GEOCHRONOLOGY AND PALEONTOLOGY OF THE PAISLEY FISH LOCALITY, SUMMER LAKE BASIN, NORTHERN LAKE COUNTY, OREGON

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ABSTRACT

The Paisley Fish Locality is a relatively recently discovered fossil locality in the northern Great Basin in south-central Oregon. Fossils, particularly fish remains, were found in faulted lacustrine deposits of pluvial Lake Chewaucan in the Summer Lake Basin. Both invertebrate and vertebrate fossils were initially found in 1995 by Mr. Larry Hills from interbedded lake beds and tephras. Gastropods, bivalves, cyprinids, catostomids, salmonids, an anuran, avians, and a badger have been thus far recognized. The question of age was initially proposed to be Pleistocene (Negrini et al. 2001) based upon tentative identification of the Mt. St. Helens Cy tephra (~45-50 ka). Later in 2015 (Kuehn et al.), a radiometric date of 3.1 to 3.2 Ma was proposed for this tephra. That age is confirmed herein by an $^{40}Ar/^{39}Ar$ date of 3.05 ± 0.07 Ma. Both dates indicate the fossils and sedimentary deposits were accumulated during the Pliocene Epoch. Lacustrine deposition in the northern Great Basin, and particularly in the Summer Lake Basin, began during the Pliocene as in other areas of the Great Basin.

Interestingly, the cypriniform fishes in the assemblages appear to have undergone hybridization with morphological characters shared between *Mylocheilus* X *Mylopharodon* and between *Catostomus* X *Chasmistes.* The latter hybrid was known previously, but the former is a new record. The co-occurrences of these cypriniforms and the trout, *Oncorhynchus lacustris*, suggest a Pliocene connection of Lake Chewaucan in southern Oregon with the Western Snake River Plain in Idaho.

Keywords

$^{40}Ar/^{39}Ar$ dating, Pliocene, Hybridization, Great Basin, Oregon, *Mylocheilus*, *Mylopharodon*, *Oncorhynchus*

INTRODUCTION

The northern Great Basin area is characterized by remnants of extensive lakes that existed principally during the last Ice Age (Allen 1984). In southern Oregon, numerous such lakes occur, such as Abert Lake, Alkali Lake, Silver Lake, Christmas Valley Lake, and Summer Lake, among many others (Figure 1). These remnants were much deeper and more extensive during the Late Pleistocene, and many of these former lakes have been named. Examples in northern Lake

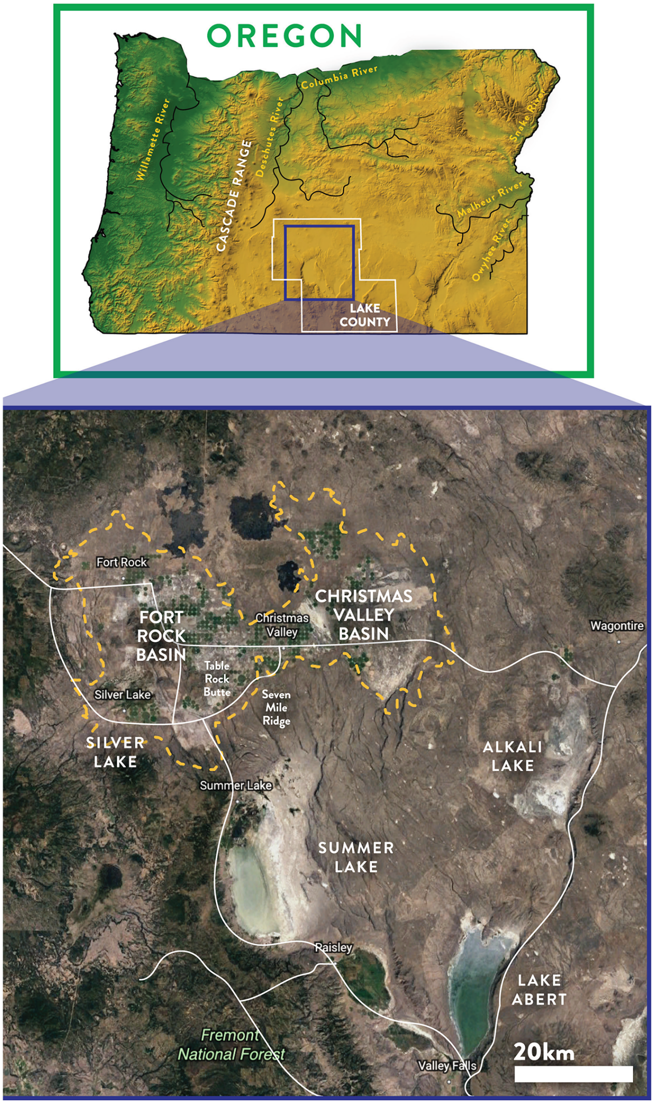

Figure 1. Lake basins in the northern portion of Lake County, southern Oregon. The dashed line represents the extent of Pleistocene Fort Rock Lake. Former levels of Pleistocene Lake Chewaucan are represented by light colored beds around Summer Lake.

County, Oregon, include Fort Rock Lake, that included what is now considered Silver Lake, Christmas Lake, and Fossil Lake (Allison 1979) and Lake Chewaucan (Allison 1982) that included present Summer Lake (Figure 2). In the latter lake basins, most sediments of Lake Chewaucan and Fort Rock Lake have been recorded from the Pleistocene Epoch (Allison 1982; Davis 1985; Cohen et al. 2000; Martin 2017; Martin et al. 2005; Negrini et al. 2001; Kuehn and Negrini 2010). However, lacustrine sediments have been recorded from more easterly and southerly lake basins during the Pliocene (e.g. Forester 1991; Hanna and Gester 1963; Smith 1984). Radiometric dates from the Paisley Fish Locality in the eastern portion of the Summer Lake Basin indicate lacustrine sediments in this basin also accumulated during the Pliocene.

Extensive lacustrine deposits occur around Summer Lake (Figures 1-2) that represent deposition of pluvial Lake Chewaucan (Allison 1982). In 1995, Mr. Larry Hills was surveying these lacustrine deposits east of Summer Lake and encountered fossil remains. Abundant invertebrates and fish remains were discovered, as well as rarer bird and mammal remains. Interbedded with the fossiliferous lacustrine deposits are coarse pumice strata and tephras. In 2001, the first attempt was undertaken to understand the geological history of the lake beds east of Summer Lake. Negrini et al. (2001) tentatively correlated a tephra layer at the top of the geological section as the ~45-50 ka Mt. St. Helens Cy tephra layer. Later in 2005, parties under the direction of the senior author initiated studies accompanied by Dr. Stephan Kuehn, now of Concord College. Dr. Kuehn collected and dated the upper tephra and derived a date of 3.1 to 3.2 Ma (Kuehn et al. 2015). We collected tephra samples and derived an $^{40}Ar/^{39}Ar$ date from the base of the section (Figure 3) as reported below. Kuehn mentioned the geology of the locality in a series of similar abstracts (Hostetler and Kuehn 2013; Hostetler et al. 2015; Kuehn et al. 2015).

