NUMBER 743 May 30, 2013

OCCASIONAL PAPERS OF THE MUSEUM OF ZOOLOGY
UNIVERSITY OF MICHIGAN

ANN ARBOR, MICHIGAN

---

# FOSSIL AND RECENT MOUNTAIN SUCKERS, *PANTOSTEUS,* AND SIGNIFICANCE OF INTROGRESSION IN CATOSTOMIN FISHES OF WESTERN UNITED STATES

Gerald R. Smith[1], Joseph D. Stewart[2], and Nathan E. Carpenter[3]

## ABSTRACT

*Catostomus* is the most diverse genus of fishes in western North America. Over thirty species of *Catostomus* and other catostomins have been classified in five recent genera, *Catostomus, Deltistes, Chasmistes, Xyrauchen,* and *Pantosteus*. Introgressed evolutionary history is apparent in all five western catostomin genera. Mountain suckers, subgenus *Pantosteus*, are small and medium-sized fishes that live in moderate-gradient streams in the foothills and mountains, from the Black Hills to Pacific coastal drainages and from western Canada to central Mexico. *Pantosteus* is distinct in its molecular as well as morphological traits, but it is polyphyletic because *Catostomus* (*Pantosteus*) *columbianus* shares unique, derived morphological traits with *Pantosteus* and mtDNA with *Catostomus* (*s.s.*), thereby identifying two genera in its ancestry. We recognize three subgroups of *Pantosteus*: *C.* (*P.*) *discobolus* group of six species is distributed in the Snake River, eastern and southern Basin and Range Province to central Mexico, the Colorado Plateau, and the Los Angeles Basin. The *C.* (*P.*) *platyrhynchus* species group consists of four species, found in the Columbia, Snake, Upper Missouri, Upper Green, Lahontan, and Bonneville basins. *Catostomus* (*P.*) *columbianus* is a separate subgroup. The *Pantosteus* fossil record is sparse. We describe three Miocene records of the *C.* (*P.*) *discobolus* group from Oregon and Washington, three Pliocene species from Idaho and Nevada, and two Pleistocene records--from the Rio Grande rift in Colorado and from the Missouri River drainage of Kansas. The Kansas record suggests a much wider range for the species during glacial periods. Miocene relatives of *C.* (*P.*) *discobolus* from three sites in Oregon and Washington, 11.5-8.5 million years old, are morphologically advanced suckers. The Pliocene species from southern Nevada is intermediate between its modern relatives in the surrounding Great Basin and Colorado Plateau. At least one of the two Pliocene mountain suckers in the Snake River drainage was probably involved in the hybrid ancestry of *C.* (*P.*) *columbianus*. The general *Pantosteus* pattern suggests an origin in the northwest Great Basin and Columbia Plateau, with a history of dispersal, isolation, and evolution southward through Basin and Range drainages to the Colorado Plateau and Mexico, and eastward across the Rocky Mountains to the Missouri drainage. Mountain suckers are adapted to moderate-gradient mountain streams and to scraping food from rocky substrate.

Key words: Catostomidae, *Catostomus*, *Chasmistes*, *Deltistes*, *Xyrauchen*, hybridization, Great Basin, Juntura, Drewsey, White Narrows, Glenns Ferry.

[1]Museum of Zoology, University of Michigan, Ann Arbor, MI 48109, U.S.A.
[2]URS Corporation, 600 Montgomery St., San Francisco, CA 94111, U.S.A.
[3]Orma J. Smith Museum of Natural History, College of Idaho, Caldwell, ID 83605, U.S.A.

## TABLE OF CONTENTS

ABSTRACT....1
INTRODUCTION....2
MATERIALS AND METHODS....6
DIAGNOSES OF CATOSTOMIDAE AND CATOSTOMINI....7
DIAGNOSIS OF *CATOSTOMUS* (*s.s.*) AND *PANTOSTEUS*....9
    Diagnosis of *Catostomus* plus *Pantosteus*....10
    Diagnosis of the subgenus *Pantosteus*....10
    Comparison of morphological and mtDNA evidence....10
    Diagnoses of *Pantosteus* species groups....10
    *Catostomus* (*Pantosteus*) *bondi*, new species....12
    Diagnoses of other groups of *Pantosteus*....15
*PANTOSTEUS* PALEONTOLOGY....16
MIOCENE FOSSIL *PANTOSTEUS* FROM OREGON AND WASHINGTON....16
    *Catostomus* (*Pantosteus*) *hyomyzon*, new species....16
PLIOCENE FOSSIL *PANTOSTEUS* FROM IDAHO....20
    *Catostomus* (*Pantosteus*) *oromyzon*, new species....21
    *Catostomus* (*Pantosteus*) *arenatus*....24
PLIOCENE FOSSIL *PANTOSTEUS* FROM NEVADA....27
    *Catostomus* (*Pantosteus*) *asitus*, new species....27
PLEISTOCENE FOSSIL *PANTOSTEUS* FROM KANSAS....29
PLEISTOCENE FOSSIL *PANTOSTEUS* FROM COLORADO....31
DISCUSSION....32
SIGNIFICANCE OF INTROGRESSION....36
EVOLUTION OF *PANTOSTEUS* BIOLOGY....38
SUMMARY AND CONCLUSIONS....39
ACKNOWLEDGEMENTS....40
LITERATURE CITED....41

## INTRODUCTION

Catostomid fishes of western North America include medium-to-large river suckers, *Catostomus* (*s.s.*), small and medium swift-water mountain suckers, *Pantosteus,* large lake suckers, *Chasmistes,* the large Lost River Sucker, *Deltistes,* and the large Razorback Sucker of the Colorado River, *Xyrauchen.* These have been classified in the Catostomini, sister group to the Moxostomini in the Catostominae (Smith 1992b; Chen and Mayden 2012). The catostomins are morphologically and molecularly diagnosable as a clade. Morphologically, the genera/subgenera are individually diagnosable as well, but molecular data uniformly cluster species of the lake sucker group with their sympatric *Catostomus* (*s.s.*) relatives, rather than other lake suckers. This has prompted speculation that the lake suckers are not a clade, but are locally-derived ecophenotypes of *Catostomus*. Chen and Mayden (2012) classified *Chasmistes, Deltistes,* and *Xyrauchen* species in *Catostomus,* close to their sympatric relatives (See also Doosey *et al.* 2010). Here we include *Pantosteus* in *Catostomus* because of the clear evidence of polyphyletic origin of *C.* (*P.*) *columbianus,* and cite evidence that supports the same logic regarding the relationships of the other genera. We discuss the merits of recognizing one non-arbitrary genus, *Catostomus*, and compare the utility of the traditional classification *vs.* the organizing principle of monophyly in a natural classification. The primary purpose of this paper, however, is to describe the morphology and the fossil record of the mountain suckers, *Pantosteus,* with three new fossil species and one new recent species, and to discuss hypotheses concerning their evolution in the geological - biogeographic context of the Basin and Range Province.

Species of *Catostomus,* subgenus *Pantosteus* (mountain suckers), are found in western North America from western Canada to central Mexico and from the Black Hills to the Columbia River drainage (Fig. 1; Smith 1966; Unmack *et al.* in revision). Fossil mountain suckers were previously known only from the Pliocene of southwestern Idaho (Miller and Smith 1967) and the Pleistocene of southern Colorado (Rogers 1985, 1992). Here we broaden the record to include descriptions and diagnoses of a new middle Miocene species from central Washington and southeast Oregon, a new Pliocene species from southern Nevada, new fossils of *C.* (*P.*) *arenatus* from the Snake River Plain*,* an older, larger species from the Snake River Plain, and Pleistocene specimens from northwestern Kansas and southern Colorado.

About a dozen recently recognizable species of *Pantosteus* were described between 1854 and 1938. Baird and Girard (1854) described *Catostomus plebeius* from the Rio Grande drainage, New Mexico, and *Catostomus clarkii* from the Gila River drainage, Arizona. Girard (1856) added *C. guzmaniensis* (a synonym of *C.* (*P.*) *plebeius*) from Mexico. Cope (1872) described *Catostomus discobolus* from the Green River, Wyoming. Cope (1874) described *Minomus platyrhynchus* from the Bonneville Basin, Utah, and *Minomus yarrowii* from the Zuni River, New Mexico. He then erected the genus *Pantosteus* for these forms in Cope and Yarrow (1875); the type species was *Minomus platyrhynchus*. Cope (in Cope and Yarrow1875) also described *Pantosteus virescens,* a large mountain sucker based on a single specimen (with erroneous locality data) determined by Snyder (1924) to be from the Weber River, in the northern Bonneville drainage, Utah. Garman (1881) described *Catostomus nebuliferus* from the Rio Nazas, Mexico, and Evermann (1893) described *Pantosteus jordani* from the Missouri drainage, South Dakota. Eigenmann and Eigenmann (1893) described *Pantosteus columbianus* from the Snake River drainage, Idaho, and Hubbs and Schultz (1932) described the same species as *Catostomus syncheilus* from the Columbia River basin, Washington. Rutter (1903) described *Pantosteus lahontan* from the Lahontan Basin, Nevada. Snyder (1908) described *Pantosteus santa-anae* from Los Angeles, California, and also reviewed (1915, 1924) previous work on the genus and clarified species synonyms, distributions, and relationships. Tanner (1932) described *Notolepidomyzon utahensis* (*=C. P. clarkii*) from the Virgin River, Utah, and in 1942 described *N. intermedius* (*=C. P. clarkii*) from the neighboring White River Valley, Nevada.

Smith (1966) revised *Pantosteus* with morphological and meristic data from 558 population samples and recognized six polytypic species, *C.* (*P.*)

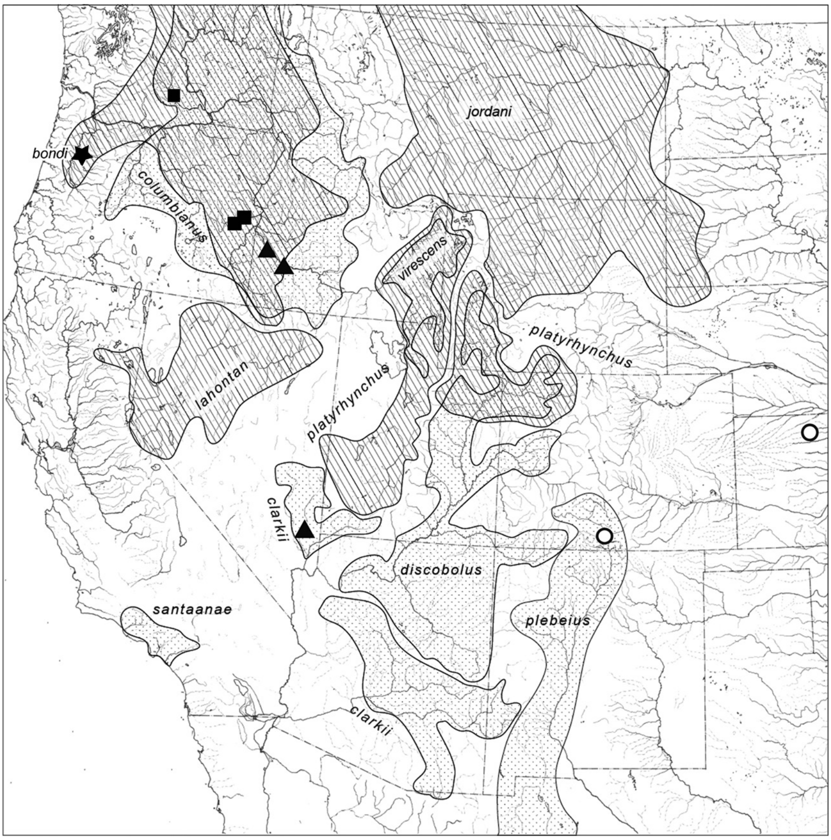

Fig. 1 a. *Pantosteus* species currently range through fluvial systems draining orogenic landscapes. Miocene and Pliocene fossil localities suggest origins in the northern Basin and Range Province and Columbia Plateau. Species in the *C.* (*P.*) *discobolus* species group are indicated by stipples; species in the *C.* (*P.*) *platyrhynchus* group are indicated by cross-hatch pattern. Miocene (square symbols) Ellensburg Formation, Washington, and Drewsey and Juntura formations, Oregon; Pliocene (triangles) Glenns Ferry Formation, Idaho, and White Narrows Formation, Nevada; Pleistocene (round symbols) Coon Creek, Kansas, and Hansen Bluff, Colorado. Recent *Catostomus* (*Pantosteus*) *bondi*, type locality (star symbol) South Santiam River, Lebanon, Oregon.

*plebeius* in the Rio Grande drainage and rivers in west-central and northern Mexico; *C.* (*P.*) *clarkii* in the lower Colorado River drainage in the Great Basin; *C.* (*P.*) *santaanae* near Los Angeles in coastal southern California; *C.* (*P.*) *columbianus* in the Columbia and Fraser river drainages in the Northwest; *C.* (*P.*) *discobolus* in the upper Colorado River drainage down through Grand Canyon, the Northern Bonneville Basin, and upper Snake River; and *C.* (*P.*) *platyrhynchus* in the Columbia drainage, Missouri drainage, Snake River drainage, Lahontan Basin, Bonneville basin, and upper Green River. Species were characterized and divergent characters were described and figured to aid interpretation of *Pantosteus* evolution.

The generic classification of species of *Catostomus* and *Pantosteus*

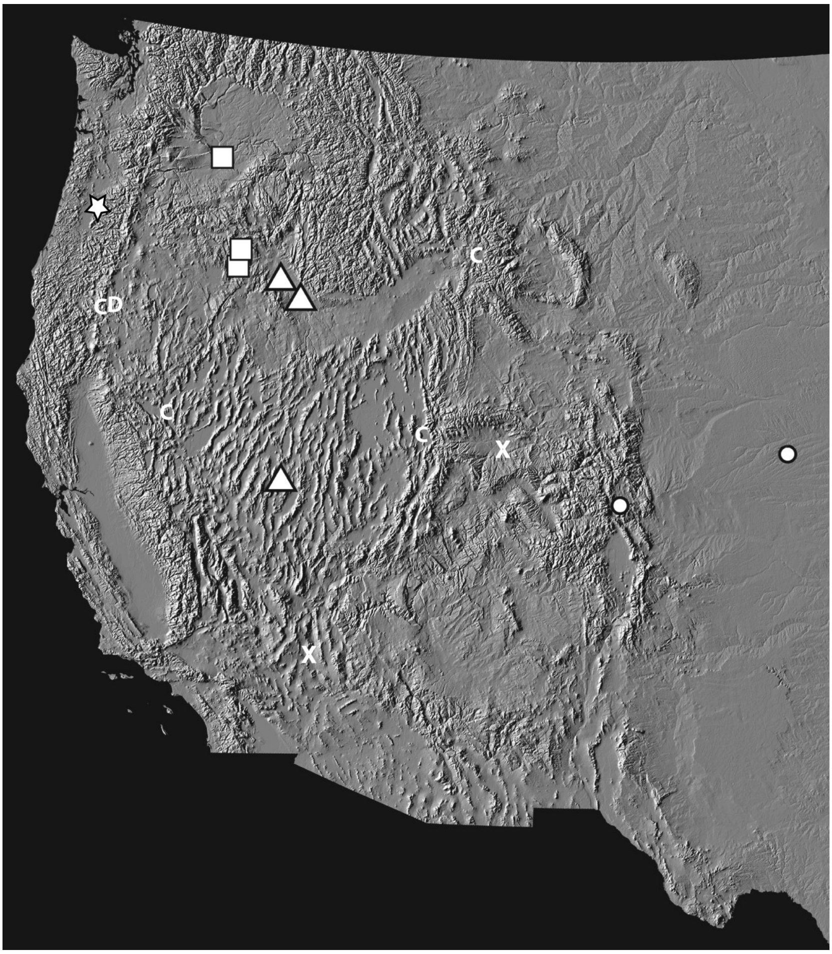

Fig. 1 b. *Pantosteus* fossil localities on a U.S.G.S. shaded relief map. Miocene (square symbols) Ellensburg Formation, Washington, and Drewsey and Juntura formations, Oregon; Pliocene (triangles) Glenns Ferry Formation, Idaho, and White Narrows Formation, Nevada; Pleistocene (round symbols) Coon Creek, Kansas, and Hansen Bluff, Colorado. Recent *Catostomus* (*Pantosteus*) *bondi*, type locality (star symbol) South Santiam River, Lebanon, Oregon. Recent Chasmistes localities marked "C" in Oregon, Nevada, Utah, and Wyomng; Deltistes marked "D" in Oregon and Xyrauchen marked "X" in the Colorado River.

changed several times, but the most important conflict continues to involve the mixed characteristics of *C.* (*P.*) *columbianus*. The mixture of generic traits in this species created a taxonomic dilemma. A possible explanation for the dilemma and a possible solution to the taxonomic problem is suggested by the characteristics and geochronological context of the fossil, *C.* (*P.*) *arenatus*, which is discussed below.

We describe new fossil species related to the *C.* (*P.*) *discobolus* group from the Late Miocene Ellensburg Formation of Washington and the Drewsey and Juntura formations of Southeast Oregon (11.5-8.5 Ma). We describe two Pliocene fossils from the Glenns Ferry Formation of southwest Idaho (4.5 and 2.4-1.9 Ma), and a species from the Pliocene White Narrows formation in southern Nevada (ca 4.6 Ma). We characterize Pleistocene fossils of *C.* (*P.*) *plebeius* from Southern Colorado (Rogers *et al.* 1985, 1992) and *C.* (*P.*) *platyrhynchus* group from northwest Kansas. The Kansas fossils are the only known fossil representatives of the *C.* (*P.*) *platyrhynchus* group. They are diagnosable as *C.* (*P.*) *jordani* from the Pleistocene Coon Creek locality in the Kansas River drainage of the Missouri drainage (Fig. 1). We also describe a new recent species in the *C.* (*P.*) *platyrhynchus* clade, from the Columbia River Basin, to update and complete diagnoses of the known species groups and species of *Pantosteus.*

Miocene and Pliocene presence of *Deltistes* and *Chasmistes* as well as *Catostomus* and *Pantosteus* in the large rift lakes of the Snake River Plain (Smith *et al.* 1982) at a time before they are known elsewhere provides more context for understanding the evolution of the Catostomini (the northwest subgenera, above, plus *Xyrauchen* from the Colorado River drainage). Miocene isolation in basins of the Great Basin and the Colorado River permitted divergence of these forms. Subsequent stream captures that assembled the Columbia, Snake, Missouri, Bonneville, Green, and Colorado river drainages, facilitated sympatry, hybridization, reticulate mixing of genes, and shared traits among species.

## MATERIALS AND METHODS

Edward D. Cope obtained fossils collected for him from the Snake River Plain in the 1860s (Cope 1870, 1883). Carl L. Hubbs and his family and students from the University of Michigan's Museum of Zoology collected fossil and Recent fishes, including *Pantosteus*, in western North America beginning in 1934. Claude Hibbard and Dwight Taylor led Michigan field crews in Idaho in the 1950s and 1960s. Most Idaho fossils were collected by surface picking disarticulated bones in fluvial and lacustrine sediments on the western Snake River Plain, from the Hagerman cliffs to eastern Oregon. Some fossil bones of *Pantosteus* were borrowed from museums and collectors that screened for mammals, with some fish bones produced incidentally. Specimens described in this study are the rare bones of mountain suckers, which normally live in swift-water habitats, not depositional environments; they were evidently transported from upstream.

Recent specimens collected for osteological preparation were eviscerated, skinned, and desiccated in the field, and cleaned by dermestid beetles in the museum. Small fish were cleared in KOH and stained with alizarin, or macerated in water or 2% KOH to yield disarticulated bones, which are then color-coded with dye, labeled, and catalogued. Disarticulated individual bones, observable in the round, offer numerous systematically informative shape characters that are sometimes less observable on whole skeletons.

Morphological traits were observed on skeletons of the University of Michigan Museum of Zoology and fossils in the University of Michigan Museum of Paleontology. The morphological parsimony phylogeny was calculated by Thomas Dowling using PAUP 4.0 (D. Swofford; Sinauer Associates).

Tests of the local ecophenotypic speciation hypotheses are based on data in relation to biogeography, genetics, and evolutionary principles. Tests of the introgression hypothesis are based on the comparison of phylogenetic trees calculated with independent data—gene trees *vs.* morphological trees. Tests of introgression require multiple heritable characters for phylogenetic reconstruction, traits that evolved at different rates, and good models of evolution for use in reconstruction (Linder and Riesberg 2004), criteria that are met by comparison of gene trees and morphological phylogenies, assuming that morphological convergence is ruled out. Detection of introgressive polyphyly requires evidence for different lineage parentage in the form of incongruent trees from separate data analyses on independent data sets, each representing a different hypothetical parent (Linder and Riesberg 2004). The decision regarding the most useful rank of genera/subgenera (if determined to be polyphyletic) depends on views regarding the optimal function of classification and names—whether the predictive benefits of adherence to the cladistic principle of monophyly in a natural classification outweighs the utility of maintaining traditional (but paraphyletic and polyphyletic) nomenclature for effective communication.

## DIAGNOSES OF CATOSTOMIDAE AND CATOSTOMINI

The Catostomidae, suckers, are cypriniform fishes, distributed from North America (*ca.* 70 species) to eastern Asia (two species). Diagnoses and fossil identifications are based on recent and fossil specimens. Larger species of catostomins are abundant as fossils in the west (Smith *et al.* 2002, and references). Specimens of *Deltistes* and *Chasmistes* are sometimes more abundant as fossils than as recent museum specimens (Smith 1975; Smith *et al.* 1982). The smaller species, *Pantosteus*, are rare in the fossil record. Two different forms of Pliocene *Pantosteus* from rift lake sediments on the Snake River Plain are described in this paper. These two plus three recent forms of *Pantosteus* are known from fluvial habitats in the Snake River drainage, including the Snake River Plain. The starting point for this study is the description of these five forms and their relatives, which requires morphological diagnoses of the lineages and their changes through time. It is useful to diagnose the major western lineages of this family with attention to both fossil and recent forms, beginning with those near the possible origin and base of the western clade, Catostomini (*Deltistes, Chasmistes, Xyrauchen, Catostomus,* and *Pantosteus*). This will include formal diagnosis of fossil and recent species, including one new recent form in the Columbia River drainage, which was revealed by molecular analysis (Unmack *et al.* in revision). The fossil record and deeper branches in the molecular phylogeny of *Pantosteus* (Unmack *et al.* in revision) suggest that the genus diverged from *Catostomus* in the middle Miocene in the Northern Basin and Range and the Columbia Plateau.

The most prominent osteological features in the diagnosis of the Catostomidae include the opercle shape with an arm-like anterodorsal process offset by a concave dorsal margin; frontoparietal fontanelle usually present but variable; post-temporal fossa large; basioccipital process uniquely heart-shaped, fenestrated, and lace-like; descending processes of 2nd - 4th Weberian ribs large and broadly sutured together; mandibular sensory canals lost; lateral ethmoid large, triradiate in cross-section, and pitted; dermosphenotic small; pharyngeal arch curved and flat with one comb-like row of 20 to 100-plus teeth in adults; teeth flat and tetragonal, each with one or two dorsally- or medially-directed points (Smith 1992b). All members of the family are tetraploids with about 100 chromosomes (Uyeno and Smith 1972) in contrast to American Cyprinidae, which are usually diploid with 50 chromosomes.

