SOUTHERN CALIFORNIA ACADEMY OF SCIENCES

BULLETIN

Volume 88   Number 3

THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.

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

Camm C. Swift

*Section of Fishes, Natural History Museum of Los Angeles County,
900 Exposition Boulevard, Los Angeles, California 90007*

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. 1A), one atlas vertebra, 1.8 mm long, R45562; five abdominal vertebrae, 1.3–1.4 mm long, R39859, R45558(2) (Fig. 1B), R45559–60; nine caudal vertebrae, 0.9–2.0 mm long, R15824, R45551 (Fig. 1C), 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. 1F); two fifth or sixth abdominal vertebrae, 1.3 mm long, R45571 (Fig. 1G, H, I), R51293.

Family Gasterosteidae

Gasterosteus aculeatus 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. 1O), 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), R21192, R45568, R45130, R45157; four abdominal vertebrae, 0.9–1.4 mm long, R18732 (Fig. 1L), R45555, R45565, R45569; one left pelvic girdle, R51294 (Fig. 1J); 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);
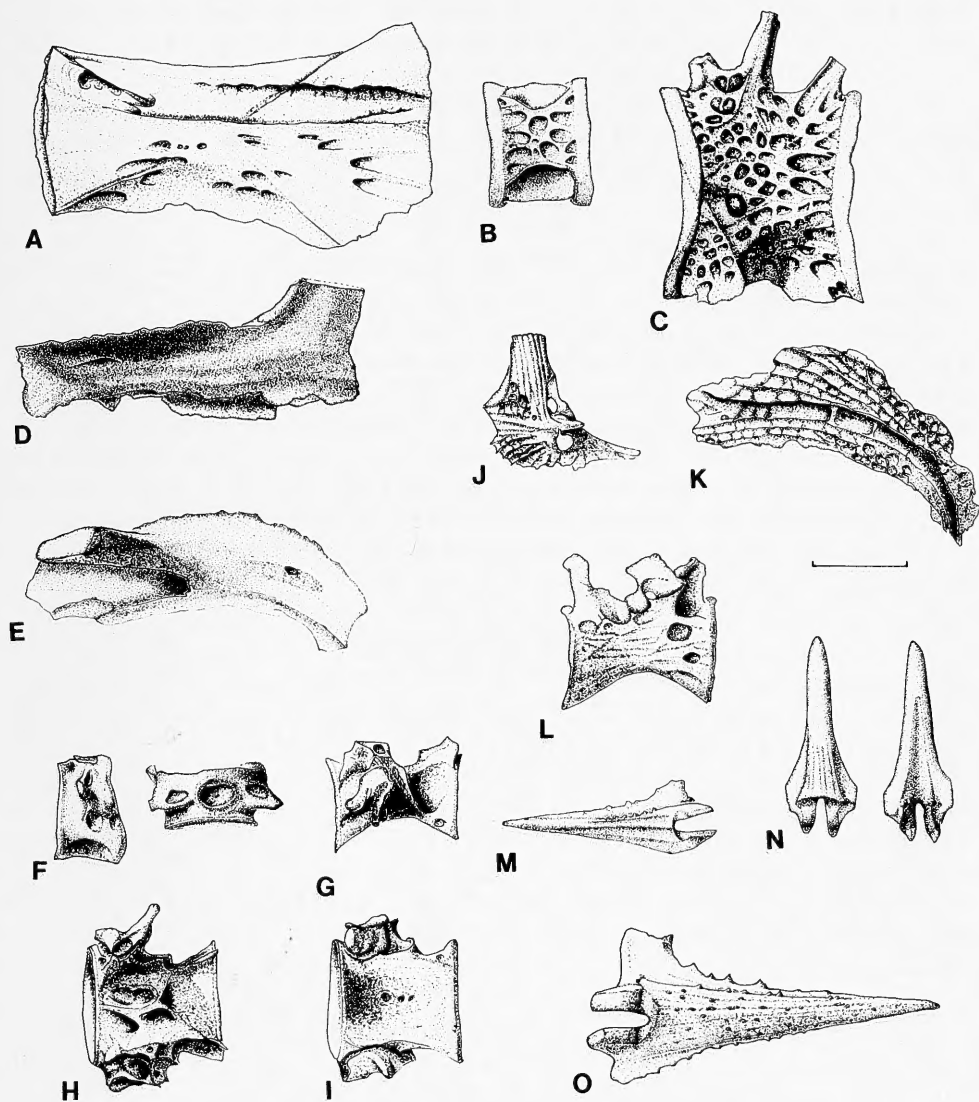
Fig. 1.   Bones of: *Salmo gairdneri*. A. Left ceratohyal. B. Abdominal vertebra. C. Caudal vertebrae. *Gila orcutti*. D. Lateral view of left dentary, anterior to left. E. Dorsal view of left dentary, anterior to right. F. Cervical vertebrae, lateral view (left), anterior to left, dorsal view (right) anterior is up. G. 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 aculeatus*. 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. O. Left pectoral spine, anterior view. Scale equals 1 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), CA, 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. 35856-1 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).

Hesperoleucas 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 are 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 surfaces 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. 1F) 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. 1C), 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: 1) 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*: all 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			1								12	4.58	4.1000
G. a. williamsoni																							
Los Angeles Basin	4	2	3	5	2	4	5	4	1	3		1	1								33	4.818	3.2639
Upper Santa Clara						1		2	1	1	2	3	2	2	4	3	1		1		24	11.9166	3.1748
G. a. microcephalus		1	1			1		4		3	2	4	3	3	3	3	1		4	2	35	11.857	4.5642

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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 deposition 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 areas (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 fossilize, 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 (Stock 1956; Harris and Jefferson 1985). However, these small endotherms, particularly passerine 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 deposits. All could survive only under the following conditions: 1) water temperature about ≤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 *Salmo 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 are also consistent with the fish fauna present into historical times.

A large literature cited exists 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 steelhead 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 *Salmo 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.

Acknowledgments

(stickleback) provided recent comparative material, and Mario Ruiz performed some of the statistical computations.

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

Joan G. Stewart

A-002, Scripps Institution of Oceanography, University of California, La Jolla, California 92093

Abstract. —The history of marine algal studies in San Diego County is reviewed. Ten taxa of Rhodophyta have ranges that extend into this southernmost part of California on the basis of recent collections. The distributions of these taxa were previously reported to terminate to the north either on the offshore California Channel Islands or on the mainland. San Diego records are summarized for four species that have been added to the California flora since Abbott and Hollenberg's *Marine Algae of California* was published (1976). Three species earlier considered rare in southern California have been found to be extremely abundant and widespread in algal turf on rocky beaches of San Diego County. Recent subtidal collections of an undescribed *Phycodrys* are treated as a major range extension of *P. cerratae,* described from central Peru. Abundant material from San Diego County sites supports the merger of *Murrayellopsis* and *Veleroa* (Rhodophyta) both at the generic and species level; for reasons of priority, *Murrayellopsis dawsonii* becomes a synonym of *Veleroa subulata.*

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

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

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

Somewhat later Setchell and Gardner, working in Berkeley, brought together all available information about Chlorophyta and Phaeophyta along the entire

Pacific coast of North America (Setchell and Gardner 1920, 1925). These two volumes include important new information about algae of southern California and Baja California, but because the introductory section describing the sources of the various records was intended to be included in a third volume on the Rhodophyta that was never prepared, it is often unclear which algae represent new records for particular areas. The detailed descriptions of habitats, morphological variation, and local distribution patterns for the green and brown algae remain useful for San Diego County despite numerous nomenclatural changes that have taken place in the intervening years.

From Snyder's time until the arrival of E. Yale Dawson in La Jolla in 1942, San Diego lacked resident phycologists. Dawson's three years of intensive work in San Diego County led to the publication of an "annotated list" of marine algae (Dawson 1945) by the San Diego Natural History Museum. This combined earlier records for the area with information based on his own collections.

With the use of SCUBA in nearshore biological studies after 1956, diving botanists could directly observe attached organisms and it was no longer necessary to depend on beach drift to describe subtidal algal populations. At Scripps Institution of Oceanography, the first diving studies of submerged algal assemblages focussed on *Macrocystis* beds, but since the early 1960's subtidal algae have been collected systematically from sites along the coast of San Diego County. New records and detailed information based on these local studies were not available at the time the first comprehensive attempt at describing the California algal flora was prepared by Abbott and Hollenberg (1976). To incorporate records of subtidal collections, data from intertidal studies, and previously published information on algal distributions into a single document, a checklist of benthic marine plants of San Diego County has been prepared for the use of marine biologists working in this part of California (Stewart 1989).

Approximately 362 species of marine algae are now known from the various habitats in San Diego County. Collections from depths beneath about 13 m, or beneath the depth of warmer summer water temperatures, disclose an algal flora rather different from the intertidal flora. Seasonal distributional patterns occur in subtidal as well as in intertidal habitats. The list (Stewart 1989) includes taxa that can be assigned to several different biogeographical categories: 1) intertidal species typical of intertidal floras both north and south of San Diego; 2) subtidal taxa that are widespread in deep-water sites along the Pacific Coast of North America; 3) intertidal species that occur intertidally or in shallow water in warmer regions of Pacific Baja California and in the Gulf of California; 4) deep-water taxa that grow intertidally or in very shallow water in central and northern California.

A group of species found in central and northern California and in northwestern Baja California is conspicuously absent from the coast of San Diego County. At least 15 of these taxa are large and could not be overlooked if they were present. Examples include such easily recognized species as *Leathesia nana, Laminaria setchellii,* large *Porphyra* thalli, and *Mastocarpus* (*Gigartina*) *papillatus.* These disjunct distributions are usually explained in terms of water temperatures. San Diego County beaches lie in the southern part of the southern California bight, a broad embayment where water circulation patterns include wide and changeable eddies as well as north-south currents. Wind and wave directions along the coast differ between seasons and affect upwelling of cold deeper water. The particular

Table 1. New Southern Range Extensions: taxa treated in MAC but not previously recorded from San Diego county.

