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Late Pleistocene Freshwater Fishes from the Rancho La Brea Deposit, Southern California

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Abstract.—Three species of Pleistocene freshwater fishes occur at Rancho La Brea, the type deposit of the Rancho La Brea Age Mammalian faunas. Remains of rainbow trout, Salmo gairdneri, (mostly isolated vertebrae) and threespine stickleback, Gasterosteus aculeatus (primarily pelvic spines), are both common. One dentary and two vertebrae represent one individual of arroyo chub, Gila orcutti. Based on pelvic and dorsal spine morphology, a relatively unarmored form of stickleback (possibly representing the recent Gasterosteus aculeatus williamsoni) existed in the Los Angeles Basin up to 30,000 years ago. Collectively the fish fossils indicate local, permanent stream conditions, and not stream transport from distant mountainous areas 10-30 km away. Absence of the more montane Catostomus santaanae and *Rhinichthys* osculus also argues against long-distance transport. As with other ectothermic organisms (and possibly small endotherms), no extinct freshwater fishes are known from the Rancho La Brea deposits.

Rancho La Brea is the largest and best known late Pleistocene terrestrial deposit in North America. It is the type locality of Rancholabrean Age mammalian faunas (Savage 1951), and also includes a large fauna of birds, amphibians, and reptiles (Gehlbach 1965; Stock 1956; Harris and Jefferson 1985; Shaw and Quinn 1986). Fine sorting for microvertebrates, invertebrates and plants has yielded three taxa of freshwater fishes. These fishes, given preliminary notice by Akersten (1980), Akersten et al. (1983), Marcus and Berger (1984), and Harris and Jefferson (1985), represent living species as have most North American Quaternary freshwater fishes thus far (Miller 1965; M. L. Smith 1981; G. R. Smith 1981).

The fish remains came from fluvial channel deposits up to 5 m deep in Pit 91 at Rancho La Brea, a rectangular pit in the northwestern area of the deposit (Marcus and Berger 1984, Fig. 8.2). The pit was opened in 1915, but remained unworked until 1969, when detailed excavation began, and continues today (Shaw 1982; Shaw and Quinn 1986). About 5% of the excavated sediment from Pit 91 has been sorted. A detailed stratigraphic interpretation of the Rancho La Brea area was given by Woodard and Marcus (1973). Marcus and Berger (1984) and Shaw and Quinn (1986) summarized much of the research to date.

Methods and Materials

The collecting methods at Rancho La Brea are published (Miller 1972; Shaw 1982). The fish fossils were compared with skeletal material of Recent taxa of the same sizes.

Seventy fish bones (Fig. 1) have been recovered and are catalogued in the George C. Page Museum, Natural History Museum of Los Angeles County, as follows:

Fossil Material

Family Salmonidae

Salmo gairdneri Richardson, rainbow trout (15 bones); one ceratohyal 4.2 mm long, R51296 (Fig. IA), one atlas vertebra, 1.8 mm long, R45562; five abdominal vertebrae, 1.3-1.4 mm long, R39859, R45558(2) (Fig. I B), R45559-60; nine caudal vertebrae, 0.9-2.0 mm long, RI 5824, R45551 (Fig. IC), R45557, R45559, R45561, R45563-64, R49533, R51295.

Family Cyprinidae

Gila orcutti (Eigenmann and Eigenmann), arroyo chub (four bones); one fragmentary left dentary, 3.6 mm long, R45570 (Fig. 1D, E); one anterior (first) vertebra, 0.6 mm long, R45572 (Fig. IF); two fifth or sixth abdominal vertebrae, 1.3 mm long, R45571 (Fig. 1G, H, I), R51293.

Family Gasterosteidae

Gasterosteus aculeams Linnaeus, threespine stickleback (51 bones); 14 right pelvic spines, some fragmentary, up to 4.1 mm long, R34195, R34817–19, R34822-23, R45553-54 (Fig. 1M), R45566-67, R47902, R47904, R51291–92; 25 left pelvic spines, some fragmentary, up to 4.8 mm long, R20861 (Fig. 10), R34807-12, R34814-16, R34820, R36592-94, R39860-61, R46213, R46606, R47039, R47903, R47901, R47903, R47907, R50325, R51290; six first or second dorsal spines, 2.2-3.6 mm high, R45552, R34813 (Fig. 1N), R2 1192, R45568, R45130, R45157; four abdominal vertebrae, 0.9-1.4 mm long, RI 8732 (Fig. IL), R45555, R45565, R45569; one left pelvic girdle, R51294 (Fig. IA one left sphenotic, R51294 (Fig. 1K).

