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DISTRIBUTION AND EVOLUTION
OF *CHASMISTES* (PISCES: CATOSTOMIDAE)
IN WESTERN NORTH AMERICA

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INTRODUCTION

The lakesuckers of the genus *Chasmistes* are midwater planktivores with numerous, dendritic gill rakers and large, terminal mouths. The terminal position of the mouth is so exceptional among the usually ventral-mouthed sucker family that it has been regarded as an extreme specialization, although certain primitive suckers (*Amyzon*, *Ictiobus cyprinellus*) and presumed sucker ancestors had or have terminal mouths. In the early larval stages *Catostomus* and other suckers have terminal mouths (Stewart, 1926: Fig. 21; Jones et al., 1978:275-297). In *Catostomus* and *Chasmistes* the mouth becomes ventral by 30 mm SL (Figs. 1,2), but the mouth of *Chasmistes* eventually becomes oblique (Figs. 4,6,7,9). The bones involved in these modifications are the dentary, maxilla, and premaxilla.

Chasmistes is the best-known genus of American Cenozoic freshwater fishes, occurring in Pleistocene to Miocene deposits of six western states, including a number of basins where the genus no

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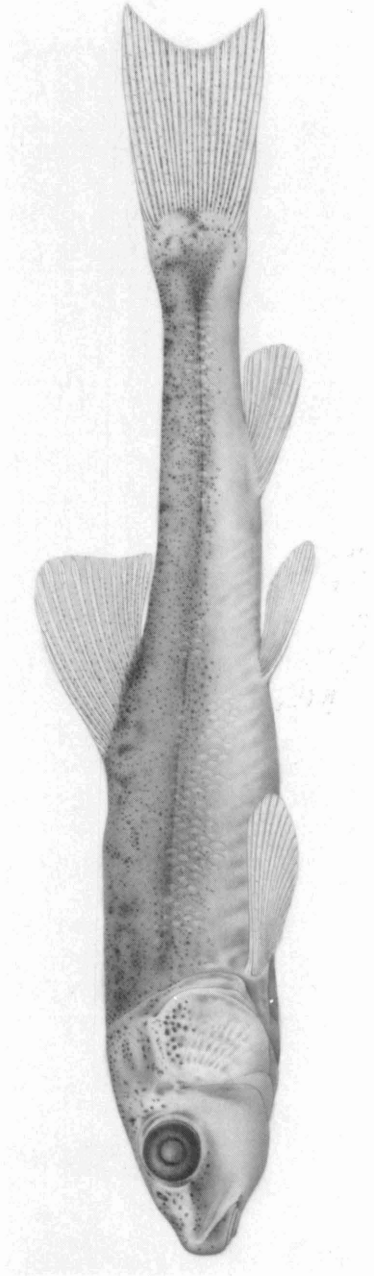


FIG. 1. Juvenile *Chasmistes cujus* (UMMZ 137054, 32 mm S.L.), drawn by Mark Orsen.

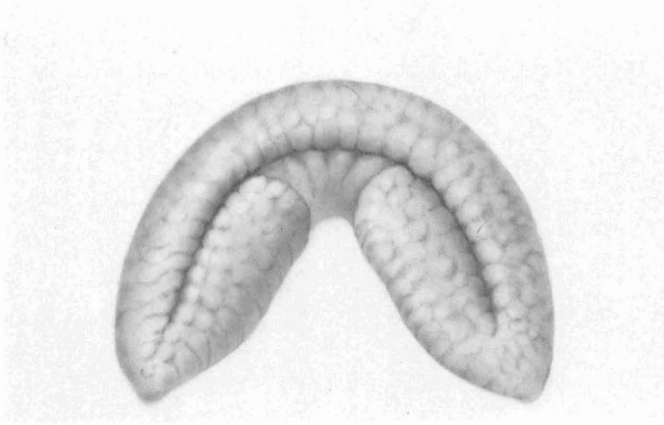


FIG. 2. Lips of juvenile *Chasmistes cujus* (UMMZ 137054, 32 mm S.L.), drawn by Mark Orsen. Separation of the lower lobes is a key character for *Chasmistes*.

longer survives (Fig. 3). Divergence and extinction have occurred in the late Cenozoic lakes of western North America to which it is or was endemic. Three contemporary species once provided a large part of the subsistence fishery for Amerinds and early settlers around Utah, Pyramid, and Klamath lakes. Now, however, only one of these, *Chasmistes cujus* Cope, survives in pure form and it is recognized as an endangered species (Koch, 1973; Miller, 1979). A fourth contemporary species, described below, is evidently now extinct.

In this paper we review the fossil and Recent species of *Chasmistes*, describe two new taxa, and discuss the distribution and evolution of the genus.

NOMENCLATURE

Synonymy of the Genus *Chasmistes* Jordan

Jordan, D. S., 1878a, Bull. U.S. Geol. and Geogr. Surv. (Hayden Surv.), 4(2):417. Type: *Catostomus fecundus* Cope and Yarrow (by original designation in footnote).

Jordan, D. S., 1878b, Bull. U.S. Nat. Mus., no. 12:149–151. More elaborate description of *Chasmistes*. Type: *Catostomus fecundus* Cope

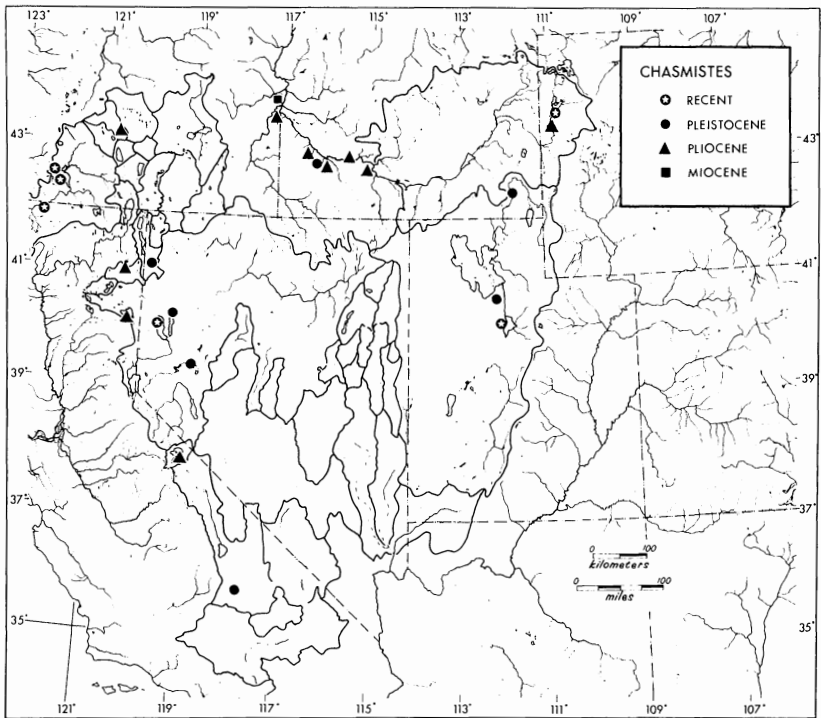


FIG. 3. Distribution of fossil and Recent *Chasmistes*.

and Yarrow [60–65 sc. in lat. line]. Description (brief) of *Chasmistes fecundus* (Cope and Yarrow), followed by a listing of specimens in U.S. Nat. Mus.

Jordan, D. S., 1878b, op. cit.:219. Reexamined *C. fecundus* with the specimens on which the genus *Chasmistes* is based, and concluded that the species was new and here described it as *Chasmistes liorus*, sp. nov. "*Chasmistes fecundus*" of Cope and Yarrow was referred back to the genus *Catostomus* as *C. fecundus* Cope and Yarrow.

Cope, E. D., 1881, Am. Nat., 15:59. Orig. descr. *Lipomyzon*; type species = *Chasmistes brevisrostris* Cope, designated by Jordan and Gilbert, 1883:132.

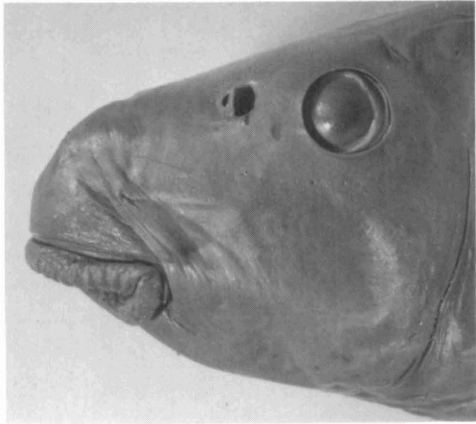
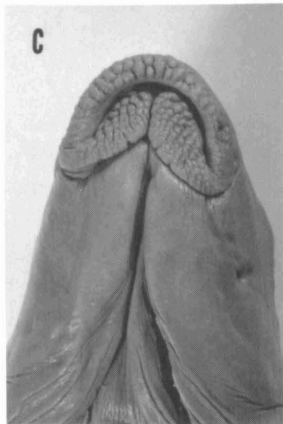
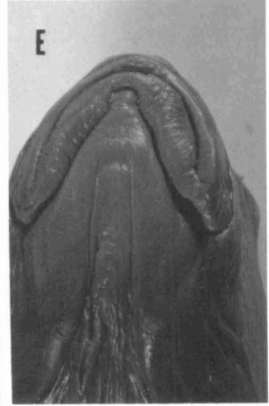
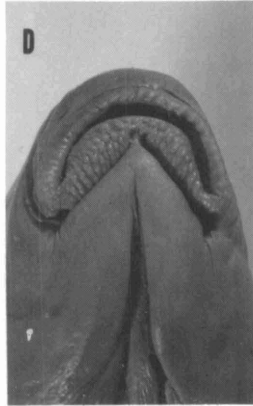
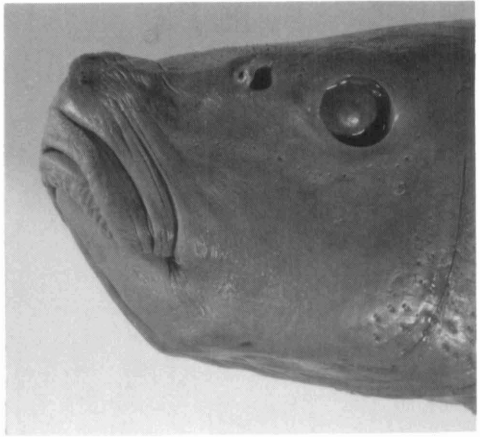
Jordan, D. S., and C. H. Gilbert, 1883 (1882), Bull. U.S. Nat. Mus., no. 16:131. *Chasmistes* Jordan. Type: *Chasmistes liorus* Jordan.

- Cope, E. D., 1883, Proc. Acad. Nat. Sci. Phila., 1883:148–150. Diagnoses and revises *Chasmistes*, including *liorus*, *brevirostris*, *luxatus*, and *cujus* sp. nov.; *Lipomyzon* relegated to synonymy of *Chasmistes*.
- Jordan, D. S., 1887, Rept. U.S. Comm. Fish and Fish., 1885:806. List of species of *Chasmistes*: *C. liorus*, *C. brevisrostris*, *C. luxatus*, *C. cujus*.
- Jordan, D. S., 1891, Bull. U.S. Fish Comm., IX:30–31. Collection of *C. liorus* in Utah Lake, summer, 1889; listing of this species and *Catostomus fecundus* from Utah Lake.
- Jordan, D. S., and B. W. Evermann, 1896, Bull. U.S. Nat. Mus., 47(1): 183. Type specimen of *Chasmistes liorus* designated as USNM 27361.
- Fowler, H. W., 1913, Proc. Acad. Nat. Sci. Phila., 1913:53. Argues that *Lipomyzon* is only available generic name for *brevirostris* and large-mouthed [lake] suckers because *fecundus*, the original type species of *Chasmistes*, is a *Catostomus*; erects subgenus *Pithecomyzon* for *Chasmistes cujus*.

ETYMOLOGY.—From the Greek, meaning one who yawns, in reference to the large, oblique mouth.

