REDESCRIPTION OF THE TYEE SUCKER, *CATOSTOMUS TSILTCOOSSENSIS* (CATOSTOMIDAE)

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ABSTRACT.—We resurrect *Catostomus tsiltcoosensis*, the Tyee sucker of Oregon coastal rivers, from the synonymy of *Catostomus macrocheilus* and compare it with its congeners. *Catostomus tsiltcoosensis* is superficially similar to disjunctly distributed *Catostomus occidentalis* of the Sacramento drainage and *Catostomus ardens* of the Upper Snake River and Bonneville Basin. However, the gill raker structure, wide frontoparietal fontanelle, location of the ninth cranial foramen, scale radii patterns, and cytochrome *b* sequences clearly align *C. tsiltcoosensis* with *C. macrocheilus* rather than *C. occidentalis*. Differences in counts of infraorbital pores and dorsal fin rays, in body depth proportions, and in cytochrome *b* sequences distinguish *C. tsiltcoosensis* and *C. macrocheilus*. Within *C. tsiltcoosensis*, specimens from each of the 4 main drainages (north to south—Siuslaw, Umpqua, Coos, and Coquille) were reciprocally monophyletic based on cytochrome *b* data but showed no differences in the morphological features examined. Both *C. tsiltcoosensis* and another Oregon coastal taxon *Catostomus rimiculus* were paraphyletic based on cytochrome *b*. Although such discordant mitochondria results can be due to introgression, incomplete lineage sorting, and paralogy, other evidence suggests that introgression and lateral transfer of mitochondria explains the cytochrome *b* pattern in *C. rimiculus*. We speculate that lateral transfer might also be responsible for the pattern in *C. tsiltcoosensis*, except that the Coquille River population appears not to have been included in recent transfers.

Key words: *Catostomidae*, Oregon, taxonomy, cytb, Tyee sucker, distribution, biogeography.

Most Oregon coastal rivers are relatively small, usually with 1 or 2 species of native freshwater ostariophysan fishes. However, several mid- to south-coastal drainages (Siuslaw, Umpqua, Coos, and Coquille) centered on the Eocene Tyee Formation (hereafter, the Tyee drainages; Orr and Orr 2000) have 7 species. Structurally, the Tyee basin extends from the Siuslaw River to the Coquille River (Heller et al. 1987, Orr and Orr 2000), but, for our purposes, we include the Sixes River north of Cape Blanco as the southernmost Tyee drainage. The adjacent drainage to the south of Cape Blanco, the Elk River, is the northernmost of the Lower Klamath drainages. The Tyee basin includes the southern Oregon Coast Range and is bound to the south by the Klamath Mountains and to the east by the Western Cascades. With respect to the fish faunas, the Tyee drainages are bound to the north and east by the 19 ostariophysan species of the Columbia River fauna and to the south by the 7 species of the Klamath River fauna (Snyder 1908a, McPhail and Lindsey 1986, Minckley et al. 1986).

Almost all Tyee drainage fishes have been described as named or unnamed endemics

(Snyder 1908a, Bisson and Reimers 1977, Markle et al. 1991) or as having unique molecular or morphological characteristics (Mayden et al. 1991, Gold and Li 1994, Pfrender et al. 2004), but most are not currently recognized as valid species. Evermann and Meek (1898) described one of those nominal taxa, *Catostomus tsiltcoosensis*, from the Siuslaw River and Tsiltcoos Lake and compared it to *Catostomus occidentalis*. Snyder (1908a) relegated the taxon to the synonymy of *Catostomus macrocheilus*, largescale sucker, because his analysis “makes it appear that no differences exist between examples from the Siuslaw and Tsiltcoos rivers [*sic*] and the lower Columbia.” Subsequent authors have simply accepted this interpretation. However, we have found that specimens often better fit the description of *C. occidentalis*, and McPhail (2007) noted that the taxonomy of Oregon coastal suckers was an unresolved problem because “molecular evidence suggests that these Oregon coastal suckers are not largescale sucker.”

The α -level diversity of *Catostomus* is fairly stable, with only 5 new taxa described since 1940 (Eschmeyer 2008). A revision of the

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subgenus *Pantosteus* (Smith 1966), as well as several phylogenies (Smith 1992, Harris and Mayden 2001) and a Great Basin faunal overview, (Smith et al. 2002) have been published. Most recent α -level work has focused on peripheral isolates (Siebert and Minckley 1986, Ward and Fritzsche 1987, McPhail and Taylor 1999), discordant genetic data (Mock et al. 2006), or problems with hybridization (Tranah and May 2006). In this study, we redescribe the suckers from central Oregon coastal streams, elevate *C. tsiltcoosensis*, and evaluate morphological and cytochrome *b* (*cytb*) sequence variation in this species and adjacent *Catostomus*.