The Catostominae (*Catostomus* plus *Minytrema, Erimyzon*, and *Moxostoma* and its relatives) are diagnosed by usual absence of supraorbital bones; frontal pores large and clustered anteriorly; metapterygoid brace or braces to the hyomandibula; and dermethmoid with a long slender anterior process (Smith 1992b).

The fossils and recent form described in this paper belong to *Catostomus* (subgenus *Pantosteus*)*,* part of a clade that is sister to the more plesiomorphic genera or subgenera, *Deltistes*, *Chasmistes*, and *Xyrauchen.* Six species of the latter three groups, the monophyletic lake suckers (in the broad phylogenetic sense), are diagnosed by a metapterygoid lamina bracing the hyomandibula; a long, gently-curved dentary; branched gill rakers; lower lip lobes usually thin and separated; wide premaxillae; a long symplectic; and a long palatine (see Appendix). The original mtDNA haplotypes of lake suckers are unknown; evidently they were replaced by mtDNA of sympatric *Catostomus* (*s.s.*) (Unmack *et al.* in revision), based on the 1-2% genetic distances (Markle *et al.* in revision) in contrast to the 8 to 10 m.y. fossil record. This introgressive history makes each of the genera polyphyletic.

*Deltistes* and *Chasmistes* are lake-inhabiting suckers with a rich late Miocene and Pliocene fossil record on the western Snake River Plain and recent representatives in the formerly connected Klamath drainage (Taylor 1960; Smith 1975; Smith *et al.* 1982; Smith *et al.* 2002). *Chasmistes* was also found at Mono Lake and Lassen County, California, Fossil Lake Oregon, and Teton County, Wyoming. *Chasmistes* survived to recent times in Klamath Lake, Oregon, Pyramid Lake, Nevada, Utah Lake, Utah, and Jackson Lake, Wyoming (Miller and Smith 1981; Cole *et al.* in prep.). *Deltistes* now lives in Klamath Lake and the Klamath and Lost River drainages. *Xyrauchen* lives in the Colorado River drainage. Pliocene *Xyrauchen* were probably fluvial as well as lentic water inhabitants; they are recorded from the Salton Sea area, southern California. (Hoetker and Gobalet 1999; UMMZ 1954:4-24). Most of these live in lakes and migrate upstream in tributaries to spawn; some *Deltistes* and *Xyrauchen* spawn in lacustrine habitats.

*Deltistes* was described as *Chasmistes luxatus* Cope 1879 and raised to generic rank by Seale (1896). It was considered a species of *Catostomus* by R.S. Eigenmann (1891), Miller (1958), Bailey *et al.* (1970), Moyle (1976, 2002), and Eschmeyer (2013), and *Deltistes* by Miller and Smith (1967) and

Bond (1994). The different classifications were based on different interpretations of intermediacy with *Catostomus snyderi vs.* distinctness of osteological traits between the *Deltistes* and *Catostomus snyderi*. The subgenus *Deltistes* is diagnosed by the long head, elongate dentary, oblique mouth, papillose lips with the lower lip lobes divided to the base, gill rakers with incipient secondary branches, small snout tubercles, and large size (to 640 mm standard length and adult weight up to 10 lbs). Evidence for introgression between *Deltistes* and *Catostomus* was noted by many authors and documented by Markle *et al.* (2005), Markle *et al.* (in revision), and various molecular studies. Two species of fossils have been described from the Miocene and Pliocene of the Snake River Plain (Smith 1975, Smith *et al.* 1982). The species is endangered because of excessive water withdrawal and depleted instream flow. They usually spawn upstream in tributaries.

*Chasmistes* Jordan 1878 has been applied to species of lake suckers in Utah Lake, Klamath Lake, Oregon, Pyramid Lake, Nevada, and Jackson Lake, Wyoming (Jordan 1878, Cope 1879, Cope 1883, Gilbert 1898, and Evermann and Meek 1898) and various fossil forms in the far west (Miller and Smith 1981). The subgenus *Chasmistes* is diagnosed by a terminal mouth, elongate dentaries, premaxillary process of the maxilla directed anteromesiad, a broad neurocranium, branched, fimbriate gill rakers, and thin lips with the lower lobes widely separated and normally lacking papillae (Miller and Smith 1981). All species have been introgressed with *Catostomus* (Miller and Smith 1981, Markle *et al.* 2005; Markle *et al.* in revision). All species are endangered, in part by the introgressive loss of their genetic integrity in the past 100 years (Miller and Smith 1981). Lake suckers were abundant and markedly more apomorphic than modern species in the Pliocene rift lake on the Snake River Plain (Smith 1975; Smith *et al.* 1982).

*Catostomus texanus* Abbott 1861 was described as a *Catostomus;* the name *Xyrauchen* was applied by Eigenmann and Kirsch in Kirsch (1889). The subgenus *Xyrauchen* is diagnosed by the elevated dorsal keel between the head and the dorsal fin, formed by large predorsal bones beneath the skin; long, fleshy, papillose, ventral lips with the lower lobes divided; elongate dentaries; deep suborbitals; gill rakers with incipient terminal branches; up to 15 dorsal rays, and large body size (to 525 mm S.L.). Hybridization between *Xyrauchen* and *Catostomus* was documented by Hubbs and Miller (1953), Holden and Stalnaker (1975), and McAda and Wydoski (1980). Introgression is verified by mtDNA of *Catostomus* in specimens of *Xyrauchen* (Doosey *et al.* 2010, Fig. 2; Chen and Mayden 2012, fig. 1).

## DIAGNOSIS OF *CATOSTOMUS* (*S.s.*) AND *PANTOSTEUS*

*Catostomus* and *Pantosteus* have more species and are more widespread than other western subgenera, but they have a less complete fossil record, probably because they live in faster water.

*Diagnosis of the subgenera, Catostomus plus Pantosteus.*—These subgenera form a morphological clade (Smith 1992b) supported by molecular data

(Unmack *et al.* in revision) and morphological traits including the relatively slender bodies, small fins, corresponding shallow anterodorsal profile of neural spines 2-3 of the Weberian apparatus, and shape of the wide ventral mouth, with fleshy, papillose lips with a partial contact between the lower lips (incompletely separated by the median notch) (Smith 1992b).

*Diagnosis of the subgenus Catostomus*.—*Catostomus* (*s.s.*) is osteologically diagnosed by an intermediate length and gently curved anterior process of the dentary (Fig. 7 e; 8 e; 9 d; 11 e-h); high dorsal keel and reduced ventral keel on the maxilla (Fig. 7 a; 10 b; 11 i); a broad plate forming the dorsal surface of the pterotic between fossae anterior and posterior to it (Smith 1966, fig. 3); slender preopercle (Smith 1966, fig. 5; interopercle not short and deep; hyomandibula with no sharp posteriorly-directed ridge lateral and anterodorsal to the opercular condyle (3 c, h); and frontoparietal fontanelle open except in *C.* (*C.*) *rimiculus* (Smith 1966, fig.3). Features of the soft-anatomy include weak cartilages on the upper and lower jaws; jaw edges rounded; deep notch between lower lips; and no notches at the outer corner of the upper and lower lips (Smith 1966, 1992b).

*Diagnosis of Pantosteus*.—This group of eleven forms is diagnosed by osteological features including the short, mesially and ventrally deflected leading edge of the dentary (Fig. 7 f-i; 8 a-d; 9 a-c, e; 11 a-d; Smith 1966, figs. 4, 5); the prominent and robust ventral keel of the maxilla, with a strong ridge for muscle attachment, low dorsal keel of the maxilla (Fig. 7 b-d; 10 a, e, f; 11j-i); plate on the dorsal surface of the pterotic reduced to a ridge between deep fossae for muscle origins (Smith 1966, fig. 3); broad, lunate preopercle (Smith 1966, fig. 5); short, deep interopercle; reduced but variable fossae lateral to the epiotic; posteriorly-directed ridge anterolateral to the opercular condyle of the hyomandibula (3 a, b, e-g) sometimes reaching high on the pterotic condyle (3 b); and frontoparietal fontanelle narrow or bridged across the midline by the skull roof (Smith 1966, fig. 3). Mouth and jaw characters include strong cartilages on the upper and lower jaws; jaw edges truncate, not convex (except in the *C.* (*P.*) *plebeius* group); shallow notch between lower lips; and notches at the outer corner of the upper and lower lips (except in some populations of *C.* (*P.*) *columbianus* [Smith 1966, pl. 1, p. 133]).

Morphologically, *Catostomus* is paraphyletic with respect to *Pantosteus,* (which is polyphyletic) because the cladistic sister of *Pantosteus* is *C.* (*C.*) *rimiculus* (Fig. 12). Equally important, *C.* (*P.*) *columbianus* has diagnostic morphological traits of both *Catostomus* and *Pantosteus,* which led Smith (1966, 1992b) to combine them. More recent analysis of mtDNA (Unmack *et al.* in revision) conflicts with morphological data in that *C.* (*P.*) *columbianus* has *Catostomus* mtDNA, confirming introgressive origin of the species (Fig. 12; see below). In addition, mtDNA provides evidence for separating the genera, depending on choice of generic criteria. Molecular data also suggests recognition of four additional species of recent *Pantosteus,* including one described below.

*Comparison of morphological and mtDNA evidence*.—Morphological cladistic analysis of the species of *Pantosteus* produces a branching structure

(Fig. 12) in which species of *Pantosteus* are apomorphic taxa of a large *Catostomus* group, consistent with the tree shown here as a hierarchy of groups nested in parentheses:

> (Outgroups (*C. ardens*, *macrocheilus*, *latipinnis*, *insignis*) (*snyderi* (*fumeiventris* (*tahoensis* (*rimiculus* (*columbianus* ((*platyrhynchus*, *bondi*, *jordani*, *lahontan*) (((*virescens*, *discobolus*) *clarkii*) *santaanae*) (*plebeius*, *nebuliferus*))))))))

The recent phylogeny, based on about one-half of the mtDNA genome (Unmack *et al.* in revision), recovered a structure in which *Pantosteus* and *Catostomus* are reciprocally monophyletic genera with *C.* (*P.*) *columbianus* included in *Catostomus* because of its mtDNA; the mtDNA tree is consistent with the following branching hierarchy:

> ((*Catostomus* [many species] including *P. columbianus*) ((*platyrhynchus*$^{n}$ group of three species) ((*plebeius* group of two species)(*santaanae* (*clarkii* (*discobolus* group of two species, *platyrhynchus*$^{b}$))))))

The mtDNA phylogeny of Unmack *et al.* (in revision) identifies a *Pantosteus* clade sister to *Catostomus* (but with *C.* (*P.*) *columbianus* in *Catostomus*). *Six* additional species are recognized within six previously recognized *Pantosteus*. *Catostomus* (*P.*) *platyrhynchus* is split into two groups: a northern group (superscript n, above), which consists of *C.* (*P.*) *jordani* from the Missouri drainage, sister to *C.* (*P.*) *lahontan* from the Lahontan drainage plus the new species from the Columbia drainage (described below); and a southern group, *C.* (*P.*) *platyrhynchus* (superscript b, above, with mtDNA derived from *C.* (*P.*) *discobolus*), which ranges from the northern and southern Bonneville Basin to the upper Snake and upper Green river drainages (Fig. 1a).

The *C.* (*P.*) *discobolus* branch of mtDNA includes *C.* (*P.*) *virescens* of the northern Bonneville tributaries and the Upper Snake River drainage above Shoshone Falls, *C.* (*P.*) *discobolus* of the upper Colorado Basin, *C.* (*P.*) *clarkii* in the lower Colorado drainage, *C.* (*P.*) *santaanae* in the Los Angeles Plain, and *C.* (*P.*) *plebeius* and *nebuliferus* in the Rio Grande and Mexico. *Catostomus* (*P.*) *discobolus* and *C.* (*P.*) *virescens* are sister to *C.* (*P.*) *clarkii* and *C.* (*P.*) *santaanae*. *Catostomus* (*P.*) *plebeius* and *nebuliferus* are sister to the remainder of the *C.* (*P.*) *discobolus* group (Unmack *et al.* in revision).

*Catostomus* (*P.*) *columbianus* is here recognized as a morphological *Pantosteus* with mtDNA of *Catostomus* (*C.*) *tahoensis;* the explanation of this combination invokes hypothesized introgressed origin because of diagnostic osteological traits mixed between a fossil form related to *C.* (*P.*) *virescens* (see below) and *C.* (*C.*) *tahoensis* (Smith 1966; Miller and Smith 1981; Smith 1992b; Appendix). Traits of the dentary and maxilla of *C.* (*P.*) *columbianus* are also shared with *C.* (*P.*) *arenatus,* which appears in the fossil record of the Snake River Plain at about the time of a spillover from the Lahontan Basin (home of *C. tahoensis*) to the Snake River Plain, discussed below under "Pliocene fossils from Idaho."

*Diagnoses of Pantosteus species groups.*—The *Pantosteus platyrhynchus* species group is diagnosed by the incomplete posterolateral crest of bone on the hyomandibula, which tapers to a terminus anterodorsal to the mid-level of the opercular condyle; the proximal limb of the dentary is usually long and slender (Smith 1966 fig. 4; Fig. 4D); pharyngeal teeth 20-40, two-pointed, sometimes forked, especially dorsally. Diagnostic traits in the soft anatomy of the *P. platyrhynchus* group include a rosette of papillae in the median anterior part of the lower lip, flanked by blank areas (Smith 1966, Pl. 1D p. 133); immaculate inter-radial membranes in the caudal fin (Smith 1966, fig. 9A); and pelvic axillary process present. This group includes *C.* (*P.*) *platyrhynchus*, *C.* (*P.*) *jordani*, *C.* (*P.*) *lahontan*, and a form in the Columbia drainage, named below. Unmack *et al.* (in revision) concluded on the basis of mtDNA and morphological examination that the Columbia River form previously referred to *Pantosteus jordani* or *C* (*P.*) *platyrhynchus* (Smith 1966) is an undescribed species, which is named here to complete diagnosis and discussion of the species of the group. It was previously referred to *Pantosteus jordani* by Gilbert and Evermann (1894), Jordan and Evermann (1896), Snyder (1915), Jordan *et al.* (1930) Schultz and DeLacy (1936), Bond (1953), and others (more complete synonymy in Smith 1966, p. 59).

### Teleostei, Catostomidae
### ***Catostomus bondi*** new species
### Fig. 2, Table 1

***Holotype***.—A female, UMMZ 249817, 118 mm in standard length, from Oregon, Linn County: South Santiam River of the Willamette drainage at Lebanon Dam, 3 miles above Lebanon. Latitude 44.6, Longitude 122.9, elevation 340 ft. Collected by Carl E. Bond and R.E Noble, May 21, 1951. The specimen has the following characteristics: head length 28 mm; width of lower jaw 8.5 mm; isthmus width 9.0 mm; caudal peduncle depth 9.5 mm; lateral line scales 89; predorsal scales 58; dorsal rays 11; pelvic rays 10; gill rakers in external row of first arch 35; gill rakers in internal row of first arch 48; number of post-Weberian vertebrae 41; frontoparietal fontanelle reduced to a small opening; fin pigment concentrated on fin rays, sparse melanophores on inter-radial membranes; pelvic axillary process present; anterior sensory papillae on lower lip in a convex-forward rosette with blank patches of lip tissue on either side.

*Paratypes*.--Four paratypes, UMMZ 162982, and two paratypes OS 18837, from the type series that included the holotype, are documented with characteristics in Table 1.

*Description*.—This somewhat variable species includes small individuals, up to 175 mm in Standard Length, with general traits of the *C. platyrhynchus* species group (Smith 1966, pp. 25, 64). The lower lips are not deeply divided, the notch is separated from the anterior edge of the lip by 3 or 4 rows of papillae; the anterior row contains 7-9 papillae in a rosette pattern with no (or few small) papillae on either side; distinct notches separate the corners where the

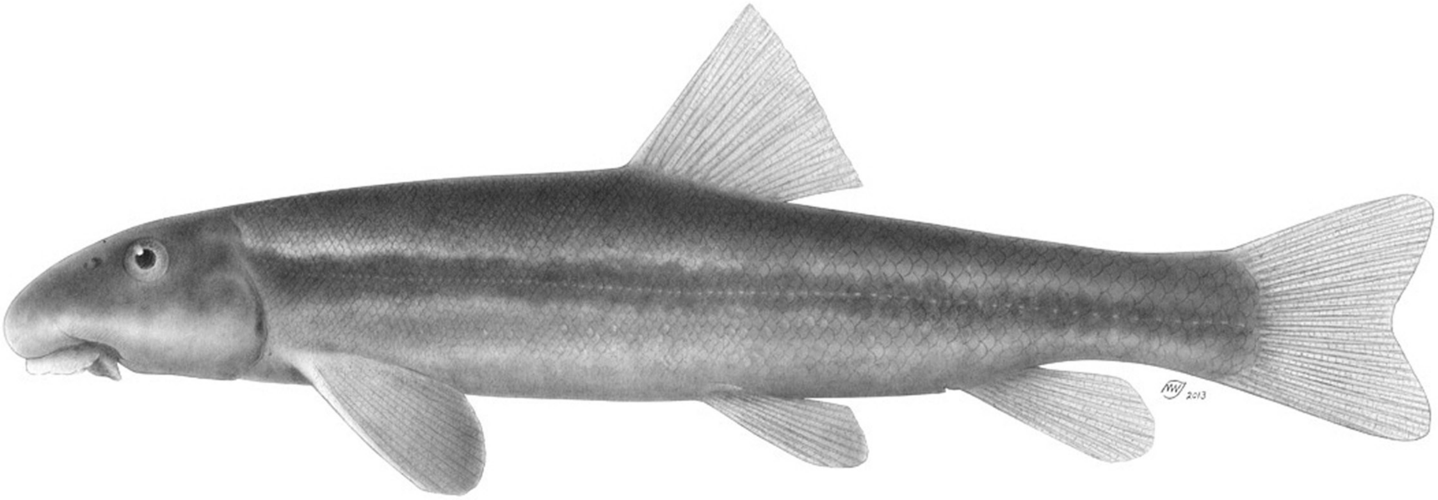

Fig. 2. Illustration of a paratype of *Catostomus* (*Pantosteus*) *bondi*, UMMZ 162982-4, 118 mm in standard length, from the South Santiam River at Lebanon, Willamette drainage, Linn Co., Oregon. Illustrated by John Megahan.

Table 1. Meristic counts and measurements of the type series of *Catostomus* (*Pantosteus*) *bondi* from the South Santiam River, Willamette drainage, Oregon, UMMZ 162982 and OSU 18837 (paratypes), and UMMZ 249850 (holotype*). S.L., standard length; Vert. post-Weberian vertebrae; L.L. lateral line scales; pDsc, pre dorsal scales; D, dorsal rays; P2, left and right pelvic rays; GRe-i, number of gill rakers in external and internal rows on the first arch; CPd%, caudal peduncle depth%; Istw%, isthmus width%; Jaw%, width of lower jaw%. Measurements given as percent standard length. Two paratypes[1] (OSU 18837) are deposited in the Ichthyological Collection at Oregon State University, Corvallis, Oregon.

| S.L. | Vert. | L.L. | pDsc | D | P2 | GRe-i | CPd% | Istw% | Jaw% |
|---|---|---|---|---|---|---|---|---|---|
| *118 | 41 | 89 | 58 | 11 | 10-10 | 35-48 | 8.0 | 7.6 | 7.2 |
| [1]110 | 42 | 82 | 56 | 11 | 9-9 | 36-44 | 8.1 | 8.3 | 7.3 |
| 129 | 43 | 86 | 53 | 11 | 9-9 | 32-44 | 7.8 | 10 | 6.9 |
| 116 | 43 | 83 | 55 | 11 | 9-10 | 37-48 | 7.9 | 10.2 | 7.2 |
| [1]123 | 41 | 80 | 50 | 11 | 9-9 | 34-48 | 7.2 | 9.7 | 7.3 |
| 108 | 41 | 81 | 50 | 11 | 9-9 | 34-44 | 8.1 | 8.3 | 7.4 |
| 116 | 43 | 85 | 56 | 11 | 9-9 | 39-44 | 7.6 | 9.8 | 7.2 |

upper and lower lips join; shallow notch between the lower lips; the lower jaw is truncate, not convex, with a cartilaginous margin, its width is 6.5-8% of standard length except in the Fraser and Similkameen drainages, Canada, where it is wider, up to 9% of standard length; isthmus width 9-10% of standard length; gill rakers 29-37 in external row and 35-57 in the internal row of the first arch; lateral line scales 70-91, (population means 77.4-81.3); predorsal scales 41-58 (mean 48); dorsal rays 10-12 (means 10.0-11.5); pelvic rays usually 9; pelvic axillary process present; caudal peduncle depth usually 9% of standard length; gas bladder reduced, not reaching pelvic origin; post-Weberian vertebrae 40-44 (mean 42); fin pigment concentrated on rays, sparse on membranes; breeding colors with a red-orange stripe above a black longitudinal stripe; fontanelle reduced to a narrow slit; maxilla with a low postdorsal keel and a deep anteroventral keel as in *C.* (*P.*) *jordani* (Fig. 10 e, f); dentary moderately robust, with a broad anterior process and a moderately wide posterior process; pharyngeal teeth two-pointed, especially dorsally; hyomandibula wide, with a strong postlateral keel, which extends up to the mid-level of the opercular condyle and beyond; pterotic condyle of hyomandibula robust and wide at the tip. Among the species in the *C.* (*P.*) *platyrhynchus* group, *C.* (*P.*) *bondi* is unusual in sharing some overlapping traits with *C.* (*P.*) *virescens* of the *C.* (*P.*) *discobolus* group in the jaw bones, hyomandibula, gill rakers, predorsal scales, and other high meristic counts (Smith 1966, table 1, fig. 21).

*Molecular characterization.*—See Unmack *et al.* (in revision) and catalog numbers for this taxon in GenBank.

*Diagnosis.*—A *Catostomus* of the *C.* (*P.*) *platyrhynchus* species group, with the following diagnostic characters: distal process of the dentary wide and robust, and proximal process of the dentary shorter than other species in the *C.* (*P.*) *platyrhynchus* group; pharyngeal teeth mostly two-pointed, dorsal teeth forked, unlike the mostly single pointed, less bifurcate teeth of *C.* (*P.*) *platyrhynchus*, but similar to *C.* (*P.*) *jordani* and *C.* (*P.*) *lahontan*; hyomandibula narrow, with a large sphenotic condyle and a broader, more robust posterodorsal tip than *C.* (*P.*) *jordani*, but similar to *C.* (*P.*) *platyrhynchus* and *C.* (*P.*) *lahontan*; opercular bone tall and narrow, the width 0.51-0.57 of the over-all height (that ratio is 0.57-0.61 in other species); combination of post-Weberian vertebrae usually 40-44 (average 1 fewer in other species of the group except *jordani*); depth of caudal peduncle usually 9% of standard length (usually 1% higher in other species); and caudal rays pigmented, inter-radial membranes with few or no melanophores (usually immaculate in other species except when introgressed with *C.* (*P.*) *virescens* [in the upper Snake River] and *C.* (*P.*) *discobolus* [in the Green River, Smith 1966 fig. 22). Differs from *C.* (*P.*) *platyrhynchus* in the Snake River above Shoshone falls (the geographically closest, potentially genetically connected relative) in having 41-58 predorsal scales (means 43-56) compared to 40-45 predorsal scales (means 42-44); usually 75-85 lateral line scales (means 77-82) compared to 80-90 lateral line scales (means 83-86); 29-37 gill rakers on the external row of the first arch *vs.* 23-31 gill rakers on the external row of the first arch; 35-51 gill rakers on the internal row of the first arch *vs.* 33-39 gill rakers on the internal row of the first gill arch.

