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Morphology and taxonomy of Klamath Basin suckers (Catostomidae)

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There are 13 or 14 genera and up to 76 species of catostomids (Nelson 1994, Harris and Mayden 2001), with 3 genera and 4 species occurring in Klamath Basin (Bond 1994): *Catostomus rimiculus* Gilbert and Snyder 1898 in Gilbert 1898 (Klamath smallscale sucker, KSS), *C. snyderi* Gilbert 1898 (Klamath largescale sucker, KLS), *Chasmistes brevirostris* Cope 1879 (shortnose sucker, SNS), and *Deltistes luxatus* Cope 1879 (Lost River sucker, LRS). Lost River and shortnose suckers are federally listed endangered species (U.S. Fish and Wildlife Service 1988), primarily occupy hypereutrophic Upper Klamath Lake (Eilers et al. 2004), and figure prominently in disputes over water allocation in the basin (Markle and Cooperman 2002).

The 2 endangered lake suckers are also part of an important lineage of large-bodied, large-water suckers, the *Xyruachen* group, that retain many primitive characters (Smith 1992a), including, in the case of *Xyruachen*, conservative sequences in at least 2 mitochondrial genes (Harris and Mayden 2001). The 4 Klamath Basin suckers are similar in overall body shape, but highly variable, and they are distinguished by feeding-related structures, adult habitat, and geography. The 2 *Catostomus* species have large lips and widely spaced gill rakers, and they are primarily river dwellers, with *C. snyderi* mostly found in the upper basin and *C. rimiculus* in the lower basin and adjacent Rogue River. *Deltistes luxatus* has smaller lips and short “deltoid” *Catostomus*-like gill rakers and is primarily found in lakes. *Chasmistes brevirostris* has small lips and many closely spaced gill suckers with secondary branching, and it is also primarily a lake dweller (Andreasen 1975, Miller and Smith 1981, Buettner and Scoppettone 1991).

Catostomids were among the first freshwater fish known to hybridize in nature (Hubbs et al. 1943). Referring to *Ch. brevirostris*, Miller and Smith (1981:22) stated they “had not seen any recently-collected specimens from (Upper) Klamath Lake that are the same as *brevirostris*” (parentheses added), that traits indicated introgression with *C. snyderi*, and that “none of the available names is applicable” to Klamath Basin populations. We examined recent specimens

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collected for a genetic study of Klamath Basin suckers to better understand their morphology and taxonomy. Genetic data support recognition of 3 of the 4 species, confirm the problematic status of **C. snyderi**, and will be reported separately. We identified specimens using key morphometric field characters, quantified those features, and then used other morphometric and meristic characters to corroborate identifications. A synopsis of each species is provided.

**STUDY AREA**

The Klamath Mountains Province and the Klamath and Rogue River basins in south central Oregon and northern California (Fig. 1) are home to many endemic species, including at least 7 fishes (Minckley et al. 1986). The region experiences the climatic interplay of the Aleutian Low and the Subtropical High leading to hot, dry summers and moderate, wet winters (Colman et al. 2004). Paleolimnological evidence from the past 45,000 years indicates Upper Klamath Lake has alternated between warm and cold water regimes over millennial time scales and has experienced over 2000 years of locally anoxic conditions after the eruption of Mt. Mazama (Bradbury et al. 2004).

In addition to the Rogue River, our genetics collections targeted 5 Klamath subbasins (Fig. 1) defined as follows: Upper Williamson—that part of the Williamson River above Klamath Marsh; Sprague—Sprague River above Chiloquin Dam, including the Sycan River; Upper Klamath—Upper Klamath Lake, lower Williamson River, lower Sprague River downstream of Chiloquin Dam, and Link River downstream of Klamath Falls; Lost River—Lost River including Clear Lake, Lower Klamath Lake, and Gerber Reservoir; and Lower Klamath—Klamath River downstream of Link River including the 3 reservoirs (J.C. Boyle, Copco, and Iron Gate) and Jenny Creek. Specimens for morphological data collected prior to the genetics collection program were also assigned to appropriate subbasins.

**MATERIALS AND METHODS**

Abbreviations for museum acronyms follow Leviton et al. (1985). We examined 1849 suckers: 1808 from the Klamath Basin and 41 from Rogue River. The most extensive data collection was on 400 adult specimens (120 **Ch. brevirostris**, 94 **D. luxatus**, 131 **C. snyderi**, and 55 **C. rimiculus**) collected for genetic analyses, of which 392 carcasses were deposited in the Oregon State University Fish Collection (8 specimens were sampled nonlethally for tissues). We attempted to obtain samples from suspected spawning groups in spring and early summer 1993–1994 and 2001, but 202 (51%) were collected outside the spawning seasons between August and November 1993 and 2001. Much additional Klamath material (1085 specimens) was obtained from juvenile collections (Markle and Simon 1993) and radiographs of the lectotype of **Ch. brevirostris** (ANSP 20950), holotype of **Ch. stomias** (USNM 48223), and holotype of **Ch. copei** USNM 48224.

