A Pliocene fossil Razorback Sucker (*Xyrauchen texanus*) from Southern California

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#### Introduction

The monotypic *Xyrauchen* (Catostomidae) lineage, containing only the razorback sucker (*Xyrauchen texanus*), has been viewed as one of the more primitive members of the western subfamily Catostominae, tribe Catostomini (Smith 1992). *X. texanus* and the Lost River sucker (*Deltistes luxatus*) are believed to be sister groups of *Chasmistes* spp. (Miller and Smith 1981; Smith 1992). These are all large-bodied genera that inhabit extensive river systems; *Chasmistes brevirostris* and *Deltistes* in the Klamath River, *C. liorus* in Utah Lake, and *C. cujus* in Pyramid Lake and the Truckee River.

The federally endangered razorback sucker is one of the larger native freshwater fishes of the Colorado Basin, reaching a total length of nearly one meter (Sigler and Miller 1963). It derives its name from the pronounced nuchal hump found in adult members of the species, a characteristic which is also present in the humpback chub *Gila cypha* and to a lesser extent the bonytail *G. elegans*, both of which are from the Colorado River system.. Much speculation surrounds the function of the hump (La Rivers 1962; Minckley 1973; Moyle 1976), and it may potentially serve as a stabilizer in the swift and deep waters of the Colorado River.

Although swimming tests utilizing Colorado River fishes with similar hump morphology have been conducted (Berry and Pimentel 1985), the specific effect of the presence of the hump on swimming performance has not been empirically tested. Minckley and Meffe (1987) found that several native fishes with the pronounced hump survived flooding in Arizona and New Mexico, while nonnative, introduced fishes lacking the hump did not. These differential responses reflect differences in evolutionary histories (Minckley and Mefee 1987), and selection for the development of humps in native fish of the Colorado River may have been an evolutionary response to certain extreme hydrological conditions of the past. Studying species with prominent humps may help us to understand its function and gain insights on the selective factors that led to the convergent evolution of this character.

A fossil specimen (Figure 1) resembling X. texanus (SBCM A768-1) that is purportedly of early Pliocene age was collected from the Anza-Borrego Desert "on the north side of the San Felipe Hills near the western boundary of Imperial County and north of State Highway 78" (Stewart and Roeder 1993). The nearly complete fossil was found inside an oval-shaped arenitic sandstone concretion. The rock was fractured lengthwise in half, with one half containing most of the skeletal material and the other half containing mostly imprints. The sandstone in which the fossil is imbedded is deltaic in nature and suggests depositition in the delta of the ancestral Colorado River and subsequent transport north and west by continental drift to the current location. It is doubtful that more precise locality and informatin on the age of the specimen will ever become available. In this paper, characters of the fossil are compared with other catostomids (*Deltistes luxatus*, Chasmistes spp.) considered to be closely related to X. texanus (Smith 1992) to determine the taxonomic position of the fossil. Comparisons were also made with *Catostomus latipinnis*, which cohabits with X. texanus in the Colorado River system and is a member of the sister genus to the Xyrauchen group (Xyrauchen + Chasmistes + Deltistes) (Smith 1992). Catostomus latipinnis also hybridizes with Xyrauchen in the Colorado River

system (Hubbs and Miller 1953) and has the potential for introgression (Buth et al. 1987, Smith 1992a). Ultimately, in this paper we assert that the fossil is *X. texanus*, with some subtle meristic and morphological variations that contrast with contemporary individuals.

# Materials and Methods

Characters were evaluated and meristic counts were made on the fossil, and on comparative specimens listed in the materials examined section. Characters considered appropriate for comparison were chosen because of their accessibility on the fossil, and for their taxonomic importance to Smith (1992: Table 1 and Appendix 1). These descriptions were of particular value, because Smith constructed a phylogeny for all species grouped in the sucker family based on these characters, in addition to examining shared habits and geographic distribution.

# **Results and Discussion**

Although portions of the fins and several vertebrae are missing from the fossil, the missing features have, for the most part, left well-defined imprints in the rock, allowing for an estimation of some diagnostic counts. Meristic counts revealed the following: 16 dorsal fin rays and pterygiophores (Figs. 1 and 2); more than 9 pectoral fin rays; at least 8 pelvic fin rays; 7 anal pterygiophores; and about 42 post-Weberian vertebrae (about 46 total).