THE GENERIC NAME.—The nomenclatural history is complex. In erecting the genus, Jordan (1878a:417) diagnosed it in a footnote and designated *Catostomus fecundus* Cope and Yarrow (1875:678–679, Pl. 32, Figs. 1, 1a) as its type. Later in the same year Jordan (1878b:149–151) gave a detailed description of *Chasmistes*, stated that it occurred only in Utah Lake, listed the material then known (all in the U.S. National Museum) which was collected by Yarrow and Henshaw in 1872, and cited USNM 20932 (now=75832) as the type species of *Chasmistes*. In an addendum to that paper, Jordan (1878b:219) re-compared *Catostomus fecundus* Cope and Yarrow with the specimens on which *Chasmistes* was based, concluded that the type species of *Chasmistes* was incorrectly identified and was undescribed, and proposed the name *Chasmistes liorus* for it. This proposal was followed by a description of *Catostomus fecundus* and reference to two lots of specimens (USNM 12984 and an unnumbered lot) that comprised part of the syntypes of that species.

Article 70 of the International Code of Zoological Nomenclature (1964:73) assumes that an author correctly identifies the nominal species designated as the type species of a new genus. If it is discovered that the type species was misidentified, the case is to be referred to the Commission. However, since in this instance the discovery was made by the original author within the same year that the new genus was proposed, since *Chasmistes liorus* Jordan is not con-



generic with *Catostomus fecundus* Cope and Yarrow but is related to the several other species of *Chasmistes* (both living and fossil), and since the generic name *Chasmistes* has been widely used for nearly 100 years, the logical course is to accept as the type of *Chasmistes* the actual species on which it was based. (See also Fowler, 1913:53, and Snyder, 1917:50.) A drawing of *Chasmistes liorus* is given in Jordan and Evermann (1900:Pl. 34, Fig. 85), based on USNM 3042 (=27361?) collected by Jordan in Utah Lake, probably in the summer of 1889 (see Jordan, 1891:30–31). However, this is evidently not the holotype of *C. liorus*, as claimed by Jordan and Evermann (1896:183) for USNM 27361, since an earlier type designation was made by Jordan (1878b:151) as explained above.

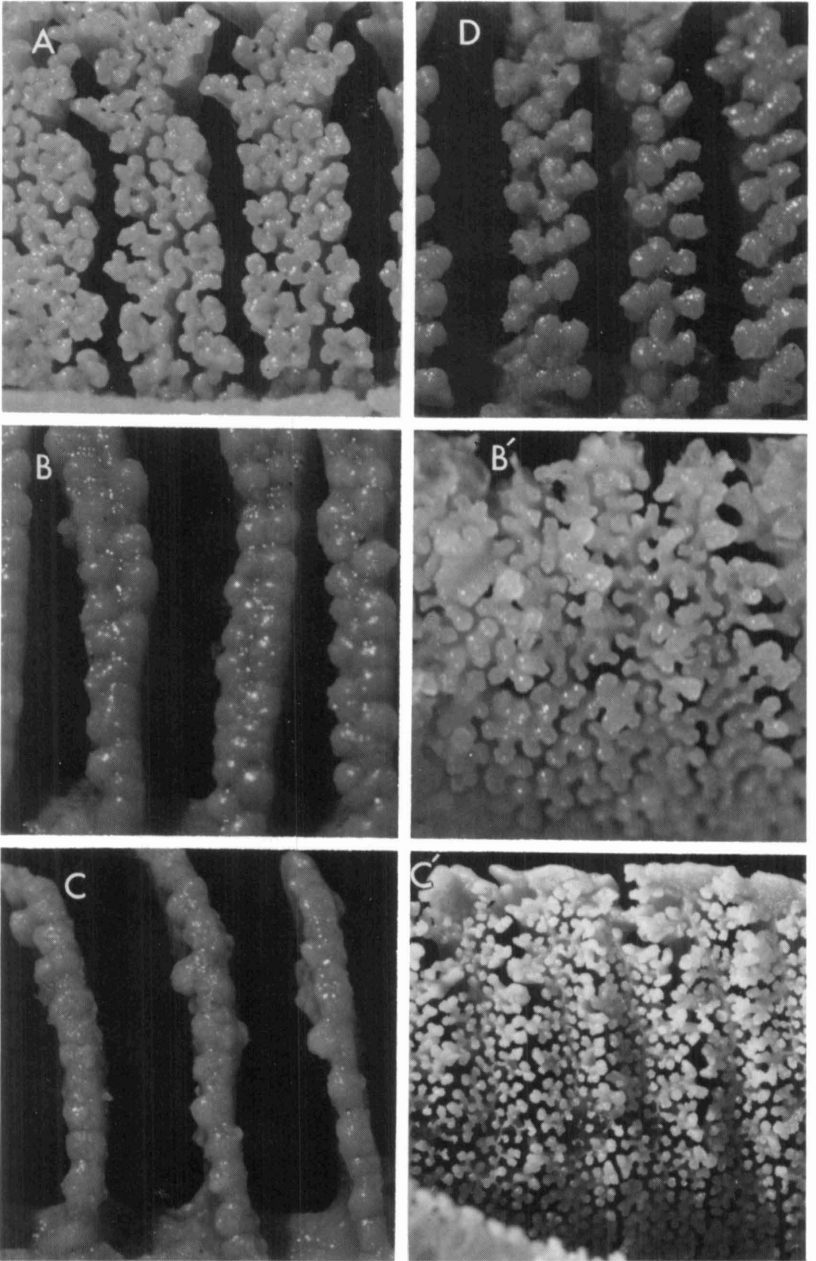
DIAGNOSIS.—Large, robust suckers with a long, broad, and deep head; mouth terminal or subterminal, moderately to strongly oblique (usually about a 45° angle), and mandible long (about equal to snout length); mouth opening wide; lateral folds well developed under maxillae; lips thin, often plicate, with scattered, weakly-developed papillae that may be obsolete (as in the lectotype of *C. brevirostris*); lobes of lower lip widely separated; eye typically in anterior half of head; gill rakers dendritic or fimbriate, flat and paddle-like on top, 38–53; pharyngeal bones weaker than usual in *Catostomus*, the teeth generally smaller; dorsal and anal fins as in *Catostomus*, the dorsal with 10–12 and the anal with 7 (rarely 8) rays. Jaw bones elongate, slender, the premaxillae wider than high; skull short and wide, the dermethmoid broader than long.

TYPE SPECIES.—*Catostomus fecundus* of Jordan (not of Cope and Yarrow) = *Chasmistes liorus* Jordan (Holotype, USNM 75832).

THE LIVING SPECIES

The living species of *Chasmistes* occurred historically in four separate drainages (Fig. 3): the Bonneville Basin (Utah Lake) in Utah, the Lahontan Basin (Pyramid Lake) in Nevada, the Klamath River Basin

FIG. 4. From Lake of the Woods, Oregon. A (ventral, lateral), *Chasmistes brevirostris* (UMMZ 166442-6); B, apparent backcross, *Chasmistes brevirostris* × *Catostomus snyderi*, to *snyderi* (UMMZ 160948-1); C, *Catostomus snyderi* (UMMZ 166441-1); D, *Chasmistes brevirostris* × *Catostomus snyderi* (UMMZ 166440-2); E, *Chasmistes brevirostris* (UMMZ 160950-1).



(Klamath Lakes and associated drainages) in Oregon and California, and the Upper Snake River Basin (above Shoshone Falls) in Wyoming and possibly Idaho. These occurrences are associated with major remnants of pluvial lakes in western United States.

Chasmistes liorus Jordan

June sucker

Chasmistes liorus Jordan, 1878b:219, Utah Lake Utah.

Catostomus fecundus, Jordan 1878a:417, 1878b:151 (misidentification in part).

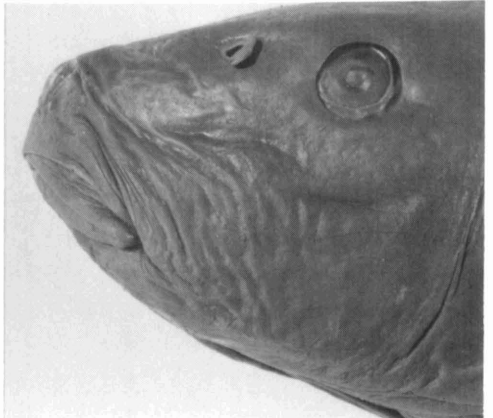
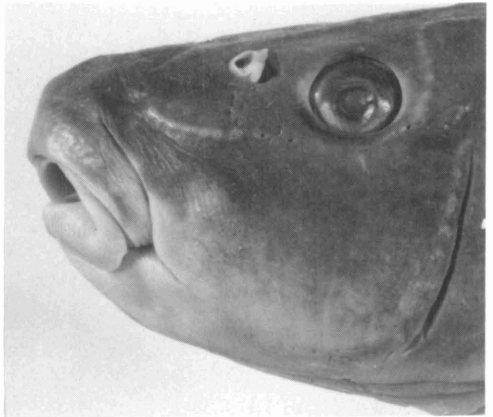
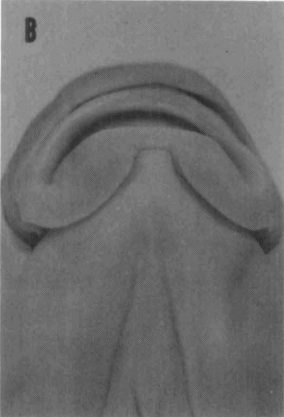
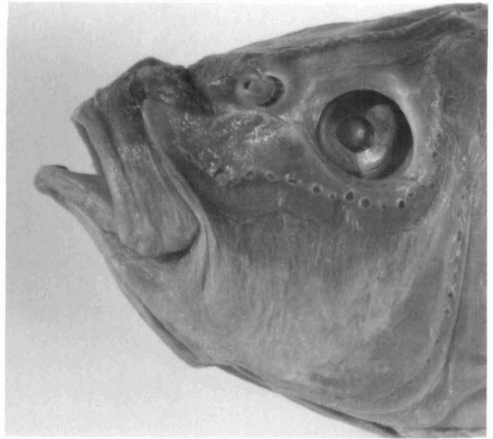
The June sucker, so-named because peak spawning time occurs that month, abounded in Utah Lake before 1900, but no individual representing the original form has, to our knowledge, been preserved in this century. The great drought of the mid-1930's, coupled with domestic use of its major spawning stream, the Provo River, decimated the suckers and other fishes in this rather shallow lake when its surface area was reduced from 93,000 to 50,000 acres (37,200 to 20,000 hectares).

"During the winter of 1934–35 the water was so shallow that hundreds of tons of suckers and carp were killed due to freezing and crowding in the few deep holes. . . . In the spring of 1935 there were no suckers to run up Provo River, something that has never happened before in the history of Utah Lake" (Tanner, 1936:167).

The description and account of *Catostomus fecundus* Cope and Yarrow (1875:678, Pl. 32) are based partly on this species. They state:

"The species is abundant in Utah Lake, and is called 'sucker' by the settlers. They run well up the rivers to spawn in June; feed on the bottom and eat spawn of better fish; spawning beds on gravel; bite at hook sometimes; are extremely numerous, and are considered a nuisance by the fisherman, but they meet with a ready sale in winter at an

FIG. 5. Gill rakers, mid-ventral part of posterior row, first arch, $\times 8$. A, *Chasmistes brevirostris* (UMMZ 166442, Fig. 4A); B, apparent backcross, *Chasmistes brevirostris* \times *Catostomus snyderi*, to *snyderi* (UMMZ 160948, Fig. 4B); C, *Catostomus snyderi* (UMMZ 166441-1, Fig. 4C); D, *Chasmistes brevirostris* \times *Catostomus snyderi* (UMMZ 166440-2, Fig. 4D); B', *Chasmistes "brevirostris"* (UMMZ 207716, Fig. 6B); C', *Chasmistes cujus* (UMMZ 191643, Fig. 6C).



average price of 2½ cents per pound.” (Fresh trout were selling for 30 cents per pound.) Suckers were captured in large numbers in winter by fishing with large nets extended through a series of holes in the ice and drawn through the lake waters.