*Range.*—This species is found in the Fraser River and tributaries to the Columbia River and Snake River below Shoshone Falls: Willamette, Boise, John Day, Yakima, Okanagan, Palouse, Owyhee, Salmon Falls, and (possibly) Salmon rivers (Smith 1966 fig. 13, part). Fossils of *C. bondi* are unknown.

*Etymology.*—The species is named for the late Prof. Carl E. Bond, formerly in the Department of Wildlife and Fisheries, Oregon State University, Corvallis, Oregon, 1950-2007, in recognition of his many contributions to the science, conservation, and management of northwestern North American fishes (see Stewart and Smith 2002).

Diagnosis of other groups of the subgenus *Pantosteus*:

The *C.* (*P.*) *discobolus* species group is diagnosed by the dorsal extension of the crest of the posterolateral sheet of bone on the hyomandibula, beyond the level of the opercular condyle, approaching the pterotic condyle on the dorsal part of the bone (Fig. 3); hyomandibula with a posterodorsal process and fossa; the dentary is short and robust (Fig. 8 d; Smith 1966, fig. 4E, F). Diagnostic traits in the soft anatomy of *C.* (*P.*) *discobolus* include smaller (12-15) lip papillae in a wide anterior row confluent with the edge of the wide, truncate lower jaw (Smith 1966, pl. 1E, p. 133) and pigmented interradial membranes in the caudal fin (Smith 1966, fig. 9B).

*Catostomus* (*P.*) *virescens* differs from *C.* (*P.*) *discobolus* in having a thicker caudal peduncle with mean depth of 8.4-8.8% of standard length (compared to 5.4-8.3% in *C.* (*P.*) *discobolus*, except *C.* (*P.*) *discobolus yarrowii*). *Catostomus* (*P.*) *discobolus yarrowii* differs in having variably-introgressed traits of *C.* (*P.*) *plebeius* (Smith 1966, p. 87-89, fig. 18; Smith *et al.* 1984; Dowling *et al.* unpublished). *Catostomus* (*P.*) *clarkii* differs from other members of the *C.* (*P.*) *discobolus* group in having larger predorsal scales (means 17-46 *vs.* 54-65 in *C.* (*P.*) *discobolus*).

*Catostomus* (*P.*) *santaanae* is diagnosed by a narrower and less truncate lower jaw; some papillae at the edges of the lower lip (Smith 1966 Pl 1C); incision in the lower lip deeper than most other species (Smith 1966 pl. 1C); silvery or lightly pigmented peritoneum; 27-41 predorsal scales; 21-28 gill rakers on the external row of the first gill arch, and 27-36 gill rakers on the internal row of the gill arch.

The *C.* (*P.*) *plebeius* species group is diagnosed by a less mesially-inflected dentary (Fig. 11 d); the extension of the lateral crest on the hyomandibula dorsad, beyond the level of the opercular condyle, approaching the pterotic condyle on the dorsal part of the bone; the proximal limb of the dentary is short and robust (Smith 1966, fig. 4B), but the distal limb of the bone is long, with an obtuse angle somewhat like *Catostomus* (*s.s.*). Diagnostic traits in the soft anatomy of *C.* (*P.*) *plebeius* include a rounded row of about 10 papillae in the median anterior part of the lower lip, roughly confluent with the narrow, rounded lower jaw (Smith 1966, pl. 1A, p. 133) and pigmented interradial membranes in the caudal fin (Smith 1966, fig. 9B).

## *PANTOSTEUS* PALEONTOLOGY

### MIOCENE FOSSIL *PANTOSTEUS* FROM OREGON AND WASHINGTON

Fossil *Pantosteus* from Miocene sediments in Oregon and Washington include dorsal fragments of hyomandibulae that share the unique diagnostic traits of the *C.* (*P.*) *discobolus* group. They are therefore interpreted to represent the lineage that later split into the Pliocene *Pantosteus* from the western Snake River Plain as well as the Snake River and Bonneville Basin *C.* (*P.*) *virescens,* the Colorado drainage *C.* (*P.*) *discobolus* and *C.* (*P.*) *clarkii*, the Los Angeles *C.*(*P.*) *santaanae,* and the Rio Grande and Mexican *C.* (*P.*) *plebeius* and *C.* (*P.*) *nebuliferus*. They represent a stem lineage, according to inference from combined fossil and molecular data (Unmack *et al.* in revision), probably not too distant in divergence and time from the stem of the *C.* (*P.*) *platyrhynchus* group. These middle Miocene specimens from Oregon and Washington are the earliest known fossils of *Pantosteus* and the earliest known catostomine suckers, the apomorphic characters suggest a longer and more complex origin and early history than previously apparent. The distinct, diagnostic partial hyomandibulae have been recovered from the Juntura Formation (11.5 Ma) and Trapa beds of the Drewsey Formation (8.5 Ma) of southeast Oregon, and the Ellensburg Formation (10.3 Ma) of central Washington.

### Teleostei, Catostomidae
### ***Catostomus (Pantosteus) hyomyzon*** New Species
Fig. 3 a, d, e, f

*Holotype*.—A partial right hyomandibula with the pterotic and opercular condyles preserved (UO F-55749), 9 mm high and 5 mm wide, from the Black Butte local fauna of the Juntura Formation, Malheur County, Oregon, col-

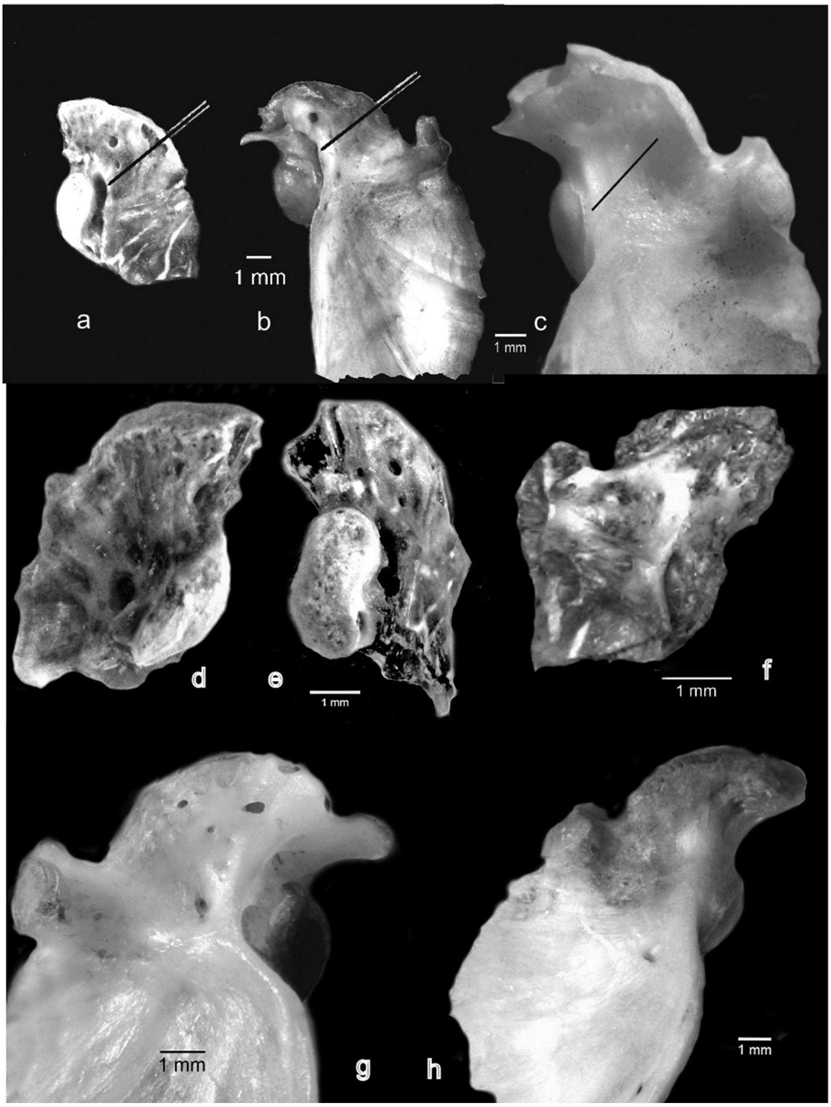

Fig. 3. *Pantosteus* hyomandibulae. Comparison of right hyomandibulae (dorsal part) of *Catostomus* (*Pantosteus*) *hyomyzon*, n. sp., holotype (UO 2337) (Figs. 3 **a**, **d**, **e**) from the Miocene Juntura Formation of Malheur County, Oregon. **b**. *Catostomus* (*Pantosteus*) *discobolus*, (UMMZ 182483). **c**. *Catostomus* (*Pantosteus*) *columbianus* (UMMZ 194641). **f.** Left hyomandibula (part) of *Catostomus* (*Pantosteus*) *hyomyzon* (UMMP 43249) from the Trapa beds of the Drewsey Formation, Malheur County, Oregon. **g**. *Catostomus* (*P.*) *clarkii* (UMMZ 162817). **h**. *Catostomus* (*C.*) *insignis* (UMMZ 162742).

lected by J.A. Shotwell and students 1955-1959.

Description.—The holotype hyomandibula is a three-dimensional fragment with a nearly complete pterotic condyle and a complete opercular condyle. The pterotic condyle is 5.9 mm long and 3 mm wide. Its posterodorsal end is broken, revealing a cavity for a posterodorsal fossa and a broken base of the posterodorsal process. The posterodorsal tip of the pterotic process ends 3.1 mm above the dorsal rim of the opercular process, which is a slightly hourglass shaped hemisphere 4 mm long and 2.2 mm wide at its slightly constricted center. The posterolateral crest of the hyomandibula extends posterodorsally to a point approximately even with the dorsal margin of the opercular condyle; it is separated from the opercular condyle by a deep groove averaging about 1.1 mm wide. The anterodorsal process of the hyomandibula is broken off, but the break shows a fossa and broken base of a process for ligament or muscle attachment. The median and lateral surfaces of the bone are marked with an intricately sculptured pattern.

*Diagnosis*.—*Catostomus* (*Pantosteus*) *hyomyzon* is diagnosed by its sharp lateral crest anterior to the opercular condyle—the crest is part of the ridge that extends from the posterior preopercular flange dorsad to near the post-dorsal point of the pterotic condyle (Fig. 3 a). There is a posterodorsal fossa, and a broken base of a posterodorsal process. The ridge is widely separated from the base of the opercular condyle by a deep groove (Fig. 3 a, e).

*Comparisons*.--The ridge, associated groove, posterodorsal fossa, and posterodorsal process are shared, but in less extreme form, with: *C.* (*P.*) *virescens, C.* (*P.*) *discobolus* (Fig. 3 b), *C.* (*P.*) *clarkii* (Fig. 3 g)*, C.* (*P.*) *santaanae, C.* (*P.*) *plebeius* and *C.* (*P.*) *nebuliferus,* but not *C.* (*P.*) *platyrhynchus* or *C.*(*P.*) *columbianus* (Fig 3 c)*;* the ridge, groove, fossa, and posterodorsal process are absent or limited to the ventral base of the opercular condyle in those species as well as in the subgenera *Catostomus* (Fig. 3 h), *Chasmistes, Deltistes*, (but not *Xyrauchen*), and other Catostomidae.

Species of *Pantosteus* in the *C.* (*P.*) *platyrhynchus* species group, *C.* (*P.*) *platyrhynchus, C.* (*P.*) *jordani, C.* (*P.*) *lahontan*, C. (*P.*) *bondi*, and populations in the upper Snake and Green River drainages, share a partially-developed crest that ends even with the middle of the opercular condyle, intermediate between *C.* (*P.*) *hyomyzon* and *Catostomus* (*s.s.*) species. They also lack the posterodorsal process and (usually) the fossa on the postdorsal tip of the hyomandibula. *Catostomus* (*P.*) *columbianus* shows a mixture of the above *Pantosteus* and *Catostomus* (*s.s.*) traits: the posterodorsal fossa is well developed and the posterodorsal processes are slightly developed as in *Pantosteus*, but the posterior ridge (Fig. 3 c) stops at the ventral edge of the opercular condyle as in *Catostomus* (*s.s.*) (Fig. 3 h).

*Provenience*.— The specimens were collected from what we hypothesize to be the Black Butte quarry 11 of Shotwell *et al.* (1963) (UO loc. 2337) in the upper member of the Juntura Formation, T. 21 S., R. 37 E., Petes Mountain Quadrangle, Malheur County, Oregon. The sparse fossil fish bones were collected from the surface, where they were lagged out below the main mammal-producing sandstone layer and an overlying ash dated at 11.5+/-0.6 Ma (Fiebelkorn *et al.* 1983).

Retallack (2004) studied the paleosols and fossil assemblages among Clarendonian basins in southeastern Oregon including Juntura, Unity, Ironside, and Baker, which seem to be similar in age. He found the tuffs in the Ironside Formation at Windglass Gulch northeast of Unity, which also produced fish fossils, to be most similar to CPTXI and CPTIX, 11.31 to 11.59 Ma, of Perkins *et al.* (1998) and close to the older date for the upper Juntura Formation. On the western edge of the Juntura Basin (152 m below the mammal quarry), 12.4+/-1.0 Ma, lavas underlie the upper and middle diatomite member of the Juntura Formation (Evernden and James 1964; Retallack 2004).

In the southern portion of the basin along the Malheur River Gorge a sequence of lava flows equivalent to the Keeney chemical sequence in the Oregon-Idaho Graben underlie and overlay the same members. The lowest Buck Mountain lavas were dated at 12.5+/-0.5 Ma (Fiebelkorn *et al.* 1983, Camp *et al.* 2003). The overlying Riverside lavas were dated at 10.14+/-0.23 Ma (Camp *et al.* 2003). (This sequence is equivalent to the Kern Basin Tuff and overlying Grassy Mountain Basalt flows, with the lowest Juntura member containing the Stinkingwater and Beulah plant and fish fossils, lying discordantly on Tims Peak basalt, placing it within the technical definition of the Deer Butte Formation.) The mammal fossils from quarry 11 indicate a Clarendonian North American Land Mammal age (NALMA). Associated fish in the Juntura Formation include *Ameiurus peregrinus*, *Ptychocheilus* sp., *Mylocheilus whitei*, *Mylopharodon* sp., ?*Lavinia*, ?*Rhinichthys*, and ?*Oregonichthys*.

*Paratypes*.—No paratypes are designated, but the fossil series from the type locality includes a partial right maxilla with traits of both *Catostomus* (*s.s.*) and *Pantosteus* (UMMP 42348, Fig. 10 c). The partial maxilla possesses a moderate mid-dorsal keel and a deep ventral keel with a strong ridge for muscle attachment diagnostic of *Pantosteus* (see below). The slender anterodorsal process and slender neck of the bone, however, are more like *Catostomus* (*s.s.*). No other catostomid bones have yet been identified from this formation.

*Etymology*.—The species name, *hyomyzon*, is from Greek, *hyo*, referring to hyoid–the distinctive, two-part dorsal margin of the hyomandibula, and "*myzo*," "suck," referring to suckers (Catostomidae).

*Referred material*.—*Catostomus* (*Pantosteus*) *hyomyzon* from the Drewsey Formation, Oregon is represented by a fragment of a right hyomandibula similar to the holotype, collected by Nathan Carpenter and Gerald Smith and field crew from the Trapa beds of the Drewsey Formation, Malheur County, Oregon, May 28, 2009. The specimen, UMMP 42349 (Fig. 3 f), is similar in size and shape to the holotype, possessing the diagnostic features of that species. A posterior part of a left maxilla (UMMP 42347, Fig. 10 d) was collected with the hyomandibula form the Drewsey Formation. The identification is uncertain because the diagnostic median and anterior processes on the anterior part of the bone are missing. The fossils were collected from ashy silts at T. 21 S., R. 35 E., Sec.17, Drewsey Quadrangle, Malheur County, Oregon, at elevations between 3750 and 3650 ft.

An age estimate of 8.5 Ma is constrained by two ash-flow tuffs. The Devine Canyon ash flow tuff (AFT) conformably overlies the upper basalts of Malheur Gorge and unconformably overlies the upper Juntura Formation within the basin interior. The Devine Canyon AFT consistently produced modern age dates of *ca.*9.7 Ma, with the latest at 9.756+/-0.020 Ma (Streck *et al.* 1999, Jarboe *et al.* 2008). The Devine Canyon AFT defines the base of the overlying Drewsey Formation. Roughly midway up the composite section a plant bed dominated by *Trapa* (water chestnut) is overlain by a thin fish-producing bed that is in turn overlaid by a second AFT dated at 8.7+/-1.0 Ma (Fiebelkorn *et al.* 1983). Walker (1979) recognized that this second AFT was likely correlative with the Prater Creek AFT from the Harney Basin to the west. The modern age date for the Prater Creek AFT is 8.48+/-0.05 Ma (Streck and Ferns 2004). The top of the Drewsey Formation lies unconformably under the Drinkwater basalt, which was dated 7.4 Ma (Fiebelkorn *et al.* 1983; Ferns *et al.* 1993).

Associated fish include *Ameiurus vespertinus, A. peregrinus, C.* (*Deltistes*) sp*., Catostomus* (*s.s.*) sp*., Ptychocheilus* sp*., Acrocheilus* sp*., Gila* or *Siphateles, ?Orthodon, Oregonichthys* sp*., Esox* sp*.,* and *Archoplites* sp. This fauna is Hemphillian NALMA.

Miocene *Catostomus* (*P.*) *hyomyzon* from Washington is represented by a fragmentary partial hyomandibulae (SDSM, not figured), similar in size and shape to the holotype. Kevin Meeks collected the specimen from the Granger Clay Pits of the Ellensburg Formation, Yakima County, Washington (46.5° N., 120.4° W.) in 2012. It is a *Pantosteus*, based on the presence of the ridge and groove lateral to the opercular condyle, but it is less complete than the holotype and Drewsey Formation specimens. G.A. Smith (1988) dated the Granger Clay Pit as *ca.*10.3 Ma. This is consistent with the presumed underlying 10.5 Ma Elephant Mountain basalt. The fossil mammals reported are consistent with a medial to late Clarendonian NALMA. The associated fishes include *Ameiurus* sp*., Mylocheilus* sp*., Rhinichthys* sp*.,* and *Archoplites* sp.

## PLIOCENE FOSSIL *PANTOSTEUS* FROM IDAHO

Data presented above demonstrate the presence of osteological traits of *Pantosteus* in the middle Miocene of Washington and Oregon, 12.3-8.5 Ma. But osteological traits of *Catostomus* (*s.s.*) and *Deltistes*, morphologically more plesiomorphic than *Pantosteus,* appear later, in the late Miocene of Idaho and Oregon (Smith *et al.* 1982; Buechler and Smith unpublished). *Catostomus* (*P.*) *arenatus,* discussed below, appears on the Snake River Plain later, *ca.* 2.4-1.9 Ma. It is a small catostomid, less than 250 mm in standard length. Rare bones of a larger, more apomorphic *Pantosteus*, about 300 mm in standard length, are described here from earlier in the Glenns Ferry Formation (4.5-4 Ma). The new fossils share most of their characteristics with *C.* (*P.*) *virescens,* which now inhabits the Snake River drainage above Twin Falls, and the Bear and Weber rivers of the northern Bonneville Basin. The fossils are related to *C.* (*P.*) *virescens, C.* (*P.*) *discobolus, C.* (*P.*) *clarkii,* and *C.* (*P.*) *santaanae*. According to inference from morphology and mtDNA sequences that define the

*C.* (*P.*) *discobolus* species group (Unmack *et al.* in revision), this new fossil form shares apomorphies of that group and probably postdates the node for the branch to the *C.* (*P.*) *plebeius* species group.

### Teleostei, Catostomidae
### ***Catostomus (Pantosteus) oromyzon*** new species
Figs. 4 b; 5 a, b; 6 a, b, c, f; 7 b, h

*Holotype*.—A right fourth rib (UMMP 43250) with the nearly complete dorsal arch and ventral ala, from Castle Creek, T. 5 S., R. 1 E., elevation 2800 ft, Rough Mountain NE Quadrangle, Owyhee County, Idaho, collected by the University of Michigan group, Summer, 1978.

*Description*.—The holotype is a right fourth rib of the Weberian apparatus (the static foundation for the sound-receptive chain of bones) of a mountain sucker that was about 300 mm in standard length. The fourth composite Weberian rib (Fig. 4 b, 5 a, 6 a) is 31.5 mm long and 14 mm (maximum) wide. It consists of a leaf-shaped ala that extends ventrolaterally from a stem-like dorsal arch, which curves dorsomesiad over the large foramen for the passage of the tripus (one of the moveable hearing ossicles, not present). The lateral surface of the highly ornamented dorsal arch extends post-dorsad where it would have attached to the last vertebra of the Weberian apparatus. The anterior surface of the ala is flat; a strong posterior rib strengthens the posterolateral surface, dorsally, and merges ventrally into the surface of the ala (Fig. 4 b, 5 a b). The strut that extended mediad, to contact the swimbladder, is broken off, but is represented by the base of a diagnostic broad mesial process. Dentaries and maxillae hypothesized to belong to *C.* (*P.*) *oromyzon* (see "*Referred Material*") are from specimens up to nearly 300 mm in standard length, from Pliocene beds at Hagerman, Twin Falls County, and Brown Cr., Owyhee County). The maxillae (Fig. 7 b) are unique among *Pantosteus* in having a relatively high dorsal keel. The dentaries have an obtuse angle between the proximal and distal processes and a longer distal process (Fig. 7 g, h).

*Diagnosis*.—The fourth composite Weberian rib of *Catostomus* (*P.*) *oromyzon* is broad, ventrally, the breadth of the ventrolateral ala is almost one-half (=44-45%) its length (this measurement is 35-40% in *Catostomus* (*C.*) *macrocheilus* [Fig. 4 a, 5 c], *C.* (*C.*) *catostomus, and C.* (*C.*) *latipinnis;* and 47% in *C.* (*P.*) *discobolus* [Fig. 5 d, 6 b]); the median edge of the bone has a semicircular notch that is bordered above by an equally broad process from which the strut to the swimbladder would have projected; the median part of the rib extends farther mesiad from the central ridge of the rib than does the lateral flange of the rib as in other *Pantosteus* of this species group, opposite to the condition in *Catostomus* (*s.s.*) (Fig. 4 a; 5 c); the anterior part of the ala is flat, not concave as in *Catostomus* (*s.s.*) or *C.* (*P.*) *discobolus* (Fig. 4 c; 5 d), *C.* (*P.*) *virescens, C.* (*P.*) *clarkii,* or *C.* (*P.*) *columbianus* (6 d, e).

*Paratype*.— A right Weberian rib 4 (Fig. 5 b, 6 f, UMMP 27128), is from the same location as the holotype: Castle Creek, T. 5 S., R. 1 E., elevation 2800 ft, Rough Mountain NE Quadrangle, Owyhee County, Idaho, August 11, 1987.