Species	Previous distribution in California	Habitat in San Diego County	New records
Antithamnion hubbsii	Santa Catalina Island	Subtidal, on bryozoan	27 m, La Jolla, JS 1991
Callithamnion catalinense	California Channel Islands	Subtidal; epiphytic, in garibaldi nests, on sponges, rocks, shells	17–37 m, numerous collections, all reproductive phases, throughout year. Specimens vary and do not consistently conform to earlier descriptions; some resemble forms of *C. biseriatum,* a widely distributed subtidal species
Callophyllis thompsonii	Monterey	drift, Imperial Beach	Several similar thalli; one identified by I. A. Abbott, JS 1141
Chondria arcuata	to Orange County	intertidal algal turf	abundant, La Jolla (see Abundance in text)
Colacodasya californica	to Orange County	on intertidal *Heterosiphonia erecta*	JS 1453, 2853, 3170 (all in November)
Gigartina tepida	to Orange County	Mission Bay Channel; 10–13 m off Pt. Loma; intertidal, La Jolla	JS 1715 (cystocarpic), det. G. I. Hollenberg; 8 additional collections
Heterosiphonia japonica	to Orange County	Subtidal, 10–23 m, on various substrates	JS 2432, 2438 cystocarpic; 13 additional collections
Pikea robusta	to Santa Barbara County	Drift, on Imperial Beach	Dawson (1945b) recorded specimens (as *P. pinnata*) from the beach near Coronado, near the area of our drift collections; JS 1153, 3225
Polysiphonia brodiaei	to Santa Monica, Los Angeles Co.	Intertidal, Bird Rock, La Jolla	JS 2294
Porphyrella californica	Laguna Beach, Orange County	On mussels and barnacles, La Jolla	abundant, high intertidal rocks, early spring

localities on the Pacific coast of Baja California where populations of "northern" algae occur, characteristically are sites strongly influenced by persistent patterns of upwelling. Seasonal sand deposition on rock surfaces, and the nature and inclination of rocky substrates, may also be important to help explain the marked contrasts between the algal vegetation of San Diego County and that to the north and south.

Unless otherwise cited, voucher specimens are filed with JS collections, presently on loan to SIO herbarium. Subtidal data are based primarily on collections made by J. R. Stewart. Individual specimens are cited in the relevant sections.

Southern range extensions. — Ten taxa of Rhodophyta with ranges that extend into San Diego County on the basis of recent collections are shown in Table 1. The distributions of these taxa previously were reported (Abbott and Hollenberg 1976) to terminate to the north either on the offshore California Channel Islands or on the mainland.
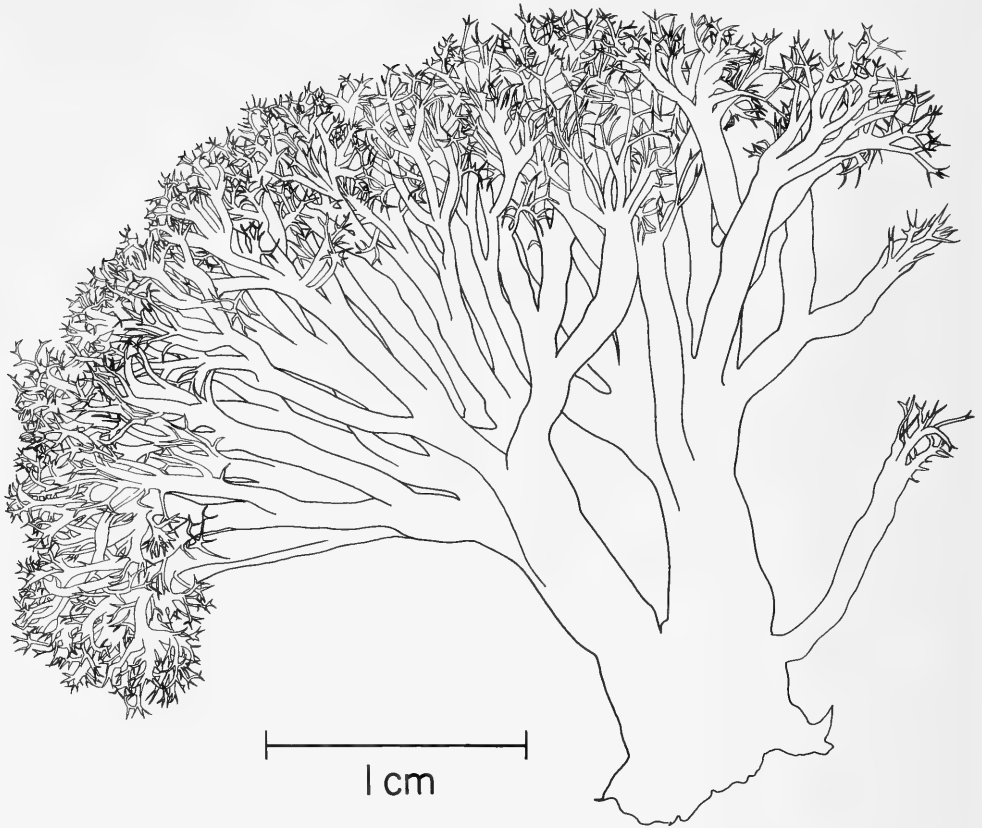
Fig. 1. *Berkeleya hyalina* (Round & Brooks) Cox. Whole plant from San Diego Co.

Species New to California. — San Diego records for species that have been added to the California flora since Abbott and Hollenberg's *Marine Algae of California* was published (1976) are summarized as follows.

Naviculaceae, Bacillariophyta

Berkeleya hyalina (Round and Brooks) Cox, a colonial benthic diatom, was identified (Chastain and Stewart 1985) on the basis of culture and field studies and microscopic examination of cleaned frustules. This species, as well as the better known *B. rutilans,* secretes and lives in tubes of mucilage that are aggregated into attached tufted thalli that resemble filamentous ectocarpoid algae. In the field, *B. hyalina* has an easily recognizable morphology (Fig. 1); details of cell and tube morphology are illustrated in the earlier report (Chastain and Stewart 1985). The species is presently known from Baja California, mainland southern California and offshore channel islands (K. A. Miller, pers. comm.) and the type locality in Togo, West Africa. In San Diego County it is often abundant in mid-intertidal habitats, April–October, on rocks or mollusc shells. Thalli grow to 3 cm high, are dark olive-brown, and slippery to the touch.

Ulvaceae, Chlorophyta

Chloropelta caespitosa Tanner. The genus and species were described (Tanner 1980) from collections in Los Angeles and Orange counties. Among specimens collected earlier from La Jolla by Dawson and originally identified as *Ulva californica,* Tanner recognized *Chloropelta* thalli. In 1976 he collected specimens from high intertidal rocks at Tourmaline Surfer Park in Pacific Beach, and in the summer of 1986 he again visited the area and located *Chloropelta* on two La Jolla beaches (Tanner, pers. comm.); I have recently collected the species from these same sites.

Cutleriaceae, Phaeophyta

Cutleria cylindrica Okam. Thalli that were conspicuously different from any previously collected San Diego species were found in Point Loma intertidal pools in the winter months 1984–87, with 1984 being a year of unusually warm water that followed a winter of unusually strong storms. The thalli were absent the following winters (1987–89). Subsequent study recognized the specimens as the same alga collected at Santa Catalina Island in 1973 and identified as *Cutleria cylindrica* by Hollenberg (1978), a species described from Japan. He discussed the similarities of this "*Cutleria*" species to *Myriogloia* and other taxa in the family Chordariaceae and questioned its affinities with Cutleriaceae. The same alga was collected by Terry Klinger subtidally from San Clemente Island several times in 1986–87, and from shallow subtidal rocks off Bird Rock in La Jolla, also in 1986.

Delesseriaceae, Rhodophyta

Apoglossum gregarium (Daws.) Wynne. The southern California plants described by Stewart (1974) as *Phrix gregarium* are delicate, minute (less than 1 cm high and 1–2 mm wide), subtidal blades that grow on sponges, bryozoans, in nests of the garibaldi fish, or with other algae in various subtidal rocky habitats. They are not rare, but difficult to recognize in the field. Reproductive as well as vegetative thalli have been collected from depths of 17–28 m at all times of the year in sites beneath the summer thermocline between La Jolla Bay and the outer kelp beds off Point Loma. Elsewhere, specimens have been collected by R. Moe (pers. comm.) subtidally at the Galápagos Islands and off Palos Verdes in Los Angeles County, and by J. R. Stewart at San Benitos Islands, Mexico.

The rippled, undulate blades are unlike any other small algal blades I am familiar with, and in freshly collected algal material are so conspicuous as to make recognition of the species obvious. I earlier (Stewart 1974) suggested that this strikingly characteristic appearance could be explained as the consequence of frequent continuing divisions in blade cells while the central and pericentral cells elongate but do not divide transversely. Growth to either side of the midline therefore forms an increasingly ruffled blade, with the "ruffles" extending to the midline, rather than observed only near the margins.

Phycodrys cerratae Daws., Acleto & Foldv. — In 1970 and again in 1981 attached *Phycodrys* blades (Fig. 3) were found in La Jolla Canyon offshore from Scripps Institution of Oceanography, San Diego County (JS 1744, 3551). The site has been observed frequently in intervening years but additional plants have not been

found. These collections could not be attributed to either of the two other species, *P. profunda* and *P. setchellii,* previously known from San Diego County. In 1940, G. J. Hollenberg collected 15 specimens of an unidentified *Phycodrys* species (Figs. 4, 5) from drift at Cabrillo Beach near San Pedro, Los Angeles County (GJH # 3102). These were later given to me by I. A. Abbott for comparison with the thalli collected in La Jolla Canyon.

The genus *Phycodrys* world-wide is large and generally conceded to be in need of monographic treatment. Pending such a study, I have identified the three southern California collections cited above as *P. cerratae.* A review of the morphology and ecology of species attributed to the genus in the eastern Pacific recognized two that were particularly similar to the unidentified specimens. Both, *P. isabellae* and *P. cerratae,* are subtidal and not often collected. The type specimen of *Phycodrys cerratae* was collected in drift material near Lima, Peru in 1960 and described and figured by Dawson et al. (1964). An isotype (Fig. 2) was deposited at HAFH, now in LAM. *P. isabellae* was described from a subtidal plant collected from the San Juan Islands, Washington (Norris and Wynne 1968). Subsequently other subtidal plants from Oregon and central California were identified as representing this latter species.

Compared with *P. cerratae* and *P. isabellae* (Table 2), the southern California specimens resemble *P. cerratae* in size, appearance of tetrasporangial sori, and in structure of the marginal bladelets. Primary blades of Hollenberg's drift specimens are to 12 cm high, to 3.5 cm wide; secondary blades are to 4.2 cm long and 1.5 cm wide. San Diego blades are to 9 cm (primary), 7 cm (secondary) high and 2 cm wide. Lateral blades are subtended by distinct stipes closely spaced on margins of primary and secondary blades. No rhizoids or other proliferations for secondary attachment from blade margins were found.