The four anterior-most vertebrae that form the Weberian apparatus are not visible, and the next 33 vertebrae in series are identifiable either by centra that are actually present or by well-defined imprints. The only portion present in the fossil that is posterior to the last visible centrum appears to be a fragment containing the origin of several caudal fin rays of both the dorsal and ventral lobes. The addition of an estimated nine caudal vertebrae in the fossil not leaving imprints is based on comparisons of similar caudal pedunclar regions in six *X. texanus* skeletons. The estimate is based on angling of neural and hemal spines, the relative position to the dorsal and anal fins, and on the position of a remnant of the lateral process of the cranial end of the third hypural.

In the *Xyrauchen* group, the anterior edge of the dermethmoid, just posterior to the median, anteriorly directed dermethmoid spine, flares out laterally and slightly posteriorly, so that in dorsal view it resembles a house with a chimney jutting straight up from the crown of the roof. Although much of the head skeleton has been tilted dorsolaterally in the fossil specimen probably as a result of torque and compression during fossilization (W. L. Minckley pers. comm), it likewise exhibits the "domed rectangle" shape described by Smith (1992: fig. 4a) and is similar in shape to *Chasmistes*. This is in contrast to the shorter, wider, and more fully rectangular shape in *Catostomus latipinnis*.

The dentaries in members of the *Xyrauchen* group are relatively long compared to other catostomids (Smith 1992) and show little or none of the ventral deflection and arching of the anterior gnathic ramus that occurs in *C. latipinnis*. The well preserved left dentary of the fossil is consistent with the shape and proportions of comparative specimens of *X. texanus*. The greatest length of the shaft of the dentary is 21 mm, and the distance from the ventral edge of the quadrate recess to the dorsal-most tip of the coronoid process measures 22 mm. The position of the prominent foramen that transverses the dentary below and near the posterior end of the gnathal ridge is also similar to that of *X. texanus* and *Chasmistes*. In these two genera the opening is oriented medial-lateral whereas in *Catostomus latipinnis* the orientation is more anterior-posterior.

The long axis of the body of the maxilla measures 27 mm in the fossil, with its posterior-most portion, the dentary process, missing. In the *Xyrauchen* group, the premaxillary (or anteromedian) process comes off of the narrow neck of the maxilla that is characteristic of catostomid fishes (Miller and Smith 1967), so that its tip is oriented anterior to the anterodorsal process. Although the neck of the left maxilla is shattered, and the anterodorsal process is the only one of the two that is visible, there is no suggestion that the premaxillary process is different from that of the *Xyrauchen* group.

While Smith (1992) reported that the lower limb of the preopercle is long in both *Xyrauchen* and *Deltistes*, and that it is relatively short in *Chasmistes cujus* and *Catostomus* 

*latipinnis*, we find this to be an equivocal character. The anterior tip of the preopercle ends five millimeters caudad of the mandibular condyle of the quadrate in the fossil.

The fossil specimen has 16 dorsal fin rays. In addition, there are two "rudimentary" anterior rays present, a number and size consistent with comparative materials of *X. texanus* (Fig.2). Fourteen or 15 rays are the norm for *X. texanus*, but ranges of 13-16 have been documented (Hubbs and Miller 1953; Sigler and Miller 1963; Minckley 1973; Moyle 1976). *Deltistes luxatus, Chasmistes* spp., and *Catostomus latipinnis* each have only 12-13 rays (Smith 1992). Our count is thus at the upper end of the range for *Xyrauchen*..

Six interneurals are found anterior to the dorsal fin of the fossil and in comparative material (Figs. 1 and 3). The number of large interneurals that comprise the hump in the fossil appears to be three. All comparative *X. texanus* specimens had three or four of these elements enlarged to contribute to the prominent hump, a range consistent with Smith (1992). *C. latipinnis* usually has 0-2 of these bones (Smith 1992), and our specimen had a single elongate element. Five comparative specimens of *Chasmistes cujus* each had only one of these bones. In all specimens except *Xyrauchen*, these elements are thin and in a line with the neural spines. The fossil clearly shows a prominent vertical recess in an impression of the prominent lead interneural in the hump, a character consistent with comparative material (Fig.3).

*X. texanus* has been shown to hybridize with *C. latipinnis* (Hubbs and Miller 1953; Buth et al. 1987, Tyus and Karp 1990) in the upper Colorado River system. This potential for hybridization may present additional problems when considering the taxonomic status of catostomid fossil material from the Colorado River drainage. In the hybrids, the hump is distinctly formed and evenly rounded, but not as pronounced as in *X. texanus* (Hubbs and Miller 1953). However, the hump that is present in the fossil is more pronounced than in even present-day *X. texanus*, which diminishes the likelihood of this being a hybrid fossil.