Abbreviations and descriptions of counts, measurements, and nominal characters are found in the Appendix and generally follow Hubbs and Lagler (1964). All vertebral and vertical fin ray counts were taken from radiographs and did not include the 4 Weberian centra. All measurements are in millimeters. We did not measure all variables for all specimens because of damage or lack of variation detected after preliminary analyses. Lip and lower jaw deformities sometimes complicated interpretation of these structures. Two Upper Williamson **C. snyderi** had incomplete development of branchiostegal membranes, creating a long gap extending from the isthmus to the symphysis of the lower jaw (OS 15903-A, B). Other specimens, mostly **C. snyderi**, had distorted jaws and lips, both of which we attributed to fixation, but which could have been deformities.

Data were analyzed using STATGRAPHICS Plus 5.0 (Manugistics 2001). Univariate characters that were not normally distributed were evaluated using Kruskal-Wallis nonparametric ANOVA to test for significant differences with comparisons adjusted using the Bonferroni correction. The relative contributions of species identification, sex, and their interaction were evaluated with multifactor ANOVA to test for significant effects after removing the effect of the other (type III sums of squares). Multivariate analyses included principal components analyses (PCA) and discriminant functions analysis (DFA) to reduce data and uncover data structure. Overall size was estimated using a 1st principal component (PCsize) of 6 body length and depth measurements not believed to be part of the initial identification
criteria (SL, HL, LOA, LOD, DDO, and DCAUDPED). Size-adjusted shape was estimated using the projection of each measurement from PCsize and summarized as shape principal components (PCshape).

Individual ages were determined by examination of annular rings on opercles (Scoppettone 1988). G. Scoppettone read the opercles of 251 fish and provided results.

**RESULTS**

**Initial Identification**

Except for 8 nonlethally sampled specimens, every preserved specimen was assigned to a species based on overall appearance, lip morphology, and our collective intuitive judgment (Douglas et al. 1989).

Length of the distance of contact between the left and right lower lips (GAPLMM) sorted specimens into recognizable groups, *Catostomus* species and *D. luxatus* plus *Ch. brevirostris* (Fig. 2). There was some difference in the slope of regression of lower lip gap and SL between the 2 *Catostomus* (*P* = 0.06, adjusted *r*² = 56.5%) but not between *D. luxatus* and *Ch. brevirostris* (*P* = 0.86, adjusted *r*² = 59.0%; Fig. 2). The 2 groups (*Catostomus* spp. and lake suckers), however, were different (*P* = 0.001). *Catostomus* species generally had a long contact distance (no lower lip gap), but 9.1% of *C. riminulus* (*n* = 55) and 7.2% of *C. snyderi* (*n* = 125) had lower lip gaps. In *Ch. brevirostris* 98.3% had a lower lip gap, and in *D. luxatus* 94.4% had a lower lip gap. The lower lip gap develops early and is present in young-of-the-year juveniles (Fig. 3). In 103 *Ch. brevirostris* 27.9–90.2 mm SL from Upper Klamath Lake (OS 13969, 13982), only 2 lacked a lower lip gap while all 51 *C. snyderi* from the Upper Williamson River (OS 13882) lacked a lower lip gap.

The posterior margin of the lower lip (LLLRM; Fig. 4) was posteriad of the ventro-posterior corner of the maxilla in 100% of *C. riminulus*, even or posteriad in 84.2% of *C. snyderi*, even or anteriad in 98.3% of *Ch. brevirostris*, and anteriad in 100% of *D. luxatus*. Lip size and presence of a gap were related: specimens with small lips ending anteriad of the maxilla had a gap in 86% of specimens, those with lips even with the corner of the maxilla had a gap in 68%, and those with the largest lips had a gap in only 10%. Expressed as a ratio to eye diameter, the GAPLMM measurement generally fell into 2 categories: less than or greater than 50% (Fig. 5).