Phycodrys isabellae has not been recognized in subtidal collections from San Diego County. The specimens from the Monterey peninsula, described by Abbott and Hollenberg (1976), are to 7 cm high but mostly smaller and as figured, the marginal bladelets tend to grow from the blade edge without a distinct stipe. Tetrasporangial sori in type material (Fig. 23, Norris and Wynne 1968) are conspicuous and discrete; the specimen illustrated as Fig. 587 (in Abbott and Hollenberg 1976) appears to show tetrasporangia in diffuse "sori" filling the space between lateral nerves. Tetrasporangia are scattered and inconspicuous on blades collected in the La Jolla Canyon. Abbott and Hollenberg (1976) describe margins of *P. isabellae* as undulate, whereas blades collected in San Diego County are flat.

In support of the assignment of southern California collections to *P. cerratae,* a species described and known only from central Peru, there are numerous other algae with similar distribution patterns. Santelices and Abbott (1978) accepted bipolar distributions for a number of species in the algal flora of Chile and report

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Fig. 2. *Phycodrys cerratae* Daws., Acleto & Foldv. Isotype, Barranco, Lima, Peru, Jan. 9, 1960, collected by Emma Cerrate 2997. AHF 75435. Resembles La Jolla canyon collection (Fig. 3) and San Pedro drift material (Figs. 4, 5) in size, midrib, margins without rhizoids, and numerous lateral bladelets.

Fig. 3. *Phycodrys cerratae.* 20 m, La Jolla Canyon, San Diego Co., 4 Sept. 1981. JS 3551.

Figs. 4, 5. *Phycodrys cerratae.* G. J. Hollenberg 3102, "cast ashore leeward side of gov. breakwater, Cabrillo Beach, San Pedro, Calif. 24 July, 1940." Annotated "*Phycodrys* n. sp. I.A.A., 1973."

Table 2. Comparison of published descriptions of two species and undescribed collections.

	Phycodrys isabellae Norris & Wynne 1968	Southern California collections, Fig. 3–5	*Phycodrys cerratae* Dawson et al. 1964, and Fig. 2
Blade length	to 7 cm	to 12 cm	to 12 cm
Blade shape	oblanceolate	both	lanceolate
Blade width	to 2 cm	to 3.5 cm	to 3 cm
Midrib	weakly developed or prominent	prominent	prominent, broad
Lateral veins	"some blades with weakly developed opposite veins from midrib"	faint, not distinct	opposite, distinct (but see Fig. 2)
Margins	sometimes denticulate, with secondary attaching rhizoids	no rhizoids, smooth	(see Fig. 2. No rhizoids shown)
Marginal bladelets	primary blade single or with few to many bladelets	to 7 cm in length, closely spaced	margins entire, or with numerous closely-spaced pedicillate bladelets to 20 mm+
Tetrasporangia	sori between lateral veins, large and distinct in photo	faint	sori between lateral veins
Gametangiathalli	described	not found	not found

(in their Tables 1, 2, and elsewhere in the text) 17 species from Chilean sites that occur in San Diego County (Stewart 1989). Dawson described the intertidal algal flora of central Peru as sharing many features in common with southern California (Dawson et al. 1964). Excluding taxa that are difficult to identify (e.g., crustose corallines), Dawson et al. (1964) list 29 species from Peru that occur in San Diego County. *Phycodrys cerratae* is added to the flora of San Diego County and thus to the California marine algal flora on the basis of the J. Stewart and G. J. Hollenberg collections cited above.

Abundance.—Three species described (Abbott and Hollenberg 1976) as occasional, relatively rare, or rare in southern California, have been found to be extremely abundant and widespread in algal turf on rocky beaches of San Diego County.

Ceramium flaccidum (Kütz) Ardissone [as *C. gracillimum* var. *byssoideum* (Harv.) Maz. and *C. taylorii* Daws. in Abbott and Hollenberg 1976]. Thalli cover coralline anchor taxa with a deep-red layer of filaments in late summer months, with peak abundance in October at La Jolla sites. The thalli are extremely fine but easily recognized by the elongated internodes contrasted with narrow nodal bands and the darker apical regions where central cells have not yet elongated (Fig. 6). All reproductive phases can be found in San Diego county material. Womersley (1978) illustrates microscopic detail of nodal cortication and provides a thorough study of the species, considering it "probably cosmopolitan in cold temperate to tropical seas."

Binghamia forkii (Daws.) Silva. Thalli (Fig. 7) are easily found between May and November on the platform rock beaches between Ocean Beach and Point Loma where they form a yellowish or greenish epiphytic mat over algal turf. Less
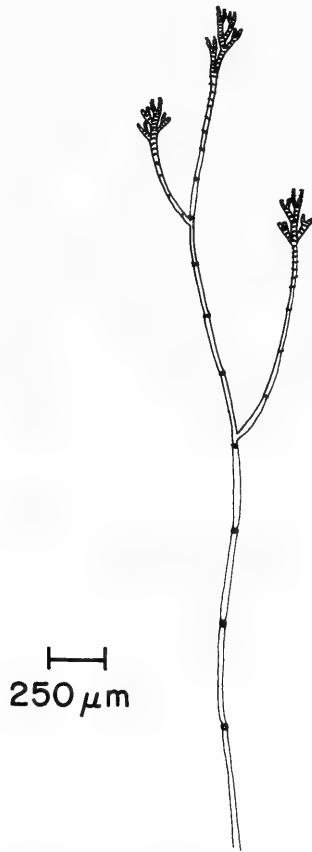
Fig. 6. *Ceramium flaccidum* (Kütz.) Ardissone. Axis with elongated proximal internodes, San Diego specimen. Long uncorticated internodes below, delicate size distinguish thalli in field.

abundant, it also grows at the same season on beaches north of Mission Bay. All reproductive phases are easily found in these intertidal habitats.

Chondria arcuata Hollenb. Thalli are dull red when growing in shaded habitats, but more commonly are pale or almost yellowish in intertidal turf. The species is illustrated by Fig. 672 in Abbott and Hollenberg (1976). Erect branches are cylindrical, often somewhat arched or curved as they grow horizontally over other algae, and secondarily attached at frequent intervals. A tuft of trichoblasts from the apical pit may be conspicuous in freshly collected or young material but in older plants or thalli that have been several hours in containers, this feature may be misleadingly absent. The species is one of the most common and abundant epiphytes growing on *Pterocladia capillacea* (Gmel.) Born. and Thur. and *Corallina pinnatifolia* (Manza) Daws. on La Jolla beaches, less common elsewhere in the County.

Taxonomic Merger: *Veleroa* and *Murrayellopsis*

Type species of these two monotypic genera, *V. subulata* and *M. dawsonii,* are small polysiphonous red algae with four pericentral axial cells and radially ar-
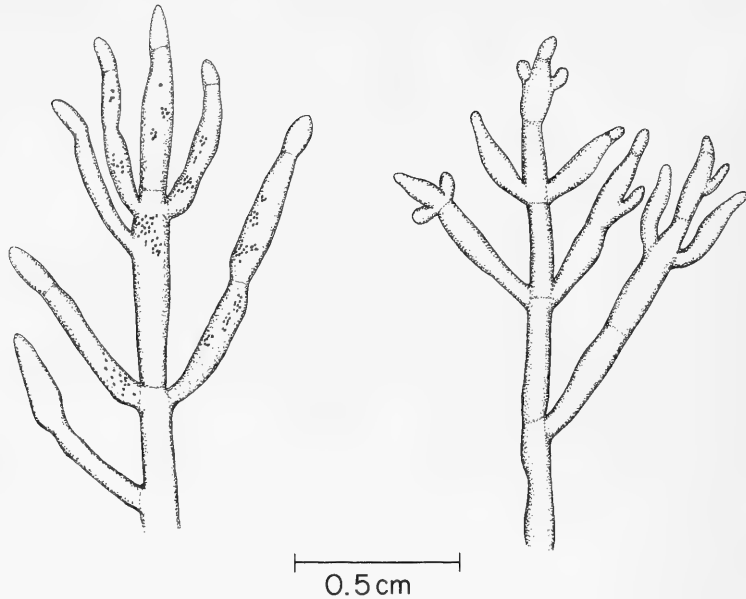
Fig. 7. *Binghamia forkii* (Daws.) Silva. Characteristic thalli, with tetrasporangial specimen on left. Whole epiphytic thallus comprises branches as shown, commonly overgrowing algal turf.

ranged monosiphonous, determinate lateral branchlets. Tetrasporangia occur in main axes rather than in stichidia. Kylin (1956) placed *Veleroa* in the *Lophothalia* group of Rhodomelaceae, a group characterized by persistent pigmented tricho-blasts termed monosiphonous branchlets by Dawson (1944, 1963) and ramuli by Abbott and Hollenberg (1976). Closely allied genera differ in the number of pericentral cells, in being corticated, or by being bilaterally branched (Kylin 1956).

Murrayellopsis was distinguished (Dawson 1963; Abbott and Hollenberg 1976) from *Veleroa* by having paired tetrasporangia in axial segments and mostly branched "trichoblasts." Post (1962, 1963) described *Murrayellopsis dawsonii* gen. et spec. nov. without mention of *Veleroa* which had been described earlier by Dawson (1944). A subsequent paper (Post 1964) added references to *Veleroa* in the text and included this genus in a key where it was distinguished from *Murrayellopsis* by the number of tetrasporangia in a segment. She stated her opinion that "in no case is *Murrayellopsis* a luxuriant *Veleroa*."

Dawson's treatment (1963) of the two species is based only on the two original descriptions as no additional collections of either were known at that time. Since then, thalli distinguishable only by the number of tetrasporangia per segment have been identified in collections from subtidal habitats along the coast of California.

Material studied:

Veleroa subulata. Holotype LAM 500006, Dawson 281d, dredged in 22 m, Tepoca Bay, 4 Feb., 1940. LAM 509949, R. Setzer 7721, 3 m, at west end of breakwater on inside, Los Angeles Harbor, 7 Nov., 1973. LAM 599947, R. Moe 2B, Palos Verdes Point, 7 m, 19 Oct. 1972. LAM 599948, R. Moe 120, Palos Verdes Point, 7 m, 19 Oct. 1972. K.A. Miller material, collected from San Miguel Island off the coast of central California, 17 Sept. 1983, 5–10 m depth, 5 slides, unaccessioned UCB.