Fossil vertebrates are rare from pluvial Lake Chewaucan, particularly from low in the section. Gobalet and Negrini (1992) recorded a Tui Chub, *Siphateles,* from higher Pleistocene sediments deposited in Lake Chewaucan with Lahontan

Figure 2. Paisley Fish Locality east of Summer Lake in northern Lake County, OR.

Basin and Fossil Lake affinities. Interestingly, as shown below, the fishes from lower in the section at the Paisley Fish Locality indicate Snake River connections.

Representatives of both the Cyprinidae and Catostomidae exhibit evidence of hybridization. Recently, Smith et al. (2018) addressed the occurrence of hybridization within the Catostomidae and noted that *Chasmistes* evolved during the Miocene in the Walker Lane trough (Faulds et al. 2005), which occurs in the shear zone between the Sierra Nevada Mountains and the western Great Basin. Sucker specimens from Summer Lake resemble *Chasmistes* "*batrachops*" and *C. spatulifer*, which exhibit hybrid influence between *Chasmistes* and *Catostomus* that

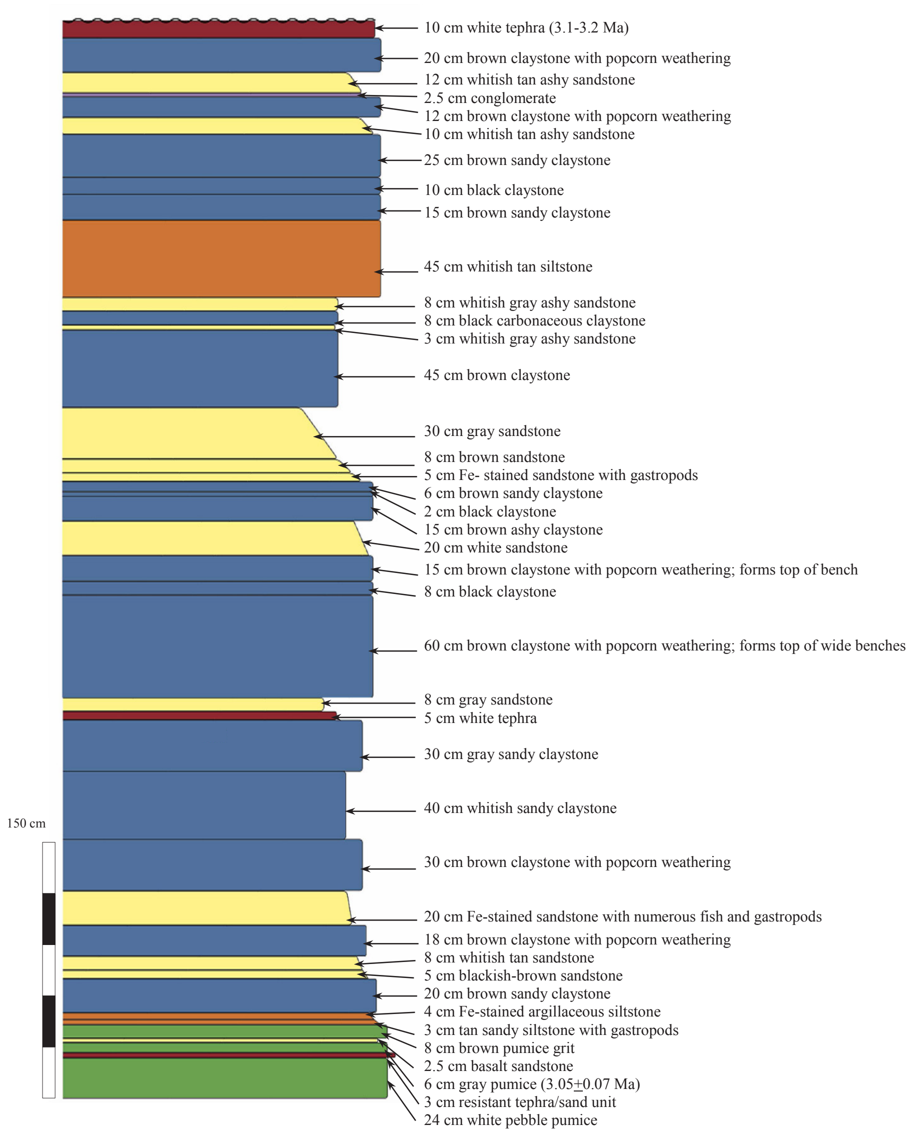

Figure 3. Lithostratigraphic section exposed at the Paisley Fish Locality, ULGM-V60.

began in the Pliocene (Smith et al. 2018:108). *Chasmistes spatulifer* occurs in the Pliocene Glenns Ferry Formation at Hagerman on the Snake River Plain (Uyeno 1961; Smith 1975; Smith et al. 1982), and *Chasmistes* cf. *batrachops* is also found in the Pliocene Ringold Formation of Washington (Smith et al. 2000) and in the Pleistocene Fossil Lake Formation in south-central Oregon (See Miller and Smith 1981:28).

STRATIGRAPHY

The fossil specimens recovered during our studies occurred at the Paisley Fish Locality, University of Louisiana Geology Museum (ULGM) locality V60. The stratigraphic section at ULGM-V60 is characterized by ferruginously stained lacustrine sedimentary units (Figure 3). These sediments are preserved in an uplifted area that appears relatively localized, owing to the faulted nature of the exposures (Hostetler et al. 2015). Interbedded within the lacustrine strata are tephras, two of which have been radiometrically dated (Figure 3). An earlier $^{40}Ar/^{39}Ar$ date of 3.1-3.2 Ma was derived from plagioclase from a tephra from the top of the section (Kuehn et al. 2015), and we here report an $^{40}Ar/^{39}Ar$ date of 3.05 ± 0.07 Ma based on hornblende from the base of the section. The ferruginous sediments coupled with these dates suggest a heretofore unknown Pliocene lithostratigraphical formational unit. The relatively localized nature of the known sediments prevents their being mapped at appropriate scales and prevents formal designation of a separate formation at this time; however, the unit is herein informally termed the Paisley Fish beds, and the stratigraphic section at ULGM-V60 (Figure 3) can be considered typical.

PALEONTOLOGY

Following the discovery of fossil specimens by Mr. Larry Hills, parties under the direction of the first author collected specimens from ULGM-V60. Some lithological units are extremely fossiliferous, whereas others are barren. The abundances allowed surface collection, layer by layer. No differences in taxa were found among the fossiliferous strata. Table 1 represents a composite list of specimens identified thus far from the Paisley Fish beds. The paleofaunal assemblage is dominated by invertebrates and fishes; birds and mammals are rare, but exceptional specimens of both vertebrate classes have been secured (e.g., Figure 4). Fossil specimens were compared to respective representatives at the University of Michigan Zoology Museum (UMMZ), University of Michigan Museum of Paleontology (UMMP), and the University of Louisiana Geology Museum (ULGM).