In general, the overall appearance was of long-snouted (*D. luxatus* and *C. riminulus*) or short-snouted (*C. snyderi* and *Ch. brevirostris*) forms and big-lip (*C. riminulus* and *C. snyderi*) or small-lip (*D. luxatus* and *Ch. brevirostris*)
forms (Fig. 6). Two ratios (GAPLMM/EYE and LAE/HD) result in 4 distinct morphotypes (Fig. 6). The LAE/HD ratio is >0.75 in 95% of D. luxatus, <0.75 in 95% of Ch. brevirostris, and <0.76 in 95% of C. snyderi.

Morphometry

PCsize accounted for 95.3% of the variance (n = 390) of 6 body length and depth measurements not believed to be part of the initial identification criteria (SL, HL, LOA, LOD, DDO, and DCAUDPED). The 2 PCshape axes accounted for 58.5% and 19.3% (77.8% total) of variance in the residual data. Mean scores of both PCshape axes were significantly different among species (P = 0.0001) with the 1st axis separating D. luxatus and Ch. brevirostris from the Catostomus species and the 2nd axis separating D. luxatus and C. rimi culus from the other 2. However, there was considerable dispersion in the data. A DFA of the shape projections correctly classified only 53.1% of specimens, but classification success varied greatly: C. rimiculus, 76.4%; D. luxatus, 63.3%; Ch. brevirostris, 57.6%; and C. snyderi, 31.5%. The most frequently misclassified species was C. snyderi, which had an almost equal probability of being classified as one of the other species (18.9%–29.1%). When restricted to fish from Upper Klamath, Upper Williamson, and Sprague subbasins, classification success was 51.5%, and when restricted to Lost River subbasin, classification success was 57.4%.

Exploratory analyses had shown that some characters were sexually dimorphic. For example, the ratio of pectoral fin length to snout to anus distance (LP1/LOA) was sexually dimorphic in all except D. luxatus (Fig. 7). Males generally had longer pectoral fins and females generally had longer pre-anal lengths, so the ratio of LP1/LOA was larger (25.4%) in males than females (23.6%), and means were significantly different (P < 0.0001) in all species except D. luxatus. Measurements associated with these features (LP1, LP1P2, LOA, LOD) were regressed on PCsize and residuals used in PCA. When size is thus removed, males still had longer pectoral fins (LP1) and shorter trunk distances (LP1P2, LOA, LOD), but only Ch. brevirostris showed significant sexual dimorphism.

Head length as a proportion of SL decreased with size and increased with age in all species except D. luxatus, in which HL/SL increased with both. For example, for 87 Ch. brevirostris, HL/SL = 0.268 + 0.0019 * AGE – 0.00014 * SL (Fig. 8; all standardized residuals <2.85, coefficients P < 0.0001, and adjusted r² = 38.8%). Age contributed more to the regression (t = 7.1) than SL (t = –4.7). Type material of 4 nominally “pure” Ch. brevirostris reported by Miller and Smith (1981) had larger heads for their size than our material. Using the above relationship, we would estimate those 4 specimens (Miller and Smith 1981: Table 4) to be 29–40 years old.

![Fig. 2. Relationship between GAPLMM and SL in Klamath and Rogue River suckers.](image-url)
Fig. 3. Lower lips of juvenile suckers, 97–107 mm SL. A and B, *C. snyderi*, OS 13739; C and D, *Ch. brevirostris*, OS 13754.

Fig. 4. Lips of Klamath Basin suckers, showing position of posterior margins ending anterior to (A, OS 15925B, LRS), even with (B, OS 15966D, SNS), or posterior to (C, OS 15894F, KLS) ventroposterior corner of maxillary (arrows); presence of lower lip gaps (D and E); and absence of lower lip gap (F).
Meristic Characters

The number of gill rakers (GILRKRANT) on the 1st arch had a strong ontogenetic or size signal (Fig. 9). The relationship for each species was expressed as gill rakers = A + B/SL. The coefficients, \( r^2 \), and sample sizes (\( n \)) were: 
- **C. rimiculus**: \( A = 26.1, B = -365, r^2 = 32.3, n = 64 \)
- **C. snyderi**: \( A = 35.1, B = -371, r^2 = 72.3, n = 257 \)
- **D. luxatus**: \( A = 29.4, B = -291, r^2 = 53.9, n = 201 \)
- **Ch. brevirostris**: \( A = 39.9, B = -453, r^2 = 58.0, n = 565 \)

All species approach an asymptote at about 200 mm SL (Fig. 9) with the predicted number of gill rakers progressing from a low of 26.1 in **C. rimiculus** to a high of 39.6 in **Ch. brevirostris**.