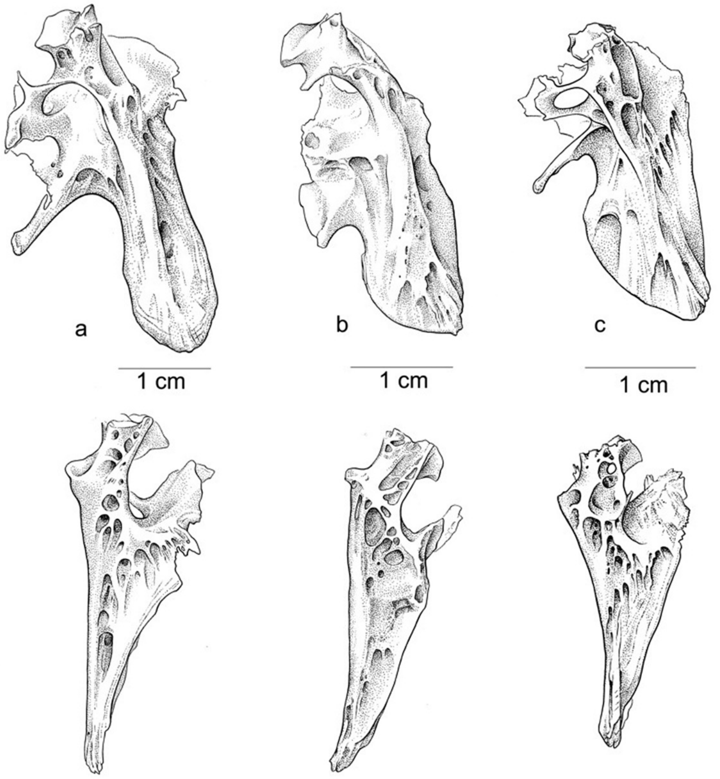

Fig. 4. Comparative illustrations of right second-fourth composite Weberian ribs, post-lateral views above, lateral views below. **a**. *Catostomus* (*C.*) *macrocheilus*, UMMZ 181694. **b**. *Catostomus* (*Pantosteus*) *oromyzon* n. sp., holotype, UMMP 42356. **c**. *C.* (*P.*) *discobolus* UMMZ 182483.

It has nearly the same dimensions and other traits as the holotype, but is lacking most of the dorsal limb.

*Referred material*.— Hagerman, Twin Falls County, Idaho: UMMP 58528, two maxillae; UMMP 58524, UMMP 58525, UMMP 58526, left dentaries, UMMP 58527, left dentaries; and Brown Cr., UMMP 69035, right dentary. *Catostomus* (*P.*) *oromyzon* dentaries differ from *C.* (*P.*) *arenatus* and *C.* (*P.*) *columbianus* in having the distal process wider and more robust, with a more posterior position of the coronoid process than *C.* (*P.*) *columbianus* (the coronoid process is similar to *C.* (*P.*) *columbianus* (Fig. 7 h) in UMMP V58526; but the rest of the dentary is like *C.* (*P.*) *oromyzon*--it is from a fish about 285 mm in standard length with a short distal process and an angle of about 110° between the distal and proximal process of the dentary). The maxillae (UMMP 58528, Fig. 7 b) are unusual in having a higher dorsal keel than other *Pantosteus*).

*Provenience*.—The Weberian rib fossils were recovered in the northeast quarter of section 21 in a relatively non-productive section of pale sediments east of Castle Creek 0.5 m north of the eastern one of two oolite outcrops. This

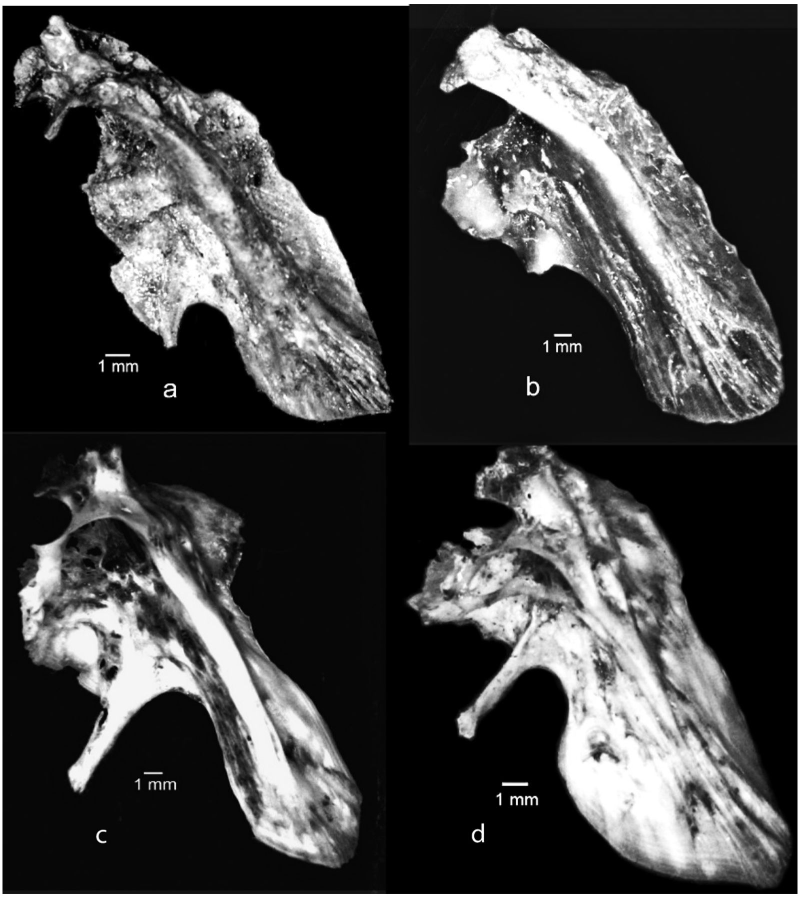

Fig. 5. Comparison of right fourth Weberian ribs, post-lateral view. **a**. *Catostomus* (*Pantosteus*) *oromyzon* n. sp., holotype, UMMP 42356. **b**. *Catostomus* (*Pantosteus*) *oromyzon* n. sp., paratype, UMMP 27128, **c**. *Catostomus* (*C.*) *macrocheilus*, UMMZ 181694. **d**. *Catostomus* (*P.*) *discobolus*, UMMZ182483.

area is stratigraphically near the base of the oolite (Swirydczuk *et al.* 1980) and 100 ft below the productive sequence of thin, horizontal, ashy silt layers in the NE quarter of sec. 27, above the oolite, 1.5 mi. southeast of the Johnson Ranch on Castle Creek (Swirydczuk *et al.* 1980). The ashy silts bearing the bones of *Catostomus* (*P.*) *oromyzon* are in the base of the transgressive phase of the Glenns Ferry lacustrine section, lateral to the Glenns Ferry basal oolite (Swirydczuk *et al.* 1979, 1980). The oolite forms laterally discontinuous, prominent cliffs on either side of Castle Creek in this tectonically disturbed area. Dentaries and maxillae were collected in the Hagerman cliffs (Ruez 2009), USGS Cen. loc. 19217, and Brown Cr. near the oolite.

Ostracodes associated with the oolite at the base of the Glenns Ferry lacustrine beds (R. Forrester pers. comm. to K. Swirydczuk, 1982) may be as old or older than those at the base of the floodplain section at Hagerman, 4.3 Ma (Ruez 2009). Therefore, the age of known *Catostomus* (*P.*) *oromyzon* may be

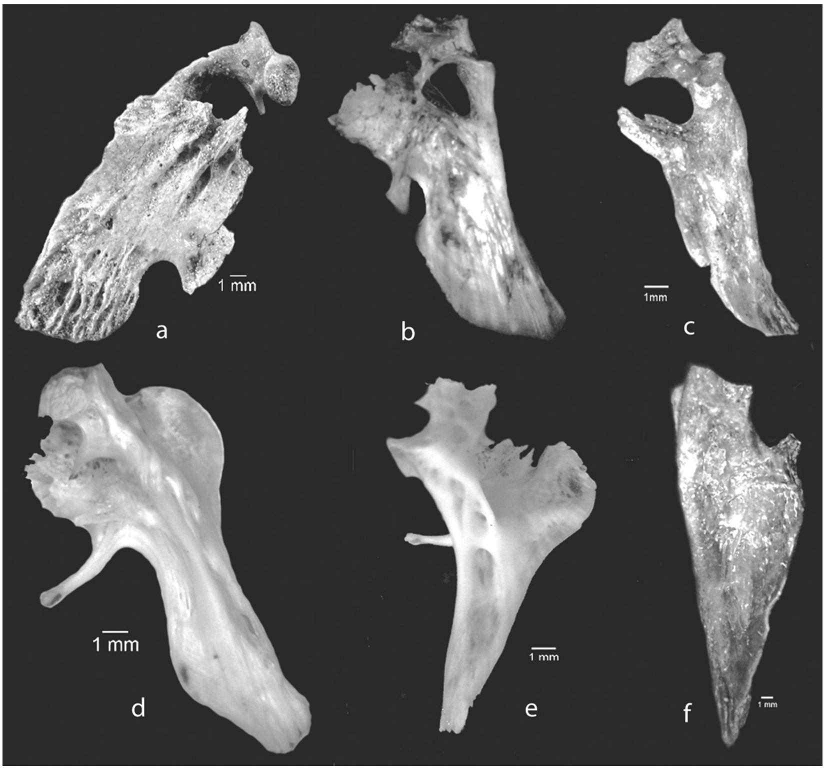

Fig. 6. Comparison of right fourth Weberian ribs. **a**. *Catostomus* (*Pantosteus*) *oromyzon* n. sp., holotype, UMMP42356, anterior view. **b**. *Catostomus* (*P.*) *discobolus* UMMZ 182483, post-lateral view. **c**. *Catostomus* (*P.*) *oromyzon* n. sp., holotype, UMMP42356, posterior view. **d**. *Catostomus* (*P.*) *columbianus*, UMMZ 194641, post-lateral view. **e**. *Catostomus* (*P.*) *columbianus* UMMZ 194641, anterolateral view. **f**. *Catostomus* (*P.*) *oromyzon* n. sp., paratype, UMMP 27128, lateral view.

slightly older than 4.3 Ma. The youngest known Chalk Hills beds are about 5.9 Ma. (By contrast, fossil dentaries of *C.* (*P.*) *arenatus* in the Glenns Ferry formation may be as old as 2.4 Ma at Sand Point (Miller and Smith 1967), but 1.9 Ma at Grandview, Jackass Butte; UOMP, UMMP).

*Etymology*.—The name "*oromyzon*" is intended to translate as "mountain sucker," the common name for *Pantosteus*. It is based on Greek "*oro,*" mountain, and "*myzo,*" "suck," referring to suckers, Catostomidae.

The younger and smaller form of *Pantosteus* collected on the Snake River Plain of Idaho, *Catostomus* (*P.*) *arenatus,* has recent descendants and a complex taxonomic history in the Columbia River drainage.

### Teleostei, Catostomidae
### ***Catostomus (Pantosteus) arenatus***
Fig. 7 g; Miller and Smith 1967, fig. 5 b, c

*Catostomus* (*P.*) *arenatus* Miller and Smith 1967:12 was described from the Pliocene Sand Point Local Fauna, *ca*. 2.4 Ma in the Glenns Ferry Formation, Owyhee County, Idaho, based on a maxilla (UMMP 55560) and a right dentary (UMMP 55559) from T. 6 S., R. 8 E., elevation 2600 ft (Miller and Smith 1967, p. 12-14, fig. 5). *Catostomus* (*P.*) *arenatus* and *C.* (*P.*) *columbianus* (recent in the Columbia and Frazer River drainages) are slightly different (Fig. 7), but are probably chronological forms of the same lineage, in part, although each is variable, with divergent populations, and the relationship is not simple. The species is identified from other localities in the Glenns Ferry Formation, including Jackass Butte, Owyhee County, Idaho (UO F31413, left dentary, UMMP 58519, left dentary, UMMP 58523, left dentary); Sand Point, Elmore County, Idaho (UMMP 59622, left dentary), and Oreana T. 4 S., R. 1 E., Sec. 7, (left dentary). Fossils of (*C.*) *P. arenatus* were found in association with *Ameiurus vespertinus*, *Catostomus cristatus, C.* (*Chasmistes*) *spatulifer, C.* (*Deltistes*) *owyhee, C.* (*D.*) *shoshonensis, Ptychocheilus arciferus, Acrocheilus latus, Lavinia hibbardi, Mylocheilus robustus, Orthodon hadrognathus, Klamathella milleri, Richardsonius durranti*, *Oncorhynchus lacustris, Prosopium prolixus, Kerrocottus divaricatus, K. pontifex, K. hypoceras,* and *Archoplites taylori* (Smith 1975, Smith *et al.* 1982). It is unlikely that *C.* (*P.*) *arenatus* actually lived with the lake community listed above. The mountain suckers more likely lived in tributaries and dispersed or were transported into the lake. *Catostomus* (*P.*) *arenatus* is *ca.*. 1.9 Ma in the Glenns Ferry Formation, Blancan NALMA (Smith 1975; Smith *et al.* 1982; Ekren *et al.* 1982; Wood 1996; Perkins and Nash 2002; Ruez 2009).

*Diagnosis*.—*Catostomus* (*P.*) *arenatus* is diagnosed by the distal limbs of the dentary short and robust (Fig. 7 g); as in the *C. discobolus* group (Fig. 7 i; Smith 1966, fig. 4 C), and a low dorsal keel of the maxilla (Miller and Smith 1967, fig. 5 C).

*C.* (*P.*) *columbianus* is further diagnosed by the incomplete dorsal extension of the crest of the lateral sheet of bone on the hyomandibula only to the level of the opercular condyle (Fig. 3 c) as in *Catostomus* (*s.s.*); intermediate width of the roofing bone on the pterotic (Smith 1966 fig. 3); the distal limb of the dentary somewhat longer (Fig. 7 g; Smith 1966, fig. 4 B); the fourth rib of the Weberian apparatus is tapered to a truncate end (Fig. 6 d, e), not broadly expanded distally or rounded as in the *C.* (*P.*) *discobolus* group (Fig. 4 c; 5 d). Diagnostic traits in the soft anatomy of *C.* (*P.*) *columbianus* include a rounded row of papillae in the median anterior part of the lower lip, confluent with the rounded lower jaw (Smith 1966, Pl. 1 A, p. 133), pigmented inter-radial membranes in the caudal fin (Smith 1966, fig. 9 B), and scale and gill-raker counts similar to *C.* (*P.*) *virescens* (Smith 1966).

*Catostomus* (*P.*) *columbianus* is the primary source of confusion in the generic classification of *Catostomus* and *Pantosteus*. This species was described in *Pantosteus* (Eigenmann and Eigenmann 1893) and in *Catostomus* (Hubbs and Schultz 1932) based on its mixture of diagnostic traits of those genera, especially in the lips, fins, and scales (Miller and Miller 1948); Miller observed that most traits diagnose this species as a *Pantosteus*. The mixture suggested that *C.* (*P.*) *columbianus* is either a product of introgressive hybridization between species of each genus or was a plesiomorphic branch from

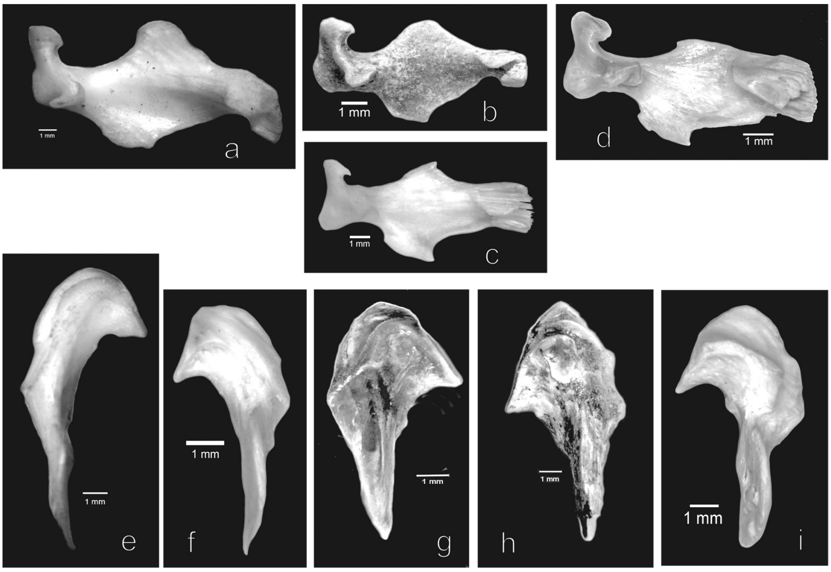

Fig. 7. Comparison of *Catostomus* (*C.*) *tahoensis*, *Catostomus* (*P.*) *oromyzon*, *Catostomus* (*P.*) *columbianus*, and *Catostomus* (*P.*) *virescens*. **a-d**, mesial views of right maxillae of **a.** *Catostomus* (*C.*) *tahoensis* (UMMZ 174437); **b**. *Catostomus* (*P.*) *oromyzon* (UMMP 58528) ; **c**. *Catostomus* (*P.*) *columbianus* (UMMZ 192601); and **d**. *Catostomus* (*P.*) *virescens* (UMMZ 180135). **e-i**, anterodorsal views of dentaries. **e**. *Catostomus* (*C.*) *tahoensis* (UMMZ 174437); **f**. *Catostomus* (*P.*) *columbianus* (UMMZ 192601); **g**. *Catostomus* (*P.*) *arenatus* (UMMP 59662 ); **h**. *Catostomus* (*P.*) *oromyzon* (UMMP 58526); and **i**. *Catostomus* (*P.*) *virescens* (UMMZ 180135).

early evolution. *Pantosteus* was classified as a subgenus of *Catostomus* (Smith 1966) because of the mixture of characters in *C.* (*P.*) *columbianus*. Molecular sequences suggest that *P. columbianus* carries *Catostomus* not *Pantosteus* mitochondrial DNA (mtDNA; Unmack *et al.* in revision) supporting the hypothesis of introgressive origin of the species. Those authors concluded that the large molecular distances between *Catostomus* and *Pantosteus* could support recognition of two genera, raising the problem of polyphyly and paraphyly. *Catostomus* (*P.*) *arenatus* bears on origin of *P. columbianus* by demonstrating the Pliocene occurrence of osteological traits shared with the modern species. Its morphological traits are partly uniquely diagnostic of *Pantosteus* and partly intermediate, and because it has *Catostomus* mtDNA (Unmack *et al.* in revision), separating the taxa at the generic level creates paraphyly of *Catostomus* and polyphyly of *Pantosteus* (or *vice versa* if *columbianus* is classified as a *Catostomus*). No evidence from nuclear DNA yet bears on this problem.

Evidence of frequent hybridization between *Catostomus* and *Pantosteus* has been reported many times (*e.g.* Hubbs *et al.* 1942; Smith 1966, 1992a). Recent evidence (Unmack *et al.* in revision) and data presented here demonstrate that the hybridization was not unique to recent times, but probably occurred in the Pliocene because the age based on molecular sequence divergence, 2.0 m.y., is consistent with possible Late Pliocene age and possible connection between the Lahontan Basin and Snake River Plain through the

Alvord Basin in the late Pliocene to Middle Pleistocene (Reheis *et al.* 2002, fig.1). The presence of *Siphateles alvordensis*, similar to the *Siphateles* from the Lahontan Basin in the Alvord Basin, supports this conncetion.

Five factors argue for hybridization and against ancient polymorphism as the explanation for the mixture of characteristics in *C.* (*P.*) *columbianus*: (1) mixed, independently segregating morphological traits are diagnostic of *C.* (*P.*) *columbianus* in fish with a divergent mtDNA sequence diagnostic of *Catostomus* cf. *C. tahoensis*; (2) evidence of variable *C.* (*P.*) *columbianus* (Smith 1966), (3) probable ancestry in variable *C.* (*P.*) *arenatus* in the Pliocene, (4) evidence of extensive modern hybridization among *Catostomus, Pantosteus,* and *C.* (*P.*) *columbianus* (Hubbs *et al.* 1943; Smith 1966); and (5) the possible concordance of the age (2.0 m.y.) based on genetic divergence of mtDNA of *C.* (*P.*) *columbianus* with the 2.4-1.9 Ma age of *P. arenatus* in the fossil record (Unmack *et al.* in revision). Many lip, jaw, scale, and bony morphological traits of *Pantosteus* are independent as demonstrated by the evident recombination of traits in F2 and backcross hybrids (*e.g.* Smith 1966, fig. 22, p. 109). These and the many significant mtDNA loci shared with *Catostomus* make coincident inheritance of many separate ancient plesiomorphic traits improbable for the combination of characters of *Catostomus columbianus*. The large numbers of recent hybrids between *Catostomus macrocheilus* and *C. columbianus* (substantial proportions of hybrids at 14 localities, Hubbs *et al.* 1943; Smith 1966) and probable hybridization between *Catostomus platyrhynchus* and *C. columbianus* in the Palouse River (Smith 1966) are consistent with the hypothesis of ancient hybridization.

## PLIOCENE FOSSIL *Pantosteus* FROM NEVADA

Fossil *Pantosteus* and other bones were collected by Dwight Schmidt (USGS), Bob Reynolds (LSA), and Quintin Lake (SBCM) from the Starvation Flat area of the Pliocene White Narrows formation in southern Nevada and deposited in the San Bernardino County Museum. Specimens in collection L3313-23-25 were carefully sorted, labeled, and prepared by volunteer William J. Kilday. All specimens were curated and made available by Eric Scott, Collection Manager. The *Pantosteus* bones are recognized as a new species, related to *C.* (*P.*) *clarkii,* which now lives in the basin, but the fossils are more plesiomorphic in some respects. The fossils include a dentary, a mesocorocoid, and a fragment of a hyomandibula. The age is estimated as 4.7-4.5 Ma (Schmidt *et al.* 1996; Reynolds and Lindsay 1999).

### Teleostei, Catostomidae
### ***Catostomus (Pantosteus) asitus*** n. sp.
Fig. 8 a, b, c, d

*Holotype.*—The holotype is a right dentary of a *Pantosteus*, 9.9 mm long and 4.3 mm wide along the symphysis (SBCM L3313-23). The bone is nearly complete except for the coronoid process. It was collected for the San Bernardino County Museum from the Pliocene White Narrows Formation at Starvation Flat, Clark County, Nevada.

*Description.*—The biting and scraping distal and anterior part of the dentary is short, 3-4 mm long, and curved ventrad and mediad to meet the left dentary at the symphysis. The angle between the symphysis and the labial edge of the bone is 50° (Fig. 8 c, d). The distal arm diverges from the proximal arm by about 135° (Fig. 8 c, d) so that the symphysis is aligned by about 30° with the proximal arm of the bone (Fig. 8 c, d). The anterodorsal surface of the distal arm is highly sculptured with a large, deep anterolateral groove (Fig. 8 d) for the labial cartilage, which is inflected over the lateral opening of the mental foramen. The posteroventral surface of the distal arm of the bone is smooth and convex anteriorly, and concave posteriorly. The median ridge extends from the posterior end of the symphysis to a point between the internal opening of the mental foramen and the abutment for the end of Meckel's cartilage (Fig. 8 b). The coronoid process is broken and abraded; the proximal end is slightly abraded (Fig. 8 a, b).

*Diagnosis*.—The dentary is diagnosed as a *Pantosteus* by the short, broad, mesially-directed distal process (Fig 8 c, d). *Catostomus* (*s.s.*) is diagnosed by a long, narrow, and less deflected distal process (Fig. 8 e). The length of this process in *C.* (*P.*) *asitus* is relatively longer and less deflected than in *C.* (*P.*) *virescens* (Fig. 7 i)*, C.* (*P.*) *discobolus, C.* (*P.*) *clarkii,* or *C.*(*P.*) *santaanae.* Its length and angle are somewhat intermediate between these species and *C.* (*P.*) *plebeius* (Fig. 11d).

*Paratypes.*—No paratype is designated.