Recent Comparative Material

Collections of Recent taxa are from the Natural History Museum of Los Angeles County (Section of Fishes) (LACM) and the University of Michigan Museum of Zoology (UMMZ); as dry skeletons (D), cleared and stained specimens (CS), bony parts (W) dissected from, or radiographs (R) of whole preserved specimens. Recent species were chosen from native southwestern U.S. forms (Culver and Hubbs 1917; Follett 1961; Moyle 1976), and since the fossils were indistinguishable from some of these, a wider range of extralimital forms was not examined. Number of specimens and size range in standard length (SL) in parentheses are for specimens actually examined. Fish specimens were measured with dial calipers and bone measurements were from an ocular micrometer (read to the nearest 0.1-0.04 mm, respectively). Pelvic spine length is the maximum length, and height was the greatest vertical distance between the proximal ends of the dorsal and ventral flanges and perpendicular to the long axis. All measurements and serration counts were made on pelvic spines dissected from the fish and with the skin and musculature removed. Dentary length was taken from the symphysis to the anterior origin of the ascending process. Unless otherwise noted collections are from California, Los Angeles County, and catalog numbers are LACM.

Family Salmonidae

***Salmo** gairdneri.* **35861-1** to 4(101-155), E Fk San Gabriel R, 16 March 1973 (D); **42371-1** to 11(52-121), trib N Fk San Gabriel R, 13 October 1972 (R, CS);

