, and *Peromyscus* are more rare and may have existed more distal to the lakeshore environment. *Neotamias*, spermophilines, *Microdipodops*, and *Peromyscus* represent newly discovered taxa at Fossil Lake. Of the rodents, *Cynomys* represents the first occurrence of the prairie dogs in the Pacific Northwest (Martin, 1996), *Castor* is very rare suggesting little moving water, *Ondatra*, which prefers ponded water, is much more common, and species of *Thomomys* may be paleoenvironmental indicators. The base of the section is dominated by *Thomomys talpoides* that now exists in High Desert area, but Units 2-4 are characterized by *Thomomys townsendii* suggesting perhaps more mesic conditions, and *Thomomys talpoides* dominates the assemblages throughout the remainder of the section, indicating a return to drier conditions.

Of the ungulates, *Equus* occurs most abundantly, rivaled only by camelids (Figure 5). Although remains are found in every unit, horses are most abundant in Unit 4, where partial skeletons appear to have been mired, and partially articulated legs remain (Figures 2, 8). The artiodactyl ungulates include peccary, camel, pronghorn, bighorn sheep, bison, and muskox. *Platygonus* is relatively rare, with most specimens occurring in Units 4 and 5. At least two camels occur, *Hemiauchenia* and *Camelops.* The greatest abundance of camels was found in Units 2, 4, and 5, but the camelids persisted well up in the section when other ungulates such as *Platygonus* disappear. The occurrences of *Ovis* and *Antilocapra* are restricted to Units 9 and 11, but many of the specimens listed as Small Artiodactyla probably represent these two taxa, greatly extending their ranges. *Bison* is poorly represented at Fossil Lake and occurs only above the unconformity separating the Irvingtonian and Rancholabrean lithostratigraphic units.

Based upon range zones and relative abundances, climatic conditions appear to have changed from cooler, somewhat moister glacially dominated conditions in the early Irvingtonian NALMA to the xeric conditions of the later Rancholabrean NALMA and today. The change is documented in Unit 6 but probably occurred above the major disconformity at the base of Unit 5. Many of the taxa in Unit 5 appear reworked, apparently including many indicative of colder mesic conditions. Overall, the vertebrate assemblages from 18 lithostratigraphic units at Fossil Lake illustrate details of the evolution of Fort Rock Lake and the conditions under which deposition occurred.

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