Our examination of the type (=lectotype) of *Catostomus fecundus* (USNM 16988) indicates that it is not a member of a species that exists today or a species that was ever collected in large numbers or deposited in museum collections. The type, and several other similar specimens collected in the last century (USNM 12894, 22493, 27362, 36815, and 41725), show a range of characters intermediate between *Catostomus ardens* and *Chasmistes liorus*, but outside the diagnosis of those species. The lips are variable, ranging between *liorus* and *ardens*. As mentioned above, Jordan's examination of *fecundus* led him to make it the basis of the genus *Chasmistes*, but he later clarified its intermediacy between the true *Chasmistes* and *Catostomus ardens*. *Catostomus fecundus* was said by Cope and Yarrow to be abundant, but they were clearly referring to all suckers in Utah Lake, not necessarily the intermediate specimens shipped back to Philadelphia for study. The fact that early knowledge of Utah Lake suckers was based on an intermediate type specimen made subsequent understanding of the problem difficult and still clouds the nomenclature. Jordan (1878b) was aware that two species were in the lake and that *fecundus* represented a unique local form unlike the widespread local *Catostomus*. It is unlikely that *Catostomus fecundus* ever existed as a distinct species in the lake.

Without access to the original material of *Chasmistes liorus* and *Catostomus fecundus* (of which few specimens now remain), Tanner (1936) erroneously synonymized both *Chasmistes liorus* and *Catostomus ardens* Jordan and Gilbert with *Catostomus fecundus* Cope and Yarrow, the earliest name for a sucker from Utah Lake. Our data demonstrate that the original population of *Chasmistes liorus* is extinct, that *Catostomus fecundus* is best regarded as a hybrid between *Catostomus ardens* Jordan and Gilbert (the third sucker described from Utah Lake) and *Chasmistes liorus*, and that a population of *Chasmistes* of hybrid origin survives in the lake and is herein given taxonomic recognition.

FIG. 6. A (ventral, lateral), *Chasmistes brevirostris* (ANSP 20959, lectotype, Klamath L.); B, *Chasmistes "brevirostris"* (UMMZ 207716, Copco Res.); C, *Chasmistes cujus* (UMMZ 191643, Pyramid L.).

Chasmistes liorus liorus

Figs. 7A, 8A, 10A

HOLOTYPE.—USNM 75832, female (probably), 282 mm SL (re-cataloged in 1914; probably originally was USNM 20932, now catalogued as *Osmerus eperlanus*), designated by Jordan (1878b:151) as "Type *Chasmistes*." This specimen, examined by RRM in 1946, has in its jar the original, much-yellowed parchment "Wheeler Survey" label, bearing original number 455, Henshaw and Yarrow, Utah Lake, Nov. 25, 1872. This is not the fish drawn by Denton (Jordan and Evermann, 1900:Fig. 85), which is USNM 27361, spec. no. 3.

Other specimens examined are listed at the end of this paper. Proportional measurements on three adults are given in Table 1. For those measurements that distinguish this subspecies from *C. l. mictus*, described below, five additional specimens were available (Table 2).

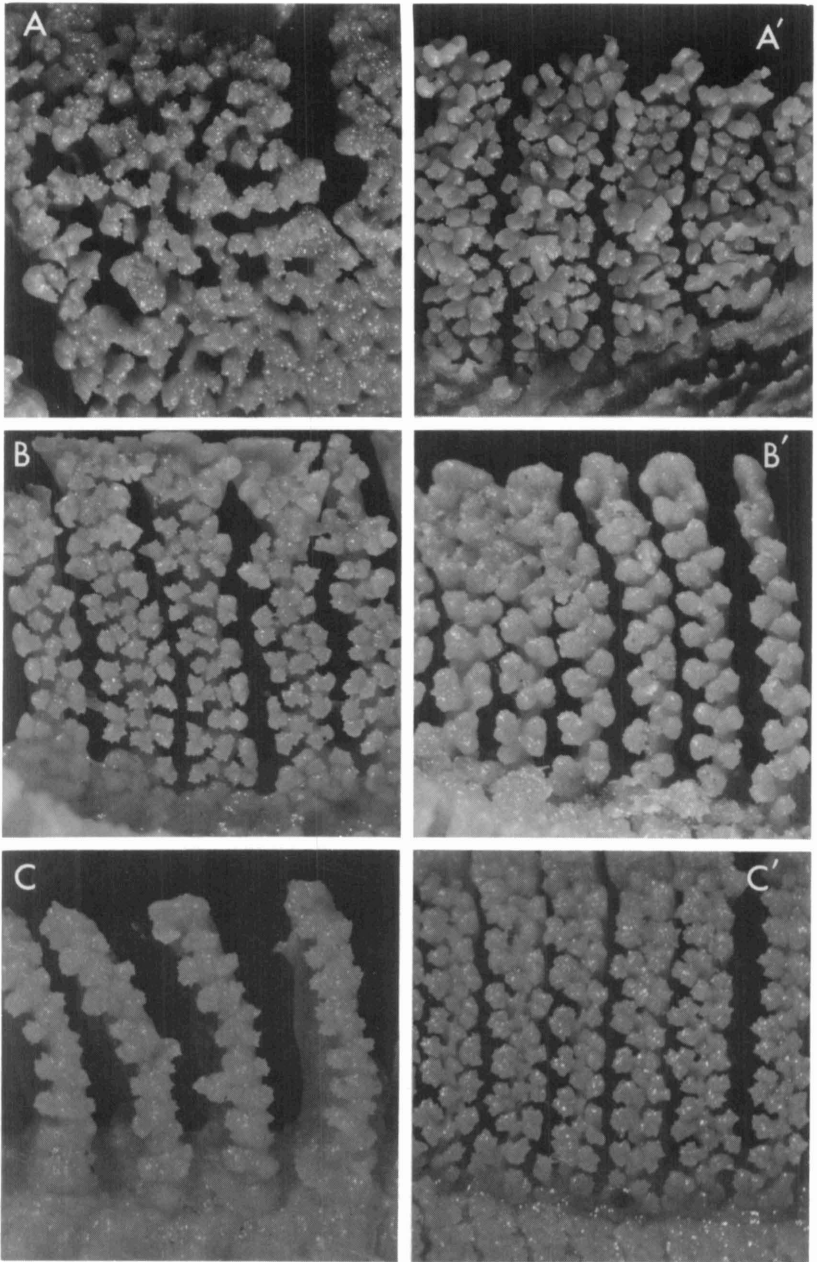
DIAGNOSIS.—A *Chasmistes* with large scales, 55 to 64 in lateral line, 9 to 11 above and 8 to 10 below lateral line, 29 to 35 before dorsal fin, 52 to 61 around body, and 19 or 20 around caudal peduncle; gill rakers in first row of first arch 45 to 53 (Table 3).

ETYMOLOGY.—From Latin, meaning smooth margin, in reference to the lack of papillae on the lips.

HABITAT AND DEPLETION.—Formerly abundant in Utah Lake, to which this species was confined except for a yearly spawning migration up tributaries, especially the Provo River, *Chasmistes l. liorus* is thought to have been depleted by the combined effects of the pollution and severe drought of the mid-1930's on Utah Lake, and the effects of agricultural and domestic use of the Provo River on reproduction (Miller, 1979). When numbers became low, extensive hybridization with *Catostomus ardens* apparently led to introgression of new traits into the population. The *Chasmistes* that returned to abundance in the 1940's and 50's is distinctly different from the original species.

FIG. 7. A (ventral, lateral), *Chasmistes liorus liorus* (USNM 27361, Utah L.); B, *Chasmistes liorus mictus* (UMMZ 203995, holotype, Utah L.); C, *Catostomus fecundus* (= *Chasmistes liorus* × *Catostomus ardens*, USNM 41725, Utah L.).





Chasmistes liorus mictus, new subspecies

June sucker

Figs. 7B; 8B, B', C', 9B, C

HOLOTYPE.—UMMZ 203995, adult male, 1.7 kg, about 395 mm SL (515 mm TL) from Utah Lake at Goshen, Utah, collected in 1978 by personnel of the Utah Division of Wildlife Resources.

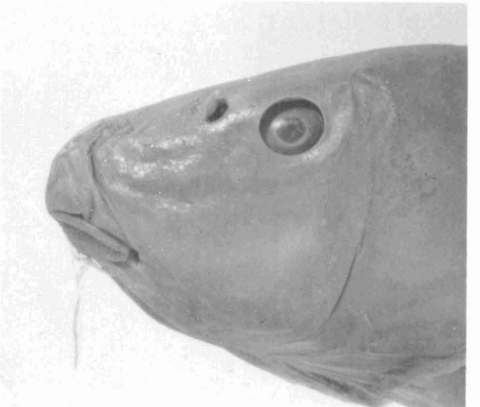
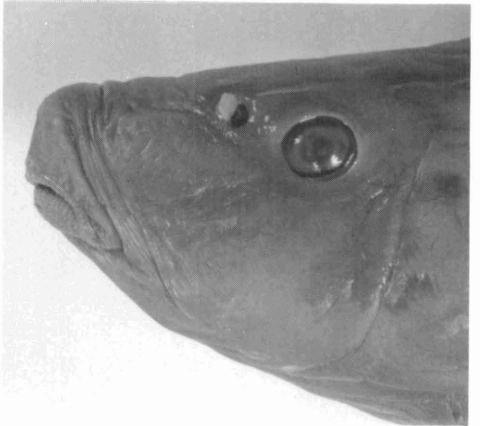
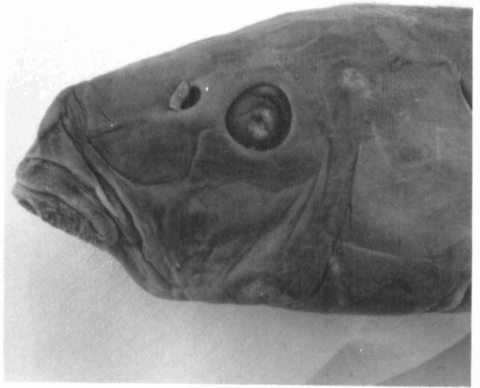
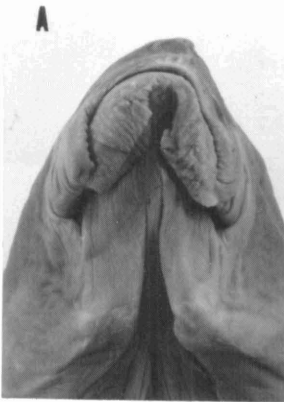
PARATYPES.—All material is from Utah Lake: UMMZ 138986(7), 299–358 mm, about 9 km S of Provo River mouth, F. Madsen, 13 Feb. 1942; UMMZ 141458(1), 309 mm, Municipal Park, Provo, C. L. and E. L. Hubbs and W. W. Tanner, 18 June 1942; UMMZ 141478(6), 285–330 mm, rock crusher, Provo, C. L. Hubbs family and W. W. Tanner, 19 June 1942; UMMZ 180680 (2 skeletons, 3 ads.), 334–395 mm, near Bird Island, B. Arnold, 21 March 1959; UMMZ 203994(3), 407–463 mm, Provo Bay Channel, Utah Div. Wildlife Res., 25 Aug. 1978; UMMZ 203996(1), 415 mm, Knolls, same coll., 23 June 1978; UMMZ 203997(3), 400–430 mm, same coll., summer 1978; and UMMZ 207720(7), 354–465 mm, S of Lincoln Pt., B. Loy, 1967.

DIAGNOSIS.—Resembling *Chasmistes l. liorus* in gill-raker structure, but more variable, and with fewer gill rakers (37 to 47—Table 3), better developed lip papillae, a less oblique mouth and shorter mandible, a shorter, slenderer head, smaller eye, smaller scales (60 to 70 in lateral line), a more anterior dorsal fin, and a somewhat longer caudal peduncle. Mouth and lips variable but readily distinguished from those of *Catostomus ardens* by the sparse papillae and subterminal position.