*Provenience*.— The fossils were recovered from Starvation Flat, T. 13 S., R. 63 E., Clark County, Nevada, San Bernardino County Museum locality L3313. More detailed locality information is on file at the SBCM. Associated fish include *Catostomus* (*C.*) *latipinnis* or *Catostomus* (*C.*) *insignis*, *Ptychocheilus* sp*., Orthodon sp., Siphateles* sp*., Rhinichthys* sp*.,* a plagopterine minnow, and numerous *Archoplites* sp.

*Etymology.*—The species name, *asitus*, is Latinized Greek meaning "without food," referring to the name of the locality at Starvation Flat.

*Referred material*.—A partial mesocoracoid (SBCM L3313-24) is a catostomid bone that matches *Catostomus* (*P.*) *clarkii* in its orientation of muscle attachments and orientation of the foramen relative to the size and position of the pectoral fin condyle. A partial dentary, (SBCM L3313-25) is a catostomid with some traits of *Pantosteus*, insofar as recognizable.

*Catostomus* (*P.*) *asitus* shows relatively plesiomorphic *Pantosteus* shape characters of the dentary. The bones are intermediate between those of *C.* (*P.*) *clarkii* and other members of the *C.* (*P.*) *discobolus* species group and *C.* (*P.*) *plebeius*. This evidence, along with the ages of the White Narrows Formation, (4.7-4.5 Ma) and the Oregon and Washington formations with the oldest *Pantosteus* (11.5-8.5 Ma) provide a perspective on the slow rate of change of the apomorphies. The fossil bones from the White Narrows Formation are morphologically intermediate between the earliest known form, *C.* (*P.*) *hyomyzon*, and the apomorphic *C.* (*P.*) *discobolus* of the Colorado Plateau.

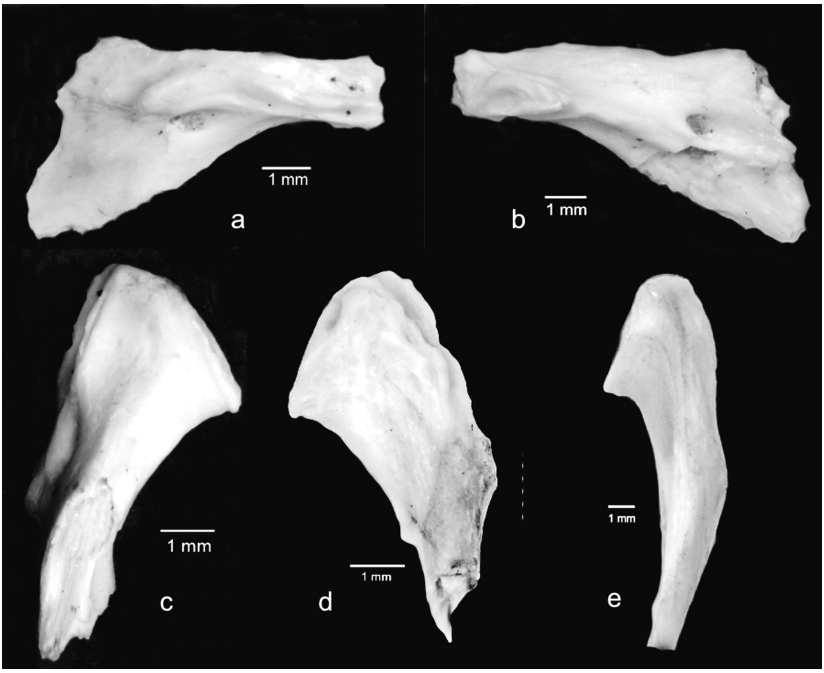

Fig. 8. Right dentaries of White Narrows Pliocene holotype, *Catostomus* (*Pantosteus*) *asitus*, **a, b, c, d** (SBCM L3313-23), **a**. Lateral view. **b**. Mesial view. **c**. Postventral view. **d**. Antero-dorsal view. **e**. Recent *Catostomus* (*C.*) *insignis*, (UMMZ 162742), anterodorsal view.

## PLEISTOCENE FOSSIL *PANTOSTEUS* FROM KANSAS

*Catostomus* (*Pantosteus*) *jordani, Pleistocene, northwestern Kansas.*— Fossils of *Catostomus* (*P.*) *jordani* from 30 Ka Pleistocene sediments in or near the Peoria Loess, at the Coon Creek locality in the Solomon River drainage, tributary to the Kansas River, North of Hill City, Graham County, Kansas. *Catostomus jordani* is represented by two dentaries (KU 64901, Fig. 9 a), and KU 64902, Fig. 9 c) and a maxilla (KU 64903, Fig. 10 e). They are recognized by their close similarity to the recent specimens of *C.* (*P.*) *jordani* (Fig. 9 b; 10 f) from the upper Missouri drainage, in streams around the Black Hills of South Dakota and Wyoming, and they indicate that the species inhabited the Solomon tributary of the Smokey Hill to Kansas River drainage in the Late Pleistocene. The dentaries are diagnosed as *Pantosteus* by the extreme mesial deflection of the distal part of the dentary. The axis of the median edge of the symphysis forms an angle of about 75° with the labial edge of the distal arm of the bone. The main axis of the distal arm is about 125° from the axis of the proximal arm of the dentary (Fig. 9 c, e). A dentary of *Catostomus* (*C.*) *commersoni* from the Coon Creek fauna, KU 64906 Fig. 9 d), by contrast, has a longer, less mesially deflected distal arm; the axis of the symphysis is nearly parallel to the axis of the proximal arm of the dentary; and the distal arm di-

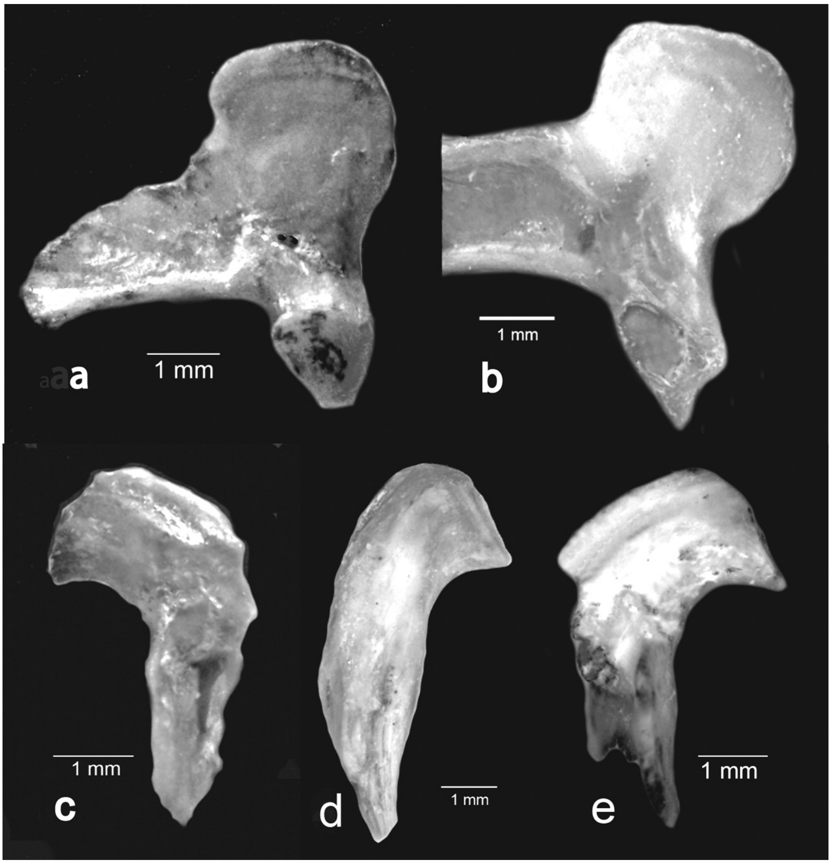

Fig. 9. *Pantosteus* and *Catostomus* dentaries from Kansas and South Dakota. **a**. *Catostomus* (*P.*) *jordani* Pleistocene left dentary, Kansas, KU 64901, mesial view. **b**. *Catostomus* (*P.*) *jordani*, recent left dentary, UMMZ 127501, South Dakota, mesial view. **c**. *Catostomus* (*P.*) *jordani* Pleistocene right dentary, Kansas, KU 64902, anterodorsal view. **d**. *Catostomus* (*C.*) *commersoni*, Pleistocene left dentary, Kansas, KU 64906, anterodorsal view. **e**. *Catostomus* (*P.*) *jordani*, left dentary, Pleistocene, Kansas, KU 64901, anterodorsal view.

verges from the proximal arm by about 160°.

The maxilla of *C.* (*P.*) *jordani* also displays apomorphic *Pantosteus* shape characters (Fig. 10 e, f). The bone is short and robust, with a low dorsal keel and an anterior-positioned ventral keel, which has a stout leading edge and a deep groove for insertion of a slip of the maxillaris muscle. The fossil (Fig. 10 e) is slightly more apomorphic than the recent maxilla (Fig. 10 f), a trend noted in some other Pliocene fossils compared to recent minnow and sucker relatives (Smith 1975). Presence of *C.* (*P.*) *jordani* in the Solomon drainage, tributary to the Kansas drainage, reveals that it was much more widespread in the Pleistocene than previously suspected. This discovery adds credence to the record of a single specimen of *Pantosteus* labeled as having been collected from the Niobrara River at Marsland, Nebraska, by W.B. Evermann in 1893 (USNM 76037). The morphology of this specimen, though ambiguous, supports this

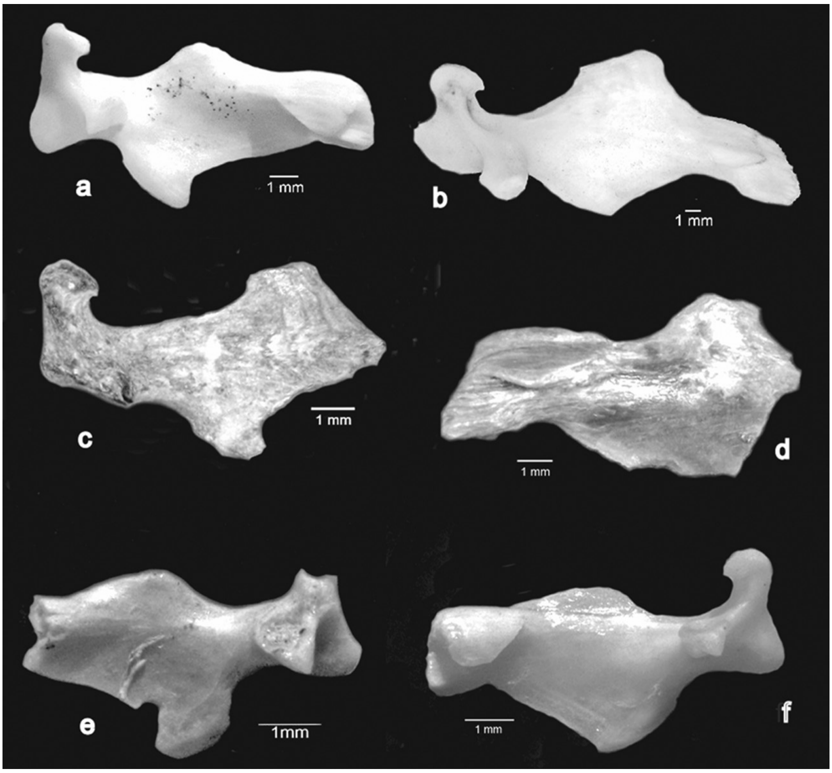

Fig. 10 Comparison of fossil maxillae, mesial view. **a**. *Catostomus Pantosteus columbianus* right maxilla, UMMZ 194641, recent, Idaho. **b**. *Catostomus macrocheilus* right maxilla, UMMZ 192602, recent, Idaho. **c**. *Catostomus* (?*Pantosteus*) sp. anterior part of right maxilla, UMMP 42347, Miocene, Juntura Formation, Oregon. **d**. *Catostomus* (?*Pantosteus*) sp. posterior part of left maxilla, UMMP 43248, Miocene, Drewsey Formation, Oregon. **e**. *Catostomus* (*P.*) *jordani* left maxilla, KU 64903, Pleistocene, Kansas. **f**. *Catostomus* (*P.*) *jordani* left maxilla, UMMZ 127501, recent, South Dakota.

interpretation (Smith 1966, p. 69). Extension of the range to Kansas suggests that other *Pantosteus* probably had broader ranges during cooler, wetter times in the past, when streams had larger volumes flowing out of the mountains.

## PLEISTOCENE FOSSIL *PANTOSTEUS* FROM COLORADO

Fossils similar to *Catostomus* (*Pantosteus*) *plebeius* were reported from 2.6 Ma to 670 Ka sediments in the Pleistocene Alamosa Formation in Southern Colorado (Rogers *et al.* 1985, 1989) in the Rio Grande Rift of the Basin and Range Province. Karel Rogers and colleagues collected many bones, including maxillae and dentaries of *C.* (*P.*) *plebeius,* from cores and outcrops as part of the Hansen Bluffs project in 1979-1986 (Rogers *et al.* 1985, table 2; fossils are deposited at the University of Colorado Museum, Boulder). Evidence for two forms of *Pantosteus,* one approaching *Catostomus* (*s.s.*) *commersoni,* was observed in specimens from outcrops (Rogers *et al.* 1985). Type "a" *Pantosteus* is plesiomorphic (Fig. 11 a, b), but similar to *P. plebeius* (Fig. 11 d) in its angular dentary, with the mesial opening of the mental foramen near the termination of Meckel's cartilage (not visible in anterodorsal view, Fig. 11 b). The maxilla has a low dorsal keel, prominent anteroventral keel, and short thick "neck" of the bone (Fig. 11 k). Type "b" is more plesiomorphic and somewhat similar to *Catostomus* (*C.*) *commersoni* and *C.* (*C.*) *leopoldi*, with a less angular dentary (Fig. 11 c) that sometimes shows the mesial opening of the mental foramen on the anterodorsal surface of the bone, a longer narrower anterolateral groove for the labial cartilage (Fig. 11 e, h) and a longer, slenderer constriction ahead of the keels on the maxilla (Fig. 11 i, j). Many fossil maxillae (Fig. 11 k) are similar to recent maxillae of *C.* (*P.*) *plebeius* (Fig. 11 l). Recent specimens of *Catostomus* (*C.*) *commersoni* have a much deeper maxilla with a prominent dorsal keel and a weaker ventral keel (somewhat similar to *C.* (*C.*) *macrocheilus*, Fig. 10 b). Dentaries in (Fig. 11 c, e-g) and maxillae (Fig. 11 i) are intermediate.

In a related issue, Koster (1959, p. 44) concluded that *Catostomus* (*C.*) *commersoni* was not native to the upper Rio Grande drainage, but the fossil evidence suggests that they probably were there in the Pleistocene and probably introgressed with *C.* (*P.*) *plebeius*. *Catostomus* (*C.*) *commersonii* is native in the adjacent Arkansas and Pecos rivers. These variable fossils possibly suggest ecological and evolutionary responses to fluctuating warm-to-cold climate change (Rogers *et al.* 1985, 1989). The catostomids are associated with *Oncorhynchus clarkii* (Cutthroat Trout), *Gila pandora* (Rio Grande Chub), and *Dionda* sp. (small minnows), as well as warm-climate ostracodes, mollusks, amphibians, reptiles, and mammals. The species represent a typical upper Rio Grande fauna (but see Rogers *et al.* 1989, p. 79).

## DISCUSSION

*Biogeography of Pantosteus.—Pantosteus* species distributions and chronology are tied to the Miocene-Pliocene topography and history of the Basin and Range Province and the Colorado Plateau in western North America (Fig. 1). Only one species, *C.* (*P.*) *jordani,* colonized east of the Rocky Mountains and extended its range through the Missouri drainage to Kansas in the Pleistocene. About a dozen species fall into two main species groups: A 'north-to-south' *C.* (*P.*) *discobolus* group in the Snake River, northern Bonneville Basin, Colorado River, Los Angeles Basin, Rio Grande, and upland drainages in central Mexico; a 'northwest-to-east' *C.* (*P.*) *platyrhynchus* group, in the Lahontan and Bonneville basins, Columbia-Snake River, Green River, and Missouri River drainages. A third lineage, *C.* (*P.*) *arenatus* and *C.* (*P.*) *columbianus* of the Columbia-Snake drainage falls, outside the two main species groups (Fig. 12) as a consequence of introgressive origin influenced by *Catostomus* (*s.s.*).

Most populations of *Pantosteus* are allopatric (Fig. 1a), but sympatric (and hybridizing) species of *Pantosteus* are found in the Columbia River, Snake River, Northern Bonneville, Green River, and Colorado River drainages (Hubbs *et al.* 1943; Smith 1966; Smith *et al.* 1982; Unmack *et al.* in revision).

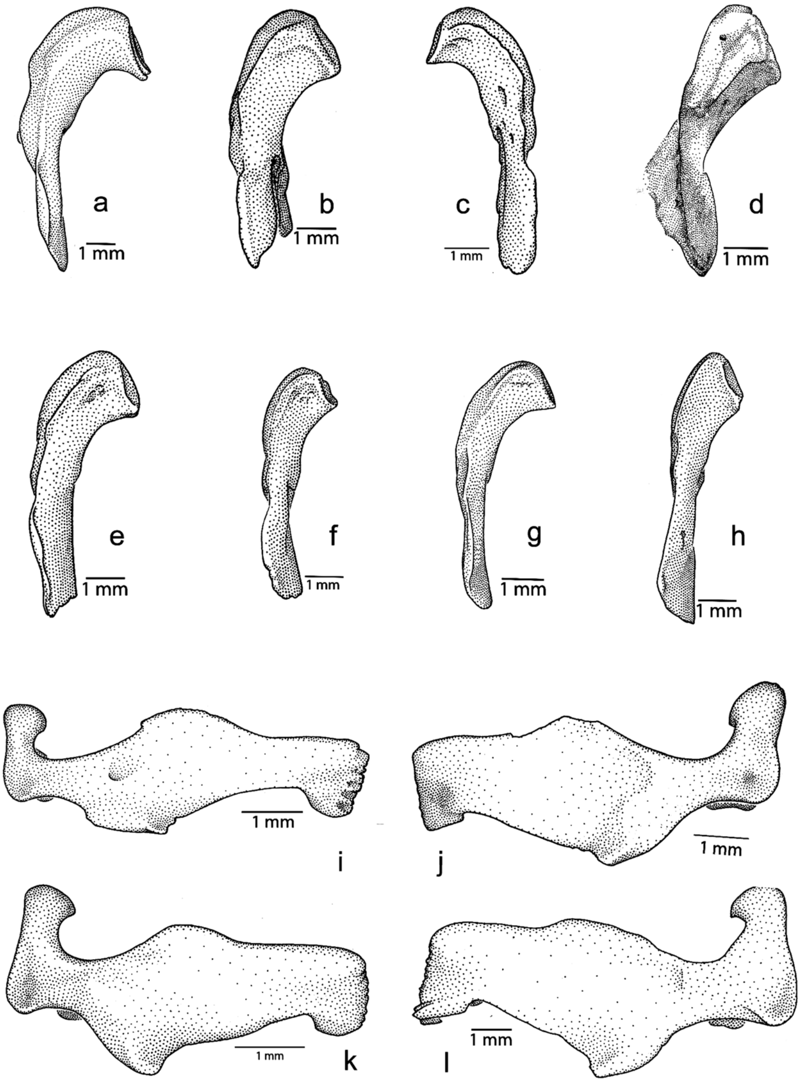

Fig. 11. *Catostomus* (*Pantosteus*) *plebeius* and variants from the Pleistocene Alamosa Formation (Rogers et al. 1985, 1989) and compared specimens from the Rio Grande drainage. Dentaries, anterodorsal view (anterior up): **a**. *Catostomus* (*P.*) *plebeius* (UMMZ 94889, NM). **b**. *Catostomus* (*P.*) cf. *plebeius* (Alamosa Fm. CT3, see Rogers et al. 1985 for stratigraphy). **c**. *Catostomus* (*P.*) cf. *plebeius* or *commersoni*i (Alamosa Fm. HA5b). **d**. *Catostomus* (*P.*) *plebeius* (UMMZ 197431, recent, Colorado). **e**. *Catostomus* (*C.*) cf. *commersoni*i (Alamosa Fm. B-80-2a). **f**. *Catostomus* (*C.*) cf. *commersoni*i (Alamosa Fm.mB-80-2b). **g**. *Catostomus* (*C.*) cf. *commersoni*i (Alamosa Fm. HA5a). **h**. *Catostomus* (*C.*) cf. *commersoni*i (Alamosa Fm. Alamosa Fm. HA5a). Maxillae, lateral view: **i**. *Catostomus* (*P.*) *plebeius* x *Catostomus* (*C.*) cf. *commersoni*i, intermediate form (left, Alamosa Fm. HA4-A80). **j**. *Catostomus* (*P.*) *plebeius* (right, Alamosa Fm. TS-1). **k**. *Catostomus* (*P.*) *plebeius* (left, Alamosa Fm. CT3-1). **l**. *Catostomus* (*P.*) *plebeius* (right, UMMZ 94889, NM).

Miocene extension of the Paleogene Nevadaplano (Ernst 2009) into high-relief drainages might have created the earliest context for evolution of mountain suckers. The earliest *Pantosteus* are middle Miocene fossils reported here from fluvial and littoral deposits in the northern Great Basin and Columbia Plateau provinces. The area was a part of the early Great Basin in Oregon and Washington, near the Columbia River basalts, the Oregon-Idaho Graben (Cummings *et al.* 2000), and the Nevada-Washington rift. Early *Pantosteus* were also present on the edges of the subsiding Western Snake River Plain and its later extension into the Basin and Range Province, as development of Miocene and Pliocene rivers and lakes provided widespread and diverse aquatic habitats in the region (Cope 1883; Malde and Powers 1966; Smith *et al.* 1982; Wood 1994; Dickinson 2006).

The Basin and Range Province, with its north-south trending valleys from Oregon to Mexico (Fig. 1 b) and eastward to the Rio Grande rift, is likely the broad landscape of Miocene and Pliocene dispersal and diversification of *Pantosteus* species, as viewed in the light of paleontological, morphological, and gene-tree evidence for the sequence of phylogenetic branching (Fig. 12; Unmack *et al.* in revision). The primary split between the *C.* (*P.*) *discobolus* group and the *C.* (*P.*) *platyrhynchus* group probably occurred in the northern Basin and Range Province. Subsequent branches of the *C.* (*P.*) *discobolus* group colonized five major Miocene rivers in the western U.S.: the Columbia, Snake, Upper Colorado, Lower Colorado, and upper Rio Grande. In the Pliocene these five were amalgamated into three rivers: the composite Columbia drainage with three species, the composite Colorado drainage with three species, and the Rio Grande with one.

Branches of the *C.* (*P.*) *platyrhynchus* group colonized precursors of the Columbia drainage, Snake River, Lahontan Basin, Bonneville Basin, Green River, and upper Missouri River (Smith 1966; Unmack *et al.* in revision), four of which contained more than one species after later connections. The divergence pattern of two species groups is supported by the morphology of bones of the skull, jaws and lips, pterygoid series, opercular series, and hyomandibula, all subject to character displacement after sympatry (Dunham *et al.* 1979).

