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Terminal Pleistocene-Early Holocene Fishes From Tulare Lake, San Joaquin Valley, California with Comments on the Evolution of Sacramento Squawfish (*Ptychocheilus grandis*: Cyprinidae)

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ABSTRACT

The fossil remains of nine species of fishes have been recovered from a late Pleistocene - early Holocene archaeological site on the ancient shores of Tulare Lake, California. The fragmentary, highly mineralized remains are from a sturgeon (*Acipenser* sp.), Sacramento perch (Centrarchidae: *Archoplites interruptus*), tule perch (Embiotocidae: *Hysterocarpus traskii*), Sacramento sucker (Catostomidae: *Catostomus occidentalis*), and the following minnows (Cyprinidae): Sacramento squawfish (*Ptychocheilus grandis*), hitch (*Lavinia exilicauda*), Sacramento blackfish (*Orthodon microlepidotus*), splittail (*Pogonichthys macrolepidotus*), and thicktail chub (*Gila crassicauda*). Sacramento squawfish in Tulare Lake attained a size in excess of 900 mm in standard length. These remains verify that the assemblage of native species known from the lowland Central Valley of California was in place at least by the end of the Pleistocene and that the species diversity was not greater than at present. No unexpected species were recovered and no additional species supporting a link with the Pliocene Snake River or Lake Idaho were present. The late Pleistocene extinctions that decimated the mammalian megafauna spared the freshwater fishes.

INTRODUCTION

The native species of fishes that inhabit the freshwater Sacramento-San Joaquin ichthyological province of California include species that are either anadromous (steelhead rainbow trout, *Oncorhynchus mykiss*; chinook salmon, *O. tshawytscha*; sturgeons, *Acipenser* sp.; and lampreys *Lampetra* sp.); had ancestors that were marine (tule perch, *Hysterocarpus traskii*; threespine stickleback, *Gasterosteus aculeatus*; and sculpins, family Cottidae); or are those that reached their present locations by freshwater routes (minnows, Cyprinidae; Sacramento sucker, *Catostomus occidentalis*; and Sacramento perch, *Archoplites interruptus*) (Moyle 1976). Studies of the Chalk Hills and Glenns Ferry formations of Pliocene Lake Idaho suggest their species were ancestral to the native central California species that reached the Sacramento River drainage by the freshwater route (Uyeno and Miller, 1965; Miller and Smith, 1967; Smith, 1975, 1981; Minckley et al., 1986). During the Miocene-Pliocene the Snake River may have flowed not into the Columbia River, but southwesterly across southeastern Oregon, northwestern Nevada and into the Feather River system of the Sacramento River drainage (Wheeler and Cook, 1954; Smith, 1981). The presence of molluscs (Taylor and Smith, 1981) and of three genera of fishes, *Archoplites*, and the minnows *Mylopharodon*, and *Orthodon* (Smith, 1975), in both Pliocene Lake Idaho and the Central Valley of California support the postulate of this freshwater connection. The genera *Ptychocheilus*, *Catostomus*, and *Gila* might also have been derived from this ancestral source or from the Colorado River system by the way of hypothetical connections between the Colorado River, Great Basin, and Central Valley.

The approximately thirty species of Lake Idaho fossil fish are noteworthy for their diversity and extreme specialization (Smith, 1975). The native fish fauna of the Sacramento-San Joaquin drainage system of the Central Valley of California is depauperate by comparison and perhaps Holocene post-glacial drying has resulted in some extinctions (Peter Moyle, personal communication 1992). Possibly man caused some extinction as is suspected for some of the late Pleistocene terrestrial megafauna. If there was a greater diversity of species in central California in the past, it should be reflected in the California fossil record, perhaps sharing additional species with the Lake Idaho deposits.