Number of gill rakers was significantly higher (\( P = 0.0001 \)) in Rogue **C. rimiculus** (\( \bar{x} = 25.6, n = 30 \)) than in Klamath **C. rimiculus** (\( \bar{x} = 24.2, n = 24 \)).

Groups of similar counts were significantly correlated. For example, all scale counts had Spearman rank correlations from 0.34 to 0.94 and \( P < 0.0001 \); and all lateralis pore counts had Spearman rank correlations of 0.35–0.74 and \( P < 0.0001 \). A reduced subset of 5 characters (GILRKRANT, LLSCALES, PAPUPRLIP, PCV, and CV) with complete data for 368 specimens provided species discrimination similar to the full data set. The first 2 PCA axes accounted for 39.0% and 24.1% (63.1% total) of the variance in the data set. A backwards stepwise DFA retained all 5 characters (Fig. 11A) and

![Graphs showing frequency of gill rakers](image-url)
correctly classified 87.6% of specimens. The most frequently misclassified species was *C. snyderi* (79.5% correct), which was generally (18.9%) misclassified as *Ch. brevirostris*. When restricted to the Lost River subbasin (*n* = 114), the DFA correctly classified 76.3%, and the most frequently misclassified species was *C. snyderi* (40% correct); it was most frequently (57.1%) misclassified as *Ch. brevirostris*. When Lost River subbasin (Fig. 11B) is excluded (*n* = 254), the DFA correctly classified 96.5%, and the most frequently misclassified species was *D. luxatus* (91.4% correct).

Sexual dimorphism was detected in 2 vertebral characters (VAO and PCV) when species effects were removed in multifactor ANOVAs (*P* < 0.02, interaction not significant). Males tended to have more precaudal vertebrae and females had more vertebrae to the anal fin origin. Differences were slight, amounting to mean differences in the range of 0.21–0.27 vertebrae. Our DFA of the 5 meristic characters for each sex slightly improved classification for males (88.9%) but not for females (86.7%).

**Synopsis of Four Species**

*Catostomus rimiculus* has an elongate body with a trunk tending toward a uniform height (Fig. 12); a relatively deep caudal peduncle (60%–71% HD); a long, angular snout; and large, fleshy, papillose lips with quite large lower lip lobes, extending well posteriad of ventroposterior corner of maxilla, and in contact along midline for a distance greater than 50% of eye diameter. There are 22–27 gill rakers in adults >200 mm SL and 42–45 post-Weberian vertebrae (98% with 44 or less). The dorsal fin origin was farther back in Rogue River *C. rimiculus* (Fig. 12), and these had fewer caudal vertebrae (Rogue mean = 18.7, *n* = 30 vs. Klamath mean = 19.7, *n* = 25), more vertebrae in front of the dorsal fin origin (Rogue mean = 15.0, *n* = 30 vs. Klamath mean = 13.7, *n* = 25), and a higher LOD/SL ratio (Rogue mean = 49.2%, *n* = 30 vs. Klamath mean = 47.8%, *n* = 25). All differences were significant (*P* < 0.001), and only the LOD/SL ratio had a sexually dimorphic component (females longer).

*Deltistes luxatus* is large (up to 1 m), and it has an elongate body with a trunk tending toward a uniform height or rising to the dorsal base (Figs. 13A, B); a relatively shallow caudal peduncle depth (40%–66% HD); a long, angular snout; and small lips with a gap in lower lobes ending anteriad of ventroposterior corner of maxilla (Figs. 13C–E). There are 23–37 (only 3 with >34) gill rakers in adults >200 mm SL and 44–48 post-Weberian vertebrae (86% with 45 or more). Lost River subbasin *D. luxatus* averaged significantly more vertebrae than those from Upper Klamath Lake (46.1, *n* = 17 vs. 45.1, *n* = 73; *P* = 0.0001); significantly more cephalic pores, for example, more infraorbital pores (38.1, *n* = 16 vs. 30.8, *n* = 73; *P* = 0.0001); and significantly smaller scales, for example, more lateral line scales (90.4, *n* = 16 vs. 81.1, *n* = 72; *P* = 0.000006).

*Catostomus snyderi* has a moderately deep body (Fig. 14); relatively shallow caudal peduncle depth (47%–66% HD); a short, rounded snout; large papillose lips ending posteriad of (68%), even with (13%), or anteriad of (18%)
ventroposterior corner of maxilla, with the lower lip gap absent in 93%; 29–40 gill rakers in adults >200 mm SL reaching adult modal count of 35.1; and 40–46 post-Weberian vertebrae (97.5%, 42–44). This was the most frequently misclassified species. There were noticeable geographic differences in head size in *C. snyderi*: for fish >300 mm SL, the average HL/SL ratios were 0.25 (Upper Williamson, n = 17), 0.24 (Lost River, n = 24), and 0.23 (Sprague, n = 26), and a Bonferroni multiple range test showed significant differences (*P* = 0.0001). The PCsize-adjusted head length showed similar trends, but only the small-headed Sprague River fish were significantly different.