Murrayellopsis dawsonii. Holotype LAM 500009, det. Erika Post, from *Hypsypops rubicunda* (garibaldi fish) nest, 12 m, New Hope Rock off Point Loma, San Diego Co., 18 April 1961. Paratype (LAM designation) LAM 500007, det. Erika Post, from vertical surface at 7 m, N.E. side of North Island, Islas Coronados, 2 June 1961. UCB 1462114, col. A. Nonomura, 10 m, sand pool, Mussel Pt., Pacific Grove, 8 Aug. 1973. CMMEX (unaccessioned), L. Aguilar 32, 20 m, Isla Todos Santos, Baja California, Mexico, 19 June 1982.

Veleroa subulata/Murrayellopsis dawsonii. Santa Barbara Co. JS 2215, 10 m, Naples Reef, May 1972; San Diego Co. JS 832a,b, 30 m, on bowl, La Jolla Submarine Canyon, 10 Nov. 1967; 906e, 27 m on rock, La Jolla Canyon, 6 Feb. 1968; 1233a-b, 22 m, inshore from Quast Rock, La Jolla, May 1969; 1381, 13 m, New Hope Rock, 5 Sept. 1969; 1809 a-b, 13 m, New Hope Rock, 23 Jan. 1971; 1877, 1878, 1896, 13 m, New Hope Rock, 13 Feb. 1971; 2420, 2434, 2435, 27 m, Quast Rock, La Jolla, 10 April 1973; 2941, 15 m, garibaldi nest, Loma Sea Cliff, Jan. 1977.

All of the above specimens fit within the original description (Dawson 1944) of *Veleroa subulata* with the following amendments.

Genus VELEROA: Irregularly arranged indeterminate branches can replace pigmented monosiphonous, determinate branchlets; tetrasporangia borne in a single or double spiral row, one or two per segment in slightly swollen upper portions of main axes and branches; carpogonial branches developed on next-to-basal cells of monosiphonous branchlets.

Veleroa subulata: Plants to 20 mm high; pericentral cells of polysiphonous erect axes and branches to 50–70 μm, more often 10–30 μm, diameter, as much as 6 diameters long; lateral branchlets to 700 μm long, each with up to 16 cells that are individually mostly less than 60 μm long and 10–40 μm diameter at base, with a basal cell about half the length of succeeding cells; branchlets simple or with up to 4 second order branchlets on lowermost cells and these infrequently once-forked; branchlets tapering to a very small sharply-pointed apical cell; tetrasporangia borne one or two per segment in up to about 15 successive segments of main axes and branches, to 60 μm diameter when mature.

Cells of polysiphonous prostrate axes of similar diameter as pericentral cells in erect axes, but often longer, to 160 μm. Polysiphonous, or multiseriate, rhizoids develop from the prostrate axes, with very long, to 300 μm, mostly narrow cells. On entangled plants, e.g., growing around bryozoans, several rhizoids grow in clumps from single segments of an axis and separately or apparently coalesced attach to substrate in a disc-like pad. In such thalli the distinction between prostrate and erect axes is lacking. Monosiphonous branchlets and rhizoids may develop from adjoining segments. The basal cell in each lateral monosiphonous branchlet is distinctly shorter than, but with the same diameter as, the more distal cells of the branchlet (Fig. 8). When branchlets detach, the basal cell usually remains and is seen on older proximal parts of the thalli as a scar cell.

Type: Dawson, 381d, growing on a small hydroid, dredged in 22 m, Tepoca Bay, Sonora, in the upper Gulf of California, 4 Feb. 1940. Herb. AHF no. 63.

When this type material was examined for the present study, no reproduction was found, suggesting that the branches photographed as Fig. 2 in Plate 72 of Dawson (1944) have been lost. The single vial representing the type collection contains mostly fragmented axes and branchlets. Cell measurements conform to
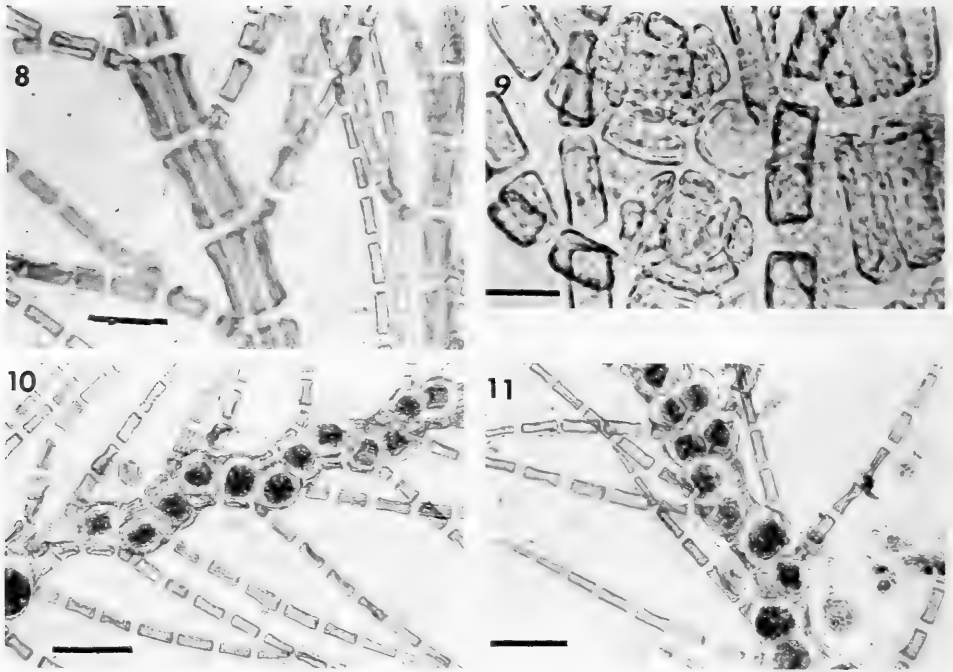
Figs. 8–11. *Veleroa subulata* Daws. Thalli collected from nests of the garibaldi on or near New Hope Rock, Pt. Loma, San Diego Co., the type locality of *Murrayellopsis dawsonii* Post. Fig. 8. JS 2941. Polysiphonous branch with monosiphonous branchlets. 1 cm scale = 80 μm. Fig. 9. JS 1809. Cystocarps on next-to-basal cell of monosiphonous branchlets. 1 cm scale = 25 μm. Fig. 10. JS 2941. Tetrasporangia in single row, smaller distally. 1 cm scale = 100 μm. Fig. 11. JS 2941. Single and paired tetrasporangia in same row. 1 cm scale = 100 μm.

the above description. In general appearance, the algae described as *Veleroa sub-ulata* are indistinguishable from any of the collections referred to *Murrayellopsis dawsonii*.

Post (1962, 1963, 1964) stated that pericentral cells in *Murrayellopsis dawsonii* were 4–5 in number but all of the material examined in this study consistently showed four. Several instances of "cortication" were observed where the peri-central cells in several adjacent axial segments were apparently replaced by ir-regularly arranged, irregularly shaped small cells. These portions of the thalli were mostly basal, lacked branching, and in the habitats where the plants were collected, were in a layer of debris or sand grains close to the substrate.

Polysiphonous branching is infrequent, but in those thalli where the axes branch, all such branches occur in the upper half or third of the axis, each one replacing a monosiphonous branchlet insofar as could be seen. A relatively densely branched axis bears up to 11 branches and each of these may bear 2,3 third-order branches which are unbranched or once-forked. The distal clustering above the long un-branched proximal portions of the axes gives a characteristic bushy aspect to individual axes. Degree of monosiphonous branchlet development parallels the extent of polysiphonous branching. Many axes are unbranched, with mostly short unbranched or once-forked branchlets; others with polysiphonous branches also bear longer, more-branched monosiphonous branchlets. Lower parts of most axes

are often unbranched or bear only short monosiphonous spine-like branchlets. Branching from the cells of the monosiphonous branchlets is also radial, apparently spiral from sequential "corners" of the single cells of the uniseriate filaments.

From the type material for *Murrayellopsis* that was collected at New Hope Rock, I segregated 19 tetrasporangial axes from the large amount of vegetative material. All were densely branched, and contained mostly paired tetrasporangia. Proximal segments, just below the swollen tetrasporangia-bearing segements, show very narrow, irregularly aligned and separated pericentral cells, indicating that tetrasporangia had been shed from these segments. Apically, distal to the swollen segments, small cells were formed in addition to immature tetrasporangia which are distinct by differential pigments. In her revision of the privately published 1962 description of *Murrayellopsis,* Post (1964) changed the number of tetrasporangia per segment from two, to 2, 3, or 4. I carefully squashed several axes to spread the tetrasporangia and in no case were more than 2 per segment found. Without this treatment, the size and congestion of the tetrads in the axis did not allow this determination. The amount of either polysiphonous or monosiphonous branching is uncorrelated with development of single or double rows of tetrasporangia.

A cystocarpic specimen (Fig. 9) and numerous tetrasporangial thalli have been collected from nests of the garibaldi on New Hope Rock as well as from other nearby rocky subtidal habitats (JS specimens). In these thalli many of the tetraspores are in paired rows as described for the type material. Some thalli, however, have only single rows of sporangia (Fig. 10); single tetrasporangia occasionally are interspersed with pairs in the same axis (Fig. 11). Figures 8–11 illustrate recent collections from the type locality for *Murrayellopsis dawsonii.* I suggest that tetrasporangia develop in a single row along an axis, in a ¼ spiral from successively arranged pericentral cells. A second row of sporangia can then develop, usually subsequent to the enlargement of those in the first row. Tetrasporangia in the first row are mostly retained while the second row develops, resulting in two rows of large tetrasporangia. The single row, one per segment (as described first for *Veleroa subulata* but now found in *Murrayellopsis* specimens) therefore appears to represent a developmental stage, rather than to characterize a distinct taxon. For this reason I propose merging the two taxa both at the generic and species level; for reasons of priority, *Murrayellopsis dawsonii* becomes a synonym of *Veleroa subulata,* typified by the few scraps now deposited in collections at LAM.