Most of the measurable differences are shown in Table 1. Additional measurements of predorsal length, head length, and eye diameter (utilizing also specimens in Table 1) are summarized in Table 2.

ETYMOLOGY.—The specific name is Latinized from the Greek word *miktos*, meaning mixed or blended, in reference to the hybrid origin of this subspecies.

FIG. 8. Gill rakers, mid-ventral part of posterior row, first arch, $\times 8$. A, *Chasmistes liorus liorus* (USNM 27361, Fig. 7A); B, *Chasmistes liorus mictus* (UMMZ 203995, Fig. 7B); C, *Catostomus fecundus* (= *Chasmistes liorus* \times *Catostomus ardens*, USNM 41725, Fig. 7C); A', *Chasmistes muriei* (UMMZ 81530, Fig. 9A); B', *Chasmistes liorus mictus* (UMMZ 141478-4, Fig. 9B); C', *Chasmistes liorus mictus* (UMMZ 138986-10, Fig. 9C).



DISCUSSION.—Three alternative explanations might be invoked to account for the existence of *C. liorus mictus* and its unusual characteristics: (1) hybrid origin, (2) rapid evolution to a new adaptive peak, and (3) increase in abundance of a formerly rare species. The third hypothesis is consistent with the possibility that *fecundus* is a rare species of some antiquity in the lake and that it increased following the decline of *liorus*. The fact that both *fecundus* and *mictus* are intermediate between *liorus* and *Catostomus ardens* suggests this explanation. The hypothesis is rejected, however, because *fecundus* and *mictus* differ completely in the number of gill rakers. If *mictus* represents a previously undescribed species of some antiquity we must still explain its hybrid-like intermediacy between *liorus* and *ardens*.

The second hypothesis, that *mictus* evolved rapidly from *liorus* following an environmental crisis resulting in a small population, is similar to an analogous situation described by Ford (1964) in Marsh Fritillary butterflies. If the character states in *mictus* represent a new adaptive peak, we must explain why it should incorporate a hybrid-like combination of characters.

The hybrid origin hypothesis is preferred because it involves a mechanism that accounts for the observed character states. It would be rejected if the characteristics of *mictus* were inconsistent with hybrid-like intermediacy between *Chasmistes liorus* and *Catostomus ardens* or if hybridization between these fishes could be shown to be unlikely. Table 3 and Figs. 7–10 present the morphological evidence. *C. l. mictus* is intermediate in the numbers of gill rakers, the shape of the gill rakers, the shape of the lips, the position of the mouth, and the shape of the jaw bones. The frequency of hybridization in the family Catostomidae has been documented thoroughly (Hubbs, 1955 and references).

Chasmistes muriei, new species

Snake River Sucker

Figs. 8A', 9A, 11A

HOLOTYPE.—UMMZ 81530, female, 371 mm SL (448 mm TL), from Snake River below Jackson Lake dam, collected 13 October 1927 by Olaus J. Murie.

FIG. 9. A (ventral, lateral), *Chasmistes muriei* (UMMZ 81530, holotype, Jackson, Wyo.); B, *Chasmistes liorus mictus* (UMMZ 141478-4, Utah L., 1942); C, *Chasmistes liorus mictus* (UMMZ 138986-10, Utah L., 1942).

TABLE I.

PROPORTIONAL MEASUREMENTS OF THREE SPECIES OF *CHASMISTES* IN THOUSANDTHS OF STANDARD LENGTH

	<i>Chasmistes l. liorus</i>			<i>Chasmistes l. mictus</i>			<i>C. muriei</i>	<i>C. cujus</i>
	Holotype ♂	MCZ 26806	USNM 27361 ♀?	Holotype ♀	4 Males	5 Females (incl. holotype)	Holotype ♀	♂
Standard length, mm	282	349	366	395	298-309(305)	317-395(346)	371	403
Predorsal length	509	519	525	494	484-493(489)	474-494(485)	536	516
Preanal length	762	785	751	759	761-804(782)	757-793(768)	787	787
Prepelvic length	582	560	593	557	534-584(563)	550-574(563)	574	588
Dorsal origin to occiput	315	328	315	311	294-316(301)	290-311(296)	327	309
Dorsal origin to caudal base	521	533	516	532	539-554(545)	530-549(539)	526	509
Tip of snout to occiput	210	216	231	225	195-207(201)	193-225(204)	234	226
Head, length	283	284	313	277	258-270(264)	249-277(261)	300	291
Depth at eye	161	179	169	167	143-151(148)	147-167(152)	167	160
Depth at occiput	185	204	198	196	166-181(176)	168-196(179)	190	186
Snout length	128	122	139	135	114-125(120)	116-135(124)	138	128
Dorsal origin to anal origin	357	369	369	361	375-391(381)	361-373(367)	341	326
Dorsal origin to pelvic origin	228	249	227	270	218-263(247)	230-270(246)	207	216
Eye diameter	38	33	40	30	30- 31(31)	26- 30(28)	36	30
Caudal-peduncle length	153	146	142	141	149-166(156)	141-168(161)	139	154
Depth	87	96	95	98	93-101(97)	94- 99(97)	92	88
Dorsal fin, depressed length	247	239	230	271	265-295(277)	244-271(253)	235	243
Basal length	176	175	162	184	177-203(188)	173-184(178)	163	153
Anal fin, depressed length	247	211	219	249	253-261(257)	219-249(229)	207	222
Pectoral-fin length	246	222	223	222	213-234(223)	208-224(215)	215	207
Pelvic-fin length	165	149	152	172	160-176(166)	153-172(158)	150	163
Caudal fin, length middle rays	165	140	150	151	146-152(148)	137-151(142)	143	143

TABLE 2
 DIAGNOSTIC DIFFERENCES IN MEASUREMENTS BETWEEN TWO SUBSPECIES OF
CHASMISTES LIORUS FROM UTAH LAKE¹

	<i>C. l. liorus</i> (8)	<i>C. l. mictus</i> (19)
Standard length, mm	282–366(334)	290–395(327)
Predorsal length	505–539(523)	467–511(486)
Head length	283–313(297)	244–277(261)
Eye diameter	33– 40(35)	26– 31(29)

¹Measurements in thousandths of SL, with means in parentheses.

SYNONYMY.—Listed as a possibly distinct form of *Chasmistes* by Miller (1965:577) and Baxter and Simon (1970:114–115), and as *Chasmistes* sp. by Smith (1978:25).

DIAGNOSIS.—A *Chasmistes* with a subterminal mouth and papillae on the lips, resembling *liorus* in gill-raker structure and most body proportions (Table 1) but slenderer (body depth about 5.0 rather than less than 4.5 mm in SL), with smaller scales, 72 vs. 55 to 70 in lateral line, about 40 vs. 30 to 35 before dorsal fin, 68 vs. 52 to 61 around body, 24 vs. 19 or 20 around caudal peduncle, and having fewer gill rakers, 40 vs. 37 to 53 (Table 3).

DISTRIBUTION.—This species is known only from the holotype and is presumed to be extinct. A geographically related species was the Pliocene *Chasmistes spatulifer* Miller and Smith, known from Lake Idaho in the ancestral upper Snake River basin (Smith, 1975; present report). However, *C. muriei* is more similar to *C. batrachops* and *brevirostris*.

COMMENTS.—We assume that this species inhabited lakes in Jackson Hole. The single specimen differs from other *Chasmistes*, except hybrids, in the presence of a subterminal mouth with papillae on the lips. It seems unlikely, on the basis of our other information on this genus, that the original population of *muriei* had this combination of characters. It is possible that the specimen possesses introgressed characters from *Catostomus ardens*.

ETYMOLOGY.—Named for the late Olaus Murie, biologist and wilderness advocate, who collected the only known specimen.

Chasmistes cujus Cope

Cui-ui

Figs. 1–2, 5C', 6C, 10D

Chasmistes cujus Cope, 1883:149.

HOLOTYPE.—ANSP 20523, a specimen about 360 mm SL in very poor condition (eviscerated, scales missing, fins broken), but clearly possessing the distinctive features of *Chasmistes*. It has 44 gill rakers on the first gill arch of the left side. Cope (1883:149) gave the number of lateral-line scales as 65.

DIAGNOSIS.—A *Chasmistes* with smaller scales than *C. liorus*: 59 to 68 vs. 55 to 62 in lateral line, 22 to 26 vs. 19 or 20 around caudal peduncle, more than 64 vs. less than 62 around body, but larger than those of *C. brevirostris*. The gill rakers number 40–47 (Table 3), fewer than in *C. liorus*. Snyder (1917) justifiably stressed the large, broad, and blunt head; the mouth is not so oblique as in the other species of *Chasmistes*. This is probably the largest of the living species, attaining lengths to 670 mm and weights to 3.5 kg (Snyder, 1917; Follett, 1967).

The most extensive accounts of this species (which bears the Indian name cui-ui, pronounced kwee-wee) were published by Snyder (1917: 50–54) and LaRivers (1962:363–372, Figs. 179–180). Before the construction of dams on the Truckee River and utilization of its waters for agriculture, this sucker made spectacular spring spawning runs for about 30 km up this river from Pyramid and Winnemucca lakes. Winnemucca Lake dried up many years ago and the water level in Pyramid Lake has been falling since about 1910. Spawning now takes place only about the margin of Pyramid Lake and is very limited, although spawning was observed by G. Kobetich in the Pyramid Lake fish ladder in 1980 (J. Deacon, pers. com.). The depth distribution of cui-ui in the lake is discussed by Vigg (1980). Since 1954 cui-ui have shown a steady decline and the future of this last-remaining pure population of the genus is problematical (Chatto, 1979; Koch, 1973, 1976; Koch and Contreras, 1972; Miller, 1979). Efforts are being made to culture the cui-ui and young are being released into Pyramid Lake, but the long-term success of this operation is unknown.

Cui-ui remains from Indian midden sites, dated from approximately 1000 to 1500 A.D., have been reported by Follett (1967, 1970, 1977, and authors cited therein) from several caves in Nevada. They were obviously prized as food by the Amerinds (Northern Paiute).

Chasmistes brevirostris Cope

Shortnose sucker

Figs. 4A,E, 5A, 6A, 10G

Chasmistes brevirostris Cope, 1879:785 (orig. descr.; comparison with *C. luxatus*; size, habits, associates; Upper Klamath Lake, Oregon).

Chasmistes stomias Gilbert, 1898:5 (orig. descr. and fig.; Upper Klamath Lake, Oregon).

Chasmistes copei Evermann and Meek, 1898:70–71 (orig. descr. and fig.; Pelican Bay, Upper Klamath Lake, Oregon).

Lipomyzon brevirostris, Fowler 1913:53 (lectotype, ANSP 20959; paralectotype, ANSP 20522; comparison with *Deltistes luxatus*, *Chasmistes stomias*, *C. copei*, and *C. chamberlaini*; suggestion of identity of *brevirostris* and *stomias*).

DIAGNOSIS.—A *Chasmistes* with a terminal, oblique mouth with weak or no papillae on the lips, and with small scales, 65 to 79 in lateral line, 21 to 25 (usually 24) scales around caudal peduncle, and 36 to 46 gill rakers (Table 3); differing from *C. liorus mictus* in the same body proportions that separate that subspecies from all other *Chasmistes* (Tables 1,2,4).

DISTRIBUTION.—Known records of native occurrence based on specimens examined are from Upper Klamath Lake (and lower tributaries). The suckers passing under the name *Chasmistes brevirostris* (Coots, 1965:Fig. 2; Moyle, 1976:231–233, Fig. 81) from Copco Reservoir, Siskiyou Co., California, are an introgressed population with traits of *Catostomus rimiculus*. The population that once lived in Lake of the Woods, Oregon, is introgressed with traits of *Catostomus snyderi*. These three populations are discussed below. They are currently under study by C. E. Bond and J. K. Andreasen, whose conclusions differ from those presented here (Andreasen, J. K., 1975, Systematics and status of the family Catostomidae in southern Oregon, Ph.D. dissertation, Oregon State University, 76 pp).