*Chasmistes brevirostris* has a moderately elongate body generally rising toward the dorsal (Fig. 15); relatively shallow caudal peduncle depth (44%–68% HD); small lips ending posteriad of (2%), even with (28%), or anteriad of (70%) ventroposterior corner of maxilla, with a lower lip gap present in 98%; 30–45 gill rakers in adults >200 mm SL reaching adult modal count of 39.9; and 41–44 post-Weberian vertebrae. Regional differentiation was most apparent in gill rakers: those from the Lost River subbasin had a mean of 35.8 (n = 66), while Upper Klamath and Klamath River *C. brevirostris* had a mean of 39.3 (n = 45).

**DISCUSSION**

Considering their current classification in 3 genera, the 4 Klamath Basin suckers were remarkably similar. The suite of morphological characters used for initial identification received mixed support, being poorly supported by other morphometric characters but well supported by meristic characters, especially when analyses were restricted geographically (Fig. 11). For some morphometric characters, sexual dimorphism and age confound interspecific signals (Figs. 7, 8). For all 4 species, there were also intraspecific geographic differences.

The great overlap in morphological characters between *C. snyderi* and *Ch. brevirostris* raises the question of their specific identity. They can be readily distinguished by lip morphology (Figs. 3, 4), different ontogenetic trends in gill raker counts (Fig. 9), and different local geographic distributions, although they are widely sympatric and identification of individuals can be problematic. In the Sprague River at Chiloquin Dam, the 2 species also have different timing of their reproductive runs. For example, in 2000 most *C. snyderi* passed through the ladder between 15 March and 5 April, while most *Ch. brevirostris* passed between 12 April and 5 May (R. Shively, USGS, Biological Resources Division, personal communication, January 2001). At springs in Upper Klamath...
Lake, ripe *C. snyderi* have not been collected with spawning *Ch. brevirostris* during collections over the past decade (L. Dunsmoor, Klamath Tribes, personal communication, August 2001). Tagging results in Klamath Basin show shoreline lake-spawners and river-spawners of *Ch. brevirostris* and *D. luxatus* seldom mix. Only 1 of 311 Lost River suckers tagged from 1985 to 1999 during spawning at in-lake springs in Upper Klamath Lake has been recaptured.

![Fig. 9. Relationships between gill rakers and size in Klamath and Rogue River suckers: A, *Catostomus* species; B, *Ch. brevirostris* and *D. luxatus.*](image)

![Fig. 10. Relationship between gill rakers and size in *Ch. brevirostris* with ontogenetic regression model. Box encloses values reported by Miller and Smith (1981) for nominally “pure” specimens.](image)
Thus, lake-spawning *Ch. brevirostris* are largely spatially segregated, and river-spawning *Ch. brevirostris* are temporally segregated from *C. snyderi* in the upper subbasins. Although the temporal modes of river-spawning fish differ, there is overlap and the 2 species co-occur on spawning grounds. It is not clear if similar spatial and temporal segregation functions in the Lost River subbasin. Although this spatial and temporal segregation does not preclude hybridization in the upper subbasins, it suggests that opportunities are reduced. There is more opportunity for interbreeding between the 2 lake suckers, but they are morphologically more distinct, suggesting less introgression.

Gilbert (1898:4) recognized 2 species of *Chasmistes* in Upper Klamath Lake which were “so similar in all their characters that it is difficult to decide to which one the name *brevirostris* properly belongs.” One with “a smaller, more nearly horizontal mouth” he referred to *Ch. brevirostris*, while he described the new species, *Ch. stomias*, which had “a larger, deeper head, with larger, more obliquely