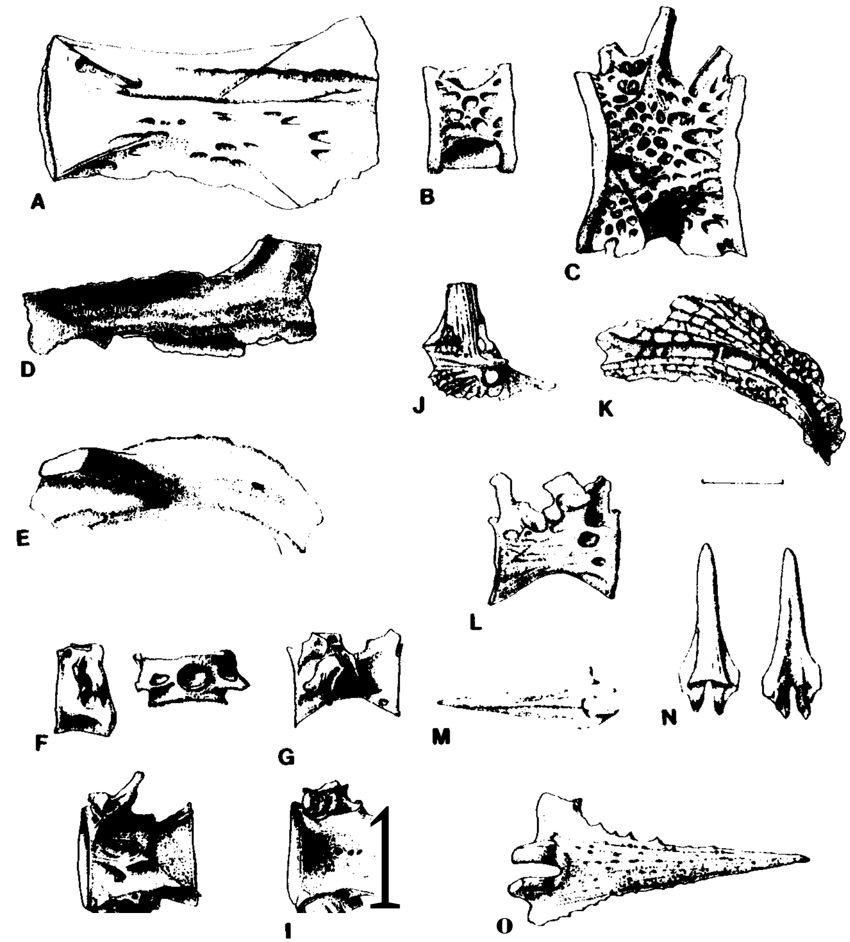

Fig. 1. Bones of: *Salmo gairdneri.* A. Left ceratohyal. B. Abdominal vertebra. C. Caudal vertebrae. *Gila orcutti.* D. Lateral view of left dentary, anterior to left. E. Dorsal view of left dentary, anterior to right. F. Cervical vertebrae, lateral view (left), anterior to left, dorsal view (right) anterior is up. 0. Abdominal vertebra, lateral view (left), anterior to left. H. Abdominal vertebra, dorsal view, anterior to left. I. Abdominal vertebra, ventral view, anterior to left. *Gasterosteus aculeams.* J. Lateral view of left pectoral girdle, anterior to left. K. Dorsal view of left sphenotic, anterior to left. L. Abdominal vertebrae. M. Right pectoral spine, anterior view. N. Dorsal spine, anterior (left) and posterior (right) views. 0. Left pectoral spine, anterior view. Scale equals I mm for all except L, for which it equals 0.5 mm.

35409-1, 2(123-126), trib W Fk San Gabriel R, 26 June 1975(R); 31858-5, 4(119-133), Malibu Cr, 7 March 1971 (R); **38578-1**, 2(100-125), Malibu Cr, 18 February 1973 (R).

Salmo clarki Richardson, cutthroat trout. **35803-1**, 2(57-64), CA, Mono Co, N Fk Cottonwood Dr, 24 July 1974 (CS); 44404-1 to 7(90-148), OR, Linn Co, Minto Cr, 23 August 1976 (W); UMMZ 179560-S, 1, 4, 5 (of 8) (133-175), NM, Taos Co, La Junta Cr, 11 July 1961 (D).

Salmo aguabonita Jordan, golden trout. 35854-1(132), ('A, Tulare Co, E Fk Kaweah R, July 1973 (D); 35857-2, 3, 5(146-172), CA, Inyo Co, Hidden L, 2 September 1973 (D).

Family Cyprinidae

Gila orcutti. 35856- I to 14(55-114), Malibu Cr, 18 November 1973(D); 42357-3, 25(36-89), upper Santa Clara R, 6 April 1979 (W).

Gila bicolor (Girard), tui chub. UMMZ 188955-S, 6(73-121), NV, Churchill Co, Little Soda L, 9 mi NW Fallon, 14 August 1979 (D); 35859-1(190), 42376-2(122), CA, Mono Co, Owens R, summer, 1970 (D); 33829-3, 4,11 to 17(182-235), CA, Mono Co, Crowley L, 17 May 1973 (D); UMMZ 177085-S, 8(98-200), CA, San Bernardino Co, Soda Lake Spring at Zzyzx Ranch, 1 July 1959 (D).

Ilesperokucas symmetricus (Baird and Girard), California roach. 35429-1, 5(35–50), CA, Santa Barbara Co, trib Sisquoc R, 16 July 1975 (W).

Rhinichthys osculus (Girard), speckled dace. 35853-1 to 6(56-63), W Fk San Gabriel R, 15 April 1973 (D).

Family Gasterosteidae

Gasterosteus aculeatus williamsoni (Girard). UMMZ 134677, 10(35-48), San Gabriel R, 27 August 1941 (W); 32591-1, 8(34-39), San Gabriel R, Whittier Narrows, 9 May 1944 (W); 43742-1, 7(43-49), and LACM JNB 10(W)74, 10(47-56), Santa Clara R, upper Soledad Canyon, 13 April 1974 (W).

Gasterosteus aculeatus microcephalus Girard. 34070-2, 10(43–50), CA, Ventura Co, mouth Santa Clara R, 27 July 1974 (W); 43743-1, 10(39–42), CA, Ventura Co, Sespe Cr, 1.0 mi W Fillmore, 23 April 1981 (W).

Gasterosteus aculeatus aculeatus. 42657-2, 9(41-63), CA, Santa Cruz Co, Struve Slough, 1 km N mouth Pajaro R, 9 June 1981 (W).

Results

The fossil bones are indistinguishable from the bones of three species of freshwater fishes extant in Los Angeles Basin streams into historical time, namely rainbow trout, arroyo chub, and threespined stickleback.