COMMENTS.—The only indisputable native *Chasmistes* of the Klamath Lakes region occurred in Klamath Lake and its lower tributaries. Three species were described from the lake but the differences are slight, and related to sex and condition. Our examination of the type specimens (Table 4) convinces us that *stomias* and *copei* are synonyms of *brevirostris*. We have not, however, seen any recently-collected specimens from Klamath Lake that are the same as *brevirostris*. Re-

TABLE 4

PROPORTIONAL MEASUREMENTS IN THOUSANDTHS OF SL OF THREE SPECIES OF SUCKERS AND THEIR HYBRIDS FROM THE KLAMATH RIVER BASIN

Specimens 1, 3-5 are from Upper Klamath Lake basin (5 is UMMZ 199198); 2 (UMMZ 166442-7), 6 (UMMZ 160948-5), and 7 (UMMZ 166441) are from Lake of the Woods; 8 (UMMZ 207712-10) and 9 (UMMZ 207716-30) are from Copco Reservoir.

[1]	[2]	[3]	[4]	[5]	[6]	[7]	[8]	[9]
	<i>Chasmistes breviostris</i>	<i>C. copei</i>	<i>C. stomias</i>	<i>Catostomus snyderi</i> × <i>Chasmistes breviostris</i>	<i>Catostomus snyderi</i> × <i>Chasmistes breviostris</i>	<i>Catostomus snyderi</i>	<i>Catostomus rimiculus</i> × <i>Chas.</i> <i>breviostris</i>	<i>Catostomus rimiculus</i>
Lectotype	Holotype	Holotype	Holotype					
Standard length, mm	335	343	306	335	357	388	405	337
Predorsal length	501	522	515	475	532	536	486	496
Prenal length	770	790	778	746	807	786	783	611
Prepelvic length	567	574	569	543	563	575	558	561
Dorsal origin to occiput	313	321	333	295	323	333	319	299
Dorsal origin to caudal base	537	516	503	564	532	536	541	513
Tip of snout to occiput	207	223	209	> 199	227	238	187	212
Head, length	284	294	303	> 286	301	284	231	253
Depth at eye	173	164	187	168	146	156	141	147
Depth at occiput	196	196	203	174	200	195	170	157
Snout length	124	127	> 121	119	146	140	117	131
Dorsal origin to anal origin	357	356	> 341	367	353	351	358	340
Dorsal origin to pelvic origin	218	213	> 196	233	236	209	237	229
Eye diameter	37	36	42	27	34	36	27	26
Caudal-peduncle length	150	151	± 135	159	145	150	152	160
Depth	96	89	88	100	95	85	92	100
Dorsal fin, depressed length	206	221	205	257	223	213	217	216
Basal length	141	144	150	172	147	140	143	146
Anal fin, depressed length	215	211	204	239	218	199	200	206
Pectoral-fin length	224	215	198	247	206	221	190	216
Pelvic-fin length	154	144	194	161	159	145	139	155
Caudal fin, length middle rays	152	157	159	135	140	132	131	129
Sex	♀?	♀	♂	♂	♀	♀	♀	♀?

cently-collected specimens examined by us have lip papillae, small mouths, too few gill rakers, short heads, small eyes, short caudal fins, short, truncate maxillae, short, angular dentaries, and right-angled premaxillae—traits distinct from *brevirostris* (Table 4; Figs. 6A, 10I) but clearly characteristic of *Catostomus snyderi*, indicating introgression with that species. If these specimens are an unbiased sample of *Chasmistes* presently inhabiting Klamath Lake, none of the available names is applicable.

Many specimens of *Chasmistes* from Lake of the Woods, Oregon, in the Klamath drainage, also differ from the type specimens of *brevirostris* and its synonyms. Some of these specimens show a mixture of traits characteristic of *Chasmistes brevirostris* and *Catostomus snyderi*, including variable gill-raker number and morphology, head length, and osteology (Tables 3,4; Figs. 4A–E, 5A–D, 10G). In a sample of 37 specimens collected in 1949 and 1952, 25 appear to be *brevirostris* (Figs. 4A,E, 5A, 10G), 11 are hybrids or backcrosses (Figs. 4B,D, 5B,D), and one is *Catostomus snyderi* (Figs. 4C, 5C).

The fish populations of Lake of the Woods were eradicated in 1952 to rid the lake of introduced carp, perch, and catfish. Many introduced species inhabited the lake. We doubt that native *Chasmistes* could have gained access to Lake of the Woods through its steeply-graded outlet (Seldom Creek) which falls from 4960 ft to 4140 ft (or 251 m) in about 13 km to upper Klamath Lake (USGS topog. sheet Lake O' Woods, 1:62,500, 1955), although C. E. Bond (in litt.) reports local testimony that suckers were present in the lake in the late 1880's. Our specimens are old individuals with large heads and small, poorly-nourished bodies. Evidently, the lake provided unsuitable habitat for these fish. *Chasmistes* can only be considered native to Lake of the Woods if it can be demonstrated that there was at some time in the late Cenozoic a relatively small difference in elevation between Lake of the Woods and Upper Klamath Lake. The known habits of living species of *Chasmistes* preclude their ascent of such a steep tributary.

An introduced and introgressed population of *Chasmistes* also exists in Copco Reservoir, California (Coots, 1965). Specimens collected by Millard Coots in 1962 and Terry Mills in 1978 and 1979 have short jaws, short heads, small scales, and reduced numbers of gill rakers, indicating introgression from *Catostomus rimiculus* (Table 4; Figs. 5B', 6B, 10H). The numbers of gill rakers range from 33 to 48 (Table 3), with the mean near 40, indicating strong *Chasmistes* traits. The morphology of the lips (Fig. 6B) and gill rakers (Fig. 5B') of many speci-

mens are also similar to typical *Chasmistes*. The sample we have seen contains no true *brevirostris*, but is about 40% "*brevirostris* > *rimiculus*" (as in Figs. 5B' and 6B, with short jaws and heads), about 55% intermediate between *brevirostris* and *rimiculus*, and about 5% "*rimiculus* > *brevirostris*" (i.e., with a trace of *Chasmistes* traits). *Catostomus rimiculus* is common in the reservoir.

Chasmistes brevirostris was recently reported from the Lost River in California (Miller, 1979). Examination of Lost River specimens by C. E. Bond revealed that they were hybrids that probably gained access from the Klamath system through "A" canal (C. E. Bond, pers. comm., 1980). This observation and our Klamath Lake interpretation suggest that the original *Chasmistes* that gained access to Copco Reservoir could have been influenced by introgression from *C. snyderi*. Nevertheless, Copco Reservoir is currently one of two refuges for a relatively intact gene pool of *Chasmistes brevirostris* and deserves protection and management.

The specimen of *Chasmistes brevirostris* reported by Ferris and Whitt (1978) from Sprague River, Oregon, is probably a hybrid, *Catostomus snyderi* × *Chasmistes brevirostris*; that recorded by Miller and Smith (1966) and by Gosline (1978—UMMZ 180686-S from Copco Reservoir) is *Catostomus rimiculus* × *Chasmistes brevirostris*.

THE FOSSIL RECORD AND OSTEOLOGY OF *CHASMISTES*

Chasmistes is represented by diagnostic bones in 11 fossil localities in California, Oregon, Nevada, Utah, and Wyoming (Fig. 3) plus 40 localities ranging from Miocene to Pleistocene on the Snake River Plain. Almost all of the fossils are from lake deposits. The significance of the distribution pattern of *Chasmistes* was first described by Taylor (1960); subsequent discoveries corroborate Taylor's hypothetical system of biogeographically connected lakes, from Lake Bonneville through the Snake River Plain to Klamath Lake, and the Western Great Basin south to Lake Searles.

Most localities are not sufficiently represented by collections to enable species descriptions. In the outline presented below, similarities are noted for the purpose of suggesting possible biogeographic and cladistic hypotheses.

Miocene

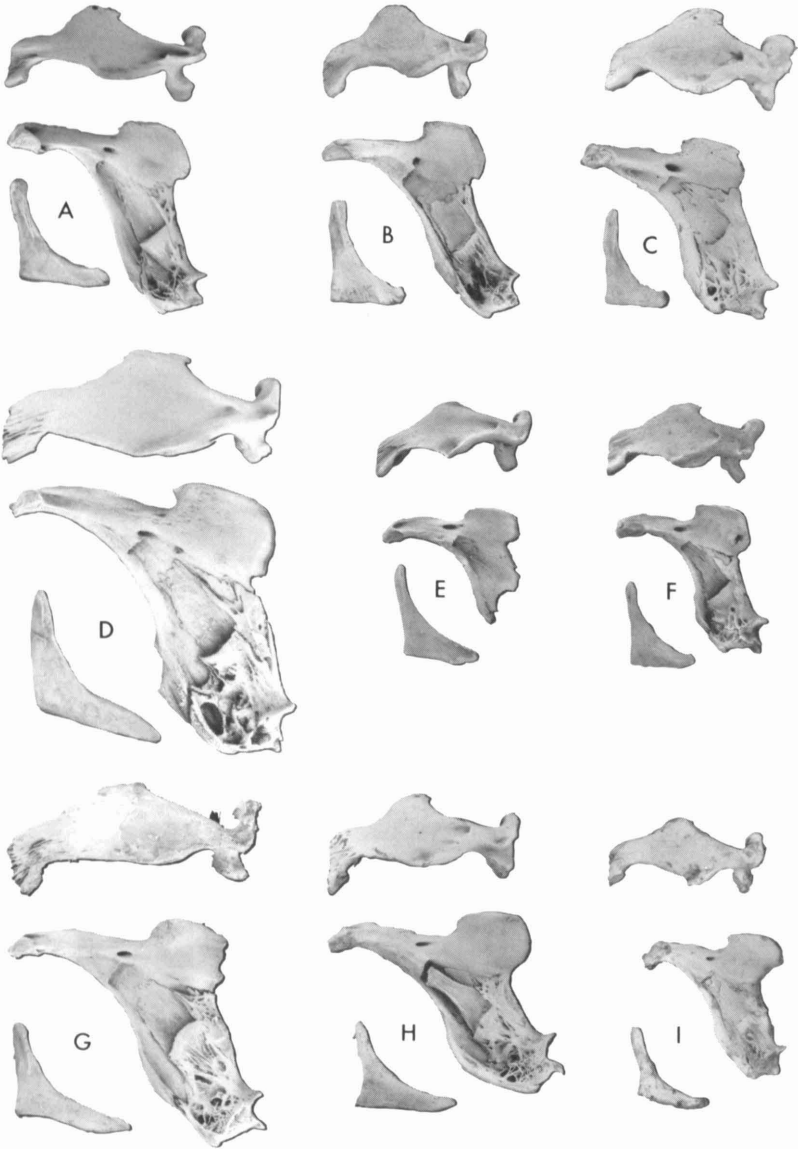
Chasmistes sp.

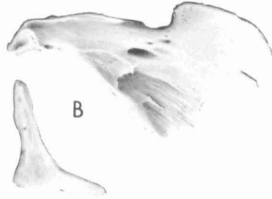
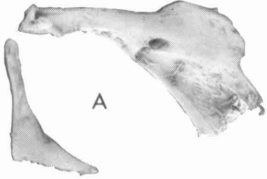
Oregon, Malheur Co.: Sand Hollow, 6 mi. W. Vale, SE $\frac{1}{4}$ Sec. 33, T 19 S, R 4 E, P. G. Kimmel, 1977 (UMMP 74499). Seven dentaries representing *Chasmistes* were collected from fluvial sands of the Deer Butte Formation. The occurrence is noteworthy as one of the earliest records of the genus, for its occurrence in fluvial beds, and because the associated fauna differs slightly from those of the Chalk Hills and Glens Ferry Formations. The associated fauna includes *Ptychocheilus* sp., *Mylocheilus inflexus* (a Miocene indicator), *Idadon* sp., ?*Orthodon* sp., *Catostomus* sp., *Ictalurus vespertinus*, and *Archoplites* sp. *Esox* is also known from the Deer Butte Formation (Cavender et al., 1970).