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Research Notes

Late Pleistocene Chipmunk, *Tamias* (Mammalia: Sciuridae), from Rancho La Brea, Los Angeles, California

The Rancho La Brea paleontological sites in Hancock Park in the western part of Los Angeles have produced one of the most impressive and complete records of late Pleistocene and early Holocene life in the world (Akersten et al. 1983; Harris and Jefferson 1985; Shaw and Quinn 1986). Early major excavations at Rancho La Brea between 1905 and 1930 sampled mostly larger organisms. This was primarily due to collecting methods that tended to overlook smaller fossils. In 1969, the Natural History Museum of Los Angeles County (LACM) began a new scientific excavation at Rancho La Brea, using modern collecting techniques, that has led to the recovery of abundant samples of smaller vertebrate fossils such as lizards, snakes, and rodents (Shaw 1982; Akersten et al. 1983). An examination of samples of these smaller fossils has revealed the presence of a chipmunk, a taxon that was previously unknown from Rancho La Brea.

The collective fossil biota recovered from Rancho La Brea represents a diverse Late Pleistocene flora and fauna. The majority of plants and animals are still represented by living forms, but Rancho La Brea is better known for its records of large, extinct mammals (Stock 1956; Harris and Jefferson 1985).

Hancock Park and vicinity is underlain by approximately 45 m of Late Pleistocene strata that Woodard and Marcus (1973) referred to the Palos Verdes Sand. Most of the thickness of the Palos Verdes Sand in this area was deposited in a shallow marine environment, but the upper 9 m to 10 m were deposited on an alluvial plain that developed between the Santa Monica Mountains and the Pacific Ocean. Fossil excavations have only penetrated to depths of a little over 8 m, but drill cores have yielded both vertebrate and marine invertebrate fossils at greater depths. Although the fine details of depositional history within any single excavation may be complex, radiometric age determinations at varying depths have shown an approximate age range of between 35,000 and 11,000 years before present for the fossils from these excavations (Woodard and Marcus 1973; Marcus and Berger 1984).

The continuing scientific excavation begun by the LACM in 1969 is centered over one of the 1915 excavations, or "Pits," as they were commonly called. This site, Pit 91, was abandoned in 1915 before removal of fossils was completed. The modern excavation, assigned the locality number LACM 6909, is approximately 9 m square, and is quarried in six-inch depth intervals using a horizontal square yard grid system commonly employed in archeological excavations (Shaw 1982). As larger fossil specimens are removed, surrounding matrix is retained for processing to recover smaller fossil specimens (pollen, seeds, small mollusks, insects and other arthropods, and small vertebrates). Over 400 tons of fossiliferous matrix have been recovered to date, but only a small percentage has been fully cleaned and the fossils removed (Akersten et al. 1983).

A substantial sample of the matrix recovered from a concentration of fossils encountered early in the new excavation (1969–1970) in the northeast corner of
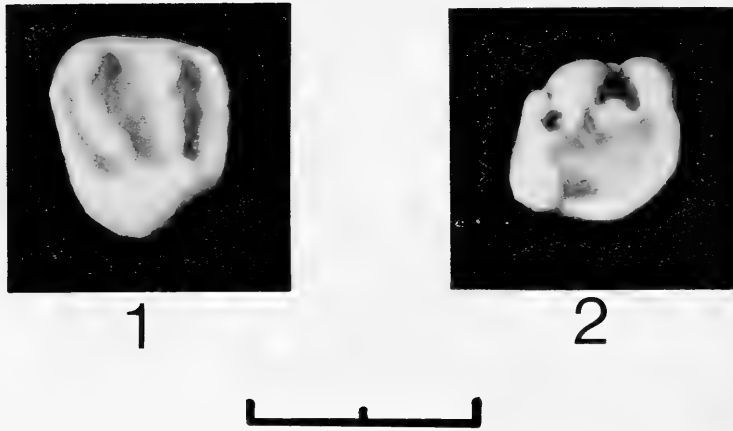
Figs. 1–2.   Teeth of *Tamias* cf. *T. merriami* from Rancho La Brea. Fig. 1, right M^1, LACMRLP 52223, occlusal view. Fig. 2, right M_1, LACMRLP 52229, occlusal view. Scale line equals 2 mm.

LACM 6909 has been cleaned (field numbers GJM 273, 275, 295, 480, 537, 539, and 550). This matrix was from grid designations N-3 and M-3 from a depth between 5 feet and 7.5 feet below datum (see Shaw 1982, for a detailed explanation of the grid and sub-locality designations). The fossils occur in fine grained silty asphaltic sandstone with lenses of brown silt, sediments that represent an infilling of an older stream channel. These stream sediments have yielded a radiometric date using ^{14}C of 32,600 ± 2800 years before present based on one specimen of a juvenile *Smilodon* left femur from this concentration (specimen number R-51285, from locality GJM 550, grid M-3 at 7–7.5 feet below datum; UCLA 1738-D; Marcus and Berger 1984).

The small fossils recovered from this northeast deposit contain a diverse assemblage of snails, lizards, snakes, and small mammals, including nine isolated chipmunk teeth that are described below. Dental terminology and measurements follow Black (1963). Measurements are made on an EPOI Shopscope optical micrometer. Taxonomy for chipmunks follows Levenson et al. 1985.

<div align="center">

Family Sciuridae Gray, 1821
Subfamily Sciurinae Baird, 1857
Tamias cf. *T. merriami* (Allen, 1889)
Figs. 1 and 2, Table 1

</div>

Material.—(Specimen numbers prefixed LACMRLP) Right M^1 (52223) from locality GJM 273; left P^4 (52226), right dP_4 (52225), left P_4 (52227), right M_2 (52224) from locality GJM 539; right M^1 (52230), left M^2 (52231), right P_4 (52228), right M_1 (52229) from locality GJM 550.

Description.—Teeth with tall lophs(ids); upper molars subquadrate in outline, protoconule and metaconule absent, metaloph only slightly constricted at connection to protocone, anterior cingulum well developed but lacking distinct parastyle, mesostyle absent; P^4 reduced antero-posteriorly, lacking anterior cingulum; lower molars narrow (labial-lingual) compared to typical *Tamias* spp., mesostylids absent, mesoconid reduced on M_1, absent on M_2, anterior cingulum well developed and well separated from protoconid in M_1, metalophid (connecting metaconid

Table 1. Measurements of teeth of *Tamias* cf. *T. merriami* from Rancho La Brea. Abbreviations: A/P = greatest anterior-posterior dimension, TR = greatest labial-lingual dimension. Measurements in millimeters.

	Specimen number								
	P^4 52226	M^1 52223	M^1 52230	M^2 52231	dP_4 52225	P_4 52228	P_4 52227	M_1 52229	M_2 52224
A/P	1.15	1.58	1.59	1.53	1.10	1.46	1.36	1.47	1.54
TR	1.43	1.75	1.86	1.86	0.90	1.15	1.04	1.46	1.66

and protoconid) incomplete in both M_1 and M_2, particularly in M_2; P_4 relatively long (compared to M_1), cusps subdued, mesostylid absent; dP_4 a smaller version of P_4 but with more reduced ectolophid and complete lingual connection of posterolophid to metaconid.

Comparisons.—The nine isolated fossil teeth were compared to samples of *Tamias merriami*, *T. sonomae* Grinnell, 1915, *T. speciosus* (Merriam, 1890), and *T. townsendii* (Bachman, 1839) from the collections of the Section of Mammalogy, Natural History Museum of Los Angeles County. These species were selected for comparison because they are either extant chipmunks which live in habitats inferred to have been present near Rancho La Brea in the Late Pleistocene (*T. merriami, T. sonomae,* and *T. townsendii*) or are those living closest to Hancock Park today (*T. merriami* and *T. speciosus*).

In overall size, the fossil teeth fall in the upper range of *T. merriami* or lower range of *T. sonomae,* and they are clearly larger than those of *T. speciosus.* The reduced P^4 resembles *T. merriami* in contrast to the other species of *Tamias* which have a more completely developed P^4 with a distinct anterior cingulum (=parastyle). In contrast, the relatively long P_4 more closely resembles *T. sonomae.* The narrowness of the lower molars most closely resembles those of *T. speciosus.* The well developed anterior cingulum and reduced metalophid on the lower molars resemble the condition in both *T. merriami* and *T. sonomae.*

The sample of fossil teeth is too small to yield information on variability, but based on the modern species examined, the fossils appear intermediate between *T. merriami* and *T. sonomae* in both size and morphology. If larger samples become available, it may be possible to demonstrate that this fossil taxon from Rancho La Brea represents a distinct species near *T. merriami* or, alternatively, it may represent a population of *T. merriami* with teeth near the upper size limit of the living populations. Goodwin and Reynolds (1989) have reported the occurrence of a large, undescribed, fossil species of *Tamias* from Kokoweef Cave in the eastern Mojave Desert which they compare to large living species of *Tamias* including *T. merriami.* The fossils from Rancho La Brea may be related to this large, Kokoweef species, but the sample is too small to draw definite conclusions.

Discussion

There are neither historic records nor previous fossil records (Miller 1971) of chipmunk in the Los Angeles Basin. Their closest occurrence to Hancock Park is 30 km northeast, across the Los Angeles Basin on the chaparral-covered slopes of the western San Gabriel Mountains (*T. speciosus*). The Santa Monica Mountains form the headwaters of the drainages crossing the Rancho La Brea area both in

the Late Pleistocene and today (Shaw and Quinn 1986). There are no documented historic records, and no modern observations of chipmunks in the Santa Monica Mountains (R. Hannum, personal communication), even though ample suitable habitat exists to support them.

This new record suggests that chipmunks previously inhabited the Santa Monica Mountains, the Santa Monica plain, and quite possibly the Los Angeles basin. Their modern absence from these areas lends further support to the well documented southward shift of more equable paleoclimates during periods of the Pleistocene, or, a less likely alternative, a change in the habitat preference of chipmunks.

It is also noteworthy that the nine *Tamias* teeth are the only record of chipmunk derived from more than 75 years of collecting at Rancho La Brea. Considerable matrix from many horizons within Pit 91 (LACM 6909) has been processed for small vertebrates, but the chipmunk specimens are restricted to a single deposit in the northeast corner of the excavation.