METHODS

Morphological Data

Cephalic lateralis pore counts follow Illick (1956), scale terminology follows Casteel (1972), and other anatomical descriptions follow Smith (1992). Other counts and measurements follow Hubbs and Lagler (1964) with emendations as described in Markle et al. (2005). For all species, we usually lacked specimens in the 200–300-mm-SL size range. For descriptive purposes, morphometric measurements were transformed as a ratio to standard length (SL). Nonnormal univariate data were analyzed using a Mann-Whitney test for comparing 2 samples and a Kruskal-Wallis test with Bonferroni correction for multiple comparisons. Statistical software PAST (Hammer et al. 2001), Statgraphics Centurion XV (StatPoint Technologies, Inc., [date unknown]), and SPSS V11.0.4 (SPSS, Inc., 2005) were used. Institutional abbreviations are as listed at <http://www.asih.org/codons.pdf> (except for OS and OSUO, which are Oregon State University Fish Collection, 104 Nash Hall, Corvallis, OR 97331-3803).

Within *C. tsiltcoosensis*, we were also interested in reducing morphological data to a few axes to examine differences between drainages. We used principal component analysis (PCA) of the covariance matrix for specimens with no missing data (Tabachnick and Fidell 2001). We used 19 meristic characters (Table 1) from 93 specimens distributed as follows: Siuslaw ($n = 22$), Umpqua ($n = 22$), Coos ($n = 14$), and Coquille ($n = 35$). We used 12 measurements (Table 1) from 88 specimens distributed as follows: Siuslaw ($n = 23$), Umpqua ($n = 17$), Coos ($n = 15$), and Coquille ($n = 33$). For

morphological data, we attempted to remove size effects by using residuals from linear regressions on SL instead of raw measurements (Reist 1986).

Molecular Data

Sequences for *cytb* were obtained from GenBank or from new material listed below. Carcasses were vouchered if available. Sequences of *Catostomus columbianus*, *Catostomus occidentalis occidentalis*, *Catostomus tahoensis*, *Deltistes luxatus*, *Moxostoma anisurum*, and *Cyprinus carpio* were obtained from GenBank.

DNA was extracted from ethanol-preserved specimens using a Qiagen DNeasy Tissue Kit (Catalog No. 69504). The mitochondrial DNA *cytb* gene was amplified from genomic DNA using primers L14724 (Schmidt and Gold 1993) and H15915 (Irwin et al. 1991). PCR reactions used 0.5- μ g genomic DNA, 5- μ L 10X buffer (0.1 M tris-HCL pH 8.5, 0.015 M $MgCl_2$, 0.5 M KCl), 5- μ L dNTP mixture (2 mM each of dATP, dTTP, dCTP, and dGTP in 10 mM tris-HCL, pH 7.9), 5 μ L of a 10- μ M solution of each of 2 primers, 0.5 μ L of Taq polymerase, and deionized water added for a final volume of 50 μ L. The amplification profile consisted of 95 °C for 45 seconds, 50 °C for 30 seconds, and 70 °C for 2.5 minutes for 32 cycles. Double-stranded DNA was purified with Qiagen QIAquick PCR purification kit (Qiagen Catalog number 28106). Purified double-stranded DNA was sequenced by MacroGen Inc. (Korea) with primers trimL14724 (5'-GTGACTTGAAAAACCAC-3'; modified from Schmidt and Gold 1993), trimH15919 (5'-AACTGCAGTCATCTCCGGTTTAC-3'; modified from Irwin et al. 1991), L15424 (Edwards et al. 1991), and H15149 (Kocher et al. 1989). Cyprinid DNA was sequenced with primers trimL14724, trimH15919, L479496, H600615, L531546, and H636652.

DNA sequences were edited and assembled in SeqEd v1.0.3 (Applied Biosystems, Inc., Forest City, CA, USA) and aligned by eye in PAUP* (Swofford 2002). Phylogenetic relationships were estimated in PAUP* using maximum parsimony (MP) and maximum likelihood (ML) (Swofford 2002). The heuristic method (1000 random additional sequences with tree bisection reconstruction for MP) was used to generate the tree. Nonparametric bootstrap analysis with 1000 pseudoreplicates and 100 random additional sequences were conducted for MP. The strict consensus topology of the most parsimonious

TABLE 1. Acronyms and descriptions of counts and measurements used in principal component analysis.