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**Fig. 11.** Discriminant functions analysis of 5 meristic characters: A, all samples (*n* = 370); B, Upper Klamath, Upper Williamson, and Sprague subbasins (*n* = 191).
placed mouth” (Fig. 15C). Cope’s (1879) description of *Ch. brevirostris* gives few clues, though he mentions that the Klamath Tribe name is “Xoooptu,” and that the Tribe did not observe it ascending the Williamson River in spring with *D. luxatus* and *Catostomus*. Gilbert (1898), on the other hand, says his *Ch. stomias* is called “K-ahp-tu” by the Klamath Tribe, and the form he refers to as *Ch. brevirostris* is not distinguished from *C. snyderi* by the Tribe, who call both “Yen.” In the 19th century it appears that the Klamath Tribe recognized a large-headed, lake-spawning fish and a small-headed, river-spawning fish in this complex. Gilbert (1898:4) recognized 2 species within the small-headed form: one with “lips thin, the lower interrupted at symphysis” (lower lip gap present), which he called *C. brevirostris* Cope; and the other with “lower lip deeply incised, with one or 2 papillae between symphysis and base of cleft” (lower lip gap absent) that he named *C. snyderi*. The 2 smaller-headed forms still exist as fish we call *Ch. brevirostris* and *C. snyderi*, but the former spawns both in Upper Klamath Lake and in the Williamson River.

Two related questions remain. What happened to the large-headed fish, and what is the correct name to apply to extant fish? Head size clearly shows age and size variation in both species (Fig. 8). Gilbert’s 3 syntypes of *Ch. stomias* are part of the nominally “pure” *Ch. brevirostris* of Miller and Smith (1981) and have head lengths that are longer (28.4%–30.3% SL) than recent specimens. Gilbert’s values for 3 short-headed *Ch. brevirostris* (22%–23.5% SL) are lower but within the range seen for current specimens (21.7%–27.5% SL). Head size in these fish has a complex ontogeny, becoming smaller with size but larger with age (Fig. 8). An old, slow-growing fish will have a larger head than a young, fast-growing fish. Our *C. snyderi* and *Ch. brevirostris* had an average age <9 years, and we estimate that Miller and Smith’s (1981) 4 nominally “pure” specimens were 29–40 years old. Large-headed fish may be old, slow-growing, lake-spawned fish, may have come from an extinct population (see discussion below), or may represent an extinct species (Miller and Smith 1981). If one is willing to accept either of the first 2 explanations, both the large-headed fish and extant populations could be referred to *Ch. brevirostris*.

Ecological changes in the Klamath Basin include hypereutrophication of Upper Klamath Lake, blocking of upstream Sprague River migration by Chiloquin Dam, irrigation diversions, loss of wetland habitat, and introductions of exotic fishes (Scoppettone and Vinyard 1991, Simon and Markle 1997, Kann and Smith 1999, Martin and Saiki 1999, Markle and Cooperman 2002). There has also been loss of spawning

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**Fig. 12.** Left lateral view of *C. riniculus*: A, Klamath River at J.C. Boyle Reservoir, OS 15909-G, 336 mm SL, female; B, Rogue River, OS 15913-D, 333 mm SL, female.
groups, especially of shoreline spawners in places such as Harriman Springs in Upper Klamath Lake (Markle and Cooperman 2002). Some of the temporal changes in morphology described above and by Miller and Smith (1981) could be due to differential sampling of these fish in the 1800s, growth rate responses to changing population densities or habitat, or hybridization.

Freshwater lakes are sites of many taxonomic problems in ichthyology that parallel the situation in Klamath Basin suckers. Lake fishes often display morphological differences in feeding-related structures (Fryer and Iles 1972, Schluter and McPhail 1992), frequently involving gill raker morphology such as in Great Lakes coregonids (Smith and Todd 1984), British Columbia sticklebacks (McPhail 1984), New Zealand smelt (Ward et al. 1989), and Klamath Basin suckers. Smith (1992b:165) notes that “differentiation in lacustrine species flocks is dominated by ecologically adaptive characters—these are usually apomorphic for intralacustrine clades, and often convergent in other species at similar depths.”

Our evidence supports Miller and Smith’s (1981) suggestion of some introgression between *Ch. brevirostris* and *C. snyderi*, especially in the Lost River subbasin. However, we disagree with the conclusion that “recently-collected specimens from (Upper) Klamath Lake” are not the same as *Ch. brevirostris*. We believe it is the appropriate name to apply to the lake-dwelling form, especially in Upper Klamath Lake. We also agree with those authors that a large-headed, thin-lipped, oblique-mouthed form is much rarer in current collections. Its head size, at least, is consistent with old, slow-growing fish that may have been more common when the system was less eutrophic and the population size larger (Markle and Cooperman 2002). Gilbert’s (1898)
Fig. 14. Morphological variation in *C. snyderi*: A, *C. snyderi*, Sprague River at Chiloquin, OS 12811, 385 mm SL, drawing by J. Tomelleri; B, *C. snyderi*, Upper Williamson at Rocky Ford, OS 15903-A, 295 mm SL; C, *C. snyderi*, Sprague River at Chiloquin Dam, OS 15893-A, 375 mm SL; D, *C. snyderi*, Lost River at Gerber Reservoir, OS 15943-B, 374 mm SL.
evidence also suggests that the forms we see today were present in the 19th century in Upper Klamath Lake and not a new product of recent anthropogenic changes. Although Chiloquin Dam may have interfered with spatial partitioning of spawning between these species in the Sprague River, seasonal differences in spawning (Scoppettone and Vinyard 1991; R. Shively, personal communication, January 2001) do not appear to have been affected by anthropogenic events, and thus an important reproductive isolating mechanism remains in the Upper Klamath Lake subbasin. The situation is less clear in the Lost River subbasin where meristic differences between *Ch. brevirostris* and *C. snyderi* blurr considerably and there is little information about spatial or temporal spawning patterns.