The dentaries are most similar to those of *C. spatulifer* of the Pliocene Glens Ferry Formation in the narrow anterior end of the ramus and the length and depth of the shelf above and behind the lateral mental foramen, but they are unique in the presence of an anteroventral flange. One of the largest *Chasmistes* we have seen is included in the sample. A terminal fragment of a left dentary has width and depth dimensions about twice those of a specimen of *C. cujus* that is 475 mm in standard length. The smallest specimen is a complete right dentary 14 mm long, with all of the adult characteristics.

Idaho, Owyhee Co.: SW of Horse Hill, Sec. 3, T 8 S, R 5 E, 3060 ft. (930 m), P. G. Kimmel, 1977 (UMMP V74247). Two dentaries from the Chalk Hills Formation are the only representatives of this genus from among thousands of specimens, yet there is no evidence that they are lag contaminants. Figs. 11H and 11I compare one specimen to the *Catostomus* with which it was found. This *Chasmistes* is relatively

FIG. 10. Dentaries, maxillae, and premaxillae of *Chasmistes* and compared formes. A, *Chasmistes liorus liorus* (USNM 28399, reduction $\times .9$), Utah Lake, Utah; B, *Chasmistes liorus mictus* (UMMZ 180680), Utah Lake, Utah; C, *Catostomus ardens* (UMMZ 183687), Salt Lake County, Utah; D, *Chasmistes cujus* (UMMZ 174435), Pyramid Lake, Nevada; E, *Chasmistes cujus* \times *Catostomus tahoensis* (UMMZ 207713-S), Pyramid Lake, Nevada; F, *Catostomus tahoensis* (UMMZ 174437), Pyramid Lake, Nevada; G, *Chasmistes brevirostris* (UMMZ 166442), Lake of the Woods, Oregon; H, *Chasmistes brevirostris* \times *Catostomus rimiculus* (UMMZ 180686), Copco Reservoir, Siskiyou Co., California; I, *Chasmistes brevirostris* \times *Catostomus snyderi* (UMMZ 199198), Sprague River, Oregon.



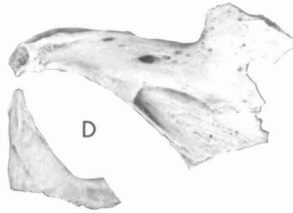
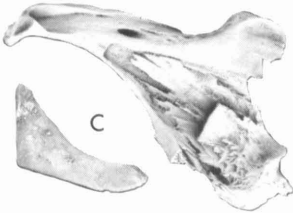


A

B

G

H



C

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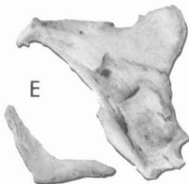
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E

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K



similar to the *Catostomus*, possibly because of the early evolutionary stage represented.

The specimens are from lake deposits. Associated species include *Rhabdofario lacustris*, *Hucho larsoni*, *Ptychocheilus arciferus*, *Acrocheilus latus*, *Mylocheilus inflexus*, *Mylopharodon* sp., *Idadon hibbardi*, *Catostomus* sp., *Ictalurus vespertinus*, and *Archoplites taylori*. *Hucho larsoni* and *Mylocheilus inflexus* are Miocene indicators.

Pliocene

Chasmistes spatulifer Miller and Smith

Chasmistes spatulifer Miller and Smith, 1967: 11 (orig. descr.; Figs. 4E–H). Smith, 1975:19–21, figs. 8, 9B. Kimmel, 1975:79. Linder and Koslucher, 1976 (partial skull from near Fossil Butte, Owyhee Co., Idaho, NE ¼ Sec. 2, T 4 S, R 2 W).

Idaho, Owyhee, Twin Falls, and Elmore Counties: Lake beds of the Pliocene Glens Ferry Formation from Hagerman west and north to the Adrian area, Malheur Co., Oregon. This species is now known from abundant material from 39 Pliocene localities (Smith, 1975; Kimmel, 1975). It is nearly restricted to the Glens Ferry Formation and its lateral equivalent in adjacent Oregon. It is part of a diverse fish fauna of nearly 25 species that inhabited E. D. Cope's "Lake Idaho." The dentaries (Fig. 11C) are extremely long and slender anteriorly; the maxillae (Fig. 11C) are anteriorly protracted with not-

FIG. 11. Dentaries, maxillae, and premaxillae of *Chasmistes* and compared forms. A, *Chasmistes muriei* (UMMZ 81530), Jackson Hole, Wyoming; B, *Chasmistes batrachops* (UMMP 74487), Pleistocene, Lake Co., Oregon; C, *Chasmistes spatulifer* (UMMP 59581), Pliocene Glens Ferry Formation, Owyhee Co., Idaho; D, *Chasmistes* sp., Pliocene (UMMP 59575, 59552, and 59422), upper Glens Ferry Fm., Owyhee Co., Idaho; E, *Ictiobus cyprinellus* (UMMZ 182021), Detroit River, Michigan; F, *Chasmistes* sp. (UMMP 74464), Pliocene, Secret Valley, Lassen Co., California; G, *Chasmistes* sp. (UMMP 74484), Pliocene, Mono Lake Basin, Mono Co., California; H, *Chasmistes* sp. (UMMP 74247), Miocene, Chalk Hills Fm., Owyhee Co., Idaho; I, *Catostomus* sp. (UMMP 74248), collected with H; J, *Chasmistes* sp. (UMMP 74499), Miocene, Deer Butte Fm., near Vale, Malheur Co., Oregon; K, *Chasmistes* sp. (UMMP 74482), Pleistocene, Airport Lake, north of China Lake, Inyo Co., California.

ably extreme anterior directions to the premaxillary process and the anterodorsal process. These features, plus the rotated symphysis indicate a large terminal mouth and planktivorous feeding. In the context of the functional morphology of planktivorous feeding, *C. spatulifer* is the most specialized species in the genus, fossil or Recent. The dentary is superficially similar to that of *Ictiobus cyprinellus* (Fig. 11E).

Chasmistes sp.

Considerable variation exists among the specimens of *Chasmistes* from the Glenns Ferry. Variation in the length of dentaries and the anterior attenuation of the maxilla suggests that more than one species is present. The variation is not allometric. The type of *spatulifer* is an extremely attenuate maxilla, so the undescribed form is the less specialized. Its maxilla differs from *spatulifer* in the thicker anterior constriction, the deeper ventral keel, and the nearly right angles between the anterior processes and the axis of the bone. It is similar to *C. cujus*. The pattern of variation is not suggestive of hybrid influence from *Catostomus*.

Chasmistes sp.

California, Lassen Co.: Secret Valley 22 mi N. Litchfield, NW ¼ Sec. 35, T 32 N, R 15 E, elevation 4400 ft. (1340 m), R. R. Miller, 1963, G. R. Smith, 1977, R. L. Elder, 1979 (UMMP 74464,65,66). Unnamed sediments including lake beds under a thick section of basalts contain a fauna with generic similarities to the Glenns Ferry Formation. The fauna includes *Rhabdofario*, *Ptychocheilus*, *Idadon*, ?*Orthodon*, and *Catostomus*, and indicates a Pliocene age.

This species is unique in the flat dorsal face and the concave ventral surface of the dentary ramus. The maxillae are similar to those of *C. sp.* of the Glenns Ferry and Chalk Hills formations.

Chasmistes sp.

California, Lassen Co.: West side of the Honey Lake "Island," Sec. 27, T 27 N, R 15 E, elevation 3995 ft. (1210 m), G. R. Smith and D. W. Taylor, 1979 (UMMP 74461,62,63). These fossils occur in highly de-

formed sediments forming cliffs along the beach of Honey Lake. The fish fauna, including *Rhabdofario*, *Gila*, *Catostomus*, and *Chasmistes*, is similar to the Pyramid Lake and Glenns Ferry faunas; it is probably of Pliocene age (Taylor and Smith, in press). The *Chasmistes* is represented by a small sample of maxillae and miscellaneous bones that are intermediate between *C. cujus* and *C. sp.* of the Glenns Ferry Formation.

Chasmistes sp.

California, Mono Co.: Mono Lake Basin; SW $\frac{1}{4}$, Sec. 35, T 3 N, R 29 E, 7100 ft. (2164 m); Sec. 33, T 3 N, R 26 E, 6976 ft. (2125 m); and NE $\frac{1}{4}$ Sec. 3, T 2 N, R 29 E, C. M. Gilbert, 1964, and R. R. Miller, 1965 (UMMP 74484,85,86). Fossils in calcareous sands below basalt.

Dentaries and maxillae from this locality are most similar to the forms from Secret Valley but the anterodorsal process of the maxilla forms a more abrupt angle with the axis of the bone. Skulls resemble *C. batrachops* of Fossil Lake, Oregon. The associated fauna includes *Ptychocheilus* sp., ?*Mylopharadon* sp., *Idadon* sp., and *Catostomus* sp.

On the basis of similarities to Secret Valley and the Glenns Ferry Formation in faunas and evolutionary grade, these fossils are judged to be Pliocene. The molluscs are also believed to be Pliocene (Taylor, 1966).

Chasmistes sp.

Wyoming, Teton Co.: Teewinot Formation. See *C. muriei* below. The specimen, a hyomandibular, was collected from USGS Cenozoic locality 19105, SE $\frac{1}{4}$ Sec. 25, T 42 N, R 116 W, by C. W. Hibbard in 1962.

Pleistocene to Recent

Chasmistes spatulifer Miller and Smith

Idaho, Owyhee Co.: "Glenns Ferry" Formation, Grand View local fauna (Jackass Butte). Three maxillae, three hyomandibulars, and two dentaries (UMMP V58516) possess the advanced characters of

spatulifer seen in specimens from the underlying strata of the upper Pliocene.

Chasmistes batrachops Cope

Catostomus batrachops Cope, 1883:151–152.

Chasmistes oregonus Starks, 1907:141–142, Fig. 32.

Oregon, Lake Co.: “Fossil Lake” (Fort Rock Basin), Sec. 8, T 26 S, R 19 E (UMMP 74487,88,89,90). These deposits have been discussed numerous times (Allison, 1966; Cope, 1889) and the *Chasmistes* has been referred to under several names: *Catostomus labiatus* Ayres (Cope, 1883), *Chasmistes oregonus* Starks (in Jordan, 1907). Because most fossils from the lake occur as deflation lag, it is possible that Pliocene fossils might be mixed with Pleistocene (Uyeno and Miller, 1963). More than one species may be represented, but sufficient fossils have not been found in place to enable biostratigraphy. The majority of *Chasmistes* are represented by bluish or black silicified bone.

Morphologically *C. batrachops* is distinguishable from *spatulifer* by a broader anterior dentary ramus, a less elongate anterior section of the maxilla, less obtuse angles between the anterior processes and the axis of the maxilla, and a less obtuse angle between limbs of the premaxilla. Resemblances are closer to the specimens from California and Nevada. The associated fauna includes a species of *Salmo* similar to *clarki*, *Gila* (*Siphateles*), and *Catostomus* or *Deltistes*.

Chasmistes cf. *C. batrachops*

California, Inyo Co.: White Hills 15 mi N. China Lake, center Sec. 11, T 24 S, R 39 E, elev. 2686 ft. (820 m), R. R. Miller, 1965 (UMMP 74482). The fossils are from gray sands and overlying diatomite.

The sample contains one dentary and one maxilla, each of which is similar to those of *C. batrachops* of Fossil Lake, Oregon, and the primitive form from the Snake River Plain. The associated “Airport Lake” mammalian fauna is early Irvingtonian according to R. Tedford (pers. comm.).