The invertebrate fossils were listed as *Vorticifex effusa*, *Gyraulus crista*, *Menetus* sp., *Pisidium* sp., as well as a limpet in Negrini et al. (2001); we noted similar invertebrate taxa. The "freshwater limpet" is surprisingly large and will be the subject of a later contribution.

Upon initial examination, the Lake Chewaucan fish fossils derived from the Paisley Fish beds show traits of five kinds of fish in three families: the Catos-

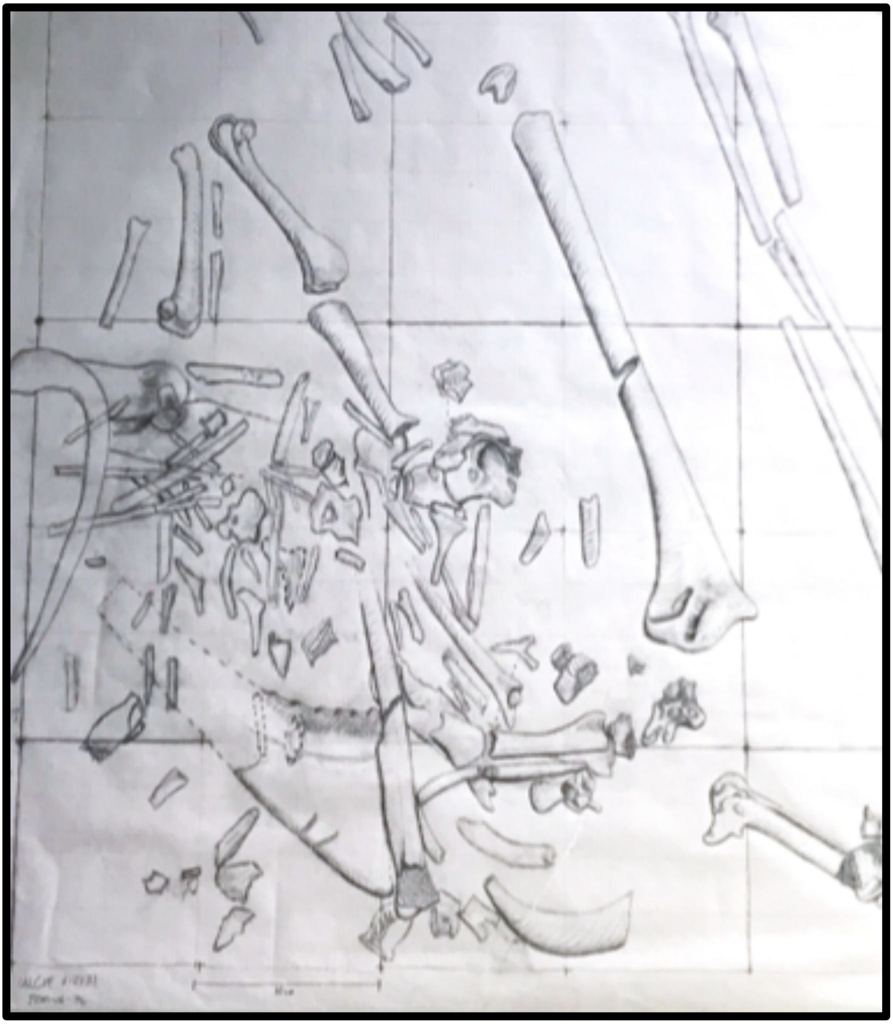

Figure 4. Field jacket map by ULGM laboratory manager, Mr. Gage Seaux, of fossil bird skeleton (ULGM V12131),* Cygnus *sp. cf.* C. hibbardi*, secured from ULGM locality V60.

tomidae, Cyprinidae, and Salmonidae. Within the Cypriniformes, the two Catostomidae (suckers) are *Catostomus* sp., common river sucker, of the Columbia-Snake River, Klamath River, and Sacramento River drainages and *Chasmistes* (Lake Sucker), of Miocene and Pliocene lakes of the Western Snake River Plain (WSRP). Two Cyprinidae (minnows), *Mylopharodon* and *Mylocheilus*, resemble common minnows of the lakes of the WSRP, *Mylopharodon hagermanensis* (Hardhead Chub) and *Mylocheilus robustus* (chub with molar teeth). Detailed examination, however, revealed unusual variation in the two suckers and between the two minnows. Apparently, no "pure" species of suckers or minnows occur in our samples.

Table 1. Fossil Taxa Collected from the Paisley Fish Locality.

Gastropoda		
	Planorbidae	
		Vorticifex sp. cf. *V. effusa*
		Menetus sp.
		Gen. et sp. indet.
Bivalvia		
	Sphaeriidae	
		Pisidium sp.
Teleostei		
Cypriniformes		
	Catostomidae	
		Catostomus X *Chasmistes* sp. cf. *Chasmistes* "*batrachops*"
		Chasmistes "*batrachops*" (probably of introgressed origin)
	Cyprinidae	
		Mylocheilus X *Mylopharodon* sp. cf. *Mylopharodon hagermanensis* (probably a hybrid swarm of introgressed origin)
Salmoniformes		
	Salmonidae	
		Oncorhynchus lacustris
Amphibia		
Anura		
	Bufonidae	
		Bufo sp.
Aves		
Anseriformes		
	Anatidae	
		Anas crecca
		Cygnus sp. cf. *C. hibbardi*
Mammalia		
Carnivora		
	Mustelidae	
		Taxidea taxus

Chasmistes can be diagnosed by its terminal mouth (Figures 5-6). The bony manifestation of this condition is the long lower jaw, especially the elongate anterior process of the lower jawbone (biting edge of the dentary, Figure 6), which forms a wider-than 90° angle with the posterior part of the bone. The maxilla has a forward-pointing antero-ventral process (premaxillary process) and low dorsal and ventral keels (Figure 5). The premaxillae are wide, and the hyomandibulars usually have a small process for muscle attachment anterior to the edge of the opercular condyle. Many other traits are diagnostic, but are not represented in our fossil sample. *Catostomus* is diagnosed by the converse of the traits of *Chasmistes* described above. The lower jaw of *Catostomus* is short, especially anteriorly, and the anterior process is angled ventrally at approximately 90°, supporting the structure of its ventral mouth (Figure 6). The maxilla is short with a mesially-pointing premaxillary process and high dorsal and ventral keels (Figure 5). The