In *X. texanus*, the hump appears about 200 days after fertilization (Minckley and Gustafson 1982) and becomes fully developed at adulthood. The prominent hump is by far the most conspicuous feature of the fossil. Even with the anterodorsal part missing (Fig. 1), it is noticeably more pronounced and the lead edge is more vertically oriented than in comparative specimens. At its apex, the hump rises 38 mm dorsally from the long axis of the body even with the top of the neurocranium, and it measures 87 mm in length from its anterior edge at the posterior end of the neurocranium to the anterior edge of the first pterygiophore. This translates to approximately 10.3% and 23.5% of the standard length of the fish, respectively. These values are greater than those of comparative materials (7.6% for twelve specimens, and 18.2% for three specimens respectively).

The estimates of 435-440 mm TL and 370 mm SL place the specimen at the lower end of the size range for adult *X. texanus* (see Moyle 1976; McAda and Wydoski 1980; Minckley 1983; Tyus 1987; Marsh 1987). The vertebral count of approximately 42 post-Weberian vertebrae (46 total) for the fossil fish was one vertebra below the range of five comparative *X. texanus* specimens (43-44 post-Weberian vertebrae, 47-48 total). Comparative specimens of *Chasmistes cujus* had 46-47 total vertebrae and *Deltistes luxatus* had 49. Smith (1992) lists the total vertebral range for *Catostomus latipinnis* as 44-45.

*X. texanus* exhibit several sexually dimorphic characters, which include pelvic and anal fin lengths, body length and weight (Minckley 1983). Males are smaller than females (Moyle 1976; McAda and Wydoski 1980; Minckley 1983; Tyus 1987; Marsh 1987), and because the length of the fossil fish fits the lower end of the range for adult *X. texanus*, this also suggests that the fossil is a male. Curvature of the last anal fin-ray is also a dimorphic trait for males (McAda and Wydoski 1980) but unfortunately, this is missing in the fossil. On the basis of pelvic fin flaring Minckley (pers. comm. Aug 17, 1992) suggested the fossil might be a male. Finally, Minckley et al. (1990) have stated that males have a more exaggerated predorsal keel (hump). This dominant character in the fossil strengthens the argument that it is a male.

## Conclusion

Analysis of character descriptions (Smith 1992) for *X. texanus, Deltistes luxatus, Chasmistes* spp., and *Catostomus* spp. revealed that the fossil fish is most similar to *X. texanus*. However, the hump morphologies of recent *X. texanus* representatives are not as exaggerated as that of the fossil specimen. In addition, the fossil has been shown to be of small size with fewer vertebrae and more dorsal rays than known *Xyrauchen* material. The species seems to vary little morphologically throughout its range (Hubbs and Miller 1953). The vertebral count of the fossil suggests greater character variation in the Pliocene.

No fossil catostomids have been identified from the Bidahochi Formation, Arizona (Uyeno and Miller 1965), and until the Anza-Borrego *Xyrauchen* specimen was discovered, fossil catostomids older than Pleistocene age were unknown (Minckley et al. 1986). The *Xyrauchen* specimen is of early Pliocene age (Stewart and Roeder 1993), which extends the *Xyrauchen* lineage back more than five million years. Late Miocene (8.5 to 5.5 million years old) *Chasmistes* and *Deltistes* from the Chalk Hills Formation of Idaho are morphologically similar to modern forms (Miller and Smith 1981; Smith et al. 1982) and indicate an even earlier divergence for the groups (Smith 1992) and likely *Xyrauchen* as well. The cyprinid species in the Bidahochi Formation are also considered modern (Minckley pers. comm. 1993). Baskin (1978) has argued that the Bidahochi Formation is late Miocene. In most respects the Pliocene fossil *Xyrauchen* specimen is similar to extant razorback suckers, but there seems to be some meristic variation including a smaller vertebral count and a relatively larger hump.

Despite these minor character variations, we consider the specimen from the Anza-Borrego desert to be *Xyrauchen texanus*. However, the meristic and morphological variations that occur in the fossil, in comparison to modern *X. texanus*, should present an interesting series of questions regarding the history and evolution of the species. Perhaps in the course of their evolution, members of the *Xyrauchen* lineage adapted to changing climate and habitat conditions through a reduction of the nuchal hump and an increase in the

number of vertebrae with corresponding increase in length.