The rainbow trout vertebrae are very similar in both the migratory (steelhead) and resident fish from the area today. Vertebrae of golden and cutthroat trouts arc typically longer in relation to their diameter than those of rainbow, but this is difficult to interpret without knowing where in the vertebral column the vertebra comes from. More diagnostic for the golden and cutthroat trouts are the ridges interspersed between the numerous excavations on the bottom, top, and sides of the vertebrae. In addition, these ridges are slightly to greatly longitudinal in orientation. The surfaccs of rainbow trout vertebrae are flat, or nearly so; the excavations appearing as holes punched in a flat surface (Fig. 1B, C). The fossil trout ceratohyal represents a fish 61 mm SL (ceratohyal length = .057 SL + .708, N = 12(48-155 mm SL), r = .990). Since the vertebrae are disarticulated, the number of trout represented is not known. The largest vertebrae represent fish about 150 mm SL.

The three bones of arroyo chub (excluding R51293, which is fragmentary) could also be from one fish 62 mm SL (dentary length = --1.672 + .0639 SL, N = 25(35-89 mm SL), r = .943). The anteriormost vertebra (Fig. IF) is not as long as in *G. bicolor, Rhinichthys osculus,* or *Hesperoleucas symmetricus.* The prominent circular pit on the ventral edge of this vertebra in *Gila orcutti* is absent or only incipiently developed in the other three species. Also in *Rhinichthys* the anterior vertebrae are wider transversely than deep, rather than circular as in the remaining species. The anterior ramus of the dentary is moderately broader and flatter laterally in *G. orcutti* than in *G. bicolor* and extremely more so than in *Hesperoleucas* and *Rhinichthys.* The abdominal vertebra is distinctive from *Rhinichthys,* but very similar to *G. bicolor* as well as *G. orcutti.*

Three morphologically defined subspecies of stickleback in California are defined by a progressive reduction of bony armor in more southerly populations, particularly the number of lateral plates (Miller and Hubbs 1969; Bell 1976). The fossil pelvic and dorsal spines of stickleback from La Brea have the relatively reduced features of unarmored threespine stickleback (Gross 1978). The complete pelvic spines have fewer poorly developed serrations along the ventral edge, about the same as fish *(G. a. williamsoni)* from the Los Angeles Basin. However, *G. a. williamsoni* from the upper Santa Clara River have more, as do *G. a. microcephalus* from farther downstream (Table 1). The fossil dorsal spines lack serrations (Fig. IC), again a condition of Los Angeles Basin *G. a. williamsoni* only. Only an occasional adult male of Los Angeles Basin *G. a. williamsoni* will have up to three serrations basally on the dorsal spines. Adult fish of both sexes from the upper and lower Santa Clara River consistently have such serrations. The serrations are even more numerous and better developed in *G. a. aculeatus.* The adult size of the fossil fish is not known. The lengths of the fossil spines do not exceed lengths of those of *G. a. williamsoni* and *G. a. microcephalus.* If they had the same proportions as recent stickleback from the Los Angeles Basin, they were 35 to 40 mm SL (standard length = 1.63 spine length + 32.2, N = *15,* r = *.16).* The low r value demonstrates considerable variability in spine length. The evidence indicates the fossil stickleback was as unarmored as the fish present into historical times in the Los Angeles Basin. The stickleback fossils represent at least 23 separate fish (the number of left pelvic spines).

The fish fossils come from three areas in Pit 91: I) stream drift from the southeast corner, also containing mollusks and abundant macroscopic plant material, 2) a lens-shaped deposit in the northeastern corner with fragmentary remains of vertebrates equal to or smaller than juvenile bison, and 3) the central-western side on the western edge of the "central bone mass" (George Jefferson, pers. comm.; Shaw and Quinn 1986). The lens-shaped deposit shows evidence of subaerial exposure. The stream drift contained all of the bones of arroyo chub, and all but two bones of the rainbow trout; the latter came from the lens-shaped deposit. Threespine stickleback came from all three areas as follows: 1) 13 bones, 2) 31 bones, and 3) 7 bones.

Discussion

Deposits at Pit 91 are a complex of stream and overbank deposits (Maloney and Akersten 1976). Bones occur in poorly sorted sandy and gravelly portions of a channel up to 8 m wide that was later invaded by liquid tar. Mammalian long

Table 1. Frequency distribution of ventral serrations on pelvic spines of *Gasterosteus aculeatus* spines 3 mm or longer.