Variable	Description
COUNTS	
PCV	Post-Weberian precaudal vertebrae without a definite haemal spine even if a haemal arch was present
CV	Caudal vertebrae with a definite haemal spine including urostyle
INTER1DEP	Number of vertebrae anterior to first dorsal fin pterygiophore including vertebrae immediately posterior to point of interdigitation with neural spines
VDO	Number of vertebrae anterior to a vertical from base of first dorsal fin ray including vertebra intersected by the vertical
VAO	Number of vertebrae anterior to a vertical from base of first anal fin ray including vertebra intersected by the vertical
VPO	Number of vertebrae anterior to a vertical from base of first pelvic fin ray including vertebra intersected by the vertical
GILRK RANT	Number of gill rakers on lateral surface of first gill arch
GILRKPOST	Number of gill teeth on the medial surface of the first gill arch
PM	Preoperculomandibular pores
IO	Infraorbital pores
IOPAE	Infraorbital pores anterior to the anterior edge of the eye
SO	Supraorbital pores
LL	Lateral line scales
SCALABVLL	Scales above lateral line
SCALBELOLL	Scales below lateral line
SCACADPED	Scales around caudal peduncle
PAPLORLIP	Rows of papillae at symphysis of lower lip
PAPUPRLIP	Rows of papillae at symphysis of upper lip
DORSAL RAYS	Dorsal fin rays
MEASUREMENT	
LAE	Snout length.
HL	Head length.
IW	Interorbital width at the least bony measurement at the narrowest point.
DP1	Body depth at origin of the pectoral fin (measure at the vertical line that cross the base of the most anterior most rays).
LOP2	Distance from tip of snout to pelvic fin origin.
LOP1_LOP2	Distance from pectoral fin origin to pelvic fin origin.
LOD	Pre-dorsal length.
LOA	Pre-anal length.
LDA	Distance from dorsal fin origin to anal fin origin.
LDOC	Distance from dorsal fin origin to middle of caudal fin base.
DCAUDPED	Caudal peduncle depth.
ED	Eye diameter

tree was used. Outgroups were *Moxostoma anisurum*, a member of the sister group to *Catostomus* (Smith 1992), and *Cyprinus carpio*.

Sequence divergence was calculated using PAUP* (Swofford 2002), based on the DNA substitution model selected by Modeltest 3.7 (Posada and Crandall 1998). The selected model was general time reversible, with some sites assumed to be invariable. Variable sites followed a gamma distribution (i.e., GTR + I

+ G). Maximum likelihood settings were as follows: nucleotide frequencies A = 0.2925, C = 0.3018, G = 0.1213, and T = 0.2844; rate matrix A-C = 0.8754, A-G = 68.2602, A-T = 0.4872, C-G = 2.4331, C-T = 11.0539, G-T = 1.0000; proportion of invariable sites (I) = 0.5694; gamma distribution shape parameter = 1.1263. An index of substitution saturation (Iss; Xia et al. 2003) was calculated in DAMBE (Xia and Xia 2001) to assess phylogenetic signal.

Catostomus tsiltcoosensis Evermann
and Meek, 1898

Tyee sucker

Fig. 1, A and B

Catostomus tsiltcoosensis Evermann and Meek, 1898: 68–69, Figure 1. (Tiltcoos Lake, Oregon). Snyder 1908a: 166 (synonym of *C. macrocheilus*); Gilbert 1998:202.

Catostomus macrocheilus (not of Girard, 1856), Snyder 1908a:167 [in part].

HOLOTYPE.—USNM 48479, 196 mm SL, Oregon, Lane County, Tiltcoos Lake, 2 December 1896, S.E. Meek.

DIAGNOSIS.—*Catostomus tsiltcoosensis* can be identified from its congeners by the following combination of characters: lateral line scales 65–80; dorsal fin rays 9–12; infraorbital pores 14–38; gill rakers 24–31 in specimens >200 mm SL; gill rakers with spines in clusters; caudal peduncle depth 6.4%–9.3% SL; lateral fields of scales with either no radii or extensions of anterior radii; and foramen for the ninth cranial nerve between the exoccipital and prootic.

DESCRIPTION.—Description based on up to 108 specimens from 2 size classes (80–186 mm and 251–442 mm SL), and proportions as percent SL, with parentheses showing mean and standard deviation: body elongate, slightly laterally compressed rising gradually to dorsal base; head moderately long 21.0–25.3 (23.2, 1.03); snout rounded and moderately long 9.0–12.9 (10.7, 0.83); least bony interorbital width 8.1–10.4 (9.1, 0.52); eye 2.6–6.0 (3.8, 0.99) declining with size; body width at base of anterior pectoral fin ray 12.1–16.0 (14.3, 0.96); body depth at vertical crossing base of anterior pectoral fin ray 14.0–19.8 (16.2, 0.92); body depth at origin of dorsal fin 15.8–23.6 (19.2, 1.50); pectoral fin length 13.1–21.3 (17.2, 1.67); pelvic fin length 11.1–18.2 (13.5, 1.35); distance from pectoral fin origin to pelvic fin origin 30.8–41.4 (35.3, 1.7); predorsal length 48.2–54.7 (51, 1.28); preanal length 74.6–83.1 (78.7, 1.68); distance from dorsal fin origin to anal fin origin 29.9–37.6 (34.2, 1.53); caudal peduncle depth moderate 6.4–9.3 (8.0, 0.70); origin of dorsal fin in midbody; dorsal fin with 10–14 fin rays (12.1, 0.62); anal fin with 7, rarely 6, or 8 fin rays (7, 0.20); pectoral fin with 17–19, rarely 16, or 20 fin rays (17.8, 0.77); pelvic fin origin posterior to dorsal fin origin, with 9–12 fin rays (10.6, 0.66); infraorbital pores 14–38 (29.4, 4.91); preopercular mandibular pores 11–34 (18.6, 4.84); supraorbital pores 12–27 (17.2, 2.78);