Chasmistes cf. *C. batrachops*

Nevada, Washoe Co.: Duck Valley, Secs. 10,11, T 37 N, R 18 E, R. Miller, 1963 (UMMP 74483). A small sample from calcareous sands contains one dentary identifiable as *Chasmistes*. The dentary is similar to *batrachops*, *brevirostris*, and *cujus*. Associated bones represent *Gila* (*Siphateles*) cf. *G. bicolor*, suggesting the assignment of Pleistocene age.

Chasmistes cf. *C. liorus*

Utah, Tooele Co.: Black Rock Late Pleistocene sediments of Lake Bonneville, Black Rock Canyon, J. H. Madsen, Jr. Large fragments of a corocoid and a dentary are referable to *Chasmistes* (Madsen and Smith, in prep.). The material is too fragmentary for more detailed analysis. The associated species are *Salmo clarki* and *Gila atraria*.

OSTEOLOGY.—The original *Chasmistes* of Utah Lake was similar to the Fossil Lake form in the long, slender dentary and maxilla (USNM 28399C, Fig. 10A). The present form, *Chasmistes liorus mictus* (Fig. 10B) is intermediate between *C. l. liorus* and *C. ardens* (Fig. 10C). The dentary ramus is short and sharply angled in dorsal view; the torsion is much reduced (the mouth is subterminal); and the maxilla is short and robust. The premaxilla is higher than wide in both forms.

Chasmistes hyomandibulars presumably related to *liorus* or *muriei* (UMMP V45740) were collected in 1961 by Bright (1967) from Pleistocene beds in the Thatcher Basin, SW $\frac{1}{4}$ SW $\frac{1}{4}$ Sec. 15, T 11 S, R 40 E, Preston Quadrangle, in southeastern Idaho.

Chasmistes *cujus*

Nevada, Churchill Co.: A partial Weberian apparatus of *Chasmistes* *cujus* (UMMP 52814) was collected from Pleistocene gravels 3–5 ft below the surface of a gravel pit near Fallon, Nevada, by J. R. Alcorn. Associated species include *Salmo clarki*, *Catostomus tahoensis*, and *Gila bicolor*.

Archaeological remains have been reported from Humboldt Cave, Churchill Co., Nevada, by Hubbs and Miller (1948) and Heizer and

Krieger (1956); from Lovelock Cave, Churchill Co., Nevada, by Follett (1967); and from Fishbone Cave, Pershing Co., Nevada, by Orr (1956). These records are not plotted on our distribution map (Fig. 3) because of the likelihood that the fish were transported from Pyramid Lake by Amerinds (Snyder, 1917; Follett, 1967). Sub-Recent remains from the north end of Winnemucca Lake (Falcon Hills sites), Washoe Co., Nevada (Follett, 1963) are plotted (Fig. 3).

OSTEOLOGY.—This is the most specialized of the Recent species in the elongation and torsion of the dentary ramus (Fig. 10D). The dentary is similar to the forms from Secret Valley and the Snake River Plain in the shape near the symphysis. The maxilla is similar anteriorly to *Chasmistes* sp. from the Snake River Plain. The premaxilla is wide.

Chasmistes brevirostris

Material from middens near Klamath Lake were reported by Hubbs and Miller (1948). We have confirmed the identification.

OSTEOLOGY.—The dentary of original *C. brevirostris* is distinct, but intermediate between those of *C. cujus* and the fossils from Fossil L., Oregon. The maxilla is similar to that from Fossil Lake. UMMZ 166442, collected in Lake of the Woods, Oregon, in 1952 is osteologically most typical of *Chasmistes* (Fig. 10G); UMMZ 180686, collected in Copco Reservoir, California, in 1961 (Fig. 10H), and UMMZ 199198 from Sprague River, Oregon, in 1975 (Fig. 10I), have short, acutely-angled dentaries, anteriorly robust, truncate maxillae, and high premaxillae, suggesting hybrid influence from *Catostomus*.

A fossil possibly related to this species is known from the Teewinot Formation of Teton Co., Wyoming (see section on Pliocene fossils). It is also possible that the Pleistocene fossil from the Thatcher Basin in southeastern Idaho (Bright, 1967, see *liorus*, above) could be *muriei*. The fossils are hyomandibulars and are diagnostic to genus but not species.

OSTEOLOGY.—The lone specimen from the Snake River (Fig. 11A) is osteologically similar to *C. batrachops* and *brevirostris*. The dentary and maxilla are long and slender. The premaxilla is higher than wide. In details of shape they are less specialized than *C. spatulifer* from the Snake River Plain.

DISCUSSION

Four Recent species of *Chasmistes* lived in the Klamath, Lahontan, Bonneville, and upper Snake drainages. The known fossil record includes late Miocene forms from the Snake River Plain, Pliocene forms from the Snake River Plain in Idaho and Oregon, and from the western edge of the Great Basin at Honey Lake, Secret Valley, and Mono Lake Basin in California, and Pleistocene forms from the edge of the Great Basin in Northern Utah, southeastern Idaho, southern Oregon, northwestern Nevada, and southeastern California. These occurrences are concordant with a distribution pattern of many other Late Cenozoic lake-dwelling animals in western North America (Taylor, 1960; in press). The distribution pattern implies historical (but not necessarily contemporaneous) existence of *Chasmistes* habitat along the northern and western edges of the Great Basin. If we could draw cladistic conclusions from an analysis of the morphology of these samples, we might shed more light on the drainage history.

Evaluation of the polarity of *Chasmistes* characters for cladistic purposes requires separation of the effects of parallelism, reversals, and introgression. The genera *Catostomus* and *Deltistes* are the most relevant group for comparison of characters to determine primitive states. *Deltistes* (and *Xyrauchen*, its osteologically similar relative from the Colorado R. drainage) might be the sister group of *Chasmistes*, based on shared fimbriate gill rakers. *Catostomus* is the most diverse and widespread genus in the tribe Catostomini (Miller, 1959). Within *Catostomus* we find the most likely primitive character states for the genus *Chasmistes*.

An alternative hypothesis, based on presence of a terminal mouth in *Chasmistes* larvae and a superficial similarity between the jaws of *Chasmistes* and *Ictiobus cyprinellus* (Fig. 11E), would involve consideration of the most primitive suckers as sister groups of *Chasmistes*. This hypothesis is rejected because *Chasmistes*, *Deltistes*, and *Catostomus* share derived character states in the ventral position of the mouth in postlarvae, as well as the shapes of the pterotics, urohyals, frontals, and much of the hyomandibulars.

If the *Chasmistes:Deltistes:Catostomus* sister-group relationships are accepted, and the resulting polarity of *Chasmistes* character states is defined, an interesting problem emerges. The most advanced

character states—the extreme anterior elongation of the maxilla and its premaxillary process and the obtuse-angled premaxillae and dentaries—are found in the Pliocene *Chasmistes spatulifer* of the Snake River Plain. Earlier and later *Chasmistes* from that area possess less advanced character states. The peak advancement in that lineage coincides with the peak diversity of the fauna of Pliocene Lake Idaho (Smith, 1975).

Cladistic hypotheses for some fossil and Recent *Chasmistes* are generated by coding character states for eight characters of the premaxillae, maxillae, and dentaries and calculating cladistic trees that show the minimum number of evolutionary steps. Character states of the samples analyzed are shown in Figs. 10 and 11. Ancestral states are coded 0 and represent *Catostomus*. Subsequent code values, 1, 2, represent more advanced steps in the morphoclines seen in the characters. Code values for *Deltistes luxatus* (not figured) are based on UMMZ 181770-S. Definitions of the characters and their states are as follows (species names refer to *Chasmistes*):

- A) Angle of premaxillary limbs: 0 (right angled) *Catostomus*; 1 (moderately obtuse) *Deltistes*, *batrachops*, *brevirostris*, *liorus*, *muriei*; 2 (obtuse) sp., *cujus*, *spatulifer*; the Mono Lake, China Lake, and Secret Valley forms are not known.
- B) Relative length of limbs of premaxillary: 0 (vertical limb longer) *Catostomus*, *Deltistes*, *muriei*; 1 (subequal) *liorus*; 2 (lower limb elongate) *brevirostris*, *cujus*, sp., *spatulifer*, *batrachops* (Fig. 11B shows a worn specimen). Other forms not known.
- C) Anterior constriction ("neck") of maxilla: 0 (thick) *Catostomus*; 1 (somewhat robust) *Deltistes*, *liorus*, *cujus*, sp.; 2 (slender) *brevirostris*, *batrachops*, *muriei*, *spatulifer*, Mono Lake, China Lake, Secret Valley.
- D) Angle of dorso-anterior process ("head") of maxilla to long axis of bone: 0 (nearly right angled) *Catostomus*, *Deltistes*, *liorus*, *brevirostris*, *muriei*, *cujus*, Mono Lake; 1 (angle obtuse) *batrachops*, sp., China Lake, Secret Valley; 2 (extremely obtuse) *spatulifer*.
- E) Angle of anteroventral (premaxillary) process of maxilla to long axis: 0 (right angle, posterior to head of maxilla) *Catostomus*, *Deltistes*; 1 (process projects anteriorly at an obtuse angle, position partly below head of maxilla) *liorus*, *cujus*, *brevirostris*, *muriei*, *batrachops*, sp., China Lake, Mono Lake; 2 (process projects strongly anteriorly, position anterior to head of maxilla) Secret Valley, *spatulifer*.

- F) Development of ventral keel of maxilla: 0 (strongly developed) *Catostomus*, *Deltistes*; 1 (modestly reduced) *liorus*, *cujus*, sp., Mono Lake, China Lake, Secret Valley; 2 (much reduced) *batrachops*, *muriei*, *brevirostris*, *spatulifer*.
- G) Angle and length of gnathic ramus relative to posterior body of dentary: 0 (slightly obtuse, short) *Catostomus*; 1 (obtuse, moderately long) *Deltistes*, *liorus*, *brevirostris*, *cujus*, China Lake, Mono Lake, Secret Valley; 2 (extremely obtuse, elongate) *batrachops*, sp., *muriei*, *spatulifer*.
- H) Angle of symphysis of dentary: 0 (parallel to gnathic ramus) *Catostomus*; 1 (sub-parallel to gnathic ramus) *Deltistes*, *liorus*, *brevirostris*, *muriei*; 2 (divergent) *batrachops*, *cujus*, sp., Mono Lake, China Lake, Secret Valley, *spatulifer*.

Possible cladistic relationships of the samples of *Chasmistes* for which characters could be scored, as well as *Catostomus* and *Deltistes luxatus*, were calculated according to the method of Kluge and Farris (1969). The preferred trees are assumed to be those that represent the branching sequence of the taxa in the fewest evolutionary steps among the character states. Several trees of about the same length were discovered. Two representative tree diagrams are given in Fig. 12.