Two species of fossils closely related to *C.* (*P.*) *virescens*—*C.* (*P.*) *oromyzon* and *C.* (*P.*) *arenatus*—lived near the rift lake that deposited the Pliocene Glenns Ferry Formation on the Snake River Plain, from 4.5 to 1.9 Ma. At approximately the same time, Pliocene *Pantosteus* in southern Nevada, *C.* (*P.*) *asitus* in the White Narrows Formation, 4.7-4.5 Ma, are intermediate in morphology and inferred to be transitional between the ancestral Miocene forms in Oregon, and modern forms to the south—*C.* (*.P*) *discobolus, C.* (*P.*) *clarkii* of the Colorado drainages, *C.* (*P.*) *santaanae* of the Los Angeles area, and *C.* (*P.*) *plebeius* and *C.* (*P.*) *nebuliferus* in the Rio Grande, southern Basin and Range, and south to central Mexico. These trends suggest that a Miocene ancestor, geographically and morphologically close to *C.* (*P.*) *hyomyzon*, diversified and spread south through the Basin and Range province in the late Miocene and Pliocene, beginning about 12.5-8.5 Ma. *Catostomus* (*P.*) *asitus* represents an intermediate morphological stage in the early Pliocene evolution of the ad-

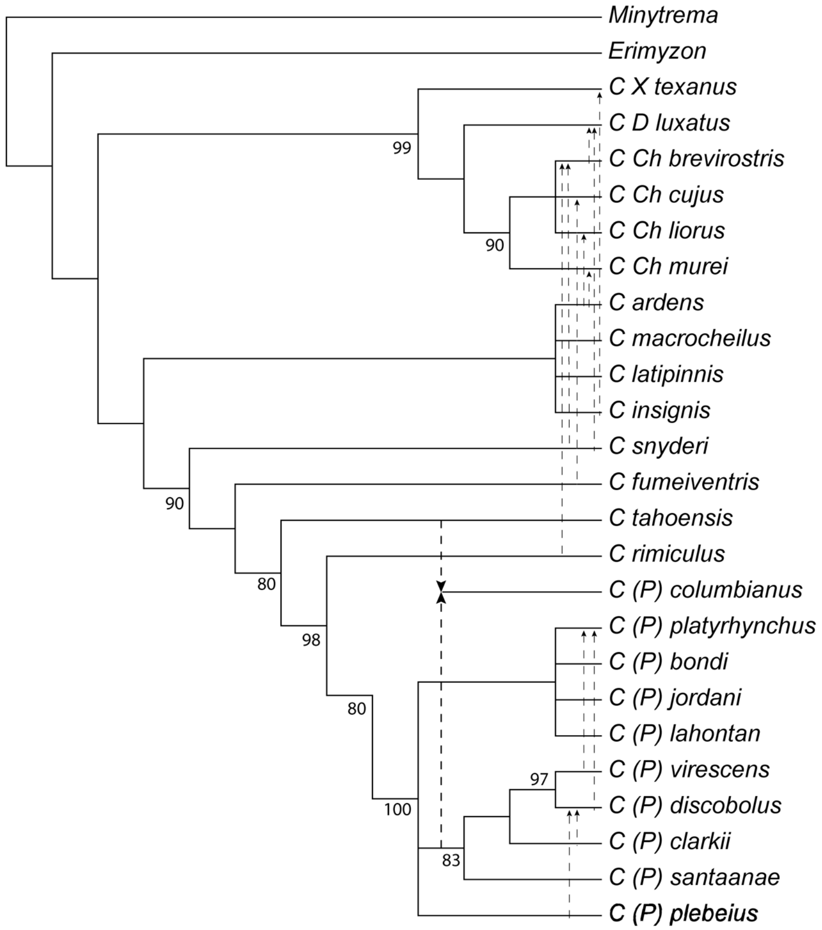

Fig. 12. Morphological phylogeny of catostomin species based on 87 morphological and biochemical characters (see Appendix). Documented introgressive transfer of mtDNA shown with dashed lines. Strict consensus of 63 trees, length = 252, CI = 0.53, RI = 0.83. Bootstrap values of 80 and above shown at nodes.

vanced feeding structures that characterize the mountain suckers, similar to the morphology seen in *C.* (*P.*) *santaanae* of the Los Angeles area.

The trend culminated in the most advanced forms, *C.* (*P.*) *discobolus* of the Colorado River in Grand Canyon and upstream, and *C.* (*P.*) *clarkii* in the lower Colorado drainages of the Great Basin below Grand Canyon. Divergence of these species began while the upper and lower Colorado River drainages were separated by the Kaibab upwarp in the late Miocene. Geological evidence in the Grand Wash trough, at the boundary of the Colorado Plateau and Great Basin, indicates that no sediments from the Colorado Plateau were deposited in the Great Basin prior to about 5.5 Ma (Lucchitta 1987; Spencer *et al.* 2001). *Pantosteus clarkii* and *discobolus* differ by about 4.0% in their mtDNA, which suggests that the last genetic exchange was 4.6 Ma (Unmack *et al.* in revision).

The *C.* (*P.*) *platyrhynchus* species group is morphologically less derived than *C.* (*P.*) *oromyzon* and the *C.* (*P.*) *discobolus* species group in some osteological traits, perhaps because it is smaller. *Catostomus* (*P.*) *bondi* of the Columbia Basin, *C.* (*P.*) *lahontan* of the Lahontan Basin, *C.* (*P.*) *platyrhynchus* of the Bonneville Basin, upper Snake River, and Green River, and *C.* (*P.*) *jordani* of the upper Missouri drainage, may have diverged in the latest Miocene. They form a polytomy on the morphological tree (Fig. 12); their divergence from each other is dated at about 6 Ma by mtDNA distances analyzed by Unmack *et al.* (in revision). This clade split from the *C.* (*P.*) *discobolus* group about 12 Ma according to molecular clock estimates (calibrated with fossil data from this paper) by Unmack *et al.* (in revision).

Figure 12 shows the branching hypothesis for this group, with hypothetical transfer of mtDNA from *Catostomus* (*C.*) *tahoensis* to the lineage of *C.* (*P.*) *arenatus* and *C.* (*P.*) *columbianus* in early Pleistocene according to mtDNA evidence (Unmack *et al.* in revision). *Catostomus* (*C.*) *tahoensis* is now restricted to the Lahontan Basin, but that drainage could have been connected to the Snake River drainage through the Alvord Basin at various times in the Pleistocene (Reheis *et al.* 2002, fig. 1) and possibly earlier. This hypothesis is supported by the presence of a relative of Lahontan *Siphateles* in the Alvord Basin. Additional evidence for drainage connections between the Lahontan and Snake River drainages is found in mtDNA haplotypes of *Rhinichthys osculus* shared across the drainage divide (Chow *et al.* in revision). The fossils related to *C.* (*P.*) *arenatus* from the Western Snake River Plain, 2.4-1.9 Ma, and *C.* (*P.*) *oromyzon* (4.5 Ma), are roughly consistent with the molecular estimate of a time of origin of *C.* (*P.*) *columbianus* in the late Pliocene, about 2.0 Ma (Unmack *et al.* in revision).

*The significance of introgression.*— Tests of introgression require multiple heritable characters for phylogenetic reconstruction, traits that evolved at different rates, and good models of evolution for use in reconstruction (Linder and Riesberg 2004), criteria that are met by comparison of gene trees and morphological phylogenies of suckers, assuming that morphological convergence is ruled out by the diversity and pattern of intermediacy of morphological characters involved. Detection of introgressive polyphyly requires evidence for different parental species as sympatric sources of diagnostic traits. Parents are typically identified on the basis of incongruent trees from separate data analyses on independent data sets, with specific character states representative of the different hypothetical parents (Linder and Riesberg 2004). It is important to remember that molecular phylogenies are gene trees, not necessarily representative of history of the fishes.

Hybridization among *Pantosteus* species and between *Pantosteus* and *Catostomus* is widespread (Hubbs *et al.* 1943; Hubbs and Miller 1953; Smith 1966; Smith 1992a). Most hybridization does not lead to introgression, presumably because many hybrids are not fertile or viable and backcrosses do not occur. Evidence of introgression is found in the Columbia Basin, upper and lower Snake River Basins, Green River Basin, Bonneville Basin, Grand Canyon, and Little Colorado River, in the form of incongruence of multiple morphological traits and also incongruence between morphology and gene trees (Smith 1966; Unmack *et al.* in revision). The indicators of past introgression in morphological traits are, with few exceptions, limited to sympatric forms that currently hybridize. The complex pattern of introgression among Klamath Basin *Chasmistes* and *Deltistes* with *Catostomus* (*C.*) *snyderi* and *Catostomus* (*C.*) *rimiculus* (Markle *et al.* 2005; Markle *et al.* in revision) demonstrates many directions of introgression, made evident by the presence of *Catostomus* mtDNA in fish with mixed *Chasmistes-Catostomus* and *Deltistes-Catostomus* morphologies. The introgression hypothesis is strongly supported by the fossil record of these forms dating from 6-8 Ma, whereas the corresponding genetic distances are only 1-2%, indicating introgressive resetting of the molecular clock. A parallel case is provided by the incongruence of *Xyrauchen* morphology and *Catostomus* mtDNA (Doosey *et al.* 2010), along with the documented current hybridization, and the mismatch of the 5 m.y. old fossil record against the 1-2% sequence divergence.

Alternatives to introgressive hybridization are not supported by evidence. Explanation of the pattern of shared traits as a consequence of character displacement is not supported because the mixture of parental characters in the hybrids involves more traits than feeding or locomotor structures in catostomids. Similar considerations apply to sympatric pairs of many western North American Cyprinidae, for example, *Algansea tincella* and *A.* (*Xystrosus*) *popoche* in Lake Chapalla (Barbour and Miller 1978), and *Gila seminuda* in the lower Colorado River drainage (DeMarais *et al.* 1992).

Tests of local introgressive hybridization *vs.* ecophenotypic speciation hypotheses are based on biogeography, genetics, and evolutionary principles. The ecophenotypic hypothesis is rejected because the Pliocene and recent record of introgressing populations shows original distinctness in the process of breaking down, not diverging. The antiquity of the fossil record relative to the minimal genetic distances is not congruent and not indicative of increasing diversification; the variety of segregating morphological traits showing biparental mixture is increasing through geological and historical times. Finally, many ecological circumstances exist where ecophenotypic speciation is predicted to occur if the capacity actually exists in the catostomid genome; yet introgression only occurs in a limited area, related to two particular clades of sympatric catostomins. Tests of the introgression hypothesis based on the comparison of phylogenetic trees use two sets of independent data—gene trees *vs.* morphological trees. Incongruence required by this test is met by *C.* (*P.*) *columbianus* with morphology from *Pantosteus* and mtDNA from *Catostomus* in the Columbia Basin (Unmack *et al.* in revision). Similarly, *Deltistes* morphology occurs with *Catostomus* mtDNA and *Chasmistes* morphology occurs with *Catostomus* mtDNA in the Klamath Basin (Markle *et al.* 2005; Markle *et al.* in revision). In the Colorado River, *Xyrauchen* morphology is found with *Catostomus* (*insignis*) DNA (Doosey *et al.* 2010; Dowling unpublished). Within *Pantosteus*, introgression has been demonstrated in descendants of *C.* (*P.*) *virescens* x *C.* (*P.*) *platyrhynchus* in the Snake River (Smith 1966), *C.* (*P.*) *discobolus* x *C.* (*P.*) *platyrhynchus* in the Green River (Smith 1966), and *C.* (*P.*) *discobolus* x *C.* (*P.*) *plebeius* in the

Little Colorado River (Smith 1966; Smith *et al.* 1983). Hybridization between *P. plebeius* and *P. discobolus* helped form *P. discobolus yarrowi* in the early Pleistocene (Fig. 12; Smith 1966; Smith *et al.* 1984; Crabtree and Buth 1987; Unmack *et al.* in revision). It is also apparent from comparison of the morphological tree (Fig. 12) and mtDNA data of Unmack *et al.* (in revision) that there was an introgressive transfer of mtDNA from *P. discobolus* in the Green River to *P. platyrhynchus* in the Bonneville Basin in the Pleistocene, possibly from the Price to the Spanish Fork drainage.

The importance of introgression is its potential role in transferring adaptive genes rapidly (not delayed by low mutation rates) between species (Arnold *et al.* 2012). The prevalence of reversed divergence in certain western clades suggests that the fragmented isolation of Basin and Range topography is a contributing factor. The persistence of introgression in certain clades in the area—Catostomidae, Cyprinidae, Salmonidae—suggests that selection for transferred traits is ambiguous under environmental circumstances common in western U.S. and in the presence of certain population genetic tolerances. The ecological and genetic circumstances that allow or perhaps favor relaxed reproductive isolation and gene exchange deserve more attention.

The decision regarding the most useful rank of genera/subgenera (when determined to be polyphyletic) depends on views regarding the optimal function of classification and higher-group names. The key question is whether the utility of maintaining the traditional nomenclature for effective communication outweighs the long-term predictive benefits of adherence to the cladistic principle of monophyly. Wide acceptance of the principle of monophyly as the foundation for natural classifications that express true ancestor-descendant relationships suggests that short-term convenience is not the higher priority. There is predictive value in genera that can encompass introgressing species with dual parentage, as opposed to an unnatural classification confounded by the unexpected phenomenon of introgression among genera.

## EVOLUTION OF *PANTOSTEUS* BIOLOGY

*Pantosteus*, mountain suckers, evolved in close association with stream gradients characteristic of the orogenic development and erosional processes that formed the Great Basin and its adjacent ranges, the Cordillera and Colorado Plateau. These fish are adapted to life in moderately-swift streams, below the cascades on mountain slopes, occupied by trout and sculpins, and above the slowly-moving waters of valley floors, occupied by *Catostomus*, most minnows, catfishes, pupfishes, percoids, and other fishes. In moderate-gradient habitats they are most closely associated with Speckled Dace, *Rhinichthys osculus*, and Rocky Mountain Whitefish, *Prosopium wlliamsoni*, whose geographic ranges and fossil record are most similar to those of *Pantosteus* (Oakey *et al.* 2004; B.A. Miller 2006; Smith *et al.* 2002).

*Pantosteus* adaptations to current stress include reduced gas-bladders, hemoglobin adapted to energy and oxygen in swift currents (Powers 1972), body size, and shape. Associated feeding adaptations include osteology of their jaws, suspensorium, pharyngeal teeth, skull, lips, mouth, gill rakers, pharynx and gut (Smith 1966). They feed on diatoms and other benthic periphyton along with small aquatic insects, crustaceans, and aufwuchs; their gill rakers form a fine sieve, their peritoneum is usually black, and their intestine is long, 5-8 times the standard length, as expected of animals that process plant matter. Their papillose, highly sensory lips and muscular jaws are adapted to locating preferred food and scraping it from stream-bed rubble; muscles of their jaws are enlarged and oriented to facilitate the unusual scraping actions with the cartilaginous jaw edges, and suction.

Divergence of species was partly driven by character displacement in feeding structures, particularly the coarse-to-fine gradient of gill rakers, which form a sieve for sorting food in the pharynx (Dunham *et al.* 1979). Their hemoglobin physiology is adapted to vigorous activity in clear, well-oxygenated water (Powers 1972). Life in clear water led to selection for brighter breeding colors than in their relatives, with brilliant reds, orange, yellows, blue, and greens. As such, they are especially valuable as indicators of good water quality and clear aquatic habitats.

All of these adaptations are rooted in the origin and dispersal of *Pantosteus* in mountain streams in the Basin and Range province (Fig. 1). The unique presence of hundreds of parallel mountain ranges, created and oriented by crustal extension, provides the hundreds of semi-isolated streams, with habitats of clear, moving, oxygenated water, rubble and gravel substrate, and periphyton food production. North-south valleys and streams provided dispersal routes among basins and ranges, which frequently changed their drainage boundaries and connections, permitting alternating diversification and dispersal of populations (Smith *et al.* 2010). The unique population genetics, adaptations, ecology, distribution, and diversity of western North American *Pantosteus, Rhinichthys,* salmonids, and cottids are examples of the evolutionary consequences of this unique style of extensional orogeny.

## SUMMARY AND CONCLUSIONS

The fossil record and deep branches in the gene trees of *Pantosteus* (Unmack *et al.* in revision) suggest that the genus diverged from *Catostomus* in the middle Miocene in the northern Basin and Range and the developing Columbia Plateau. The first known *Pantosteus*, the middle Miocene *C.* (*P.*) *hyomyzon* of Oregon and Washington, supports a Miocene origin in the north. Later diversification and spread southward are suggested by phylogenetic branching sequences and the current range of the *P. discobolus* species group through the Snake River Plain, Basin and Range, and south to the Rio Grande and Mexico, and Colorado Plateau. *Pantosteus asitus* from the early Pliocene of southern Nevada is intermediate in morphology, age, and geography between the ancestral forms in the north and *C.* (*P.*) *clarkii* of the Basin and Range portion of the Colorado drainage, *C.* (*P.*) *santaanae* in the Los Angeles Basin, *C.* (*P.*) *discobolus* of the Colorado drainage, and the *C.* (*P.*) *plebeius* group in the Rio Grande and other Mexican drainages in the southern Basin and Range

Province. *Catostomus* (*Pantosteus*) *asitus* is known from a time immediately after the connection of the upper Colorado River on the Colorado Plateau with the Lower Colorado River in the Great Basin (5.5 Ma), but was probably in the Lower Colorado Basin earlier.

Pliocene fossils of *C.* (*P.*) *oromyzon* (4.5 Ma) and *C.* (*P.*) *columbianus* (2.4-1.9 Ma) occur on the Western Snake River Plain. *Catostomus* (*P.*) *oromyzon* was probably ancestral to *C.* (*P.*) *virescens* and others of the *C.* (*P.*) *discobolus* species group according to shared, derived characters. Morphological and geographic data suggest that *C.* (*P.*) *oromyzon* or *C.* (*P.*) *virescens* is also an ancestor, through introgression with *Catostomus* (*C.*) *tahoensis*, of *C.* (*P.*) *arenatus* and *C.* (*P.*) *columbianus* (Fig. 12) (Unmack *et al.* in revision).

The *C.* (*P.*) *platyrhynchus* species group and *C.* (*P.*) *plebeius* are represented by fossils of *C.* (*P.*) *jordani* in northwest Kansas (30 Ka) and forms of *C.* (*P.*) *plebeius* from the Rio Grande rift in southern Colorado (2.6-0.67 Ma). *Catostomus* (*P.*) *plebeius* occurs within the Basin and Range Province; *C.* (*P.*) *jordani* is east of the Rocky Mountains. These Pleistocene fossils are too young to calibrate rates or estimate times of origin. Their genetic distances suggest origins earlier than the known fossil ages (Unmack *et al.* in revision).

Mountain sucker adaptations, such as small body size, unique jaws for scraping benthos from rocks, gill rakers for straining food particles, high-energy hemoglobin physiology, and reduced gas-bladders for occupation of rivers with moderately swift currents, were probably driven by habitats associated with steep topographic relief. The fluctuations between diversification in isolation and dispersal through stream captures in the Miocene, Pliocene, and Pleistocene, were responsible for divergence of about a dozen species in the northern and southern Great Basin and surrounding drainages of the Colorado Plateau, Sierra Nevada, and Rocky Mountains. The distribution of species was initially correlated with Miocene drainage configurations, at least in the north. Geological background of the Mexican *Pantosteus* is still to be determined. Later Miocene and Pliocene dispersal followed major stream captures that connected the Columbia to the Snake River, the upper Colorado River to the lower Colorado River, and capture of the upper Missouri River from Hudson Bay drainages. These events were followed by occasional periods in which the Lahontan and Bonneville basins were tributaries to the Snake River, at least in the Pleistocene, assembling the current distribution patterns of *Pantosteus* in the intermountain West.

## ACKNOWLEDGMENTS

Prof. Pat Packard and her College of Idaho students collected many fossils from the Snake River Plain, now in the College of Idaho's Orma J. Smith Museum of Natural History. Dr. Claude Hibbard of the Museum of Paleontology and Dr. Robert Miller of the Museum of Zoology and their students at the University of Michigan collected fossils and comparative specimens beginning in the 1950s. The University of Oregon's J. Arnold Shotwell and students collected many specimens on which this work is based. The Shotwell collections are curated in the University of Oregon Museum of Natural and Cultural History (UO). We are indebted to Dr. Shotwell for his extensive fieldwork, his monumental collections, and his many published contributions to vertebrate paleontology. We thank Dr. Edward Davis, Fossil Collections Manager, for permission to borrow and examine University of Oregon specimens. Dr. Eric Scott, Vertebrate Collection Manager at the San Bernardino County Museum loaned Nevada fossils from that museum. Douglas Nelson, Collection Coordinator of the Division of Fishes, Museum of Zoology (UMMZ) and Gregg Gunnell, former Vertebrate Collection Coordinator in the Museum of Paleontology (UMMP), managed collections and records at the University of Michigan. Dr. William Sanders (UMMP) prepared key fossils. Kevin Meeks collected specimens from the Ellensburg Formation, Washington, which were sent to us by Mr. Meeks and loaned by James Martin and Sally Y. Shelton, Collection Manager at the Museum of Geology and Paleontology of the South Dakota School of Mines and Technology. Howard and Darlene Emry, Neal Schornack, Bill Belknap, John Eldredge, Keith Smith, and Phillip Smith assisted collection of specimens in Malheur County, Oregon, in May, 2009. We thank John Zancanella of the BLM in Oregon, for his assistance with permits to collect fossils. John Megahan of the Museum of Zoology drew maps and the fish in Fig. 2. Bonnie Miljour, Emily Damstra, Carrie DiLorenzo, and John Megahan illustrated specimens and maps. Prof. H. Don Cameron of the Classics Department of the University of Michigan helped form Latinized Greek names of fossil species. We thank Dr. John B. Burch and Dr. Janice L. Pappas for editorial work. Thanks to Tom Dowling and an anonymous reviewer for helpful suggestions.

## SUPPLEMENTAL MATERIAL

UMMZ publications: http://www.lsa.umich.edu/ummz/fishes/personnel/grsmith/publications/supp_materials/UMMZ_OP_743_supp.html).

## LITERATURE CITED

Abbott, C. C. 1860. Description of four new species of North American Cyprinidae. Proceedings of the Academy of Natural Sciences of Philadelphia, 12: 473-474.

Arnold, M.L., J.P. Hamlin, A.N. Brothers and E.S. Ballerini. 2012. Natural hybridization as a catalyst of rapid evolutionary change, pp. 256-265, *in* Evolution in the fast lane: Rapidly evolving genes and genetic systems, R.S. Singh, J. Xu, and R.J. Kulathinal (eds.) Oxford University Press.

Baird, S. F., and C. Girard. 1854. Descriptions of new species of fishes collected in Texas, New Mexico and Sonora, by Mr. John H. Clark on the U.S. and Mexican Boundary Survey, and in Texas by Capt. Stewart Van Vliet, U.S.A. Proc. Acad. Nat. Sci. Philadelphia. 7:24- 29.

Barbour, C.D., and R.R. Miller. 1978. A revision of the Mexican fish genus *Algansea*. University of Michigan Museum of Zoology Miscellaneous Publications, 155: 1-72.

Bond, C. E. 1953. Occurrence of the mountain sucker, *Pantosteus jordani*, in the Willamette River system, Oregon. Copeia 1953(2): 116.

Camp, V. E., M. E. Ross, and W. E. Hanson. 2003. Genesis of flood basalts and Basin and Range volcanic rocks from Steens Mountain to the Malheur River Gorge, Oregon. Geological Society of America Bulletin 115(1):105-128.

Cope, E. D. 1870. On the fishes of a fresh water Tertiary in Idaho, discovered by Capt. Clarence King. Proc. Amer. Phil. Soc., 11:538-547.

Cope, E. D. 1872. Recent reptiles and fishes. Report on the reptiles and fishes obtained by the naturalists of the expedition, pp. 432-443 *in*: Part IV: Special Reports, *in*: Preliminary report of the U.S. Geol. Survey of Wyoming and portions of contiguous territories, by F.V. Hayden.