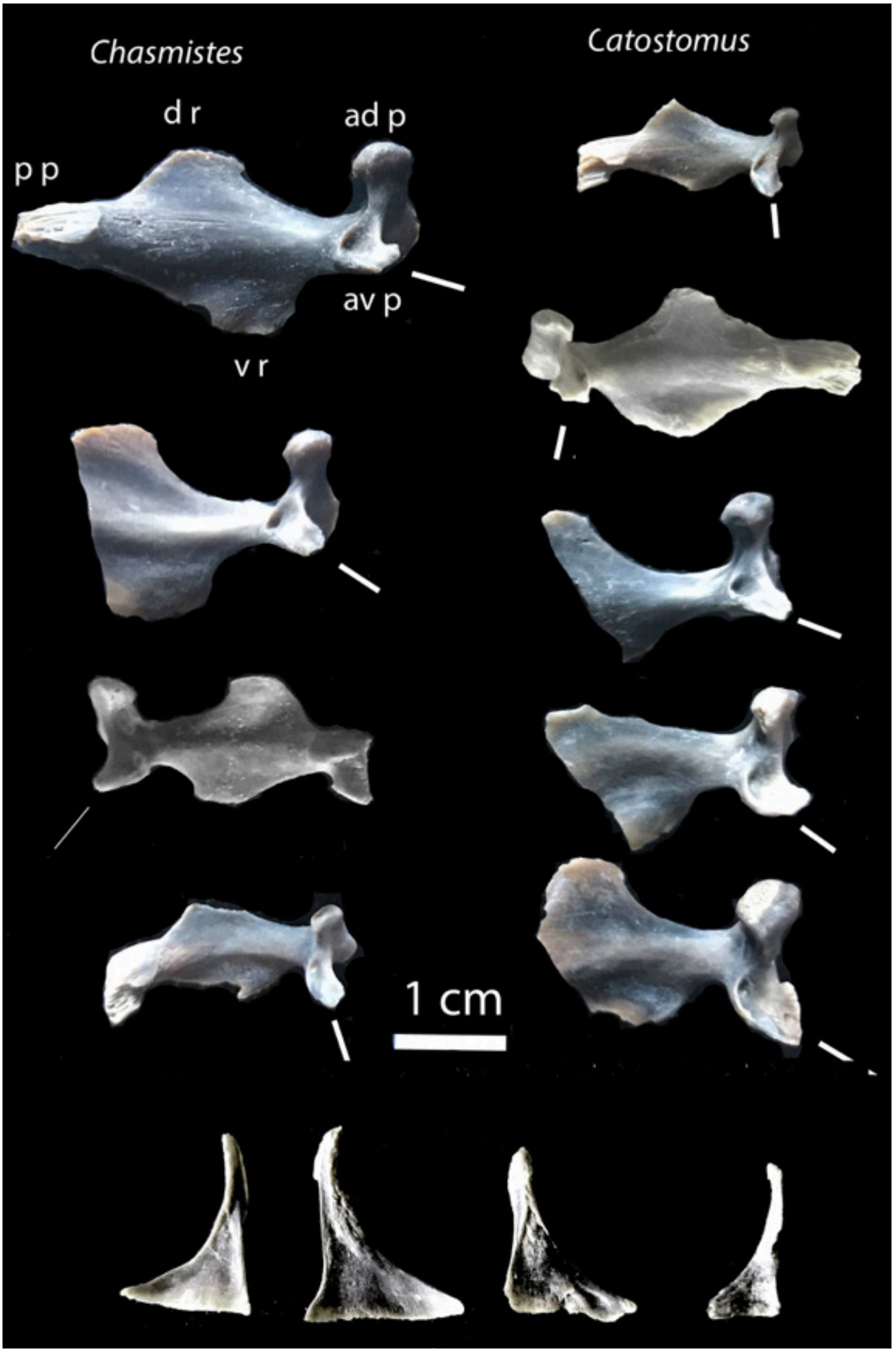

Figure 5. Maxillae and premaxillae of fossil Catostomidae from the Paisley paleofauna. Left maxilla of* Chasmistes *cf.* C. batrachops*, mesial view, ad p, antero-dorsal process, av p, antero-ventral (premaxillary) process, d r, dorsal ridge, v r, ventral ridge, p p, posterior process. Top nine, variable* Chasmistes *and possible* Catostomus *(top right). Bottom row, premaxillae. Tic marks indicate orientation of premaxillary process.

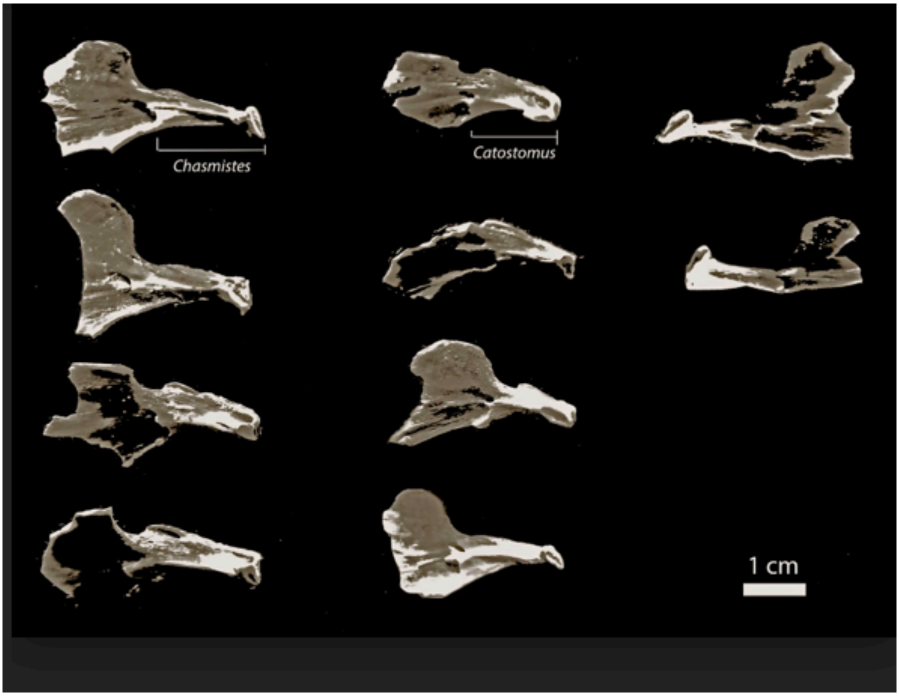

Fig. 6. **Chasmistes batrachops** ***dentaries from the Paisley paleofauna. Right column most like*** **Chasmistes batrachops,** ***with long biting edge of dentary at wide angle from posterior part of the mandible; left column,*** **Catostomus** ***and intermediate specimens (middle column), with shorter anterior limb at nearly right angles to posterior part of mandible.***

premaxillae are narrow, and the hyomandibula has no elevated process anterior to the opercular condyle (Figure 7).

The sample of *Catostomus* and *Chasmistes* shows a predominance of intermediate individuals (Figures 5-7), with few if any *Catostomus* without some individual traits of *Chasmistes* on their jaw bones. Several *Chasmistes* are similar but not identical to the typical forms of lake suckers in the Pliocene Glenns Ferry Lake on the WSRP. There is no consistency in which of the many maxillary and dentary traits seem incongruous on individual bones. The bones resemble *Chasmistes* "*batrachops*", which has been reported from many Pliocene lakes in western United States (Miller and Smith 1981; Smith et al. 2018). *Chasmistes* "*batrachops*" is variable and is suspected of being based on introgressed individuals between *Chasmistes* and *Catostomus* in several lakes.