	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	N	$\bar{x}$	S.D.
La Brea fossils	4				2	2		1		2			>								2	4.58	4. 0
G. a. williamsoni																							
Los Angeles Basin	4	2	[illegible]	5		4	5	4	1	3		1	1								[illegible]	4.8 8	3. 6
Upper Santa Clara						1		2	1	1	2	3	2	2	4	3	1		1		24	1 9 66	3. 48
G. a. microcephalus		1	1			1		4		[illegible]	2	4	3	3	3	3	1		4	2	35	1 857	4.5 2

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bones, predominantly from carnivores and scavengers, are generally aligned in the direction of the channel and show little wear or abrasion. Silt and blue-green clays lateral to the channel contain most of the plant fossils, but fewer vertebrate fossils. Plant fossils are from several distinct plant communities including closed cone pine forest, relict coast redwood, inland dry foothills, and nearby pond or marsh. Two primary agencies of deposi tion are believed responsible for the present geological facies: entrapment of animals in soft asphalt pools during warm weather and subsequent asphalt invasion of stream collected bone concentrations (Woodard and Marcus 1973; Maloney et al. 1974; Marcus and Berger 1984; Harris and Jefferson 1985).

Ecological indications from the plant fossils are that the Pit 91 deposits were accumulated at a time when winters were wetter and summers dry but cooler than today (Marcus and Berger 1984). Radiocarbon dates for the sites where the fish fossils were found range from 25,000 ± 1,000 to 33,000 ± 1,750 yr BP (Marcus and Berger 1984), and at that time the sea level was somewhat higher, possibly to within a few kilometers of La Brea (Nardin et al. 1981; Nardin 1983). Late Pleistocene climates varied widely, but coastal arc,.. (including La Brea) apparently fluctuated much less because the marine influence maintained Mediterranean climatic conditions (Johnson 1977; Miller 1971; Harris 1985).

Seven species of fishes inhabited the inland freshwaters of southern California into historical time, namely ***Lampetra tridentata*** (Pacific lamprey), ***Lampetra*** cf. *pacifica* (Pacific brook **lamprey**), *Salmo gairdneri*. *Gila orcutti*. ***Rhinichthys osculus***, ***Catostomus santaanae***, and ***Gasterosteus aculeatus*** (Culver and Hubbs 1917; Follett 1961; Moyle 1976). All seven species occurred in the Los Angeles River, which flowed westward three to four km south of La **Brea** until 1851 when its course was fixed by man to the present southerly route to San Pedro (Shepard and Wanless 1971). Lampreys lack bone and would not fossilise, and ***Rhinichthys*** and ***Catostomus*** have not been found. These last two species exist today in mountainous tributaries of the Los Angeles River in the San Gabriel Mountains, farther **upstream** than *Gila* or *Gasterosteus*. The lack of ***Rhinichthys*** and ***Catostomus*** indicate (tentatively) no long-distance transport of fish to the site. In addition, although the individual fossils are **disarticulated** and sometimes broken, they show little or no abrasion, presumably reflecting local deposition of an *in situ* fauna.

As with other ectothermic organisms, amphibians and reptiles (Gehlbach 1965) and insects (Miller 1982), no evidence exists for prehistoric extinctions among the freshwater fishes at La Brea in the last 32,000 years. However, in the last 45 years the Pacific brook lamprey disappeared (Hubbs 1967), and the unarmored threespine stickleback became an endangered species (Moyle 1976).

Considerable extinction occurred among the larger birds and mammals. Little or none is documented for the small birds **and** mammals, i.e., **passerines**, rodents **(St** 1 1956; Harris and Jefferson 1985). However, these small endotherms, **particul.** **sserine** birds are difficult to identify and future work may disclose extinct **forms**. Otherwise, whatever led to the megafaunal extinctions did not lead to elimination of small aquatic vertebrates nor of **endothermic** ones.

The presence of fossils of these three fish species is additional evidence arguing for permanent, small riparian stream conditions in the area of the La **Brea** **its**. All could survive only under the following conditions: **1)** water **tempera** bout **22°C**, 2) dissolved oxygen ≥ **8‰**, due to large deep pools, adequate ground water inflow, and/or shaded conditions, and 3) available hiding places to provide protection from predators (Moyle 1976). The three fossil taxa present an ecologically graded series with *Saline gairdneri* requiring the coldest and most oxygenated water (Moyle 1976). *Gila orcutti* requires the warmest and least oxygenated water (Castleberry and Cech 1986), and *Gasterosteus aculeatus* has intermediate requirements (Feldmuth and Baskin 1976). The abundance of fossil stickleback and trout suggest an environment on the cooler side of this range that could be attributed to colder climate than today or local spring-fed conditions. However, by themselves, the fish remains arc also consistent with the fish fauna present into historical times.