The late Tertiary to Holocene freshwater fish fossil record of central California is limited. Casteel and Hutchison (1973) have documented the presence of Sacramento blackfish, *Orthodon microlepidotus*, within its present range during the Pliocene and Pleistocene, and Casteel and Rymer (1975) found Sacramento blackfish, Sacramento perch, and threespine stickleback from the Cache formation (Pliocene or Pleistocene) near Clear Lake, Lake County, California. The Plio-Pleistocene *Damalichthys saratogensis* described by

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Casteel (1978) is probably a freshwater derivative of the primarily marine family Embiotocidae. Subfossil scales from tule perch and Sacramento perch have been recovered from cores of Clear Lake, Lake County that date to 25,000 years before present (y.b.p.) (Casteel et al., 1977; Hopkirk, 1988). Sacramento perch scales and Sacramento blackfish pharyngeal teeth that date from 25,000 to 100,000 y.b.p. have been recovered from cores of Tulare Lake (Atwater et al., 1986). Jordan (1927) identified a new species of squawfish, *Ptychocheilus tularis* and ctenoid scales of Sacramento perch from lake bottom clay of Tulare Lake. He speculated the material was Pleistocene. Uyeno and Miller (1963) surmised the squawfish was the same as *P. grandis*. The only study to suggest that additional freshwater-derived species may have existed in the past is that of Casteel and Adam (1977). In addition to finding early Pleistocene remains of an undetermined salmonid, hardhead (*Mylopharodon conocephalus*), Sacramento blackfish, and Sacramento perch, they found a tiny cyprinid dentary (designated genus a) with possible affinities to Lake Idaho, and the first vertebra of an undetermined catostomid designated genus b.

Numerous studies have been undertaken on the fish remains recovered from archaeological sites within the Sacramento-San Joaquin ichthyological province of central California (Schulz and Simons, 1973; Casteel, 1974a; Schulz, 1979; Gobalet, 1990a). Some of these studies have provided evidence of range extensions of extinct species (Gobalet, 1990a). Jordan (1907) reported remains of hardhead and the Sacramento squawfish from Quaternary cave deposits in Shasta County. None of these studies on Holocene materials has unearthed unexpected fishes in the region, though some of these remains date to 7,500 y.b.p. (Gobalet, in press and unpublished data on Monterey County archaeological site CA-MNT-234).

The fossil and subfossil fish remains reported here from the shores of Tulare Lake date from the late Pleistocene to early Holocene. The purpose of the present paper is to record this Pleistocene fossil assemblage, to determine whether the species diversity was higher during the Pleistocene, to document additional ichthyological connections with the Lake Idaho fauna in the past, and to evaluate the size of the Sacramento squawfish represented to determine possible affinities with the Colorado squawfish, *Ptychocheilus lucius*.

THE WITT SITE LOCALITY

The fish remains in this study were collected from the ancient Witt archaeological site described by Riddell and Olsen (1969). It is officially recorded as site CA-Kin-32 in the State of California Archaeological Inventory. The locality consists of a stretch of old lake shoreline on the western side of the Tulare Lake Basin in Kings County, California (Figure 1). It is approximately 4.8 km in length by 0.8 km in width. The area today is nearly featureless terrain that gently slopes up from the lake basin to a low-lying east to west trending bulge in the valley floor known as Dudley Ridge. Historic stands of Tulare Lake were as high as 66 m above sea level. The Witt Site lies at about 58.5 m indicating the archaeological site was associated with a smaller body of water than the historic lake, now vanished. The uppermost portion of the site has been cultivated and is disturbed. The soils consist of fine sand and alkali silt with some small waterworn pebbles. Any large rocks present have been introduced by humans.