#### Materials Examined

Fossil *Xyrauchen* specimen: SBCM A768-1; *Xyrauchen texanus:* ASU 13760, ASU 13905, ASU 13906, ASU 14621, ASU 14622, ASU 14623, ASU 14624, ASU 14625, ASU 14626, ASU 14880, ASU 14881, ASU 14882, ASU three unnumbered skeletons; *Deltistes luxatus:* UCMP 122582; *Chasmistes cujus:* KWG 346, KWG 351, KWG 359, KWG 399, KWG 488; *Catostomus latipinnis:* ASU 13844. Institutional abbreviations indicate the following: SBCM (San Bernardino County Museum), ASU (Arizona State University), UCMP (University of California Museum of Paleontology), KWG (K. W. Gobalet, personal collection at CSU Bakersfield).

#### Acknowledgments

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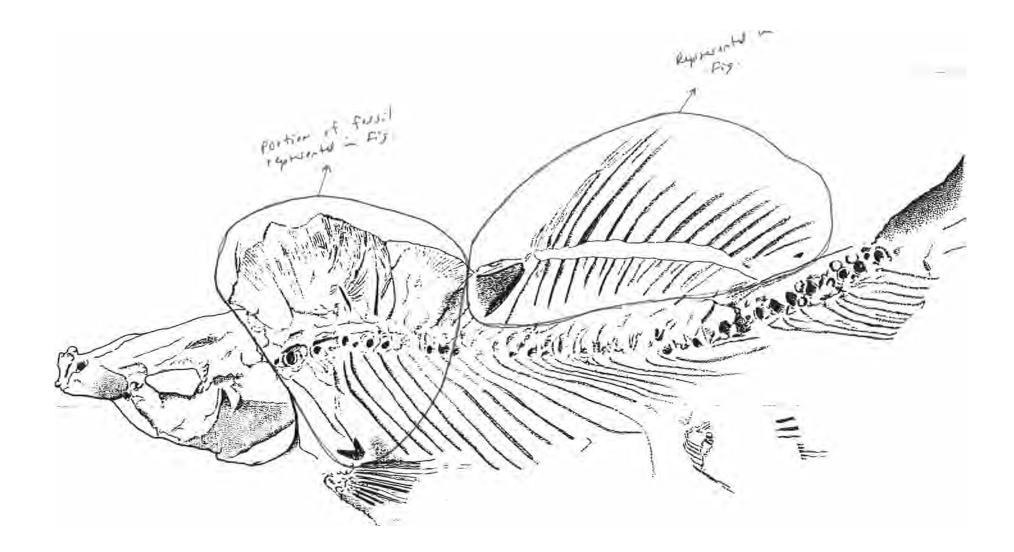
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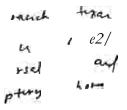
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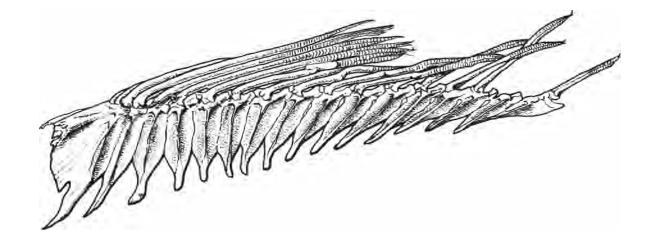
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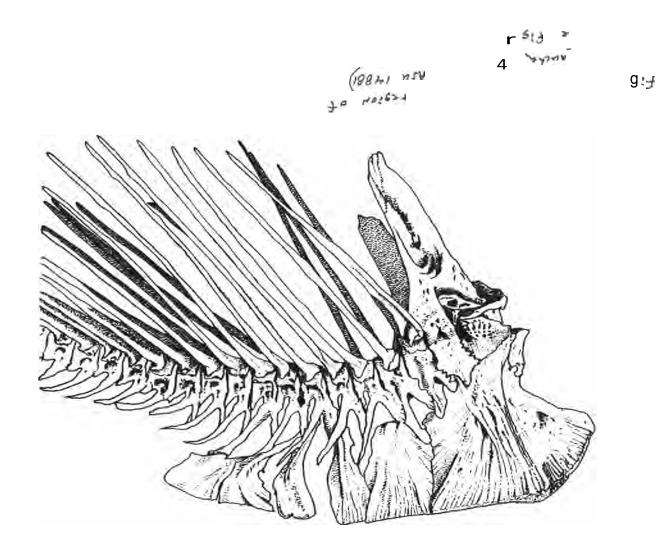














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November 24, 1997

Dear Bill-

Thank you so much for looking this over. Please be brutal and correct any of the many "personal contributions" we have attributed to you. I will not soon forget how I had screwed-up your evaluation of the fishing "weirs" in the Salton Basin. (Have you come up with an aerial view of those yet?)

Many thanks,

Ken Gobalet

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