The fossils found with the chipmunk teeth do not have a strikingly different composition from the typical collective assemblage recovered from the Rancho La Brea deposits, although there are subtle differences. The associated large fossils are those typical at Rancho La Brea including the carnivores (sabretooth, *Smilodon*; large lion, *Felis atrox*; wolf, *Canis dirus*; and coyote, *C. latrans*) and large herbivores (large ground sloth, *Glossotherium*; horse, *Equus occidentalis*; *Bison* sp.; pronghorn, *Capromeryx*). Large fossils from the northeast corner deposit are not as numerous nor as well preserved as are the smaller biota. R. Lamb (personal communication) provided the following about the fossil mollusks: "All but the rarest species of land and freshwater mollusks identified from Pit 91 are found in the same deposit as the chipmunk. The land snails associated with the chipmunk fossils are characteristic of riparian environments. A quantitative analysis of all mollusks shows an increase in individuals of permanent water and streambank species in the stratigraphic levels bearing chipmunks." Only one of the three fish identified at Rancho La Brea is present (Swift 1989), the threespine stickleback, *Gasterosteus aculeatus.* There is a diverse snake assemblage (La Duke 1983) with the garter snake, *Thamnophis sirtalis* forming 70% of the snakes; however, this is also the common snake in other, well-sampled sites. The skink, *Eumeces skiltonianus* Baird and Girard, 1852, and the alligator lizard, *Gerrhonotus multicarinatus* Blainville, 1825, form 76% of the lizard fauna, a slightly larger percentage than in other areas of Pit 91 examined to date. The small mammals associated with the chipmunk are all those previously recognized at Rancho La Brea (Harris and Jefferson 1985) with the exception of the bats, mole, and desert shrew, but these missing taxa are generally rare.

Considered together, this fossil assemblage does not appear to contain clear evidence to explain the restricted occurrence of chipmunk in the northeast deposit. The assemblage, including the chipmunk, suggests a riparian habitat surrounded by more open and/or brushy terrain. There is ample evidence from other studies of the fossil plants and animals that Rancho La Brea has preserved several communities including costal sage shrub, chaparral, deep canyon, and riparian (Templeton 1964; Warter 1976; Shaw and Quinn 1986). Consequently, the preferred habitat of present-day *T. merriami* (chaparral and foothill scrub) was present during the span of time represented by the Rancho La Brea deposits and is present

today in the Santa Monica Mountains. The restriction of chipmunks to a single, small fossil deposit and their present-day absence in ample, suitable habitat in the adjacent Santa Monica Mountains are thus a bit enigmatic. One possible reason for this restricted fossil occurrence of *Tamias* is that the deposit that yielded the specimens is one of the oldest sampled at Rancho La Brea and conditions may have been slightly different from those that prevailed during later times.

In conjunction with this study, all sciurid specimens recovered from Pit 91 and the other Rancho La Brea excavations (over 500 specimens) were also examined. Notable by its absence is the tree squirrel, *Sciurus griseus* Ord, 1818 (see also Shaw and Quinn 1986). The paleoecological reconstructions for the Late Pleistocene at Rancho La Brea certainly support the presence of the oak/foothill woodland association favored by this tree squirrel today. Acorns, the preferred food of *S. griseus,* are common as fossils at Rancho La Brea (Templeton 1964). Additionally, this squirrel is currently found in close association with *T. merriami* in the coast ranges of central California.

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David P. Whistler, *Section of Vertebrate Paleontology, Natural History Museum of Los Angeles County, 900 Exposition Blvd., Los Angeles, California 90007.*

A Note on the Ontogenetic Age of the Rancho La Brea Hominid. Los Angeles, California

Although human remains from Pit 10, Rancho La Brea (now Hancock Park) have been known since 1914 (Merriam 1914) they have received little attention by physical anthropologists or anatomists. Kroeber examined the remains of "La Brea Woman" (LACM HC 1323) with Merriam in 1914 (Heizer 1962) but did not publish a report; his notes were eventually published posthumously (Kroeber 1962). In that publication Kroeber assessed the age of the individual as "perhaps 25 years old" but did not discuss how that age was determined. In 1981 the cranium, mandible and a few post cranial bones of "La Brea Woman" received a more systematic assessment (Bromage and Shermis 1981) but that study dealt only superficially and incompletely with the ontogenetic age of the individual. It is the purpose of this note to reassess that age based on a fuller analysis of the preserved cranial and post cranial indicators.

Bromage and Shermis (1981) estimated the age of the La Brea hominid at 25–30 years based largely on dental attrition. They suggested that the dentition showed "third stage dental wear" yet gave no reference, discussion or comparative data to support that estimate. They appear, in fact, to have used Brothwell's ageing classification (1972), which contains a "third stage dental wear" phase consistent with the features on LACM HC 1323 that they cite. If they have, in fact, used Brothwell's system they should have noted the possible inaccuracies resulting from use of a system which does not include or consider the often heavily attrited coastal California materials. Brothwell's ageing classification was based on British materials from the Neolithic through Medieval periods. Bromage and Shermis supported their age assessment by pointing out that all of the adult teeth had erupted at the time of death ($=14+$) and that the medial epicondyle of the humerus had fused ($=16+$). They suggested, without discussion or any supporting data, that a lack of fusion of the iliac crest may have been due to "dietary deficiencies."

In the current study, initial analysis of all the hominid skeletal materials from Pit 10 suggests that only a single individual is represented. All the remains are from a small individual of very delicate build and there is no duplication of materials. Features of the innominate, such as a wide sciatic notch and a moderately developed preauricular sulcus, suggest that the individual is female. None of the preserved long bones are complete enough for a secure stature estimate.

Re-evaluation of the La Brea hominid materials allows a more precise, and younger, age than that estimated by either Kroeber or Shermis and Bromage.

The dental eruption sequence appears to have been complete although all of the anterior dentition was lost post mortem. In the maxilla, 3 teeth remain: the $RM^{1,2}$ and the LM^1. Alveoli for the missing molar teeth are present and suggest that these teeth were in full eruption at death. An ectopic right canine may have been present but this issue does not affect the estimated age of the individual. In the mandible, only a single tooth remains, the LM_3 which was impacted; the

occlusal surface of this tooth was rotated mesially with the long axis of the tooth at approximately 45 degrees to the long axis of the horizontal ramus. Radiographically the root apices of this tooth appear to be closed. Radiographic and visual examination suggest that a similarly impacted M_3 may have been present on the right but was lost ante mortem. McKern and Stewart (1957) reported that the third molars in their study (on males only) had generally erupted between 17 and 22 years. Other authors have reported, however, a much longer eruption period; Romanes (1972), for example, reported that third molars may erupt between 13 and 25 years.

Most authors are now in agreement that closure of the cranial sutures show such high individual variability that they should not be used as age indicators (i.e., Hrdlicka 1939; Singer 1953; Brooks 1955; McKern and Stewart 1957; Krogman 1962). Closure of the spheno-occipital synchondrosis (the "basilar suture"), however, is an exception and shows high consistency of age at closure (McKern and Stewart 1957). Moreover, ossification of post cranial bones from secondary or epiphyseal centers provides an important and reliable source of information regarding ontogenetic age. Although variability exists in rates of closure between different individuals and between the sexes, most ossification activity at epiphyseal centers can be shown to occur during a consistent and restricted span of time. Variability in epiphyseal closure rates between races seems to be relatively minor: "Intra-racial variability is much more marked than inter-racial differences" (Krogman 1962:32). Several sources are available for assigning age to post cranial remains (Stevenson 1924; Todd 1930; Stewart 1934; Krogman 1962); however, the largest and best documented study of epiphyseal closure was published by McKern and Stewart in 1957. It should be noted that McKern and Stewart's data were derived from male Korean war dead and while sexually homogeneous the sample was racially mixed. In males, growth is slower than in females and occurs over a longer time period; therefore ontogenetic age estimates derived from male data would represent maximum values for a female individual, as the La Brea hominid undoubtedly is (see above).

In the cranium of the La Brea hominid the spheno-occipital synchondrosis is not fused (confirmed by radiographs), although it is in the last phase (Stage 3) of fusion. McKern and Stewart (1957) indicate that complete fusion of this synchondrosis took place in 97% of their male sample by 19 years and in 100% by 21 years of age. Huschke's foramina are present bilaterally (contra Bromage and Shermis); however since these foramina, normally present during ossification of the tympanic plate, usually close by the 5th year (Clemente 1985) their presence, while of interest, has no bearing on the age determination of this individual.

The post cranial remains of the La Brea hominid are incomplete and few in number: a fragmentary scapula, right humerus, radius (side?; destroyed for radiocarbon dating), ulnar shaft (side?), right femur (now lost), left femur (destroyed for radiocarbon dating but represented by a cast), left innominate, cervical (N = 2) and lumbar (N = 2) vertebrae. Of this material, the scapula and innominate contain at least two epiphyseal centers which had not yet completely fused. On the innominate, much of the iliac crest was lost, apparently through post mortem abrasion, and the condition of the diaphyseal/epiphyseal interface cannot be determined. However, at the anterior superior iliac spine a small portion of the iliac crest is preserved and is fused. Posterior to this fused area, at the superior surface

of the iliac diaphysis, a few vertical striations, characteristic of an active, fusing diaphyseal surface are seen. At 5.1 cm posterior to the anterior superior iliac spine, at the superior terminus of the acetabulo-cristal buttress, a small area of epiphysis is adherent to the diaphyseal surface. The closure of the iliac crest at the anterior superior iliac spine and in the middle third of the crest are consistent with a "partial fusion" stage (Webb and Suchey 1985). In that study of 116 females, 100% of their sample aged 16 and 17 years demonstrated a similar "partial fusion" stage; this stage could continue, however, until 23 years of age. In no individual was full fusion present before the age of 18 years. Although the scapula contains a number of secondary ossification centers, only the acromial center on this specimen is undamaged enough for evaluation. On the lateral margin of the acromion process there is a small area of fusing epiphysis consistent with a Stage 1 fusion. Again, confirmation of active fusion was confirmed radiographically. In McKern and Stewart's male data (1957) 40% of their sample showed complete fusion by 17 years; 95% of their sample showed complete fusion by 21 years and all had fused by 23 years.

It is clear from the cited evidence that the La Brea hominid had not yet reached full adult status at the time of death although a precise determination of her age is not possible. Difficulties are encountered because although inter-racial variability in closure of the basi-occipital synchondrosis and the post-cranial epiphyses in recent populations is relatively minimal we do not know that this was also the case for pre-contact southern California populations. Moreover, the undoubted female status of the La Brea hominid means that her age in years would very likely be somewhat less that the skeletal age of the all-male comparative sample of McKern and Stewart. Nevertheless, the fully erupted adult dentition suggests that an age younger than 17 years is unlikely, while the evidence of the unfused spheno-occipital synchondrosis and the unfused condition of the acromial and iliac crest epiphyses suggest that an age of more than 18 years is also unlikely. A reasonable estimate of the age of the La Brea hominid would therefore seem to be 17–18 years.