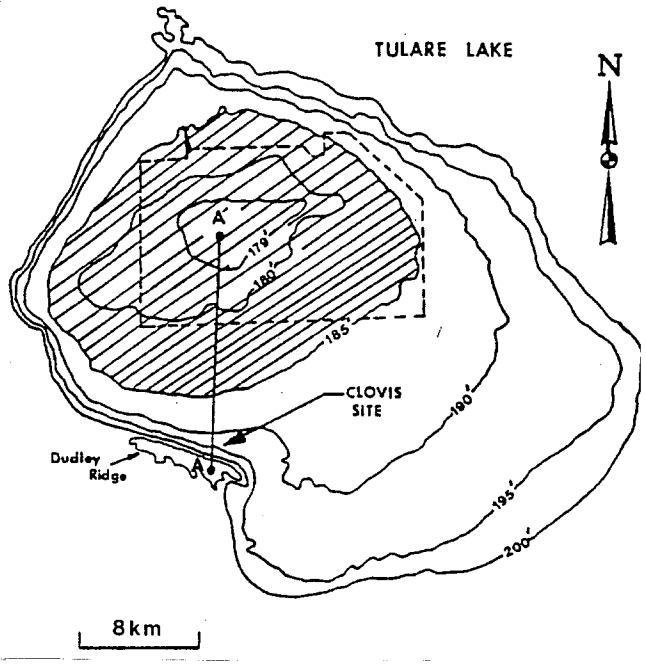

Fig. 1. Map of Tulare Lake showing location of Witt Clovis site. Hatched area indicates extent of hypothetical lake stand at 185 feet (56.4 m) in elevation with lake center at approximately 36° 02'N, 119° 44'W and Witt Clovis site at approximately 35° 56'N, 119° 58'W. Dashed lines indicate current boundary of Tulare Lake (adapted from Willig, 1991).

No scientific investigations were made here until the summer of 1991 when an on-going testing program was initiated. The fish remains were collected from five, one-meter square, archaeological test units (40 to 90 cm in depth) in which the soil was water screened through either 3.2 or 1.6 mm mesh screens. Bone, stone artifacts, and shell fragments of the mollusc *Anodonta* are abundant in a shallow cultural deposit that overlies the Blakeley Canal silt which lacks vertebrate remains. A complete discussion of the history and geology of the lake and the stratigraphy of the basin is found in Atwater et al. (1986).

AGE OF THE FAUNAL ASSEMBLAGE

The antiquity of the Witt Site has been established through the associated temporally-diagnostic cultural materials, the associated faunal remains, and a body of radiometric dates. Substantial numbers of temporally-diagnostic stone artifacts include specific types widely recognized to be associated with late Pleistocene and early Holocene Paleo-Indian populations in North America. The earliest of these are projectile points and other tools attributed to the Western Clovis cultural complex (Riddell and Olsen, 1969; Willig and Aikens, 1988; Willig, 1991). The Witt locality has produced more Clovis projectile points than any other site in western North America. Also abundant are cultural materials diagnostic of early Holocene occupations. These include numerous chipped stone crescents (Tadlock, 1966; Riddell and Olsen, 1969) and projectile points and knives assigned to the Western Stemmed point series (Willig and Aikens, 1988). The Witt Site is widely recognized by archaeologists as one of the oldest known sites in California (Moratto, 1984; Chartkoff and Chartkoff, 1984).

Recent test excavations have revealed the area of the early occupations may also have been used during later periods of prehistory. Some test units have produced shell beads (*Olivella biplicata*) that are temporally sensitive and indicate a brief use between about A.D. 1300 and 1500. One of the fossil-bearing test units (TU-12-1) was located at the eastern end of the Witt Site in a location where no evidence of late inhabitation was noted. The majority of the fish remains recovered can be attributed to the earlier inhabitation owing in part to mineralization of the bone and stratigraphic association with other highly mineralized vertebrate remains (Fenenga, 1991). The remains of 17 species of mammals (Table 1) are of expected late Pleistocene/early Holocene taxa. Heavily mineralized human remains were also recovered.

Uranium-Thorium datings were used because little or no organic fraction remains in the mineralized specimens (Table 2). The dates include two determinations on human skull fragments (Taylor et al., 1984). The others are on elements derived from Pleistocene taxa. There also is one radiocarbon (^{14}C) dating on unidentified bone fragments. These support a late Pleistocene-early Holocene age for the deposits.

Together the dating techniques that have been employed each support a late Pleistocene to early Holocene age for the majority of the archaeological assemblage at the Witt Site.

TABLE 1. Species Represented Among the Fossil Mammalian Remains from the Witt Site, Tulare Lake, California.

Glossotherium harlani	Harlan's ground sloth
Lepus californicus	black-tailed jack rabbit
Thomomys cf. T. *bottae*	valley pocket gopher
Castor canadensis	beaver
Canis latrans	coyote
Canis dirus	dire wolf
Felis atrox	lion
Mustela vison	mink
Mammuthus columbi	Columbian mammoth
Equus occidentalis	western horse
Equus conversidens	Mexican horse
Camelops hesternus	yesterday's camel
Cervus elaphus nannodes	tule elk
Odocoileus hemionus	mule deer
Antilocapra americana	pronghorn
Euceratherium collinum	shrub ox
Bison antiquus	bison

TABLE 2. Radiometric Dates on Mineralized Bone from Tulare Lake, California.