Cope, E. D. 1874. On the Plagopterinae and the ichthyology of Utah. Proceedings of the American Philosophical Society, 14:129-139.

Cope, E. D. 1879. The fishes of Klamath Lake, Oregon. American Naturalist, 13: 784-

785.

Cope, E. D. 1883. On the fishes of the Recent and Pliocene lakes of the western part of the Great Basin, and of the Idaho Pliocene lake. Proceedings of the Academy of Natural Science, Philadelphia, 35:134-167.

Cope, E. D., and H. C. Yarrow. 1875. Report upon the collections of fishes made in portions of Nevada, Utah, California, Colorado, New Mexico, and Arizona, during the years 1871, 1972, 1873, and 1874. Rept. Geogr. and Geol. Expl. and Surv. W. 100th Meridian (Wheeler Survey), 5:635-703.

Crabtree, C.B., and D.G. Buth, 1987. Biochemical systematics of the catostomid genus *Catostomus*: assessment of *C. clarki*, *C. plebeius* and *C. discobolus* including the Zuni sucker, *C. d. yarrowi*. Copeia 1987, 843–854.

Cummings, M.L., J.G. Evans, M.L. Ferns, and K.R. Lees. 2000. Stratigraphic and structural evolution of the Middle Miocene synvolcanic Oregon-Idaho Graben. Geological Society of America Bulletin, 112(5): 668-682.

DeMarais, B.D., T.E. Dowling, M.E. Douglas, W.L. Minckley, and P.C. Marsh. 1992. Origin of *Gila seminuda* (Teleostei: Cyprinidae) through introgressive hybridization: implications for evolution and conservation. Proceedings of the National Academy of Sciences, USA, 89: 2747-2751.

Dickinson, W.R. 2006. Geotectonic evolution of the Great Basin. Geosphere 2(7):353-368.

Doosey, M.H., H.L. Bart, Jr., K. Saitoh, and M. Miya. 2010. Phylogenetic relationships of catostomid fishes (Actinopterygii: Cypriniformes) based on mitochondrial ND4/ND5 gene sequences. Molecular Phylogenetics and Evolution 54(3): 1028-1034.

Dowling, T.E., C. Secord, *et al.* (In preparation). The mountain sucker complex in the Little Colorado River and San Juan tributaries of NE Arizona: Phylogeography and conservation.

Dunham, A.E., G.R. Smith, and J.N. Taylor. 1979. Evidence for ecological character displacement in western American catostomid fishes. Evolution 33(3): 877-896.

Eigenmann, R.S. 1891. Description of a new species of *Catostomus* (*C. rex*) from Oregon. American Naturalist v. 25 (no. 295): 667.

Eigenmann, C.H., and R.S. Eigenmann. 1893. Preliminary description of new fishes from the northwest. American Naturalist, 27 (1893), 151-154.

Ekren, E.B., D.H. McIntyre, E.H. Bennett, and R.F. Marvin. 1982. Cenozoic stratigraphy of western Owyhee County, Idaho, *in* Bonnichsen, B. and Breckenridge, R.M. eds., Cenozoic Geology of Idaho , Idaho Bureau of Mines and Geology Bulletin, 26, 215-235.

Ernst, W.G. 2009. Rise and fall of the Nevadaplano. International Geology Review, 51 (7-8):583-588.

Eschmeyer, W.N. 2013. Catalog of Fishes. California Academy of Sciences.

Evermann, B.W., 1893. Description of a new sucker, *Pantosteus jordani*, from the upper Missouri basin. Bulletin of the United States Fish. Commission, 12 (1892), 51-56.

Evermann, B. W., and S. E. Meek. 1898. A report on salmon investigations in the Columbia River basin and elsewhere on the Pacific Coast, in 1896. Bulletin of the U.S. Fish Commission 17(1897): 15-84.

Evernden, J. F., and G. T. James. 1964. Potassium-argon dates and the Tertiary floras of North America. American Journal of Science, 262:945-974.

Ferns, M. L., *et al.* 1993. Geologic Map of the Vale 30 X 60 minute quadrangle, Malheur County, Oregon, and Owyhee County, Idaho. Oregon Department of Geology and Mineral Industries GMS-77.

Fiebelkorn, R. B., G. W. Walker, N. S. McLeod, E. H. McKee, J. G. Smith. 1983. Index to K-Ar determinations for the State of Oregon. Isochron-West, 37:3-60.

Garman, S., 1881. New and little-known reptiles and fishes in the collections. Bulletin of the Museum of Comparative Zoology, 8: 85-93.

Gilbert, C. H. 1898. The fishes of the Klamath River Basin. U.S. Fish Commission Bulletin, 1897: 1-13.

Gilbert, C. H. and B. W. Evermann 1894. A report upon investigations in the Columbia River basin, with descriptions of four new species of fishes. Bulletin of the U. S. Fish Commission, 14 (16): 169-207.

Girard, C. 1856 (1857). Researches upon the cyprinoid fishes inhabiting the fresh waters of the United States west of the Mississippi Valley, from specimens within the Smithsonian Institution. Proceedings of the Academy of Natural Sciences, Philadelphia, 7: 165-213.

Harris, P.M. and R.L. Mayden. 2001. Phylogenetic relationships of major clades of Catostomidae (Teleostei: Cypriniformes) as inferred from mitochondrial SSU and LSU rDNA sequences. Molecular Phylogenetics and Evolution, 20(2): 225-237.

Holden, P.B., and C.B. Stalnaker. 1975. Distribution of fishes in the Dolores and Yampa River systems of the upper Colorado basin. Southwestern Naturalist 19(4): 403-412.

Hubbs, C.L., and R.R. Miller. 1953. Hybridization in nature between the fish genera *Catostomus* and *Xyrauchen*. Papers of the Michigan Academy of Science, Arts, and Letters, 38 (1952): 207-233.

Hubbs, C.L., and L.P. Schultz. 1932. A new catostomid fish from the Columbia River. University of Washington Publications, Biology, 2(1): 1-13.

Hubbs, C.L., L.C. Hubbs, and R.E. Johnson. 1943. Hybridization in nature between species of catostomid fishes. Contributions of the Laboratory of Vertebrate Biology, University of Michigan, 22:1-76.

Hoetker, G.M., and K.W. Gobalet. 1999. Fossil Razorback Sucker (Pisces: Catostomidae, *Xyrauchen texanus*) from southeastern California. Copeia ,1999: 755-759.

Jarboe, N.A., R.S. Coe, P.R. Renne, J.M.G. Glenn. 2008. Quickly erupted volcanic sections of the Steens Basalt, Columbia River Basalt Group: Secular variation, tectonic rotation, and the Steens Mountain reversal. Geochemistry, Geophysics, Geosystems, 9(11):1-24.

Jordan, D.S. 1878. Contribution to North American Ichthyology III. B.—A synopsis of the family Catostomidae. Bull. U.S. National Museum, 12: 97-237.

Jordan, D.S., and B.W. Evermann. 1896-1900. The fishes of North and Middle America: a descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, north of the Isthmus of Panama. Bulletin of the United States National Museum 47: 3313 pp.

Jordan, D. S. , B. W. Evermann and H. W. Clark. 1930. Check list of the fishes and fishlike vertebrates of North and Middle America north of the northern boundary of Venezuela and Colombia. Report of the U. S. Commission of Fisheries, 1928 (2): 1-670.

Kirsch, P. H. 1889. Notes on a collection of fishes obtained in the Gila River, at Fort Thomas, Arizona, by Lieut. W. L. Carpenter, U. S. Army. Proceedings of the United States National Museum, 11 (754): 555-558.

Koster, W. J. 1957. Guide to the fishes of New Mexico. University of New Mexico Press. Albuquerque. 116 pp.

Linder, C.R., and L.H. Riesberg. 2004. Reconstructing patterns of reticulate evolution in plants. American Journal of Botany 91(10): 1700-1708.

Lucchitta, I., 1987. The mouth of the Grand Canyon and the edge of the Colorado Plateau in the upper Lake Mead area, Arizona: Boulder, Colorado, Geological Society of America, Rocky Mountain Section, Centennial Field Guide, 2: 365–370.

McAda, C.W., and R.S. Wydoski. 1980. The razorback sucker, *Xyrauchen texanus*, in the upper Colorado River basin, 1974-76. Technical papers of the U.S. Fish and Wildlife Service, 99: 1-15.

Malde, H.E., and H.A. Powers. 1962. Upper Cenozoic stratigraphy of western Snake River Plain, Idaho. Bulletin of the Geological Society of America, 73: 1197-1220.

Markle, D.F., M.R. Cavalluzzi, and D.C. Simon. 2005. Morphology and taxonomy of Klamath Basin suckers, Catostomidae. Western North American Naturalist 65(4): 473-489.

Markle, D.F., T.E. Dowling, G.J. Tranah, E.W. Carson, D. W. Wegman, and B. May. (in revision). Recovering phylogeny in an inbreeding syngameon of suckers.

Miller, B.A. 2006. The phylogeography of *Prosopium* in western North America. M.S. Thesis, Brigham Young University, 157 pp.

Miller, R.R., and R.G. Miller. 1948. The contribution of the Columbia River system to the fish fauna of Nevada; five species unrecorded from the state. Copeia, 1948: 174-187.

Miller, R.R., and G.R. Smith. 1967. New fossil fishes from Plio-Pleistocene Lake Idaho. Occasional Papers of the Museum of Zoology, University of Michigan, 654: 1-24.

Moyle, P. B. 2002. Inland Fishes of California. University of California Press, 502 pp.

Oakey, D. D., M.E. Douglas, and M.R. Douglas. 2004, Small fish in a large landscape: diversification of *Rhinichthys osculus* (Cyprinidae) in western North America: Copeia, 2004: 207-221.

Perkins, M.E., F.H. Brown, W.P. Nash, W. McIntosh, W.K. Williams.1998. Sequence, age and source of silicic fallout tuffs in middle to late Miocene basins of northern Basin and Range Province. Geological Society of America Bulletin, 110:344-360.

Perkins, M. E. and B. P, Nash. 2002, Explosive silicic volcanism of the Yellowstone hotspot: The ash fall tuff record: Geological Society of America Bulletin, 114 (3): 367-381.

Powers, D.A. 1972. Hemoglobin adaptation for fast and slow water habitats in sympatric catostomid fishes. Science, 177(4046):360-362.

Reheis, M.C., Sarna-Wodjcicki, A.M., Reynolds, R.L., Repenning, C.A., Mifflin, M.D., 2002. Pliocene to middle Pleistocene lakes in the western Great Basin: ages and connections. In: R. Hershler, D.B. Madsen, and D.R. Curry, (eds.), Great Basin Aquatic Systems History: Smithsonian Contributions to Earth Sciences 33, 53–108.

Reynolds, R. E., and E. H. Lindsay. 1999. Late Tertiary basins and vertebrate faunas along the Nevada-Utah border, pp. 469-478 *in* D.D. Gillette (Ed.) Vertebrate Paleontology in Utah. Utah Geological Survey Miscellaneous Publication, 99-1: 553 pp.

Retallack, G. J. 2004. Late Miocene climate and life on land in Oregon within a context of Neogene global change. Palaeogeography, Palaeoclimatology, Palaeoecology, 214: 97- 113.

Rogers, K.L., C.A. Repenning, R.M. Forester, E.E. Larson, S.A. Hall, G.R. Smith, E. Anderson, and T.J. Brown. 1985. Middle Pleistocene (Late Irvingtonian: Nebraskan) climatic changes in south-central Colorado. National Geographic Research, 1(4): 535-563.

Rogers, K.L., E.E. Larson, Gary Smith, D. Katzman, G.R. Smith, T. Cerling, Yang Wang, R.G. Baker, K.C. Lohmann, C.A. Repenning, P. Patterson, and G. Mackie. 1992. Pliocene and Pleistocene geologic and climatic evolution in the San Luis Valley of south-central Colorado. Palaeogeography, Palaeoclimatology, Palaeoecology, 94: 55-86.

Ruez, D.R., Jr. 2009. Revision of the Blancan (Pliocene) mammals from Hagerman Fossil Beds National Monument, Idaho. Journal of the Idaho Academy of Science, 45 (1): 1-143.

Rutter, C. 1903. Notes on fishes from streams and lakes in northeastern California, not tributary to the Sacramento Basin. Bulletin of the United States Fish Commission, 22 (1902): 143-148.

Schmidt, D.L., W. R. Page, and J.B. Workman. 1996. Preliminary geological map of the Moapa West Quadrangle, Clark County, Nevada. U.S.G.S. Open-File Report 96-521.

Schultz, L.P. and A.C. DeLacy. 1936. Fishes of the American Northwest. A catalogue of the fishes of Washington and Oregon, with distributional records and bibliography. Journal of the Pan-Pacific Research Institute 11 (1, 4).

Seale, A. 1896. Note on *Deltistes*, a new genus of catostomid fishes. Proceedings of the California Academy of Science 2 (5): 269.

Shotwell, J. A. *et al.* 1963. The Juntura Basin: Studies in earth history and paleoecology. Transactions of the American Philosophical Society, New Series, 53: 42-69.

Smith, G. A. 1988. Sedimentology of proximal to distal volcaniclastics dispersed across an active foldbelt: Ellensburg Formation (late Miocene), central Washington. Sedimentology 35:953-977.

Smith, G.R. 1966. Distribution and evolution of the North American catostomid fishes of the subgenus *Pantosteus*, genus *Catostomus*. Miscellaneous Publications of the Museum of Zoology, University of Michigan, 129: 1-132.

Smith, G.R. 1975. Fishes of the Pliocene Glenns Ferry Formation, southwest Idaho. University of Michigan Museum of Paleontology Papers on Paleontology, 14:1-68.

Smith, G.R. 1992a. Introgression in fishes: Significance for paleontology, cladistics, and evolutionary rates. Systematic Biology, 41(1): 41-57.

Smith, G.R. 1992b. Phylogeny and biogeography of the Catostomidae, freshwater fishes of North America and Asia, pp. 778-826 in R.L. Mayden (Ed.), Systematics, Historical Ecology, and North American freshwater fishes. Stanford University Press, 969 pp.

Smith, G.R., C.E. Badgley, T.P. Eiting, and P.S. Larson. 2010. Species diversity gradients in relation to geological history in North American freshwater fishes. Evolutionary Ecology Research 12: 693-726.

Smith, G.R. and W. Buechler. In preparation. *Catostomus* and *Archoplites* from the Clarendonian Pickett Creek diatomite, southwest Idaho.

Smith, G.R., T. Dowling, K.W. Gobalet, T. Lugaski, D. Shiazawa, and R.P. Evans. 2002. Biogeography and timing of evolutionary events among Great Basin fishes, pp. 175-234, *in* R. Hershler, D.B. Madsen, and D.R. Currey, (Eds.) Great Basin Aquatic Systems History. Smithsonian Contributions to Earth Sciences, Number 33, 405 pp.

Smith, G.R., J.G. Hall, R.K. Koehn, and D.J. Innes. 1983. Taxonomic relationships of the Zuni Mountain sucker, *Catostomus discobolus yarrowi*. Copeia 1983(1):37-48.

Smith, G.R. and R.K. Koehn. 1971. Phenetic and cladistic studies of biocemical and morphological characteristics of *Catostomus*. Systematic Zoology, 20(3): 282-297.

Smith, G.R., K. Swirydczuk, P.G. Kimmel, and B.H. Wilkinson. 1982. Fish biostratigraphy of late Miocene to Pleistocene sediments of the western Snake River Plain, Idaho, p. 519-542 *in* B. Bonnichsen and R.M. Breckenridge (Eds.), Cenozoic Geology of Idaho. Idaho Bureau of Mines and Geology Bulletin, 26, 725 pp.

Snyder, J.O. 1908. Description of *Pantosteus* santa-anae, a new species of fish from the Santa Ana River, California. Proceedings of the United States National Museum, 34: 33-34.

Snyder, J.O. 1915. Notes on a collection of fishes made by Dr. Edgar A. Mearns from rivers tributary to the Gulf of California. Proceedings of the United States National Museum, 49:573-586.

Snyder, J.O. 1924. Notes on certain catostomid fishes of the Bonneville system, including the type of *Pantosteus virescens* Cope. Bulletin of the United States National Museum, 64: 1-6.

Spencer, J.E., L. Peters, W.C. McIntosh, and P.J. Patchett. 2001. 40Ar/39Ar geochronology of the Hualapai Limestone and Bouse Formation and implications for the age of the lower Colorado River, *in* R.A. Young, and E.E. Spamer, eds., The Colorado River: Origin and Evolution: Grand Canyon, Arizona, Grand Canyon Association Monograph 12, p. 89–91.

Spencer, J.E., G.R. Smith, and T.E. Dowling. 2008. Middle to Late Cenozoic geology, hydrography, and fish evolution in the American Southwest, pp. 279-299 *in* M.C. Reheis, R. Hershler, and D.M. Miller (eds.): Late Cenozoic Drainage History of the Southwestern Great Basin and Lower Colorado River region: Geologic and Biotic Perspectives. Geological Society of America Special Paper 439.

Stewart, M.M, and Smith, G.R. 2002. Carl and Lenora Bond. Copeia: 2002 (4): 1154-1156.

Streck, M. J., J.A. Johnson, M.L. Grunder. 1999. Field guide to the Rattlesnake tuff and High Lava Plains near Burns, Oregon. Oregon Geology 61(3): 64-76.

Streck, M. J., and M. Ferns. 2004. The Rattlesnake tuff and other Miocene silicic volcanism in eastern Oregon, in Haller, K.M. and Woods, S.H., (Eds.), Geological Field Trips in southern Idaho, Eastern Oregon, and northern Nevada. Idaho Department of Geosciences, Boise State University, p. 2-17.

Swirydczuk, K., B.H. Wilkinson, and G.R. Smith. 1980. The Pliocene Glenns Ferry Oolite II: Sedimentology of oolitic lacustrine terrace deposits. Journal of Sedimentary Petrology, 50(4): 1237-1248.

Swirydczuk, K., G.P. Larson, and G.R. Smith. 1982. Volcanic ash beds as stratigraphic markers in the Glenns Ferry and Chalk Hills Formations from Adrian, Oregon, to Bruneau, Idaho, p.543-558 *in* B. Bonnichsen and R.M. Breckenridge (Eds.), Cenozoic Geology of Idaho. Idaho Bureau of Mines and Geology Bulletin, 26, 725 pp.

Tanner, V.M. 1932. A description of *Notolepidomyzon utahensis*, a new catostomid from Utah. Copeia, 1932 (3): 135-136.

Tanner, V.M. 1942. A review of the genus *Notolepidomyzon* with a description of a new species (Pisces, Catostomidae). Great Basin Naturalist, 3: 27-32.

Taylor, D.W. 1960. Distribution of the freshwater clam, *Pisidium ultramontanum*: a zoogeographic inquiry. American Journal of Science, 258A (Bradley Volume): 325-334.

Unmack, P. J., T.E. Dowling, N.J. Laitinen, C.L. Secor, RL. Mayden, and G.R. Smith. (in revision). Influence of introgression and geological processes on evolution of western North American mountain suckers (*Pantosteus*, Catostomidae). Molecular Biology and Evolution.

Uyeno T., and Smith G.R. 1972. Tetraploid origin of the karyotype of catostomid fishes. Science 175:644–645.

Walker, G. W. 1979. Revisions to the Cenozoic stratigraphy of Harney Basin, Southeastern Oregon. United States Geological Survey Bulletin, 1475:35p.

Wood, S. H. 1994. Seismic expression and geological significance of a lacustrine delta in Neogene deposits of the Western Snake River Plain, Idaho. American Association of Petroleum Geologists Bulletin 78(1): 102-121.

## APPENDIX: a) CODES FOR *CATOSTOMUS* CHARACTER MATRIX

Reduced from Smith (1992, with additional characters added and non-applicable characters omitted). Question marks indicate uncertainty or variability. Characters 67-75 from Ferris and Whitt (1978) and Buth (1979). Characters 76-85 from Smith and Koehn (1971).

1 Premaxillary shape: 0=lateral wing longer than dorsal process; 1=lateral wing slightly shorter than dorsal process (Miller and Smith 1981 fig. 10 C); 2= lateral wing much shorter than dorsal process.

2 Premaxillary process of maxilla: 0=Premaxillary process of maxilla projects mesially from anterior constriction ahead of central keels and anterodorsal process of bone (Fig. 7 b); 1=process shifted anteriorly to below anterodorsal process (Fig. 10 e); 2=process directed anteromesially (Miller and Smith 1981 fig. 10 D, G, 11 A-D).

3 Posterior third of maxilla: 0=posterior third of maxilla elongate and slender ahead of postventral downward end (Fig. 11 i); 1= posterior limb robust and short posterior to maxillary keels (Fig. 10 a, d, f).

4 Anteroventral keel under midsection of maxilla: 0=with low profile (Fig. 11 i); 1=prominent keel similar to dorsal keel (Fig. 7 b); 2=keel anteriorly more prominent than dorsal keel and bearing a strong anterior ridge for muscle attachment (Figs. 7 c, d; 10 a, e, f).

5 Length and angle of anterior process of dentary: 0=anterior limb of dentary short and little deflected; 1=anterior limb short and strongly deflected (Figs. 8 a-d; 9 a-c); 2=anterior limb moderately long and moderately deflected (Fig. 8 e, 9 d); 3= anterior arm long and only slightly deflected (Miller and Smith fig. 10 B, D. G; 11 A-D). (States are unordered.)

6 Proximal part of dentary and articular-angular: 0=short and broad (Miller and Smith 11 E; 1=long and slender (Miller and Smith fig. 10 B).

7 Dentary, mesial mental foramen: 0=near anterodorsal edge of distal process (Miller and Smith fig. 10 A,-D); 1=equidistant between edge and Meckel's cartilage (Fig. 11 c); 2=nearer terminus of Meckel's cartilage (Fig. 8 b).

8 Palatine, length of mesopterygoid process relative to the length of the maxillary process, measured from the focus of the three main processes of the palatine (Smith et al. 2013, fig. 7 e): 0=short; 1=subequal; 2=long.

9 Palatine, angle of mesopterygoid to maxillary and dermethmoid

processes, ventral view (vomerine socket aspect, Smith et al. 2013, fig. 7 e, f, g): 0=mesopterygoid process aligned with maxillary process; 1=mesopterygoid process aligned between maxillary and dermethmoid processes.

10 Palatine, 0= sharp lateral keel from anterodorsal end of maxillary process to lateral side of mesopterygoid process (Smith et al. 2013, figs. 7 e, f, g) ; 1=no sharp lateral keel, but a vestigial short rounded ridge, from maxillary process to mesopterygoid process.

11 Dermethmoid, anterior process: 0=short and broad (Smith 1992, fig. 4 c); 1=short, broad, ventrally deflected; 2=intermediate length and slender; 3= long and slender (Smith 1992, fig. 4 a, b). (Unordered.)

12 Dermethmoid shape, anterior view: 0= flat dorsal profile; 1= convex dorsal profile.

13 Urohyal shape: 0=hypohyal processes reduced to facets (Smith 1992, fig. 2 e, l); 1=hypohyal processes well developed, horizontal lamina shield-shaped (Smith 1992, fig. 2 m),; 2=hypohyal processes well developed, horizontal lamina elongate and tapered posteriorly. (Unordered.)

14 Metapterygoid braces for ventral process of hyomandibula: 0=strong ridge or processes brace the hyomandibula (Smith 1992, fig. 3 c, d); 1= weak ridge or processes contact the hyomandibula (Smith 1992, fig. 3 a).