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G. E. Kennedy, *Department of Anthropology, University of California, Los Angeles, California 90024.*

The Natal Pterylosis of Closed-nest Building
Tyrant Flycatchers (Aves: Tyrannidae)

The tyrant flycatchers (Tyrannidae) are perhaps the most diverse and dominant family of New World passerine birds (Traylor and Fitzpatrick 1982). Although the systematics, morphology, behavior, and ecology have received much attention (Traylor 1977, 1979; Traylor and Fitzpatrick 1982 and references therein) the natal pterylosis has been described for only a few temperate zone species (Wetherbee 1957, 1958) of this largely Neotropical family.

This paper provides detailed information on the natal pterylosis of seven species in six genera of Neotropical tyrannids (Table 2); field observations of additional species are also summarized in Table 1. One newly hatched nestling (stage A, Wetherbee 1957) of the Slaty-capped Flycatcher, *Leptopogon superciliaris,* was collected 11 km north of Maracay, Est. Aragua, Venezuela on 26 June 1972 by C. T. Collins; an additional two specimens (stage A) were collected, from one nest, 1 km west of Macas, Prov. Morona-Santiago, Ecuador on 13 August 1988 by M. Marin A. Single specimens of the Common Tody Flycatcher, *Todirostrum cinereum,* Yellow-breasted Flycatcher, *Tolmomyias flaviventris,* Rusty-margined Flycatcher, *Myiozetetes cayanensis,* Social Flycatcher, *Myiozetetes similis,* and Great Kiskadee, *Pitangus sulphuratus* and two specimens of the Pied Water-tyrant *Fluvicola pica* were collected at Fundo Pecuario Masaguaral, 45 km south of Calabozo, Est. Guarico, Venezuela between 22 April 1979 and 27 May 1980 by B. T. Thomas. The specimen of *Pitangus sulphuratus* had pin feathers emerging through the skin (Stage B); all of the others were late stage embryos or newly hatched (Stage A) (Wetherbee 1957). The classification of the Tyrannidae followed here is that of Traylor (1977, 1979); common names are those of Meyer de Schauensee (1966).

Specimens were examined under a binocular dissecting microscope and the number and distribution of natal downs (neossoptiles) in each species recorded (Table 2). The terminology for neossoptile tracts and regions within tracts follows Wetherbee (1957). Neossoptiles were present in the coronal, occipital regions and scapular tract in all nine specimens with downs present; the specimen of *Tolmomyias* was completely naked! The spinal and caudal tracts had neossoptiles present in 8 of these 9 specimens. Alar, ventral, and postauricular neossoptiles were present only in *Fluvicola, Myiozetetes,* and *Pitangus.* Ventral cervical neossoptiles, which are only infrequently observed in passerine birds, were present in only the single specimen of *Myiozetetes similis.*

Each of the closed-nest building species considered here (Table 1) has chicks which are either naked at hatching or have a relatively low total number of neossoptiles in a small number of tracts. By contrast eighteen specimens from ten genera of open-cup nesting tyrannids averaged 401 neossoptiles (range 154–607) (Wetherbee 1967; Collins, in prep). Although the number and distribution pattern of passerine neossoptiles has proven in some cases to reflect taxonomic affinities (Collins and Kemp 1976), that is unlikely to be the case here as one or more "groups" of genera (Traylor and Fitzpatrick 1982) in each of three proposed

Table 1.   Natal down pattern in closed-nest building tyrant flycatchers.

Species	Total number of neossoptiles	Source
Elainiinae		
Paltry Tyrannulet (*Zimmerius villissimus*)	dense long grey down	Skutch, 1960:471.
Ocre-belled Flycatcher (*Mionectes oleaginea*)	"sparse but long grey natal down" 52	Skutch, 1960:568. Collins, in prep.
Slaty-capped Flycatcher (*Leptopogon superciliaris*)	53–64	this study
Common Tody Flycatcher (*Todirostrum cinereum*)	16	this study
Slaty-headed Tody Flycatcher (*Todirostrum sylvia*)	"tufts of grey down on the crown occiput, shoulders and middle of back"	Skutch, 1960:495.
Eye-ringed Flycatcher (*Rhynchocyclus brevirostris*)	"sparse but rather long grey down"	Skutch, 1960:511.
Yellow-breasted Flycatcher (*Tolmomyias flaviventris*)	0	this study
Yellow-olive Flycatcher (*Tolmomyias sulphurescens*)	"devoid of down"	Skutch, 1960:502.
Fluvicolinae		
Pied Water-tyrant (*Fluvicola pica*)	154–156	this study
Royal Flycatcher (*Onychorhynchus mexicanus*)	"utterly naked"	Skutch, 1960:526.
Ruddy-tailed Flycatcher (*Terenotriccus erythrurus*)	"devoid of down"	Skutch, 1960:535.
Sulphur-rumped flycatcher (*Myiobius sulphureipygius*)	"devoid of down"	Skutch, 1960:545.
Black-tailed Flycatcher (*Myiobius atricaudus*)	"devoid of down" "naked"	Skutch, 1960:552 Gross, 1964
Tyranninae		
Rusty-margined Flycatcher (*Myiozetetes cayanensis*)	185	this study
Social Flycatcher (*Myiozetetes similis*)	252 "sparse light grey down"	this study Skutch, 1960:441.
Gray-capped Flycatcher (*Myiozetetes granadensis*)	"sparse light grey down"	Skutch, 1960:418.
Great Kiskadee (*Pitangus sulphuratus*)	269	this study

subfamilies of the Tyrannidae (Traylor 1977, 1979) are represented by the genera considered in this study. Of greater significance is an ecological correlation among all of the genera considered here—they all build covered, domed, or ball-shaped nests, a habit which is thought to have been evolved independently in all three subfamilies (Traylor and Fitzpatrick 1982). Although the reason for the absence or reduction in number of neossoptiles has been considered by a number of authors, with little agreement (see Wetherbee 1957:353), this pattern does seem

Table 2. Distribution and counts of neossoptiles.

Region	Leptopogon superciliaris			Todi-rostrum cine-reum	Fluvicola pica		Myioze-tetes similis	Myioze-tetes caya-nensis	Pitangus sulphura-tus
Ocular[b]	—	—	—	—	6/9	4/5	11/11	9/9	18/18
Coronal	7/7	7/6	7/6	5/5	10/10	8/8	19/19	6/6	16/16
Postauricular	—	—	—	—	2/2	0/0	2/0	—	1/1
Occipital	4/4	4/3	4/3	1/1	5/5	4/3	8/8	3/3	6/6
Cervical	—	—	—	—	—	—	2/2	—	—
Middorsal	7/6	8/8	6/6	—	7/7	9/9	17/16	6/7	20/21
Pelvic[c]	—	—	—	—	0	3	3	4	5
Scapular	6/6	6/6	4/5	3/1	5/10	8/8	13/12	13/13	15/17
Femoral	0/2	0/0	0/0	—	6/6	7/6	11/10	12/12	15/15
Ventral	—	—	—	—	10/5	8/9	9/16	23/10	10/10
Caudal	6/6	6/6	6/6	—	3/3	6/6	6/6	5/6	6/6
Crural	—	—	—	—	3/6	6/4	8/10	8/7	7/8
Primaries	—	—	—	—	1/1	0/0	—	—	—
Secondaries	2/1	0/0	0/0	—	8/8	0/0	2/2	1/1	—
Greater Secondary Coverts		—		—	5/6	10/11	6/8	5/4	9/8
Middle Secondary Coverts		—		—	2/3	7/5	7/5	6/5	7/7
Lesser Secondary Coverts		—		—	—	—	1/1	—	—
Carpal Remix Covert		—		—	0/0	1/1	0/1	—	—
Patagial Coverts		—		—	—	—	—	—	—
Total	64	60	53	16	154	156	252	185	269

[a] *Tolmomyias flaviventris* was entirely naked and omitted from this table.
[b] Number of neossoptiles (right/left).
[c] Single midline row; all other tracts bilaterally paired.

to be common in taxa which utilize enclosed, cavity or domed nests. In the Tyrannidae an open cup nest is most common, and, has been thought to be primitive (Traylor and Fitzpatrick 1982). If so, the absence or reduced number of neossoptiles in some tyrannid genera is most likely to be also derived along with the closed nesting habit. It is interesting to note that *Pitangus* and *Myiozetetes* build loosely constructed bulky, ball-shaped nests in rather conspicuous open places in trees or other structures (Traylor and Fitzpatrick 1982: Fig. 3g; Skutch 1960). The remaining genera considered here (Table 1) all build tightly woven, globular or pyriform shaped nests frequently suspended from an overhanging twig or root (Traylor and Fitzpatrick 1982: Fig. 3i-3l). *Pitangus* sometimes builds an initially open cup-shaped nest which is gradually covered over during later stages of incubation. This is perhaps indicative of a more recently derived tendency and shows an evolutionary pathway from a primitive open to a derived closed, type of nest construction (Traylor and Fitzpatrick 1982:16). *Pitangus* and *Myiozetetes* also show the least reduction in number of neossoptiles which would be in keeping with species having only recently derived the habit of building a closed nest. The Piratic Flycatcher, *Legatus leucophaius,* which pirates covered nests of other species and the Sulphur-bellied Flycatcher, *Myiodynastes luteiventris,* which builds its cup-shaped nest in a cavity in a dead tree or old woodpecker hole both seem to have the denser down covering typical of open-nesting tyrannids (Skutch 1960)

from which they also may be more recently derived. Apparent exceptions to the above noted correlation are the Golden-crowned Spadebill, *Platyrinchus coronatus,* which builds an open cup nest and yet has nestlings which are entirely naked (Skutch 1960:335), and the Paltry Tyrannulet, *Zimmerius vilissimus* which builds a closed, domed nest with a side opening, and yet has "on its crown, back, sides, long grey down which is dense for a passerine" (Skutch 1960:471).

Information on the natal pterylosis of tyrant flycatchers still is drawn from a few individuals constituting only a small fraction of the 374 species and 88 genera of the Tyrannidae. Included are forms representing only part of the broad range of morphological and geographical diversity which occurs in this dominant New World family. When detailed information on the natal pterylosis is available for a greater array of taxa it is possible that some clearer taxonomic as well as ecological correlates will be found.