mouth subterminal with large fleshy lips, covered with papillae; 1–2 rows of papillae across the symphysis of the lower lip; 2–4 rows on the upper lip (2.1, 0.28); 2–8 rows on lower lip (5.6, 1.01); gill rakers on lateral surface of the gill arch 23–31 (27.0, 1.55) with spines in clusters; gill rakers on medial surface of the gill arch 27–38 (34.1, 2.19); lateral line scales 65–80 (72.1, 3.37); scales above lateral line 11–17 (13.1, 1.01); scales below lateral line 8–14 (10.3, 1.20); scales around caudal peduncle 19–28 (22.2, 2.13); lateral field of scales usually with parallel extensions of anterior radii, but lateral field may be completely full of radii (OS 12810, Siuslaw River) to almost no radii (OS 15433, Coquille River; Fig. 2B); post-Weberian vertebrae 42–46 (44, 0.68), 23–26 precaudal vertebrae (24.8, 0.71); vertebrae anterior to first dorsal fin pterygiophore including vertebrae immediately posterior to point of interdigitation with neural spines 9–12 (10.0, 0.81); vertebrae anterior to a vertical from base of first dorsal fin ray including vertebra intersected by the vertical 12–16 (14.1, 0.72); vertebrae anterior to a vertical from base of first anal fin ray including vertebra intersected by the vertical 30–33 (31.8, 0.72).

COMPARISONS.—*Catostomus tsiltcoosensis* has fewer lateral line scales (65–80) than *C. columbianus*, *Catostomus catostomus*, *Catostomus latipinnis*, *Catostomus rimiculus*, and *C. tahoensis*, which have more than 80 lateral line scales (Bond 1994, La Rivers 1994, Wydoski and Whitney 2003). Specimens >200 mm SL have fewer gill rakers (24–31) than *Catostomus snyderi* (29–40) and *Catostomus ardens* (32–39; Smith 1992). *Catostomus tsiltcoosensis* has more dorsal fin rays (10–14, 98% have 11 or more) and a shallower caudal peduncle depth (6.4%–9.3% SL) than *Catostomus warnerensis* (9–10 rays, 8.3%–11.7% SL) and *Catostomus fumeiventris* (10 rays, 9.3%–10.6% SL; Miller 1973). It is most similar superficially to the *C. occidentalis* complex and *C. macrocheilus*. Compared to *Catostomus microps* and *C. occidentalis*, *C. tsiltcoosensis* has gill rakers with spines in clusters (Fig. 2A) rather than simple ridges with spines, lateral fields of scales with either no radii or extensions of anterior radii rather than numerous slanting radii (Fig. 2B, 2C), a wider frontoparietal fontanelle, a foramen for the ninth cranial nerve between the exoccipital and prootic (mostly on the exoccipital), and a shallower caudal peduncle (>9.5% SL; Smith

Fig. 1. *Catostomus tsiltcoosensis*, collected from Woahink Creek, Oregon, on 25 April 2009: A, 395-mm-SL tuberculate, running ripe male; B, 440-mm-SL running ripe female. *Catostomus macrocheilus*, collected from Willamette River near Corvallis, Oregon, on 1 May 2009: C, 420-mm-SL tuberculate male; D, 440-mm-SL ripe female.

Fig. 2. A, dorsal view of branchial basket of *Catostomus tsiltcoosensis*, Coquille River, OS 15433, 415 mm SL, anterior to left. B, *C. tsiltcoosensis*, Coquille River, OS 15433, 260 mm SL, dorso-lateral field of scale, anterior to left. C, *Catostomus occidentalis occidentalis*, Rush Creek, California, OS 5111, 380 mm SL, dorso-lateral field of scale, anterior to left.

Fig. 3. *Catostomus tsilcoosensis* and *Catostomus macrocheilus*: A, scatter plot of infraorbital pores and dorsal fin rays; B, comparison of regression of body depth at dorsal fin origin and caudal peduncle depth, assuming common intercepts. For *C. tsilcoosensis*, $Y = 3.47075 + 2.20652 * X$, and for *C. macrocheilus*, $Y = 3.47075 + 2.76822 * X$ (slopes differ $P < 0.0001$, adjusted $R^2 = 97.1\%$).

1992). Within the *C. occidentalis* complex, *C. tsilcoosensis* also has more lateral line scales than *C. o. mniotiltus* (58–65; Ward and Fritzsche 1987). It has been confused with *C. macrocheilus* (Snyder 1908a) but can be distinguished by the combination of fewer dorsal fin rays, fewer infraorbital pores, and deeper caudal peduncle depth (Fig. 3).

Univariate analyses of morphometric and meristic data found no clear differences among fish from the major Tyee drainages. The first 2 axes of the PCA of residual morphometric characters explained 27.7% and 19.1% of the variation, respectively, and did not indicate evidence of differences in suckers from the 4 coastal drainages (Fig. 4A). The first 2 axes of the PCA of meristic characters explained 45.2% and 19.8%

of the variation, respectively, and also did not indicate evidence of differences in suckers from the 4 coastal drainages (Fig. 4B).