Uranium Series (230Th) Dates	Years Before Present
Unidentified bone	18,779
Unidentified bone	12,230 ± 71
Mammoth tooth	65,336 ± 3,445
Mammoth tusk	10,778 ± 488
Scapula (*Camelops*?)	17,745 ± 867
Horse metapodial	15,696 ± 370
Human bone	15,800
Human bone	11,380 ± 70
Radiocarbon (14C) Dates	
Unidentified bone fragments	7,325 ± 420

METHODS

The identifications made here are based on comparisons with skeletons listed in the materials examined section. Only pharyngeals and basioccipitals recovered from archaeological sites were available for the identification of the extinct thicktail chub, *Gila crassicauda*. As a result, thicktail chub remains may be more abundant than indicated.

Most of these remains are vertebrae. The vertebrae of tule perch, (family Embiotocidae), and Sacramento perch, (family Centrarchidae), are the only endemic members of their respective families in California freshwaters. While making their vertebrae easy to identify, possibly some embiotocid or centrarchid vertebrae represent additional species. All sucker vertebrae are assumed to be Sacramento suckers, since they are indistinguishable between species. But they, like the many cyprinid vertebrae, might represent species not hitherto known from California.

Vertebrae of cyprinids and catostomids are similar but distinguishable. Precaudal vertebrae of cyprinids possess a dorso-ventrally oriented bony strut from the dorsal edge of the socket of the parapophysis to the neural spine base that distinguishes them from vertebrae of the Sacramento sucker. Most caudal vertebrae of cyprinids bear a narrow ventrally projecting process from the posteroventral portion of the centrum that is lacking or rudimentary in the Sacramento sucker. Specific indentification of small cyprinid vertebrae are tentative.

Published equations for calculating the size of Sacramento squawfish from their vertebral width (Casteel, 1974a, 1976) were generated from individual squawfish too small to be useful in determining the size of squawfish bearing the huge vertebrae recovered from the Tulare Lake deposits. Specimens of large Sacramento squawfish obtained from the upper Kern River were measured and their bodies skeletonized. A regression of average precaudal vertebral width versus standard length was generated using 12 *Ptychochelius grandis* ranging from 122 mm to 662 mm standard length (SL), seven *P. oregonensis* ranging from 180 mm to 464 mm in SL and four *P. lucius* from 353 mm to 544 mm SL (see material examined section). Since all these squawfish have similar body form, this lumping increased the sample size of larger specimens. Such a lumping was previously used by Casteel (1974b) for otoliths of *Catostomus* sp. and by Gobalet (1989) for cyprinid vertebrae. The resultant regression was used to estimate the size of the Sacramento squawfish from which ten particularly large precaudal vertebra had been recovered.

Common and scientific names used here follow Robins et al. (1991) except that *Hysterocarpus traskii* is the prioritized spelling for the tule perch (Hubbs et al., 1979).

MATERIAL EXAMINED

Institutional abbreviations are as listed by Leviton et al. (1985). Specimens lacking catalog numbers, indicated by standard length (SL), and those numbered KWG are in the collection at California State University, Bakersfield. *Acipenser transmontanus*: KWG 410, KWG 236, KWG 286. *A. medirostris*: KWG 409. *Oncorhynchus mykiss*: 470mm SL. *Gila crassicauda*: CAS 18378, 16 pharyngeals, 3 basioccipitals. *G. bicolor*: KWG 376, KWG 274mm SL. *Lavinia exilicauda*: KWG 254. *Mylopharodon conocephalus*: CAS 25798, CAS 66053, CAS 66054, CAS 66050, CAS 66045, CAS 66046, CAS 66047, CAS 66049, 195mm SL. *Orthodon microlepidotus*: KWG 443, KWG 256, partial skull. *Pogonichthys macrolepidotus*: 265mm SL, 154mm SL, 174mm SL, 203mm SL. *Ptychocheilus grandis*: AMNH 47109SD-C, AMNH 471105D-C, CAS 26104, CAS 66190, CAS 66108, CAS 66109, CAS 66185, KWG 243, 243mm SL, 607mm SL, 122mm SL, 648mm SL, 644mm SL. *P. lucius:* CAS 66217, CAS 66191 (#938), CAS 66191 (#945), CAS 66191 (#939). *P. oregonensis*: AMNH 47154SD-C, AMNH 47153SD-C, AMNH 47152SD-C, KWG 404, KWG 454, KWG 347, 180mm SL. *Catostomus occidentalis*: KWG 240, KWG 277. *C. tahoensis*: 252mm SL. *C. platyrhynchus*: 98mm SL. *Archoplites interruptus*: 245mm SL, 2 skeletons. *Hysterocarpus traskii*: 141mm SL, 144mm SL, 104mm SL.