Mylopharodon bones are typically diagnosed by short, wide dentaries and a coronoid process angled slightly posteriorly (Figure 8). Its pharyngeal arches have a short anterior process, a prominent corner (Figure 9), and a long, tapered post-dorsal process with an abrupt angle on the post-ventral edge (Figure 9). The lateral surface of the arch has large, open, nutrient foramina, with thin walls separating them. The tooth formula is normally 2,5-4,2, i.e. left-to-right, there

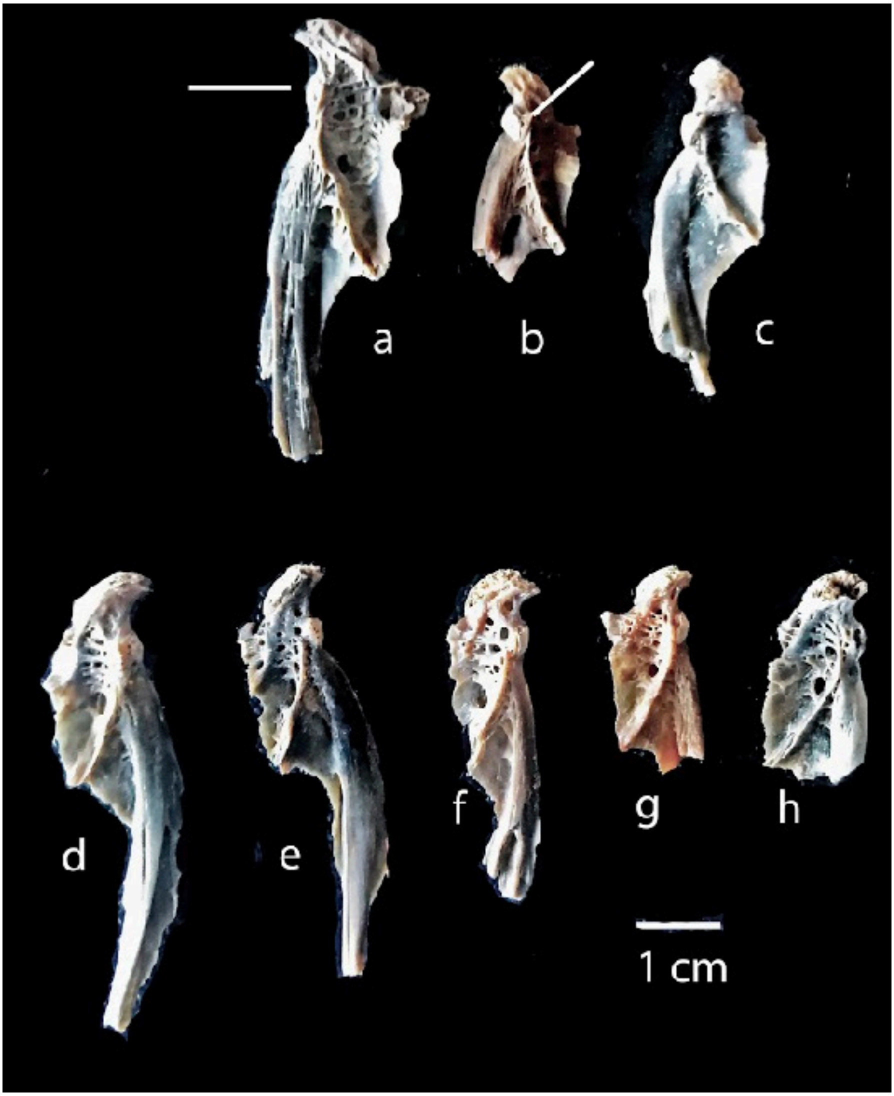

Figure 7.* Catostomus x Chasmistes *intermediate hyomandibulas; a,* Catostomus-*like, with no raised muscle attachment ahead of opercular condyle of right hyomandibula (note tic mark); b,* Chasmistes-*like, with a distinct raised muscle attachment ahead of opercular condyle; d-f are left hyomandibulas.

are 2 teeth in each minor row, 5 teeth on the left major row and 4 teeth on the right major row. The teeth are typically rounded and semi-molariform, but sometimes worn flat terminally (Figure 9). The teeth occluded with a basioccipital pad on the base of the neurocranium as in other North American minnows except *Mylocheilus*. *Mylocheilus* had longer, narrower dentaries than *Mylopharodon* in the Pliocene (Figure 8). *Mylocheilus* on the WSRP had a tooth formula that

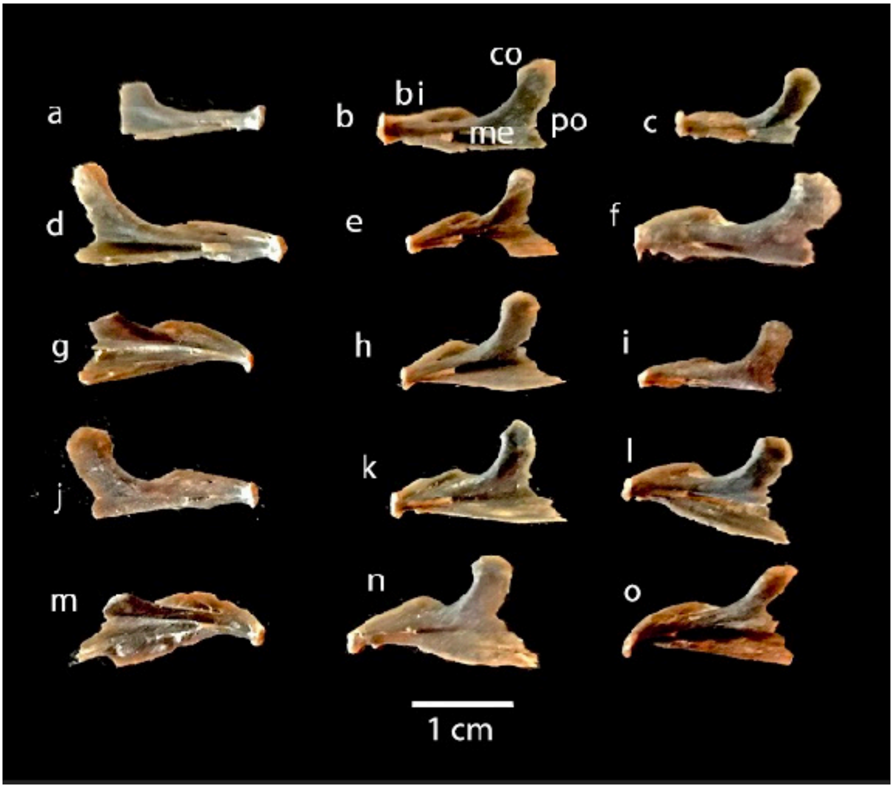

Figure 8. Left and right dentaries of hybrid swarm of dentaries like* Mylocheilus *cf.* M. robustus *(a, b, d, i) and* Mylopharodon cf. M. hagermanensis *(c, e to h, J to o). Mesial view except lateral view f. bi, biting edge; co, coronoid process; me, groove for Meckel's cartilage; po, posterior. Biting edge of* Mylocheilus robustus *typically long and straight; biting edge of* Mylopharodon hagermanensis *short and flared laterally.

evolved through time from 2,5-4,2 to 0,4-4,0 by gradual loss of individual teeth in adults as the body size evolved to larger size through time (Smith et al. 1982). The anterior and posterior processes of the arches are small, but bodies of the arches are large and robust often with limited nutrient foramina separated by massive nearly solid bone (Smith and Cosell 2002). The middle teeth (and 1 and 5 in adults) are molariform with flat terminal surfaces that occluded with their opposites (Figure 9).