Acknowledgments

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Charles T. Collins and Kathleen M. McDaniel, *Department of Biology, California State University, Long Beach, California 90840.*

A New Species of the Genus *Traubella*
(Siphonaptera: Ceratophyllidae)

Among fleas found on canyon mice (*Peromyscus crinitus*) collected in south-western Utah were several specimens of an undescribed species of *Traubella* Prince, Eads and Barnes 1976, the first time this genus had been found in the state. The present paper describes this new taxon.

Traubella grundmanni, new species
Figs. 4–7

Diagnosis. —Selected generic characteristics shared with *Traubella neotomae* (I. Fox, 1940) include: head with frontoclypeal tubercle present but scarcely noticeable; eye relatively small and lightly pigmented except for outer rim; trabecula centralis present; row of minute setae (one to three setae in width) extending full length of dorsal margin of antennal fossae in both sexes. Labial palps five-segmented and about 90 percent as long as forecoxae. Apical spinelets present on first four abdominal terga. One long and two minute flanking antepygidial setae in male, and three long, well-developed antepygidial setae, each of a different length but center one longest, in female. Penis rods not coiled. Ventral anal lobe of female similar in shape, and number, arrangement and size of setae for both species.

The description that follows compares the new species with *Traubella neotomae* (I. Fox, 1940), the only other known species in the genus.

Modified Abdominal Segments, Male. —Finger longer than fixed process (Fig. 4) rather than equal (Fig. 1), finger almost flat-topped (Fig. 4), not gradually tapered (Fig. 1), and with about 6–7 marginal, unpigmented or lightly pigmented, mostly long, tapering setae of unequal lengths; of these the anterior seta longest, and one (usually the third or fourth seta posterior to apex) much shorter and less developed than others. Apex of fixed process (Fig. 4) somewhat less rounded than in *neotomae* (Fig. 1), tipped with one seta rather than three. Two acetabular setae in about the same position but longer than the two in *neotomae*.

Modified Abdominal Segments, Female. —Anal stylet with one long apical seta and two minute setae along its shaft, as opposed to stylet with one long apical seta flanked by a shorter ventrolateral subapical seta. Posterior border of sternum VII variable (Fig. 7) with deep sinus separating upper narrow, well developed lobe from much broader lower lobe compared to a shallow sinus and broadly rounded, scarcely differentiated upper and lower subequal lobes (Fig. 2). Differences in numbers and position of setae on sternum VII as in Figs. 2 and 5.

Bulga of spermatheca (Fig. 6) approximately the same length as *neotomae* (Fig. 3) but much narrower in diameter and with slightly concave upper and lower borders, not inflated with well rounded upper border and straight lower border; hilla strongly bent and about the same length in both species, but narrower and without sclerotized tip in *grundmanni*.

Size (total length mm, mounted specimens). —Males (N = 3), range 2.7–3.2, average 2.9; Females (N = 9), range 2.8–3.7, average 3.4.
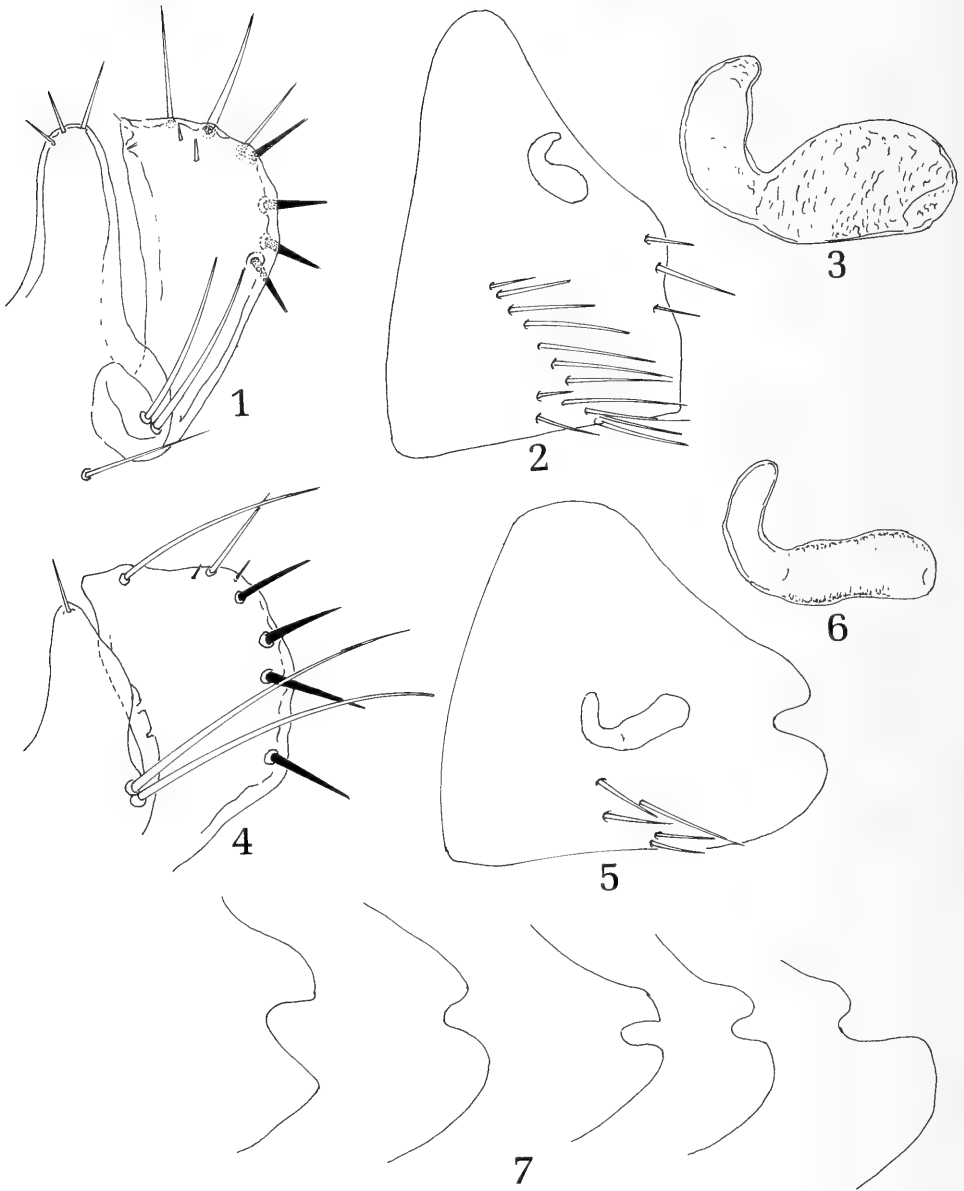
Figs. 1–3. *Traubella neotomae.* Fig. 1, finger and fixed process of male; Fig. 2, sternite VII of female; Fig. 3, spermatheca.

Figs. 4–7. *Traubella grundmanni,* n. sp. Fig. 4, finger and fixed process of male; Fig. 5, sternite VII of female; Fig. 6, spermatheca; Fig. 7, variation in outline of posterior margin, sternite VII of female.

Types. — Holotype male and Allotype female ex *Peromyscus crinitus stephensi* Mearns 1897 (H.J.E. host no. 19135) collected at mouth of Snow Canyon, 3.2 km northeast of Ivins: Washington County, Utah, elev. 945.5 m, 19 November 1988, H. J. Egoscue original numbers 11179 and 11181, respectively.

Paratypes, one male, one female, same data, H. J. Egoscue; two males, five females, same host species, location and elevation, 19 November 1988, H. J. Egoscue; one male, same host and location, elevation 950 m, 17 December 1988, J. Kucera; one female, same data, 18 December 1988, J. Kucera; one male, one female, same data, R. E. Elbel.

Additional material.—Two males (very badly damaged), host unknown, collected 28 or 29 December 1961 at the type locality by A. W. Grundmann and unknown students.

The holotype and allotype will be deposited in the U.S. National Museum, Washington, D.C. Paratypes collected by me will remain, at least temporarily, in my collection; those borrowed from R. E. Elbel and J. Kucera are being returned.

This new species is named for Dr. Albert W. Grundmann, Professor Emeritus, Department of Biology, University of Utah, in recognition of his many years of teaching and research in the field of parasitology and for providing the first specimens of this flea.

Discussion.—*Traubella neotoma* (I. Fox 1940) (Figs. 4–7), type host, *Neotoma lepida,* was originally described by Fox (1940) as a species of *Amphipsylla.* Prince et al. (1976) carefully reviewed the controversial taxonomic history of the taxon and corrected the situation by erecting the genus *Traubella* to hold *neotomae.* They also adequately discussed the many similarities between *Traubella* and *Malaraeus* and indicated the closest affinities of *Traubella* were with what was then called the *telchinus* group (*eremicus, sinomus* and *telchinus*) with which *Traubella* was compared.

Traubella grundmanni is known only from the type locality, where its preferred or true host appears to be *Peromyscus crinitus stephensi.* Special efforts to find *grundmanni* on other species of small mammals at Snow Canyon were unsuccessful. More intensive year-around collecting at Castle Cliff and environs less than 32 km distant on the west slope of Beaver Dam Mountains yielded no specimens of the new flea from either woodrat nests or numerous hosts of several rodent species which, however, included very few canyon mice.

The type locality of *grundmanni* is located among colorful sandstone formations in what is often called "red rock country." Dominant shrubs along the dry wash leading out of Snow Canyon include creosote bush, *Larrea tridentata,* and sand sagebrush, *Artemisia filifolia.* But the lava flows and cliffs favored by canyon mice there are very sparsely vegetated and lack characteristic shrubs. The climate in this part of Utah is characterized by low annual rainfall, wide ranges in temperatures, long, hot summers and relatively mild winters—conditions probably quite similar to those in southern California and other parts of the arid southwest where *Traubella neotomae* has been reported (Prince et al. 1976). Both species of *Traubella* are apparently winter fleas.

Acknowledgments

Research Resources, National Institutes of Health to the University of Utah. Permission to use drawings based on photomicrographs of *Traubella neotomae* in The Rothschild Collection of Fleas, The Ceratophyllidae: Key to the Genera and Host Relationships, by Traub, Rothschild and Haddow (1983) was given by Academic Press and Meriam Rothschild.

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Harold J. Egoscue, *Post Office Box 787, Grantsville, Utah 84029.*

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Holmes, T. Jr., and S. Speak. 1971. Reproductive biology of *Myotis lucifugus.* J. Mamm., 54:452–458.

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