Fig. 15. A, *Ch. brevirostris*, Sprague River at Chiloquin, OS 5306, 365 mm SL, drawing by J. Tomelleri; B, *Ch. brevirostris*, Upper Klamath Lake at Oxxy Spring, OS 15953-A, 342 mm SL; C, large-headed, thin-lipped lake form of *Ch. brevirostris*, holotype of *Ch. copei*, USNM 48224.
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University).

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APPENDIX. Description of meristic, morphometric, and nominal characters used in morphological analyses.

<table>
<thead>
<tr>
<th>Meristics</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>PCV</td>
<td>Post-Weberian precaudal vertebrae without a definite hemal spine even if a hemal arch was present</td>
</tr>
<tr>
<td>CV</td>
<td>Post-Weberian caudal vertebrae with a definite hemal spine including urostyle</td>
</tr>
<tr>
<td>INTER1DFP</td>
<td>Number of vertebrae anterior to first dorsal fin pterygiophore including vertebra immediately posterior to point of interdigitation with neural spines</td>
</tr>
<tr>
<td>VDO</td>
<td>Number of vertebrae anterior to a vertical from base of first dorsal fin ray including vertebra intersected by the vertical</td>
</tr>
<tr>
<td>VAO</td>
<td>Number of vertebrae anterior to a vertical from base of first anal fin ray including vertebra intersected by the vertical</td>
</tr>
<tr>
<td>VPO</td>
<td>Number of vertebrae anterior to a vertical from base of first pelvic fin ray including vertebra intersected by the vertical</td>
</tr>
<tr>
<td>GILRKRAKT</td>
<td>Number of gill rakers on lateral surface of first gill arch</td>
</tr>
<tr>
<td>PGRVAGR</td>
<td>Number of gill rakers on medial surface of first arch anteriad of all gill rakers on the lateral surface of the arch</td>
</tr>
<tr>
<td>PREOPMNPOR</td>
<td>Preoperculomandibular pores</td>
</tr>
<tr>
<td>INFORBPOR</td>
<td>Infraorbital pores</td>
</tr>
<tr>
<td>SUPORBPOR</td>
<td>Supraorbital pores</td>
</tr>
<tr>
<td>LLSCALES</td>
<td>Lateral line scales</td>
</tr>
<tr>
<td>LLPECTPOR</td>
<td>Number of lateralis pores on cleithrum from supratemporal canal to first lateral line scale</td>
</tr>
<tr>
<td>DSCALEROW</td>
<td>Diagonal scale rows</td>
</tr>
<tr>
<td>SCALEADF</td>
<td>Scales anterior to dorsal fin</td>
</tr>
<tr>
<td>SCALABVLL</td>
<td>Scales above lateral line</td>
</tr>
<tr>
<td>SCALBELOLL</td>
<td>Scales below lateral line</td>
</tr>
<tr>
<td>PAPUPRLIP</td>
<td>Rows of papillae at symphysis of upper lip</td>
</tr>
<tr>
<td>PAPLORLIP</td>
<td>Rows of papillae at symphysis of lower lip</td>
</tr>
<tr>
<td>SACACAPDF</td>
<td>Scales around caudal peduncle</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Morphometrics</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>SL</td>
<td>Standard length (measurements made on preserved specimens)</td>
</tr>
<tr>
<td>LAE</td>
<td>Snout length</td>
</tr>
<tr>
<td>LPE</td>
<td>Distance from tip of snout to posterior margin of eye</td>
</tr>
<tr>
<td>HL</td>
<td>Head length</td>
</tr>
<tr>
<td>IW</td>
<td>Interorbital width at narrowest point</td>
</tr>
<tr>
<td>WPI</td>
<td>Width of body at pectoral fin bases</td>
</tr>
<tr>
<td>DPI</td>
<td>Depth of body at anterior margin of pectoral fin bases</td>
</tr>
<tr>
<td>DDO</td>
<td>Depth of body at dorsal fin origin</td>
</tr>
</tbody>
</table>
### Morphometrics (continued)