COLORATION.—Body color in preservative dark on dorsum; light on ventrum and lower half of body; peritoneum white posteriorly grading to dusky gray or black near anterior swimbladder chamber and pericardial cavity. Based on observations in Woahink Creek, spawning females with golden, yellow-green base color on head, body, paired fins, dorsal and caudal fins; leading-edge paired fins light; anal fin pink to light rose colored; scales with black margins; and lower head and belly white (Fig. 1). Males similarly colored except lower head and belly bright yellow with contrasting broad, black lateral stripe. Both black stripe and yellow belly

Fig. 4. Principal component analysis plots for suckers from major Tyee drainages. Ellipses are 95% confidence intervals as determined in PAST. Symbols are Coos (x), Coquille (Δ), Siuslaw (+), and Umpqua ($\circ$). A, first 2 axes using residuals from regression of 12 measurements on SL; B, first 2 axes using 19 meristic characters.

coloration disappear rapidly when fish disturbed, captured, or not spawning. Spawning colors similar to *C. macrocheilus*, both sexes with yellow on lower head and belly and color persistent after capture (Fig. 1C, 1D). Male breeding tubercles large and prominent on anal fin and lower caudal fin and smaller on leading edges of paired fins.

MOLECULAR PHYLOGENY.—A total of 1042 base positions were included in the analysis. Of these, 199 were informative, 148 were parsimony uninformative, and 695 were constant. Of the 199 informative characters, 20 were first position and 4 were second position. The index of substitution saturation ($Iss = 0.154$) was significantly lower ($P < 0.0001$) than the critical index of substitution saturation $Iss.c$ for

symmetrical trees ($IssSym = 0.749$) or asymmetrical trees ($IssAsym = 0.449$), suggesting little saturation with significant phylogenetic information. MP analysis yielded 18 trees with 602 steps, consistency index ($CI = 0.7027$), retention index ($RI = 0.9523$), and rescaled consistency index ($RC = 0.6692$). The consensus topology of the MP analysis was 605 steps, $CI = 0.6992$, $RI = 0.9515$, and $RC = 0.6653$. The consensus topology of the 18 MP trees and the topology from the ML analysis (likelihood score 4143.10372) were similar, but the MP tree (Fig. 5) had somewhat more resolution and is shown here.

Both trees contained a northern clade and a southern clade. The northern clade contained *C. macrocheilus*, *C. tsilcoosensis*, *C. columbianus*,

Fig. 5. Strict maximum parsimony consensus tree for *cytb* sequences from western Oregon suckers showing lack of monophyly for *Catostomus tsiltoosensis* and *Catostomus rimiculus*. Tree constructed from 18 trees (602 steps), with *Moxostoma anisurum* and *Cyprinus carpio* as outgroups; final tree is 605 steps long with consistency index = 0.6992, retention index = 0.9515, and rescaled consistency index = 0.6653; branch lengths proportional to changes; numbers on nodes are bootstrap values greater than 50%; numbers on terminal elements represent unique haplotypes within a drainage.

Fig. 6. Map showing distribution of *Catostomus tsiltcoosensis*, *Catostomus macrocheilus*, and *Catostomus rimiculus* in western Oregon; inset shows map location in western North America.

and *C. tahoensis*. The southern clade contained *C. rimiculus*, *C. occidentalis*, and the 3 other Klamath species: *C. snyderi*, *Chasmistes brevirostris*, and *D. luxatus*. Although *C. macrocheilus* was monophyletic, both *C. tsiltcoosensis* and *C. rimiculus* were not (Fig. 5). For *C. tsiltcoosensis*, 3 taxa (*C. macrocheilus*, *C. tahoensis*, and *C. columbianus*) were embedded

within it; and for *C. rimiculus*, 3 Klamath species were embedded (Fig. 5). Within *C. rimiculus*, the Rogue River fish were monophyletic and all Rogue River *C. rimiculus* were reciprocally monophyletic, with the clade containing all 4 Klamath River taxa.

Pairwise sequence divergence between northern and southern clades was 12.0%–20.9%.

Sequence divergences between *C. macrocheilus* and *C. tsiltcoosensis* from each drainage were as follows: Siuslaw plus coastal lakes, 1.6%–2.2%; Umpqua, 1.7%–2.5%; Coos, 1.4%–2.0%; and Coquille, 2.8%–3.8%. Within *C. tsiltcoosensis*, sequence divergence between Coquille and all others was 2.6%–4.1%. Sequence divergence between all Rogue River *C. rimiculus* and all 3 nominal genera of Klamath River fish was 1.2%–2.1%.

DISTRIBUTION AND ECOLOGY.—*Catostomus tsiltcoosensis* is found in coastal Oregon streams and lakes from the Siuslaw River south to the Sixes rivers. Among coastal streams south of the Columbia River, *C. macrocheilus* is only found in the adjacent Nehalem River; and there are no museum records or Oregon scientific-take permit records (S. Miller, Oregon Department of Fish and Wildlife, personal communication, April 2009) for suckers from the Miami River to the Alsea River. Thus, *C. tsiltcoosensis* is adjacent, west and south of the distribution of *C. macrocheilus* and north of *C. rimiculus* (Fig. 6). Evermann and Meek (1898) reported that specimens from the Siuslaw River were obtained in “brackish water,” and Snyder (1908a) reported that large schools follow the tide and venture “some distance into the brackish water.” Several reports by Oregon Department of Fish and Wildlife (ODFW) biologists also suggest that *C. tsiltcoosensis* can tolerate some salinity. For example, adult salmon traps set at the head of tidewater in the South Coos River have caught thousands of suckers in the fall (T. Rumreich, ODFW, personal communication, 2009).