A large literaturec ists on the selection by piscine predators, particularly trout, for fully, or at least well, armored stickleback (Wootton 1976; Gross 1978; Bell 1984). Native trout do not occur with the only remaining population of *G. a. williamsoni* in the upper Santa Clara River (Bell 1978). However, unarmored stickleback were known from the Los Angeles and San Gabriel River systems which also harbored runs of steclhead trout *Salmo gairdneri* (Hubbs 1946). If poorly armored stickleback necessitates lack of piscine predators (or at least lack of trout), perhaps their interaction was limited to a few weeks during midwinter high flows when adult trout migrated to, and young smolts descended from, headwater tributaries lacking stickleback. The present evidence indicates all three species lived in some proximity on the Los Angeles Basin. They could have occupied separate habitats but still had their remains washed together in the stream deposits of Pit 91.

The fossils come from three separate places within Pit 91 and were separated over as much as 10,750 years (including error). Thus dry-warm periods as well as wet-cool ones could be included. The fact that only small taxa or small specimens of larger ones were taken indicates small, local tributaries rather than a main drainage.

This is the first fossil record for *Gila orcutti*, but *Saline gairdneri* and, particularly *Gasterosteus aculeatus* have extensive fossil records in the western United States (G. R. Smith 1981; M. L. Smith 1981; Cavender and Miller 1982; Bell 1973; Bell et al. 1985). Recently fossil stickleback have been discovered in Pleistocene beds of Lake Manix in the Mojave drainage (Roeder 1985). Bell (1982) discovered recent stickleback living in Holcomb Creek, a tributary to the Mojave River, but subsequent electrophoretic analysis suggests they were introduced with trout from the Santa Clara River (D. Buth, pers. comm.). These fossils will be of great interest, since this gap separates distinct evolutionary lines in each taxon today.

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Notes on Marine Algae of San Diego County luding Merger of *Murrayellopsis with Veleroa*

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Abstract.-The hist of marine algal studies in San Diego County is reviewed. Ten taxa of Rhodop ta have ranges that extend into this southernmost part of California on the basi of recent collections. The distributions of these taxa were previously reported to erminate to the north either on the rill r 'alifornia Channel Islands or on th mainland. San Diego records are summar ed for l species that have been ad d to the California flora since Abbott and Hollenberg's *Marine Algae of California* as published (1976). Three species earlier considered rare in southern California ve been found to be extremely abundant and widespread in algal turf on rocky aches of San Diego County. Recent subtidal collections of an undescribed *Ph odrys* are treated as a major range extension of *P. cerratae,* described from central eru. Abundant material from San Diego County sites supports the merger of *M rayellopsis* and *Veleroa* (Rhodophyta) both at the generic and species level; for reasons of priority, *Murrayellopsis dawsonii* becomes a synonym of *Veleroa sub lata.*

During early days of exploration in alifornia, ship-based studies focussed primarily on the coast between Montere and San Francisco. Vancouver's expedition with Menzies as a biologist, howev r, spent nearly 2 weeks in San Diego late in 1793 before sailing south to El Rosario 'n Baja California, thence to Hawaii (Jepson 1929). The few plants preserved fro this voyage were described in scattered reports; the only alga that might have n collected near San Diego is the species now known as *Egregia menziesii.* W k of early collectors of marine algae throughout California has been described b Papenfuss (1976).

In 1885, Daniel Cleveland, a 60 year resident San Diego, listed the algal species he had collected "at San Diego" in Orcutt' checklist of the flowering plants of southern and Baja California (Cleveland 18). This was the first published information for marine algae on the coast of Sa Diego County. Both he and Edward Palmer, another local botanist, sent specime s to Farlow at Harvard to be identified and, if new to science, to be named. These wo early phycologists were recognized by the names of several species that were rst collected locally (*Sargassum palmeri; Ozophora, Platysiphonia,* and *Pterosip nia clevelandii*).

During the years just before and after 1900, Mary Snyder co ected extensively from San Diego beaches and sent material to herbaria throu out the United States. Snyder's specimens were cited by other workers but her llections never were assembled as the basis for local floristic analyses.

Somewhat later Setchell and Gardner, working in Berkeley, bro ht together all available information about Chlorophyta and Phaeophyta alon the entire