The cladistic hypotheses (Fig. 12A, B) demonstrate extensive homoplasy—reversals and parallelisms—among the character states. The shortest tree (Fig. 12B, 20 steps) has most of the hypothetical evolutionary changes concentrated in the history prior to the emergence of the specialized Pliocene form, *C. spatulifer*. Furthermore, most of the characters (ADGH) are seen to have evolved in parallel. Inspection of the hypothetical sequence reveals that elimination of some of the parallelisms requires homoplasy in other characters, for example C and F. This hypothesis suggests that most of the active evolution in the group was ancient, perhaps associated with the period of active speciation (as suggested by Stanley, 1979), followed by a relatively steady period. The tree is geographically rather concordant (Smith and Koehn, 1971). Branches in Fig. 12B are rotated (without altering the sequence) to place the taxa roughly in their northeast to southwest order. Only *muriei*, from Jackson, Wyoming, is seriously discordant, being aligned with its sister group, *batrachops* and *spatulifer* from Oregon and adjacent Idaho, on the basis of shared elongate dentaries. However, this cladistic hypothesis is consistent

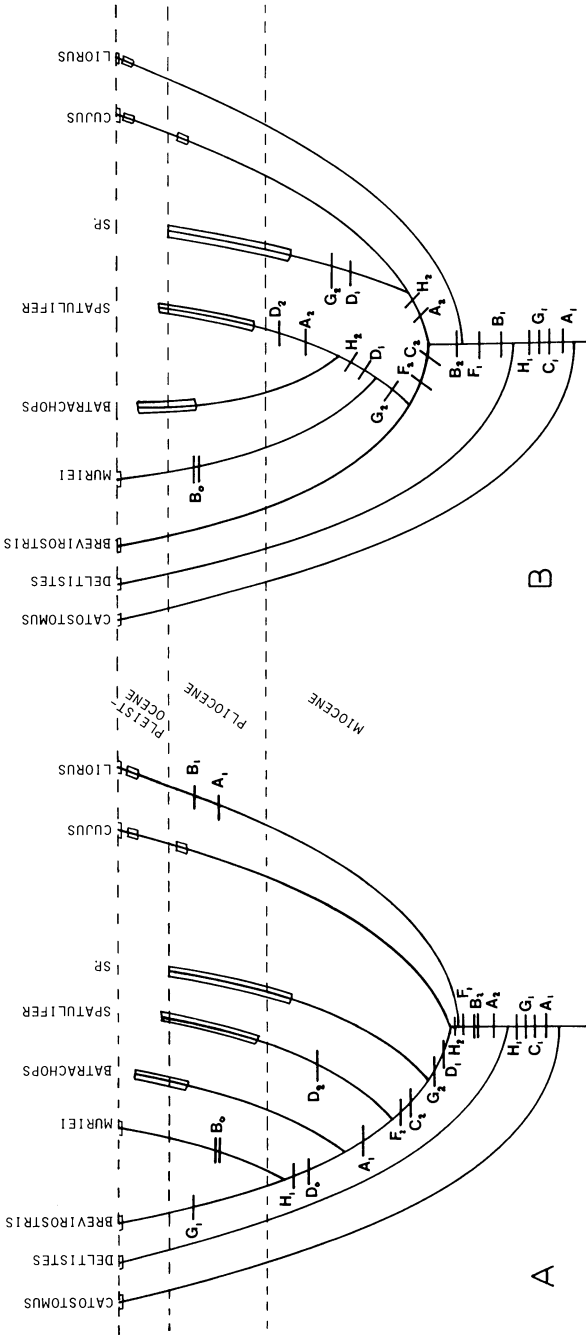


FIG. 12. Hypothetical branching sequences of *Chasmistes* in relation to *Catostomus* and *Delistetes*. At the base of each cladogram the hypothetical ancestor possessed standard character states of *Catostomus*, scored 0 for characters A-H. See text for definitions. Tree A was constrained to have character states of the oldest known fossil near the base. It is less parsimonious than tree B. Most of the later steps in A are reversals; those in B are parallelisms.

with late Miocene continuity of the upper Snake River drainage through southern Oregon (Taylor, in press).

An alternate cladistic hypothesis is presented in Fig. 12A (22 steps). This tree is the outcome of an attempt to make the oldest known (fossil) character states ancestral in *Chasmistes*; it constrains the Recent species, *liorus* and *brevirostris*, to show more recent evolution. The tree differs in its polarity and is less parsimonious. Most characters show reversals rather than parallelisms and more of the steps occur later in time, as intended. The constrained and non-parsimonious tree shows the cladistic consequences of the hypotheses that *Chasmistes* sp. of the Snake River Plain is ancestral and that later evolution in *liorus* and *brevirostris* involved reversals. This hypothesis is interesting in light of evidence that *liorus* and *brevirostris* have been influenced by introgression from the species of *Catostomus* with which they are sympatric in the Bonneville and Klamath basins. The tree is geographically concordant except that *muriei* is linked in a sister-group relationship with the Oregon forms, as in the alternative hypothesis. Geographically, *muriei* would be expected to be close to the Bonneville form (*liorus*), as are the other fishes in the upper Snake River drainage. *C. muriei* is also similar to *brevirostris* rather than *liorus* in its small scales; its papillose lips are unique in the genus, however.

The fossil forms from Secret Valley, Mono Lake, and China Lake are not shown on the cladistic trees because of missing data. When their positions are calculated on the basis of the characters available, the Mono and China Lake forms appear close to *batrachops*. The Secret Valley form is the sister species of *spatulifer* on the basis of shared anterior projection and position of the premaxillary process of the maxilla.

Although the cladistic hypotheses are not entirely acceptable because of the extensive homoplasy in the available characters, they suggest some conclusions. The Great Basin forms, *liorus* and *cujus*, seem to be relicts of the ancestral *Chasmistes*, and as such indicate a possible area of earliest evolution of the genus. A northwestern vicariant of the early form gave rise to the clade distributed along the Snake River Plain to central Oregon and south along the east side of the Sierras: *Chasmistes* sp., *spatulifer*, *batrachops*, *brevirostris*, and the undescribed forms from Secret Valley, Duck Valley, Honey Lake, Mono Lake, and China Lake. *C. muriei* is a member of this group that remained in the upper Snake River drainage. The branching sequence within this group is questionable, but both hypotheses imply that most of the differentiation occurred early, followed by relative

stasis in the Pliocene and Pleistocene. Recent evolution could have been a result of introgression, especially in *liorus* and *brevirostris*.

If any of these forms possess primitive *Catostomus*-like characters because of introgression, their placement on a cladogram could be erroneous. In particular, it is possible that the material of *liorus* and *brevirostris* is influenced by introgression. Similarly, the Pleistocene China Lake form could be primitive in appearance because of introgression, rather than as a primitive offshoot of the genus. There is no assurance that elimination of favorable habitat and resulting hybridization weren't occasionally caused by Pleistocene interpluvial desiccation as well as recent cultural mismanagement.

Apparent hybridization in every known population of this genus and introgression in almost every population is unusual even in fish biology. In each case the hybridization seems to have been associated with reduction of favorable habitat or numbers of *Chasmistes*, presumably leading to mixed-species spawning associations, as observed by Hubbs (1955:18). The result has been a rapid shift to morphological characters intermediate between *Chasmistes* and the local *Catostomus* in Utah Lake, Klamath Lake, Lake of the Woods, and Copco Reservoir.

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MATERIAL EXAMINED

Chasmistes liorus liorus.—UTAH: ANSP 20126-29 (2), Utah L., Cope, 1882; BMNH 1881.3.14.229, USNM 27361 (1), ca. 355 mm, Utah L., Jordan; BMNH 1883.12.14.236, USNM 28399 (1), ca. 245 mm, Utah L., Madsen, 1881; CAS-SU 11782-83 (2), Utah L., Madsen, 1895? MCZ 26806 (1), 349 mm, Utah L., Jordan, 1880; USNM 27361A-C (3), ca. 332–372 mm, Utah L., Jordan; USNM 28399A-C (3), Utah L., Madsen, 1881; USNM 75832 Holotype, 282 mm, Utah L., 1872.

Chasmistes liorus mictus.—see text.

Catostomus ardens × *Chasmistes liorus liorus*.—UTAH: BMNH 1881.3.14.230 (1), Utah L., 1881; USNM 12894, Paralectotype of *Catostomus fecundus* (1), Utah L., Yarrow and Henshaw, 1872; USNM 16988, Lectotype of *C. fecundus* (1), 392 mm, Utah L., Yarrow and Henshaw, 1872; USNM 22493 (1), ca. 244 mm, Provo, Yarrow and Henshaw, 1872; USNM 27362 (1), ca. 330 mm, Utah L., Jordan, 1889; USNM 26737, 1 skeleton, and 28398 (2), 302–358 mm, Utah L., Madsen, 1881; USNM 36815 (1), 290 mm, Utah L.; USNM 41725 (3), 254–319 mm, Utah L., Jordan, 1889.

Catostomus ardens × *Chasmistes liorus mictus*.—UTAH: UMMZ 207723 (1), 358 mm, Utah L., Madsen, 1942; UMMZ 207721 (1), 457 mm, Utah L., S of Lincoln Pt., Loy, 1967; UMMZ 207722 (1), 350 mm, Utah L., Arnold, 1959.

Catostomus ardens.—UTAH: UMMZ 85943 (1), 193 mm SL, Utah L., Tanner, 1926; UMMZ 141451 (4), 61–340 mm, Jordan R., Hubbs and Tanner, 1942; UMMZ 141457 (1), ca. 360 mm, Utah L., just S of Provo R. mouth, Hubbs and Tanner, 1942; UMMZ 176875 (2), 209

mm, Sevier R., 1953; UMMZ 192939 (2), 168, 183 mm, Utah L., 5 mi S Provo R. mouth, Madsen, 1942; UMMZ 207714 (4), 299–345 mm, Jordan R., Salt Lake Co., 1960; ANSP 20126-29 (1), Utah L., Cope, 1882; USNM 20337 (1), ca. 275 mm, Utah L., Yarrow, 1872; USNM 27363 Syntype (1), 387 mm, Utah L., Jordan, 1880; USNM 28400 (1), 435 mm, Utah L., Madsen, 1881; USNM 41658 (1), 255 mm, Utah L., Jordan, 1889.

Chasmistes muriei.—see text.

Chasmistes cujus.—NEVADA: ANSP 20523, Holotype, ca. 360 mm, Pyramid L., Cope; UMMZ 133839 (10) & 133839-S (1), mouth of Truckee R., Alcorn, 1941; UMMZ 137054 (1), 32 mm, Pyramid L., near mouth of Truckee R., Miller, 1939; UMMZ 161964 (2), 530, 540 mm, Pyramid L. at mouth of Truckee R., LaRivers, 1950; UMMZ 174435-S (1), 505 mm, Pyramid L., Johnson and LaRivers, 1958; UMMZ 174436-S (1), 475 mm, Pyramid L., Johnson and LaRivers, 1958; UMMZ 191634 (4), 405–435 mm, Pyramid L., Madsen and Carbine, 1935.

Chasmistes brevirostris.—OREGON: ANSP 20959, Lectotype, Klamath L., Cope; ANSP 20522, Paralectotype (1), Klamath L., Cope; USNM 48223, Holotype of *Chasmistes stomias*, Upper Klamath L., Gilbert et al., 1894; USNM 48224, Holotype of *Chasmistes copei*, Upper Klamath L., Meek and Alexander, 1896; UMMZ 160950 (11), 305–370 mm, Lake of the Woods, Locke, 1949; UMMZ 166442 (14), 310–370 mm, & UMMZ 166442-S (1), Lake of the Woods, Bond et al., 1952.

Chasmistes "brevirostris" (Catostomus snyderi × Chasmistes brevirostris).—OREGON: UMMZ 199198 (1), Sprague R., Chiloquin-Klamath Co. line, Andreasen, 1975; UMMZ 160948 (7), 285–370 mm, Lake of the Woods, Locke, 1949; UMMZ 166440 (4), 310–354 mm, Lake of the Woods, Bond et al., 1952.

Catostomus snyderi.—OREGON: UMMZ 130600 (13), 39–141 mm, Upper Klamath Lake, Hubbs, 1934; UMMZ 136679 (29), 31–59 mm, Sycan R., Miller, 1939; UMMZ 146507 (6), 103–433 mm, Lost R., Needham and Smith, 1941; UMMZ 166441 (1), 400 mm, Lake of the Woods, Bond et al., 1952; UMMZ 179363 (1), 52 mm, Upper Klamath Lake, Bailey, 1955.

Chasmistes "brevirostris" (Catostomus rimiculus × Chasmistes brevirostris).—CALIFORNIA: UMMZ 180686 (2), 352, 365 mm, and UMMZ 180686-S (1), Copco Res., Riley, 1961; UMMZ 207716 (19), 351–443 mm, and 15 specimens returned to Terry Mills, Calif. Fish & Game,

Copco Res., Mills et al., 1978–1979; CAS 26305 (1), 374 mm, Copco L., Coots, 1962.

Catostomus rimiculus.—CALIFORNIA: UMMZ 207712 (12), 281–379 mm., Copco Res., Mills and Mamika, 1978.

Catostomus tahoensis × *Chasmistes cujus*.—NEVADA: UMMZ 207713-S (2), Pyramid L., Smith, 1968.

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