Spawning was observed in Woahink Creek, which links Woahink Lake and Tsiltcoos Lake, on 25 April 2009 and presumably was of fish from Tsiltcoos Lake. Nuptial males in breeding color were generally aggregated downstream of masses of females. During spawning over gravel and cobble, multiple spawners participated, often with 2 males along the side of a female.

ETYMOLOGY.—The common name, Tyee sucker, refers to the geological Tyee Formation and its present drainages. The name is derived from the native American trade language, Chinook Jargon, for chief or king.

DISCUSSION

Current taxonomy, which treats the Tyee sucker as a synonym of *C. macrocheilus*, is partly an artifact of history. Evermann and Meek

(1898) thought many of the western large-scaled suckers, including *C. ardens* and *C. latipinnis*, were similar; and they directly compared their new species, *C. tsiltcoosensis*, with *C. occidentalis*. Snyder (1908b) also thought the complex of large-scaled suckers of Columbia (*C. macrocheilus*), coastal Oregon (*C. tsiltcoosensis*), Klamath (*C. snyderi*), and Sacramento (*C. occidentalis*) were difficult to diagnose and relegated *C. tsiltcoosensis* to the synonymy of *C. macrocheilus* (Snyder 1908a). Part of the diagnostic problem of *C. tsiltcoosensis* is not differentiating it from *C. macrocheilus*, as current taxonomy suggests, but rather differentiating it from *C. occidentalis*, as originally suggested by Evermann and Meek (1898). Characters such as scale morphology and *cytb* sequences suggest substantial differences between *C. tsiltcoosensis* and *C. occidentalis*. The *cytb* analysis supports Snyder (1908a) by placing *C. tsiltcoosensis* in a northern clade with *C. macrocheilus*, *C. tahoensis*, and *C. columbianus* and *C. occidentalis* in a southern clade with the Klamath suckers. Based on *cytb* data, *C. ardens* is also with the northern clade (Dowling, personal communication, April 2009).

Not surprisingly, among the complex of coarse-scaled suckers, populations of species found in multiple drainages are also difficult to distinguish from each other using standard morphology (*C. occidentalis*—Ward and Fritzsche 1987, Moyle 2002; *C. ardens*—Mock et al. 2006). We also found this true for *C. tsiltcoosensis* (Fig. 4); however, *cytb* sequences suggested that populations from different drainages (Siuslaw plus adjacent coastal lakes Umpqua, Coos, and Coquille) were reciprocally monophyletic and that intraspecific divergence of the Coquille River population was particularly deep (2.6%–4.1%). Sequence divergence of Coquille River suckers from *C. macrocheilus* (2.8%–3.8%) was similar to divergence of Coquille River suckers from all other *C. tsiltcoosensis* (2.6%–4.1%), whereas divergence between *C. macrocheilus* and the non-Coquille *C. tsiltcoosensis* was much less (1.4%–2.5%). Similar, relatively deep genetic divergence is also seen in *C. ardens* from different drainages, where mitochondrial sequence divergence is 4.5% between morphologically similar fish from the Snake River and Bonneville Basin (Mock et al. 2006).

The *cytb* gene tree was also paraphyletic for both *C. tsiltcoosensis* and *C. rimiculus* (Fig. 5). However, for *C. rimiculus*, both morphology (Markle et al. 2005) and nuclear microsatellites

(Tranah and May 2006) corroborate monophyly and suggest the paraphyletic result of the *cytb* data (Fig. 5) was due to lateral transfer of mitochondria within the sucker fauna of Klamath Basin (Dowling et al. unpublished data). Similar discordant mitochondrial phylogenies are found in other groups of vertebrates and may be attributed to introgression, incomplete lineage sorting of ancestral polymorphisms, or paralogy (Irwin et al. 2009, Wiens et al. 2010). We speculate that our paraphyletic *cytb* result might also be due to secondary contact and lateral transfer of *cytb* between one or more northern populations of *C. tsiltcoosensis* and *C. macrocheilus*. Potential contact events were during late Pliocene and Pleistocene, when a former tributary of the proto-Willamette River was captured by a westward flowing stream to become the Umpqua River (Diller 1915, Baldwin 1959) and during late Pleistocene when the Long Tom River, a tributary of the proto-Siuslaw River, was captured by the Willamette River (Baldwin and Howell 1949). After an initial transfer, exchange among *C. tsiltcoosensis* in different drainages could have been facilitated by low-elevation (2–12 m above sea level), perennial freshwater lakes (Orr and Orr 2000) and/or a lower (130-m) Pleistocene sea level (Fleming et al. 1998). Evidence of some salinity tolerance in *C. tsiltcoosensis* also supports lowland conjunction as a possible contact mechanism, but reciprocal monophyly in *cytb* suggests isolation has subsequently been effective. Segregation of the Coquille population from other Tyee drainages at Cape Arago is problematic but may have been facilitated by raised terraces both onshore and offshore (Orr and Orr 2000). Such terraces also isolate the much smaller Sixes River; the DNA of suckers in this river has not been analyzed. If the Coquille population's mitochondria have not been influenced by lateral transfer, its *cytb* sequences may more accurately track species phylogeny.