The sample of *Mylopharodon* and *Mylocheilus* also shows a predominance of intermediate individuals (Figures 8-9). The dentary and pharyngeal specimens are most like those of *Mylopharodon hagermanensis*, but the specimens are not homogeneous; all have some traits suggestive of *Mylocheilus*. No individuals of *Mylocheilus* occur in our sample, but it is a unique fish and recognizable fragments of its phenotype are inconsistently apparent in various *Mylopharodon* dentaries and most pharyngeal arches and teeth (Figures 8-9).

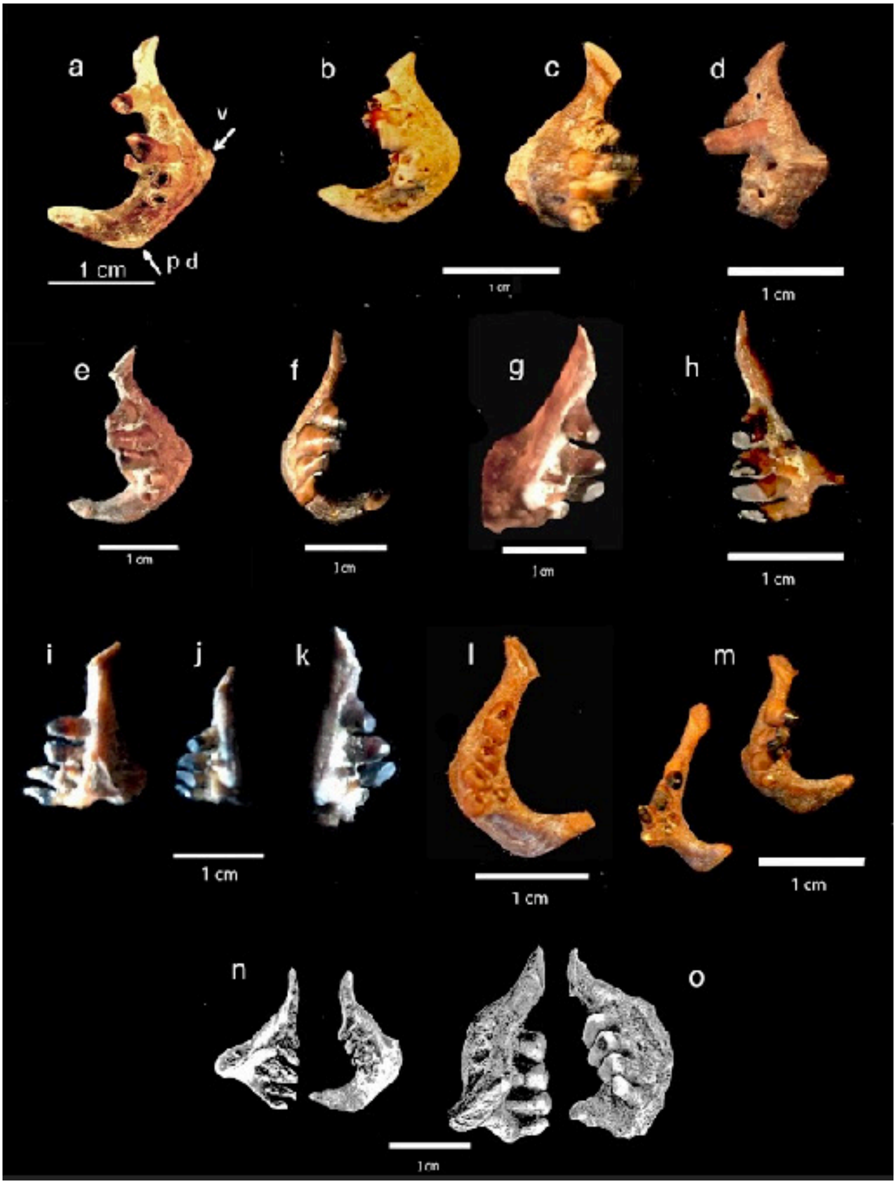

Figure 9. Pharyngeal arches and teeth of* Mylopharodon *sp. from the Paisley locality and comparative arches of* Mylopharodon *and* Mylocheilus *from the WSRP. Anterior toward top of page; scale bar equals 1 cm. Specimens a, b, d, e, g, k, n are from the left side, usually with five teeth (or sockets) in the main row and two in the minor row. Right side: c, f, h, I, j, l, o, usually with four teeth in the main row (but five in l). Mesial to ventral views of a-f, l, m, approximately dorsal views of g, h, I, j, k. In specimens a, n, angle v (ventral corner) are prominent in* Mylopharodon*, as in a, d, g, n, but rounded in the others, as in* Mylocheilus *(o), and angle p d (posterior) is sharp in* Mylopharodon*, as in a, f, l, m, n, but rounded or intermediate in others; n, Glenns Ferry* Mylopharodon hagermanensis *(dorsal [l] and ventro-mesial [r] views of left pharyngeal arch and teeth);* Mylocheilus robustus *(dorsal and ventro-mesial views of left pharyngeal arch and teeth).