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>LOP2</td>
<td>Distance from tip of snout to pelvic fin origin</td>
</tr>
<tr>
<td>LOP1_LOP2</td>
<td>Distance from pectoral fin origin to pelvic fin origin</td>
</tr>
<tr>
<td>LOD</td>
<td>Pre-dorsal length</td>
</tr>
<tr>
<td>LID</td>
<td>Distance from tip of snout to insertion of dorsal fin</td>
</tr>
<tr>
<td>LOA</td>
<td>Pre-anal length</td>
</tr>
<tr>
<td>LIA</td>
<td>Distance from tip of snout to insertion of anal fin</td>
</tr>
<tr>
<td>LDA</td>
<td>Distance from dorsal fin origin to anal fin origin</td>
</tr>
<tr>
<td>LDOC</td>
<td>Distance from dorsal fin origin to middle of caudal fin base</td>
</tr>
<tr>
<td>LDIC</td>
<td>Distance from dorsal fin insertion to middle of caudal fin base</td>
</tr>
<tr>
<td>CPD</td>
<td>Least caudal peduncle depth</td>
</tr>
<tr>
<td>LP1</td>
<td>Length of longest pectoral fin ray</td>
</tr>
<tr>
<td>LP2</td>
<td>Length of longest pelvic fin ray</td>
</tr>
<tr>
<td>LPEOD</td>
<td>Distance from posterior margin of eye to origin of dorsal fin</td>
</tr>
<tr>
<td>LPOA</td>
<td>Distance from pelvic fin origin to anal fin origin</td>
</tr>
<tr>
<td>SPMLL</td>
<td>Projected distance from tip of snout to posterior margin of lower lip with mouth closed</td>
</tr>
<tr>
<td>LDMM</td>
<td>Distance from symphysis of lower jaw to lateroposterior margin of lower lip lobe</td>
</tr>
<tr>
<td>GAPLMM</td>
<td>Distance from dorsal symphysis of lower jaw to point where lower lip lobes separate or thickness of lower jaw if lobes not in contact</td>
</tr>
<tr>
<td>AIOPAE</td>
<td>Distance from anterior most infraorbital pore to anterior margin of eye</td>
</tr>
<tr>
<td>SAIOP</td>
<td>Distance from tip of snout to anterior most infraorbital pore</td>
</tr>
<tr>
<td>POMMM</td>
<td>Perimeter of mouth</td>
</tr>
<tr>
<td>AOMMM</td>
<td>Area of mouth</td>
</tr>
</tbody>
</table>

### Nominal

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
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</thead>
<tbody>
<tr>
<td>LLGAP</td>
<td>Gap between lower lip lobes: ( Y ) = present when lower lip lobes do not contact; ( N ) = absent when lower lip lobes contact; ( T ) = teratological; ( A ) = when a gap is present anteriorly but lips touch posteriorly</td>
</tr>
<tr>
<td>LLLRM</td>
<td>Posterior extent of lower lip scored relative to a vertical through ventroposterior corner of maxilla: ( A ) = lip ending anterior to; ( E ) = even with; and ( P ) = posterior to vertical</td>
</tr>
<tr>
<td>VERTFUSION</td>
<td>Presence (( Y )) or absence (( N )) of fusion among vertebrae</td>
</tr>
<tr>
<td>GRFUSION</td>
<td>Presence (( Y )) of absence (( N )) of fusion among gill rakers</td>
</tr>
<tr>
<td>LTNASALFLP</td>
<td>Condition of left nasal flap: ( A ) = absent; ( D ) = deformed; ( C ) = nare; ( N ) = does not cover nare</td>
</tr>
<tr>
<td>RTNASALFLP</td>
<td>Condition of right nasal flap: ( A ) = absent; ( D ) = deformed; ( C ) = nare; ( N ) = does not cover nare</td>
</tr>
<tr>
<td>PREOPBRANCH</td>
<td>Branching (( Y )) or absence (( N )) of branching in preoperculomandibular canal</td>
</tr>
<tr>
<td>INFBRANCH</td>
<td>Branching (( Y )) or absence (( N )) of branching in infraorbital canal</td>
</tr>
<tr>
<td>SUPBRANCH</td>
<td>Branching (( Y )) or absence (( N )) of branching in supraorbital canal</td>
</tr>
</tbody>
</table>