Recognition of *C. tsiltcoosensis* as a taxon separate from *C. macrocheilus* more adequately reflects both morphological and molecular evidence and highlights an unrecognized area of endemism. Our *cytb* analysis suggests the Tyee fauna is related to the Columbia fauna and that the boundary at Cape Blanco separates Columbia Tyee fishes from Klamath fishes. The zoogeographic boundary at Cape Blanco is also found in the genetic structure and life histories

of anadromous salmonids (Waples et al. 2001) and in some *cytb* lineages of *Rhinichthys osculus* (Pfrender et al. 2004). For primary freshwater fishes, the origin of this pattern is likely related to the sequential Miocene and Pliocene connections and disconnections of the Snake River and Lake Idaho with the Columbia, Klamath, and Sacramento rivers (Taylor and Smith 1981, Smith et al. 1984, 2000, Wagner et al. 1997). If this view of drainage evolution is correct, our *cytb* data also suggest that the Coquille River, and perhaps other Tyee drainages, were initially isolated early in the sequence.

This and other work (Mock et al. 2006) to characterize western suckers and diagnose taxa have shown that morphologically similar forms can differ greatly in molecular markers, while morphologically distinct forms, even co-occurring nominal genera, can be indistinguishable with molecular markers (Tranah and May 2006, Cole et al. 2008, Dowling et al. unpublished data). The former seems to occur when there are allopatric distributions, and the latter occurs when there is sympatry. Both occurrences create dilemmas with implications for conservation (Cole et al. 2008) and taxonomy and underscore the need for wider taxon sampling of western fishes and for multiple lines of evidence—mitochondrial markers, multiple unlinked nuclear markers (Wiens et al. 2010), morphology, and ecological characters.

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APPENDIX. Material examined. Specimens are listed alphabetically by species and grouped by drainage. Symbols preceding the catalog number are as follows: an asterisk (*) indicates both DNA sequences and morphological data were collected; a solid circle (●) indicates only DNA sequences were collected; and no symbol indicates only morphological data were taken. Following the catalog number is the sample size in parentheses, standard length, date of collection, and GenBank accession numbers.

Catostomus ardens

Bear Lake, Utah—OS 6573 (2), 94–129 mm, 11 June 1959.

Catostomus macrocheilus

Columbia River (main stem)—*UW 49018 (1), 326 mm, 8 November 2003, EU 676840; ●OS 17858 (1), 400 mm, 9 October 2004, EU 676834. **Willamette River**—OS 10591 (4), 130–182 mm, 24 August 1981; OS 14388 (1), 140 mm, 7 September 1993; OS 15718 (2), 138–153 mm, 1 July 1996; OS 16654 (1), 184 mm, 29 August 1997; OS 16656 (2), 152–216 mm, 25 June 1997; OS 17111 (2), 144–153 mm, 25 August 1998; OS 17860 (1), 326 mm, 24 June 2004; OS 17862 (4), 306–345 mm, 6 April 2004; *OS 17863 (6), 275–360 mm, 2 April 2004, EU 676835–EU 676837; *OS 17873 (4), 370–435 mm, 5 April 2004, EU 676835, EU 676839–EU 676840; ●OS uncataloged tissue F43 (1), 159 mm, 20 July 1992, EU 676833; ●OS uncataloged tissue F44 (1), 165 mm, 20 July 1992, EU 676839. **Santiam River**—OS 6039 (1 skeleton), 360 mm, 30 May 1977. **Pudding River**—OS 14389 (1), 112.4 mm, 21 September 1993. **Marys River**—OS 16107 (1), 109.15 mm, 1 July 1998. **Long Tom River**—OS 16821 (1), 158 mm, 15 July 1998; OS 13135 (3), 160–175 mm, 11 July 1991; OS 17712 (1), 125.7 mm, 22 September 1998. **Nehalem River**—USNM 58115 (7), 79–172 mm, 1879.

Catostomus occidentalis

Goose Lake, Oregon—OS 3157 (2), 102–121 mm, OS 17953 (22), 12–280 mm. **San Joaquin River, California**—OS 5208 (4), 114–157 mm. **Sacramento River, California**—OS 5111 (1), 380 mm; OS 8017 (5), 40–51 mm.