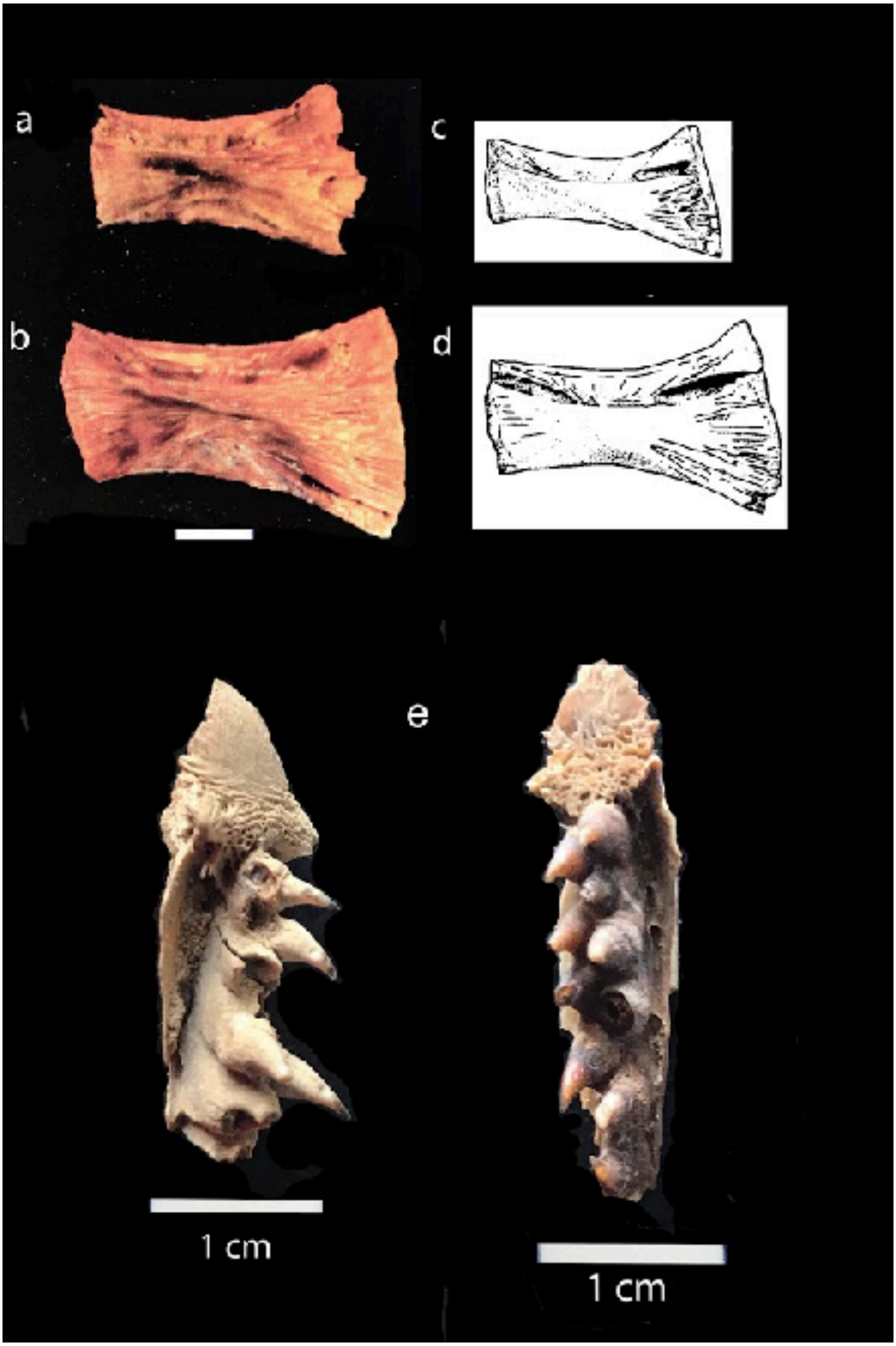

Figure 10. Fossil* Oncorhynchus *ceratohyals and prevomers from the Paisley paleofauna. a, b, ceratohyals of* Oncorhynchus lacustris *from the Paisley paleofauna; c,* Oncorhynchus clarkii*, modern, Oregon; d,* Oncorhynchus mykiss*, modern, Oregon; e, two prevomers of* Oncorhynchus *from the Paisley paleofauna.

The trout (Salmonidae, salmon and trout) at the Paisley site is represented by *Oncorhynchus lacustris*, a large trout ancestral to Rainbow and Redband Trout in western North America today. *Oncorhynchus lacustris*, an inland Pacific trout in the Paisley Fish beds, is similar to *Oncorhynchus lacustris* of the Miocene and Pliocene Western Snake River Plain (WSRP). *O. lacustris* is represented in the Paisley paleofauna by two complete prevomers and several complete ceratohyals among hundreds of elements. The prevomer (e.g. ULGM 14511, Figure 10) has two longitudinal rows of large teeth with enlarged bases and sharp points. The ceratohyal is a flat trapezoid throat bone, longer than deep and expanded posteriorly (Figure 10), which is readily distinguished from that of the Cutthroat Trout (*Oncorhynchus clarkii*), in which the ceratohyal is always less deep relative to its length (Stearley and Smith 1993). The occurrence of *O. lacustris* in the Summer Lake Basin and in the Glenns Ferry Formation in southern Idaho suggests an early connection of the two areas in the Pliocene.

The amphibians are represented by a single robust femur of a toad (ULGM 12107), likely a species of *Bufo* such as *B. woodhousei* or *B. boreas*. However, more diagnostic elements must be secured before a reliable species designation can be assigned.

Thus far, two bird taxa have been identified: *Anas crecca*, the green-winged teal, and *Cygnus* sp. cf. *C. hibbardi*, an extinct swan. The teal is represented by associated wing elements (ULGM 12054), whereas the swan (ULGM 12131) is represented by an associated skeleton (Figure 4). The type specimen of *C. hibbardi* was collected from the Hagerman West 2 Locality, which represents a lacustrine environment deposited during the Pliocene, rather than from the Pleistocene American Falls area as indicated by Brodkorb (1958). The Glenns Ferry localities also produced salmonid and cyprinid specimens similar to those occurring at the Paisley Fish Locality (Smith 1975).

A single mammal is known thus far from the Paisley site, an associated skeleton (ULGM V12148) identified as *Taxidea taxus*, the extant badger. This specimen is identical to the living species and significantly larger than *Pliotaxidea*, which occurred during the late Miocene and apparently gave rise to *Taxidea* in the Pliocene.

DISCUSSION

Oncorhynchus lacustris, Chasmistes, Mylopharodon, and *Mylocheilus*, as represented by traits in hybrids in the Paisley paleofauna, all have their nearest relatives in the Late Miocene and Pliocene lakes of the WSRP (Smith et al. 1982). Aquatic connections between the Miocene and Pliocene lakes of the WSRP and Klamath and Pit River drainages in Lake County were proposed by Wheeler and Cook (1954), Taylor (1960), Smith et al. (2000), and Stearley and Smith (2016). *Chasmistes spatulifer*, *Mylopharodon hagermanensis*, and *Mylocheilus robustus*, endemic to the Pliocene Glenns Ferry Lake are the closest relatives of the Paisley suckers and minnows, based on shared traits. This allows comparison of morphologies and hypotheses about species, ancestors, or introgression as explanations for the mixed phenotypes.

The Paisley fossil fishes are unique as far as is known in that species of two genera of suckers and two genera of minnows have broken down their reproductive barriers and formed two hybrid swarms. Individuals of *Chasmistes* and *Catostomus* are not cleanly identifiable with their parental species or genera. Similarly, *Mylopharodon* and *Mylocheilus* are so thoroughly mixed phenotypically that all individuals in our samples appear to have mixed ancestry. In former years the intermediates might have been considered ancestral taxa, but we now know that the four genera existed in modern form at least 10-6 Ma. Hybrid swarms of modern *Chasmistes* in Klamath Lake, Utah Lake, Jackson Lake, and Palisades Reservoir may be modern consequences of ancient hybridization (Smith et al. 2018). Fossils suggest past hybridization of this combination in the Pliocene Glenns Ferry Lake, Owens Lake, and other lakes in the Walker Lane transfer zone between the Sierras and Great Basin (Smith et al. 2018). All of these localities have Miocene or later hydrographic connections (Smith et al. 1982; Smith et al. 2000; Smith et al. 2002).