15 Angle formed by Weberian ribs 2-4 to each other: 0=less than 65°; 1=50°-60°; 2=70°-90°; 3=90°-105°.

16 Pterygoid plate of quadrate: 0=elongate posterodorsally; 1=anterodorsal-postventral and posterodorsal-anteroventral dimensions subequal; shortened posterodorsally.

17 Vertebral number, mean: 0=40-42; 1=43; 2=44-45

18 Lateral ethmoid-dermethmoid contact: 0=widely separated (Smith 1992, fig. 4 a, b); 1=proximate or in contact (Smith 1992, fig. 4 c).

19 Pterotic dermal plate or ridge: 0=broad dermal plate; 1=narrow dermal plate; 2=plate reduced to a ridge.

20 Fronto-parietal fontanelle: 0=wide; 1=width reduced; 2=left and right frontals and parietals in contact, fontanelle largely absent.

21 Subtemporal fossa: 0=exoccipital excluded from the fossa; 1=shal-

low with exoccipital corner at least minimally present in the fossa.

22 Epiotic process: 0=present (Smith 1992, fig. 4 a, b); 1=absent (Smith 1992, fig. 4 c, d).

23 Basioccipital anteroventral keel: 0=a single, sharp keel (Smith 1992, fig. 1 d); 1=a double or complex keel; 2=a low profile rounded ventral ridge. (Unordered.)

24 Ceratohyal: 0=shortest distance from basihyal to epihyal (posterior ceratohyal) about 20% longer than greatest depth of ceratohyal (Smith 1992, fig. 2 q); 1=shortest distance from basihyal to posterior ceratohyal about equal to greatest depth of ceratohyal Smith 1992, fig. 2 s); 2=shortest distance from basihyal to posterior ceratohyal about 20% shorter than greatest depth of ceratohyal.

25 Supraorbitals: 0=present (Smith 1992, fig. 4 c); 1=absent (Smith 1992, fig 4 a).

26 Suborbital shape: 0=robust and deep (Smith 1992, fig. 1 a, c), 1=fragile and deep, 2=fragile and slender. (Unordered.)

27 Frontal lateralis pores: 0=small and scattered (Smith 1992, fig. 4 c); 1=large and clustered (Smith 1992, fig. 4 a, b).

28 Intercalar: 0=a flat plate; 1=a narrow plate or rod

29 Infraorbital number: 0=4 infraorbitals (Smith 1992, fig. 1 a); 1=2-3 infraorbitals.

30 Hyomandibula, width of midsection: 0=slender (Fig. 3 h); 1=intermediate; 2=broad.

31 Hyomandibula, postdorsal crest: 0=short, reaches dorsally to level of ventral edge or midsection of opercular condyle (Fig. 3 c, h); 1=reaches to midsection or top of opercular condyle; 2=reaches past opercular condyle to pterotic condyle Fig. 3 a, b).

32 Hyomandibula, postdorsal foramen and process: 0=no fossa or prominent processes at convex postdorsal tip Fig. 3 h); 1=concavity and simple cup-like process at postdorsal tip (Fig. 3 c); 2=deep fossa and one or two prominent processes at postdorsal tip (Fig. 3 b, g).

33 Preopercle shape: 0=tall and slender (Smith 1966, fig. 5 a); 1=shorter and deeper but not half-moon shaped; 2=slightly concave and asymmetrical half-moon shaped (Smith 1966, fig. 5 c).

34 Ventral pterotic depression posterior to subtemporal fossa, formed by the intercalar meeting with the postlateral wing of the pterotic and the epiotic cone of the pterotic: 0=with minimal foramina between bones--bypassed by a large dorsal foramen between the pterotic, posttemporal, and epiotic; 1=present with one or two major foramina between the pterotic and intercalar, one or more entering the pterotic and sometimes the intercalar. (Unordered.)

35 Pharyngeal arch: 0=low triangular cross-section with fewer than 55 often robust teeth; 1=high triangular cross-section with more than 55 weak teeth in adults.

36 Pharyngeal teeth, shape: 0=Teeth with posteriorly directed dorsal point above a laterally flat, terminally rounded cusp; 1=Teeth with a single dorsal cusp at proximal end, grading to two sharp cusps at distal (dorsal) half of arch.

37 Median branchial ridges on gill arches: 0=median ridge visible between ends of internal and external rows of rakers (Smith 1992, fig. 5 c d); 1=bridged over and hidden by branching rakers (Smith 1992, fig. 5 e, f).

38 Lower lip lobes: 0=thin, length shorter than ½ width, as measured along rows of papillae (Miller and Smith 1981, figs. 6, 7); 1=lip lobes about as long as wide (Miller and Smith 1981, fig. 4 c; Moyle 2002, fig. 68); 2=length of lobes longer than width (Moyle 2002, fig. 74).

39 Lower lip papillae: 0=weak papillae in rows (Miller and Smith, 1981, fig. 4 a, 6 c, 7 a, 9); 1=intermediate papillae; 2=strong papillae (Miller and Smith, 1981, fig. 4 c).

40 Median notch between lower lip lobes: 0=wide and deep, full separation of lobes(Miller and Smith 1981, figs. 6, 7); 1=deep to base of lobes, but not wide, lobes in contact (Miller and Smith 1981, fig. 4 c); 2=moderate separation of lobes--an anterior bridge of papillose tissue between lobes (Smith 1966, pl. 1 A, B); 3=a shallow posterior notch between lower lobes (Smith 1966, pl. 1 C-E).

41 Notches between lateral edges of upper and lower lips: 0=no lateral notches, upper and lower lips continuous (Smith 1966, pl. 1 B); 1=weak lateral notches; 2=strong lateral notches (Smith 1966, pl. 1 D, E).

42 Outer surface of upper lip: 0=with strong papillae (Smith 1966, pl. 1 B); 1=with weak papillae (Smith 1966, pl. 1 A); 2=smooth, lacking papillae (Smith 1966, pl. 1 D, E).

43 Body depth relative to length: 0=depth slightly more than 25% of standard length (Minckley 1973, fig. 74; Moyle 2002, fig. 72, 73); depth about 25% of standard length (Moyle 2002, fig. 68); depressed, depth usually 20% to 22% of standard length(Moyle 2002, fig. 64).

44 Head length as a proportion of standard length: 0=25% or more (Moyle 2002, figs. 72, 73); 1=about 23%- 24%; 2=less than 22%.

45 Gas bladder size: 0=fully developed, longer than 1/3 standard length and larger than 2X eye diameter; 1=reduced to less than 1/3 standard length and little more than eye diameter.

46 Caudal peduncle depth as proportion of standard length: 0=more than 9.4%; 1=8.3% to 9.4%; 2=usually less than 8.3%.

47 Lower jaw cartilage: 0=weak and rounded (Smith 1966, pl. 1 A); 1=moderate, rounded (Smith 1966, pl. 1 B); 2=strong and truncate (Smith 1966, pl. 1 D, E).

48 Maximum body size: 0=2-6 kg, 1 m; 1=usually 100 g to 2 kg, 30-70 cm; 2=usually less than 100 g, less than 20 cm.

49 Height of neural arch 2-4 of Weberian Apparatus: 0=elevated to height of 4X diameter of centrum; 1=about 1.5-2X centrum diameter; 2=reduced to about centrum diameter.

50 Posterior radii of lateral scales, annual incremental increase: 0=annual increase increments, ca. 5,10,15; 1=annual increase increments, ca. 3,6,12.

51 Lateral scale shape: 0=obovate; 1=with well-developed corners.

52 Anterior and lateral radii on lateral scales: 0=few; 1=few radii extend in parallel into lateral fields; 2=numerous lateral radii. (Unordered.)

53 Number of scale rows around caudal peduncle: 0=17 or more; 1=typically 16.

54 Mean number of predorsal scales: 0=fewer than 39; 1=40-49; 2=more than 50.

55 Mean number of lateral line scales: 0=fewer than 44; 1=55-60; 2=61-74; 3=75-87; 4=88 or more.

56 Mean number of dorsal fin rays: 0=14-16; 1=12-13; 2=11; 3=9-10.

57 Mean number of gill rakers on outer row of first arch in adults: 0=22-25; 1=30-40; 2=40-50.

58 Gut length: 0=fewer than 5 coils; 1=6 or more coils.

59 Peritoneum pigment: 0=absent or sparse; 1=dusky to black.

60 Caudal fin pigment: 0=present on rays and membranes; 1=sparse or absent on interradial membranes, concentrated on rays.

61 Nuptial color, lateral band: 0=absent; 1=blue or black; 2=red or orange. (Unordered.)

62 Ninth cranial nerve exit: 0=between exoccipital and pro-otic; 1=through exoccipital.

63 Facial lobe length (as proportion of brain length): 0=more than 22%; 1=0.12%-0.19%; 2=7%-10%.

64 Vagal lobe length (as proportion of brain length): 0=32%-38%; 1=25%-29%; 2=18%-23%.

65 Median optic fissure: 0=present; 1=absent.

66 Vagal lobe shape: 0=swollen, occludes facial lobe; 1=contact over posterior facial lobe; not in contact behind facial lobe.

67 Gpi-B: 1=functional diploid; 2=duplicate.

68 G3pdh-A: 1=functional diploid; 2=duplicate.

69 Ak-A: 1=functional diploid; 2=duplicate.

70 Pdh-A: 1=functional diploid; 2=duplicate.

71 Ldh-B: 1=functional diploid; 2=duplicate.

72 sAat-A: 1=functional diploid; 2=duplicate.

73 Ald-C: 1=functional diploid; 2=duplicate.

74 sMdh-A: 1=functional diploid; 2=duplicate.

75 sMdh-B: 1=functional diploid; 2=duplicate.

76 Hemoglobin, anodal: 0=single strong band; 1=3 strong and 3 weak bands; 2=3 strong and 4 weak bands. (Unordered.)

77 Hemoglobin, cathodal: 0=absent; 1=2 weak bands; 2=strong band with intermediate mobility; 3= strong band with high mobility; (Unordered.)

78 Esterase Ia’: 0=absent; 1=present.

79 Esterase Ia: 0=absent; 1=present.

80 Esterase Ib: 0=present; 1=absent.

81 Transferrin 1: 0=absent; 1=present.

82 Transferrin 2: 0=absent; 1=present.

83 Transferrin 3: 0=absent; 1=present.

84 Transferrin 4: 0=absent; 1=present.

85 Transferrin 5: 0=absent; 1=present.

86 Fusion of Weberian vertebrae two and three: 0=incomplete; 1=complete.

87 Lower lip papillae, anterior rosette pattern flanked by bare spaces: 0=pattern absent (Smith 1966, pl. 1 B, E); 1=pattern present (Smith 1966, pl. 1 D).

Appendix B. Catostomin species-by-character matrix (1)

| Character # | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Minytrema* | 3 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Erimyzon* | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 |
| *C Xyrauchen* | 1 | 2 | 1 | 0 | 3 | 0 | 0 | 2 | 0 | 0 | 3 | 1 | 2 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| *C Deltistes* | 3 | 2 | 1 | 1 | 3 | 0 | 0 | 2 | 0 | 0 | 3 | 1 | 2 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 |
| *C Ch brevirostr.* | 1 | 2 | 1 | 0 | 3 | 0 | 2 | 2 | 0 | 0 | 3 | 0 | 2 | 1 | ? | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | ? | 1 | 0 | 1 | 0 | 0 | 0 |
| *C Ch cujus* | 1 | 2 | 1 | 0 | 3 | 0 | 2 | 2 | 0 | 0 | 3 | 0 | 2 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| *C Ch liorus* | 1 | 2 | 0 | 0 | 2 | 0 | 2 | 1 | 0 | 0 | 3 | 0 | 2 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| *C Ch murei* | 1 | 2 | 1 | 0 | 3 | 0 | 2 | 2 | 0 | 0 | 3 | 0 | 2 | 1 | ? | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| *C ardens* | 3 | 1 | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 2 | 1 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| *C macrocheil.* | 3 | 1 | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 1 | 1 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| *C latipinnis* | 3 | 1 | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 1 | 1 | 2 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| *C insignis* | 3 | 1 | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 1 | 1 | 2 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| *C snyderi* | 2 | 1 | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 2 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| *C fumeivent.* | 2 | 1 | 1 | 0 | 2 | 0 | 2 | 2 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 0 |
| *C tahoensis* | 2 | 1 | 1 | 0 | 2 | 0 | 0 | 1 | 1 | 0 | 3 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 1 | 2 | 1 | 0 | 0 | 0 |

Appendix B. continued.

| Character # | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *C rimiculus* | 3 | 1 | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 2 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 2 | ? | 1 | 2 | 1 | 0 | 0 | 1 |
| *C P columbia.* | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 1 | 2 | 2 | 0 | 1 | 1 | 1 | 0 | 2 | 2 | 1 | 2 | 1 | 0 | 0 | 1 |
| *C P platy.* | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 0 | 2 | 0 | 1 | 1 | 3 | 2 | 0 | 0 | 2 | 2 | 1 | 0 | 2 | 1 | 1 | 2 | 1 | 1 | 0 | 1 |
| *C P bondi* | 2 | 1 | 1 | 2 | 1 | 1 | 2 | 1 | 1 | 0 | 2 | 0 | 1 | 1 | 2 | 2 | 0 | 0 | 2 | 2 | 1 | 0 | 2 | 2 | 1 | 2 | 1 | 1 | 0 | 1 |
| *C P jordani* | 2 | 1 | 1 | 2 | 1 | 1 | 2 | 1 | 1 | 0 | 2 | 0 | 1 | 1 | 3 | 2 | 0 | 0 | 2 | 2 | 1 | 0 | 2 | 2 | 1 | 2 | 1 | 1 | 0 | 1 |
| *C P lahontan* | 2 | 1 | 1 | 2 | 1 | 1 | 2 | 1 | 1 | 0 | 2 | 0 | 1 | 1 | 2 | 2 | 0 | 0 | 2 | 1 | 1 | 0 | 2 | 2 | 1 | 2 | 1 | 1 | 0 | 1 |
| *C P virescens* | 2 | 1 | 1 | 2 | 1 | 0 | 2 | 1 | 1 | 1 | 2 | 0 | 1 | 0 | 3 | 2 | 2 | 0 | 2 | 3 | 1 | 0 | 2 | 2 | 1 | 2 | 1 | 1 | 1 | 2 |
| *C P discobolus* | 2 | 1 | 1 | 2 | 1 | 0 | 2 | 1 | 1 | 1 | 2 | 0 | 1 | 0 | 3 | 2 | 2 | 0 | 2 | 3 | 1 | 0 | 2 | 2 | 1 | 2 | 1 | 1 | 1 | 2 |
| *C P clarkii* | 2 | 1 | 1 | 2 | 1 | 0 | 2 | 1 | 1 | 1 | 2 | 0 | 1 | 0 | 2 | 2 | 2 | 0 | 2 | 3 | 1 | 0 | 2 | 2 | 1 | 2 | 1 | 1 | 1 | 2 |
| *C P santaana.* | 2 | 1 | 1 | 2 | 1 | 0 | 2 | 1 | 1 | 1 | 2 | 0 | 1 | 0 | 3 | 2 | 0 | 0 | 2 | 3 | 1 | 0 | 2 | 2 | 1 | 2 | 1 | 1 | 1 | 2 |
| *C P plebeius* | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 0 | 2 | 0 | 1 | 1 | 3 | 1 | 0 | 0 | 1 | 3 | 1 | 0 | 2 | 1 | 1 | 2 | 1 | 1 | 0 | 2 |

Appendix B. continued.

| Character # | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Minytrema* | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 2 | 1 | 0 | 0 |
| *Erimyzon* | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 0 |
| *C Xyrauchen* | 0 | 2 | 0 | 1 | 1 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 3 | 0 | 2 | ? | 0 |
| *C Deltistes* | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 3 | 1 | 2 | ? | 0 |
| *C Ch brevirostr.* | 0 | 0 | 0 | ? | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 2 | ? | 0 |
| *C Ch cujus* | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 2 | ? | 0 |
| *C Ch liorus* | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 2 | ? | 0 |
| *C Ch murei* | 0 | 0 | 0 | ? | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 2 | ? | 0 |
| *C ardens* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 2 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 1 | 0 | 0 |
| *C macrocheil.* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 2 | 2 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 2 | 1 | 1 | 0 | 0 |
| *C latipinnis* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 2 | 2 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 2 | 3 | 1 | 1 | 0 | 0 |
| *C insignis* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 2 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 1 | 0 | 0 |
| *C snyderi* | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 2 | 2 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 3 | 2 | 1 | 1 | 1 |
| *C fumeivent.* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 2 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 3 | 3 | 1 | 1 | 1 |
| *C tahoensis* | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 2 | 2 | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 2 | 3 | 3 | 1 | 1 | 1 |

Appendix B. continued.

| Character # | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *C rimiculus* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 2 | 2 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 0 | 2 | 3 | 3 | 1 | 1 | 1 |
| *C P columbia.* | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 2 | 2 | 2 | 1 | 0 | 2 | 1 | 0 | 1 | 1 | 2 | 1 | 0 | 0 | 2 | 0 | 2 | 3 | 2 | 1 | 1 | 1 |
| *C P platy.* | 1 | 1 | 2 | 0 | 0 | 1 | 0 | 2 | 2 | 3 | 2 | 2 | 2 | 2 | 1 | 1 | 2 | 2 | 2 | 0 | 0 | 2 | 0 | 1 | 2 | 3 | 1 | 1 | 1 |
| *C P bondi* | 1 | 1 | 2 | 0 | 0 | 1 | 0 | 2 | 2 | 3 | 2 | 2 | 2 | 2 | 1 | 1 | 2 | 2 | 2 | 0 | 0 | 2 | 0 | 2 | 2 | 2 | 1 | 1 | 1 |
| *C P jordani* | 1 | 1 | 2 | 0 | 0 | 1 | 0 | 2 | 2 | 3 | 2 | 2 | 2 | 2 | 1 | 1 | 2 | 2 | 2 | 0 | 0 | 2 | 0 | 1 | 2 | 3 | 1 | 1 | 1 |
| *C P lahontan* | 1 | 2 | 2 | 0 | 0 | 1 | 0 | 2 | 2 | 3 | 2 | 2 | 2 | 2 | 1 | 1 | 2 | 2 | 2 | 0 | 0 | 2 | 0 | 1 | 2 | 3 | 1 | 1 | 1 |
| *C P virescens* | 2 | 2 | 2 | ? | 0 | 1 | 0 | 2 | 2 | 3 | 2 | 2 | 2 | 2 | 1 | 1 | 2 | 1 | 2 | 0 | 0 | 2 | 0 | 2 | 3 | 2 | 1 | 1 | 1 |
| *C P discobolus* | 2 | 2 | 2 | 0 | 0 | 1 | 0 | 2 | 2 | 3 | 2 | 2 | 2 | 2 | 1 | 2 | 2 | 1 | 2 | 0 | 0 | 2 | 0 | 2 | 3 | 2 | 1 | 1 | 1 |
| *C P clarkii* | 2 | 2 | 2 | 0 | 0 | 1 | 0 | 2 | 2 | 3 | 2 | 2 | 2 | 2 | 1 | 1 | 2 | 1 | 2 | 0 | 0 | 2 | 0 | 0 | 2 | 3 | 1 | 1 | 1 |
| *C P santaana.* | 2 | 2 | 2 | 0 | 0 | 1 | 0 | 2 | 2 | 3 | 2 | 2 | 2 | 2 | 1 | 1 | 1 | 2 | 2 | 0 | 0 | 2 | 0 | 1 | 2 | 3 | 0 | 1 | 1 |
| *C P plebeius* | 1 | 2 | 2 | 1 | 0 | 1 | 0 | 2 | 2 | 2 | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 2 | 2 | 0 | 0 | 2 | 0 | 1 | 2 | 3 | 0 | 1 | 0 |

Appendix B. continued.

| Character # | 60 | 61 | 62 | 63 | 64 | 65 | 66 | 67 | 68 | 69 | 70 | 71 | 22 | 73 | 74 | 75 | 76 | 77 | 78 | 79 | 80 | 81 | 82 | 83 | 84 | 85 | 86 | 87 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Minytrema* | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 2 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1 | 0 |
| *Erimyzon* | 0 | 0 | 1 | 2 | 1 | 1 | 0 | 2 | 1 | 2 | 2 | 2 | 2 | 1 | 1 | 2 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1 | 0 |
| *C Xyrauchen* | 0 | 2 | 1 | 1 | 0 | 0 | 1 | 2 | 2 | 2 | 2 | 2 | 1 | 1 | 2 | 1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1 | 0 |
| *C Deltistes* | 0 | 2 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 2 | 2 | 2 | 1 | 1 | 2 | 1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1 | 0 |
| *C Ch brevirostr.* | 0 | 2 | 1 | 1 | 1 | 0 | 1 | 2 | 2 | 2 | 2 | 2 | 1 | 1 | 2 | 1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 |
| *C Ch cujus* | 0 | 1 | 1 | ? | ? | ? | ? | 2 | 2 | 2 | 2 | 2 | 1 | 1 | 2 | 1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1 | 0 |
| *C Ch liorus* | 0 | 1 | 1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1 | 0 |
| *C Ch murei* | 0 | 1 | 1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 |
| *C ardens* | 0 | 2 | 0 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 |
| *C macrocheil.* | 0 | 2 | 0 | 1 | 1 | 1 | 0 | 2 | 1 | 1 | 2 | 2 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *C latipinnis* | 0 | 1 | 0 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 |
| *C insignis* | 0 | 1 | 0 | 1 | 1 | 1 | 1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 |
| *C snyderi* | 0 | ? | 1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *C fumeivent.* | 0 | 1 | 0 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | 0 |
| *C tahoensis* | 0 | 2 | 1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |

Appendix B. continued.

| Character # | 60 | 61 | 62 | 63 | 64 | 65 | 66 | 67 | 68 | 69 | 70 | 71 | 22 | 73 | 74 | 75 | 76 | 77 | 78 | 79 | 80 | 81 | 82 | 83 | 84 | 85 | 86 | 87 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *C rimiculus* | 0 | 2 | 1 | 1 | 2 | 0 | 1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | ? | 0 |
| *C P columbia.* | 0 | 2 | 1 | 1 | 2 | 1 | 1 | 2 | 1 | 2 | 2 | 2 | 1 | 1 | 2 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *C P platy.* | 1 | 2 | 1 | 1 | 2 | 1 | 2 | 1 | 1 | 2 | 2 | 2 | 1 | 1 | 2 | 1 | 2 | 2 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 |
| *C P bondi* | 1 | 2 | 1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | 1 |
| *C P jordani* | 1 | 2 | 1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | 1 |
| *C P lahontan* | 1 | 2 | 1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 2 | 2 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 |
| *C P virescens* | 0 | 1 | 1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 |
| *C P discobolus* | 0 | 1 | 1 | 1 | 2 | 1 | 2 | 1 | 2 | 2 | ? | 2 | 2 | 1 | 2 | 1 | 1 | 3 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | ? | 0 |
| *C P clarkii* | 0 | 2 | 1 | 1 | 2 | 1 | 2 | 1 | 2 | 2 | 2 | 2 | ? | ? | ? | ? | 1 | 3 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| *C P santaana.* | 0 | 2 | 1 | ? | ? | ? | ? | 1 | 2 | 2 | 2 | 2 | ? | ? | ? | ? | 1 | 3 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| *C P plebeius* | 0 | 2 | 1 | ? | ? | ? | ? | 1 | 2 | 2 | 2 | 2 | 1 | 1 | 2 | 1 | 1 | 3 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 |