Catostomus rimitulus

Klamath River main stem—OS 15908 (4), 136–190 mm, 22 June 1993; OS 15909 (8), 231–411 mm, 5 November 1993; *OS 17877 (10), 333–408 mm, 22 July 2004, EU 676816–EU 676820. **Jenny Creek**—OS 12520 (2), 128 mm, 13 September 1990; OS 12821 (3), 118–156 mm, 26 June 1979; OS 12822 (1), 121 mm, 1979; OS 12823 (1), 124 mm, 2 August 1979; OS 12824 (1), 130 mm, 16 August 1979; OS 12825 (1), 120 mm, 19 May 1979; OS 12826 (2), 79.35–102 mm, 25 October 1980; OS 12827 (5), 146–175 mm, 1979; OS 12828 (1), 112 mm, 19 August 1979; OS 12829 (2), 125–132 mm, 29 August 1979; OS 12831 (2), 126–132 mm, 28 August 1979; OS 12832 (2), 131–160 mm, 24 August 1979; *OS 13737 (3), 125–181 mm, 17 June 1992, EU 676816; OS 17784 (3), 101–144 mm, 27 August 2001.

Spencer Creek, OS 17785 (1), 184 mm, 24 April 1997; *OS 17879 (1), 180 mm, 1 April 2004, EU 676822; *OS 17880 (3), 236–338 mm, 29 April 2005, EU 676817, EU 676823, EU 676824; *OS 17881 (1), 150 mm, 18 May 2004, EU 676817; *OS 17882 (1), 177 mm, 20 May 2005, EU 676817. **Smith River—OS 5234 (5), 210–241 mm, August 1975. **Rogue River main stem**—OS 8090 (6), 109–133 mm, 4 October 1979; OS 11013 (11), 97–127 mm, 11 September 1981; *OS 15913 (23), 315–405 mm, 23 August 1993, EU 676810, EU 676813–EU 676815; OS 17135 (5), 79–112 mm, 15 September 1998; *OS 17878 (1), 350 mm, 16 May 2006, EU 676809; *OS 17883 (1), 92 mm, 20 May 2005, EU 676812. **Elk Creek**—*OS 17875 (4), 315–400 mm, 13 May 2005, EU 676809–EU 676811; *OS 17876 (1), 110 mm, May 2005, EU 676809. **Rough and Ready Creek**—OS 16161 (3), 72–131 mm, 14 August 1997. **Bear Creek**—OS 17874 (1), 158 mm, 10 May 2005.**

Catostomus tsitlicoosensis

Tsitlicoos Lake—USNM 48779 (1), 207 mm. **Tenmile Lake**—USNM 124386 (2), 192–201 mm. **Siuslaw River**—OS 12810 (1), 183 mm, 23 August 1990; *OS 15461 (13), 251–401 mm, 7 June 1995, EU 676827–EU 676829; OS 15465 (4), 87–129 mm, 7 June 1995; OS 16806 (4), 91–134 mm, 3 June 1998; OS 16813 (2), 85–119 mm; OS 16871 (2), 121–135 mm, 3 June 1998. **Woahink Lake**—*OS 13656 (3), 350–372 mm, 11 March 1992, EU 676827. **Woahink Creek**—OS 17962 (1 skeleton), 440 mm, 25 April 2009. **Umpqua River**—*OS 15427 (5), 340–416 mm, 28 April 1995, EU 676830, EU 676831; OS 16200 (2), 80–81 mm, 7 August 1997; OS 17869 (2), 105–143 mm, 7 July 2004; OS 17870 (3), 99–113 mm, 8 July 2004; *OS 17871 (1), 343 mm, 9 July 2005, EU 676831; *OS 17872 (10), 303–367 mm, 19 August 2004, EU 676830–EU 676832. **Coos River**—*OS 17859 (3), 301–395 mm, 16 September 2004, EU 676841; *OS 17861 (3), 353–382 mm, 20 August 2004, EU 676841, EU 676842. **Millicoma River**—*OS 15442 (8), 286–408 mm, 11–15 May 1995, EU 676841, EU 676842; OS 15879 (6), 99–138 mm, 25 June 1997; OS 15880 (4), 128–150 mm, 6 June 1997; OS 16351 (1), 152 mm, 19 August 1997; OS 16320 (1), 101 mm, 2 September 1997. **Coquille River**—USNM 58353 (10), 90.1–172.3 mm, 1879; USNM 62253 (10), 90.7–183.5 mm, 1899; OS 15433 (4), 270–415 mm, 29 April 1995; *OS 17864 (2), 345–362 mm, 15 October 2003, EU 676846; OS 17866 (1), 352 mm, 24 October 2003; *OS 17867 (3), 350–442 mm, 23 January 2004, EU 676843, EU 676847; *OS 17868 (5), 298–345 mm, 6 June 2003, EU 676843, EU 676844. **Sixes River**—USNM 62250 (2), 330–350 mm, 1879; USNM 58153 (2), 86.8–114 mm, 1879.

Catostomus warnerensis

Warner Creek—USNM 55597 (1), 245 mm, holotype; **Honey Creek**—USNM 125638 (6), 94–142 mm; OS 2440 (1), 157 mm, 30 June 1954. **Hart Lake**—OS 3557 (4), 84–116 mm, 29 August 1949; OS 13219 (2), 345–365 mm, 28 June 1991.