RESULTS AND DISCUSSION

Nine species of fishes were present (Table 3). This assemblage of fishes existed in the lowland marshes and sluggish waters of the central valley of California prior to recent catastrophic environmental changes (Schulz and Simons, 1973; Moyle, 1976). Schulz and Simons (1973) have subdivided these fishes into three categories: those that prefer sloughs, valley lakes, ponds and marshes including stream backwaters: Sacramento perch, tule perch, hitch (*Lavinia exilicauda*), thicktail chub and Sacramento blackfish; those that occupy a wide variety of habitats: splittail (*Pogonichthys macrolepidotus*), Sacramento squawfish and Sacramento sucker; and main channel moving-water forms: hardhead, steelhead rainbow trout, salmon and sturgeon.

Notably absent from the fossil remains reported here are remains of the hardhead, salmon, and steelhead rainbow trout. Hardhead tend to be riverine forms found at 270 - 420 meters elevation in the foothills (Moyle and Nichols, 1973). Since salmon are found in abundance at some archaeological sites (e.g. Contra Costa County, Gobalet, 1990b) their absence suggests lack of availability in the lacustrine habitat of Tulare Lake. The rarity of sturgeon remains further suggests that Tulare Lake was cut off much of the time from the anadromous species, a viewpoint supported by the tributary flows (Atwater et al., 1986). The California roach, *Hesperoleucas symmetricus*, and speckled dace, *Rhinichthys osculus*, are both Central Valley fishes that would be difficult to recover because of their small size and same habitat restriction as hardhead, salmon, and steelhead rainbow trout.

These results are consistent with and extend the findings of a Pleistocene squawfish by Jordan (1927) and of Sacramento perch scales and Sacramento blackfish pharyngeal teeth by Atwater et al. (1986) from core samples of Tulare Lake dated at 25,000 to 100,000 y.b.p. These remains reflect the lack of change of the freshwater fish fauna from at least the Pleistocene to present.

The size of the Sacramento squawfish here is striking. Ten precaudal vertebral centra measure from 15.5 mm to 22.5 mm in horizontal diameter. The linear regression generated by the measurement of 23 individuals in the genus *Ptychocheilus*, yielded a relationship of: standard length (mm) = 48.8 mm + 39.2 centrum width (mm), r^2= 0.97. The individual fishes from which the fossil vertebrae came thus ranged in standard length from 650 mm to 930 mm. Although huge by current standards, Moyle (1976) indicates the

TABLE 3. Fish Remains From Late Pleistocene-Early Holocene Archaeological Site CA-KIN-32 located on Tulare Lake, California.

common name	taxon	elements identified
Sacramento perch	*Archoplites interruptus*	224 vertebrae, 2 angulo-articulars, 3 cleithra, vomer, maxilla, pelvic, exoccipital, pterygiophore, lachrimal, basioccipital, premaxilla
tule perch	*Hysterocarpus traskii*	18 vertebrae
Sacramento sucker	*Catostomus occidentalis*	125 vertebrae, 2 opercles, basioccipital
minnow family	Cyprinidae	386 vertebrae, 2 ceratohyals, 4 basioccipitals, pharyngeal
splittail	*Pogonichthys macrolepidotus*	pharyngeal, basioccipital, opercle
hitch	*Lavina exilicauda*	vertebra, 2 ceratohyals, cleithrum, 3 pharyngeals, basioccipital
Sacramento blackfish	*Orthodon microlepidotus*	6 vertebrae, 3 pharyngeals, dentary, pleural rib, opercle, 2 basioccipitals
Sacramento squawfish	*Ptychocheilus grandis*	pharyngeal, 12 vertebrae, (width to 22.5mm)
thicktail chub	*Gila crassicauda*	pharyngeal, basioccipital
minnow or Sacramento sucker	Cyprinidae or *Catostomus occidentalis*	144 vertebral, and other fragments
white or green sturgeon	*Acipenser transmontanus* or *A. medirostris*	2 scutes, 2 bone fragments