Genetic evidence for these catostomid hybrid connections is presented in Smith et al. (2018). DNA and phenotypic evidence combined demonstrate mixed parentage in Klamath Lake, Utah Lake, Pyramid Lake, Jackson Lake, and Palisades Reservoir. In each of these, *Chasmistes* mitochondrial DNA has been replaced by *Catostomus* mtDNA, from sympatric or formerly sympatric species. Both Lake Suckers and River Suckers spawn in the same tributaries, usually separated by season and locality. Lake Suckers are terminal-mouthed planktivores with unique adaptations for filter feeding on zooplankton in large lakes; *Catostomus* are generalized benthivores. The climate variation hypothesis proposes that they spawn separately and diverge ecologically during wet times and mix during arid times when low instream flow forces them onto the same spawning riffles.

Mylopharodon and *Mylocheilus* rarely hybridize and rarely backcross so introgression was unknown until discovery of the Paisley fossils. The uncorrelated admixture of fossil traits and extreme inter-trait and inter-individual variation (Figures 8-9) demonstrate the interaction of generations of mixed backcross genomes (as in F2s of Anderson and Stebbins 1954) with some possibly incompatible genes. We assume that extreme climatic fluctuations distorted the water cycle and ecological interactions enough to cause hybridization and introgression. Additional paleoecological research is necessary to test these ideas. Future sedimentology with micropaleontology and isotope analysis might reveal the nature of environmental changes that could lead to such extreme disruption of ecology and behavioral responses in two clades of fishes.

The fishes also constrain environmental and hydrographic interpretations. The *Chasmistes*, *Mylocheilus*, and *Oncorhynchus lacustris* were large lake species up to a meter long. *Mylopharodon* and *Catostomus* are medium-sized fluvial species that adapt easily to lakes. The descendants of these are smaller-bodied species—*Mylocheilus caurinus*, the living species endemic to the Columbia River drainage, *Mylopharodon conocephalus*, the extant endemic in California, and *Oncorhynchus mykiss* subspecies, modern Redband Trout primarily in the Columbia drainage, are often limited in their growth by smaller aquatic habitats.

The Paisley specimens are slightly on the small side of the size range, indicating a shallower lake habitat, at least seasonally. Temperature and rainfall were probably similar to today, with seasonality that produced arid conditions. The remarkable introgression within two pairs, the suckers *Chasmistes* and *Catostomus,* and minnows, *Mylopharodon* and *Mylocheilus*, indicate environmentally-caused breakdown of reproductive isolation dependent on stable water volume in lakes and tributary streams. Reproductive isolation in these fishes depends on segregation of time and place of spawning. Seasonal reduction in tributary in-stream flow is hypothesized to lead to breakdown in stability-dependent reproductive isolation and formation of introgressed hybrid swarms (Smith et al. 2018).

The ranges of the vertebrate fossils suggest a Pliocene time of deposition. Of the fishes, the *Oncorhynchus lacustris* is very similar to the Redband Trout, and Smith et al. (2002) indicated a trout similar to the *Oncorhynchus mykiss* lineage occurring in the Pliocene of the WSRP in Idaho and Oregon, similar to the trout of the Paisley Fish Locality in Oregon. The catostomid swarm, *Catostomus X Chasmistes* sp. cf. *Chasmistes* "*batrachops*" is similar to *Chasmistes* "*batrachops*" and *Catostomus spatulifer* common in the Glenns Ferry Formation (Smith et al. 2002). *Chasmistes* "*batrachops*" also occurs occur in the Pliocene Ringold Formation (Smith et al. 2000) among others; it ranges from Miocene to Pleistocene (Miller and Smith 1967, 1981). The Cyprinidae are dominated by hybrids of *Mylocheilus* X *Mylopharodon*. *Mylopharodon* and *Mylocheilus*, particularly related to *Mylopharodon hagermanensis* and *Mylocheilus robustus* in the Glenns Ferry Formation. *Mylocheilus* also occurred in the Great Basin during the Miocene and Pliocene (Smith et al. 2002).

The identifications of the birds suggest a Pliocene time of deposition. *Anas crecca* ranges from the Pliocene to present (e.g. Emslie 1992), and *Cygnus* sp. cf. *C. hibbardi* has only been found in the Pliocene Hagerman sites in the Glenns Ferry Formation of Idaho. The only mammalian specimen known from the assemblage is *Taxidea taxus*, a partial skeleton (ULGM V12148), which appears in the Pliocene Blancan NALMA and persists today; the preceding Hemphillian NALMA was characterized by its ancestor, *Pliotaxidea.* Therefore, the known mammal suggests a Blancan or later time of deposition. The mammals from the Glenns Ferry Formation in Idaho and the Ringold Formation in southeastern Washington where similar fishes occur also indicate a Blancan NALMA. Therefore, the known biostratigraphic information correlates with the radiometry, indicating deposition of the Paisley Fish beds during the Pliocene Epoch.

CONCLUSIONS

The paleontological locality, ULGM-V60, in the Summer Lake Basin, Lake County, Oregon, produces invertebrate and vertebrate fossils, particularly snails and fish. Occasionally, clams, "limpets," birds, and mammals may also occur, and these may be exquisitely preserved. The snails, clams, fish, shore birds, and lithologies indicate a shallow lacustrine environment of deposition. Such fossil assemblages are common in Pleistocene lacustrine deposits within the Summer and Fort Rock basins (Martin et al. 2005; Martin 2017). Therefore, radiometric dates that indicated a Pliocene age of deposition were initially surprising. Two

$^{40}Ar/^{39}Ar$ dates from different parts of the Paisley Fish Locality (ULGM-V60) lithological section and from separate dating laboratories indicate deposition occurred approximately 3 million years ago (Figure 3). The Pliocene date indicates that the lacustrine depositional regime in the northern Great Basin that persists to the present apparently was initiated earlier than the Pleistocene Ice Age. This reflects similar earlier depositional histories elsewhere in the Great Basin as noted by Smith et al. (2002), Forester (1991), and Hanna and Gester (1963), among others.

The fossil fishes reported here from the Paisley Fish Locality are unique because species of two genera of suckers and two genera of minnows have broken down their reproductive barriers and formed two hybrid swarms. The five kinds of fish represented in the paleofauna and its hybrid swarms are all remarkably similar to counterparts in the Miocene Chalk Hills Lake (Kimmel 1975) and especially the Pliocene Glenns Ferry Lake on the WSRP. They do not share this level of identity with any other Great Basin, coastal, Columbia drainage, or other lakes. We infer that the Pliocene Chewaucan drainage was intimately connected with outlets from Glenns Ferry Lake to the Klamath and associated Sacramento drainages in the Pliocene (Taylor 1960; Stearley and Smith 2016). The Snake River connections occurring with Lake Chewaucan during or before the Pliocene, later change to a Lahontan Basin drainage connection in the Pleistocene (Reheis et al. 2002) based upon the occurrence of a Tui Chub, *Siphateles* from Pleistocene sediments deposited in pluvial Lake Chewaucan (Gobalet and Negrini 1992).

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