largest known Sacramento squawfish attained a standard length of 1150 mm. Miller (1955) made a similar calculation to determine that a Colorado squawfish recovered from a Sobaipuri Indian trash heap in the San Pedro River, Arizona was about 1350 mm in standard length. Even prehistorically it appears the Sacramento squawfish did not attain the size of its cousin in the Colorado River drainage which may have attained two meters in total length (Holden and Wick, 1982). These numbers however, indicate they were closer in size than many realize, particularly since the two meter length is an estimate.

P. prelucius of the Lake Bidahochi Formation in Arizona is the oldest known fossil of the genus and is closely aligned with *P. lucius* (Uyeno and Miller, 1965). Baskin (1978) argues that this formation is late Miocene. In isolation, *P. lucius*, the largest North American cyprinid, may have changed little from the ancestral Miocene form (Carney and Page, 1990). This suggests that large size is ancestral and that *P. grandis* (and *P. oregonensis* and *P. umpquae*) are derived. Since the Sacramento squawfish vertebrae do not approach the size of *P. lucius* they do not provide evidence of a similarity through exceptional size with *P. grandis* from the late Pleistocene of California. Size reduction prior to the late Pleistocene may account for this or it may be that *P. prelucius* is not ancestral, that speciation in the genus is north to south, and that the sister group *Mylopharodon* and the individual species of *Ptychocheilus* diverged prior to the Miocene (Mayden et al., 1991). This is the parsimonious explanation in part because a prehistoric connection between the Colorado River and California Central Valley is not known.

The remains represented here which are probably from 8,000 to 19,000 years old have not yielded additional species to strengthen the proposed link between the native California species and fishes of the Pliocene Glenns Ferry Formation of Lake Idaho. Both localities share the following genera: *Catostomus, Ptychocheilus, Gila* (though thicktail chub are extinct), *Mylopharodon, Orthodon,* and *Archoplites*. Large species lacking from central California but present in Pliocene Lake Idaho are the freshwater dispersing sucker genus *Chasmistes,* and the cyprinid genera *Acrocheilus, Mylocheilus,* and *Richardsonius* (though these genera are found in adjacent drainages), the extinct *Idadon,* and the catfish genus, *Ictalurus*. California lacks native catfishes (Moyle, 1976). Catostomid and cyprinid vertebrae of additional species may have been present but indistinguishable from those of other family members. Extinction of these forms prior to the late Pleistocene in the central valley of California is still plausible.

The ancestry of the endemic Central Valley genera *Lavinia* and *Pogonichthys* is unknown. Smith (1975) has remarked on the diversity and extreme specialization of the Lake Idaho species in relation to North American fish faunal counterparts. He suggested that more generalized forms may have evolved from specialized forms and that the generalized *Pogonichthys* may have evolved from the specialized *Idadon*. A simpler explanation might have the ancestors of the California and Lake Idaho forms becoming separated before the radiation of species in Lake Idaho, thus a specialized *Idadon* evolved in Lake Idaho and a less specialized form (*Pogonichthys*) remained in the Central Valley of California. Though *Lavinia* is only known from the Holocene (Smith, 1981) a cleithrum from Pleistocene cores (Atwater et al. 1986) was questionably attributed to *Lavina exilicauda* (Gobalet, unpublished data).

SUMMARY

The nine species of fishes reported here from late Pleistocene to early Holocene Indian middens on the shores of Tulare Lake suggest the continuity of the fish fauna in their sluggish water environment from at least the late Pleistocene onward and the lack of morphological change. These remains do not indicate a greater diversity of fish forms in the Central Valley of California during the late Pleistocene and do not provide further links with the species of the Pliocene Glenns Ferry Formation of Idaho. The terrestrial megafaunal extinctions of the late Pleistocene did not extend to the California freshwater fishes and man did not cause the extinction of any California freshwater fishes until the 1900's. These abundant remains and the associated human elements suggest the site was a fishing camp of great antiquity.

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