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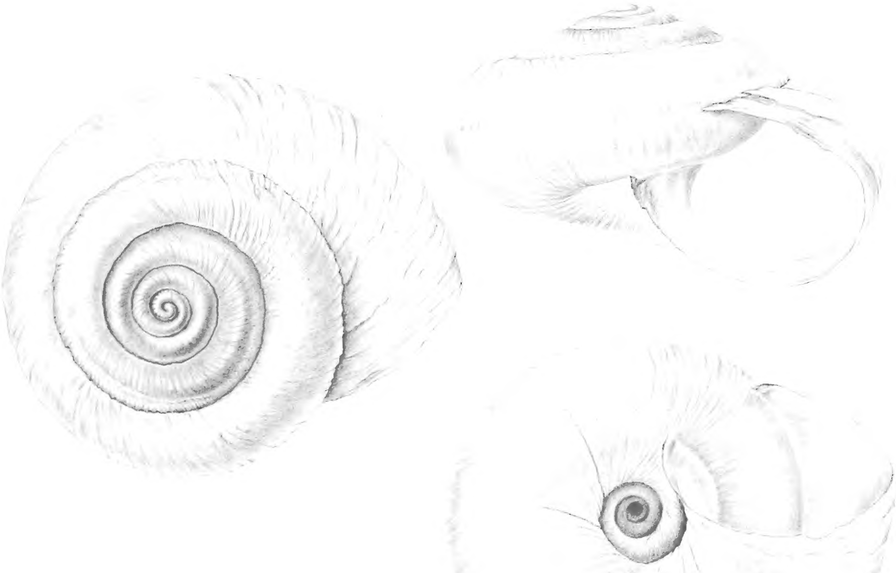

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Rediscovery of *Radiocentrum avalonense* (Hemphill in Pilsbry, 1905) (Gastropoda: Pulmonata)

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Abstract.—The land snail species originally described as *Oreohelix avalonensis* Hemphill in Pilsbry, 1905, was rediscovered on Santa Catalina Island, California, after being "lost" for nearly 80 years since its original collection. It is narrowly distributed on south-facing slopes on the southeastern part of the island, in association with a coastal sage scrub plant community. Dissection of the reproductive system confirms placement in the oreohelicid genus *Radiocentrum.* Disjunctions in the range of *Radiocentrum* correspond to the arid environments of the Sonoran and Chihuahuan deserts and probably date from late Pleistocene time. A lectotype is designated for the species.

In January or February of 1902 the conchologist Henry Hemphill visited Santa Catalina Island, California, and collected a large series of live oreohelicid snails, presumably in the vicinity of the town of Avalon. From this original collection Hemphill distributed specimens to collectors and museums throughout the country, many under the name "*Helix alternatus* var. *avalonensis.*" The find was first reported by Stearns (1902) and the snail later described by Pilsbry (1905), quoting a manuscript of Hemphill's, as *Oreohelix avalonensis.* Over the years many prominent malacologists have visited Catalina Island in search of this snail. Repeated failure to find it led to the suggestion that it might have become extinct (Bequaert and Miller 1973), perhaps through over-collecting (Smith 1970) or expansion of the settlement of Avalon. Because Catalina Island is well outside the range otherwise known for the Oreohelicidae, some workers suspected a mixup of locality labels, which has been known to happen with Hamphill's material (Roth 1982).

During a field survey of land mollusks on Catalina Island in December 1978, the senior author (FGH) unexpectedly found recently dead shells of an *Oreohelix*-like snail on a steep, south-facing slope about 4 km south of Avalon. No living snails were located in a brief survey of the area, nor on a second reconnaissance in 1979. A third trip was made to the same locality in January 1982 by all three authors. On the second day of field work, during a heavy, early-morning rainstorm, the junior authors (BR & WBM) discovered six live snails in an area which had been thoroughly examined the day before. Subsequent dissection and comparisons revealed that these snails were indeed the elusive species originally collected by Hemphill and confirmed that the proper generic assignment is to the genus *Radiocentrum.*

Additional field work extended the known range (based on recently dead shells) approximately 0.5 km to the northwest and 1.6 km to the southeast. No *Radiocen-*

trum have yet been found on other parts of the island in spite of extensive searching by the senior author. Since Hemphill did not specify his original locality, except as "Santa Catalina Island," we can only speculate that it was near the town of Avalon or in Avalon Canyon as the name implies. The original locality may have been destroyed in the course of Avalon's growth or through natural vegetational changes. Our findings indicate that the species' present range is probably restricted to the southeast end of the island on south-facing slopes, in coastal sage scrub habitats dominated by *Salvia* and *Opuntia.*

Because the species is rare and localized and would be threatened by unrestrained collecting, in this report locality information is given only in general terms. Detailed data are on file at the Santa Barbara Museum of Natural History and available for research and management purposes.

The following institutional abbreviations are used: ANSP, Academy of Natural Sciences, Philadelphia; CAS, California Academy of Sciences; CM, Carnegie Museum; SBMNH, Santa Barbara Museum of Natural History; SDMNH, San Diego Museum of Natural History; SUPTC, Stanford University Paleontological Type Collection (now at CAS); UCM, University of Colorado Museum; USNM, National Museum of Natural History, Smithsonian Institution.

Order Sigmurethra
Family Oreohelicidae
Radiocentrum Pilsbry, 1905

Type-species: *Oreohelix chiricahuana* Pilsbry, 1905, by original designation.

Diagnosis.—Oreohelicids with embryonic shell of about 1½ radially ribbed whorls; penis tripartite, walls of anterior part plain or furnished with pilasters, middle part papillose or with oblique ridges internally, posterior part ridged inside, wide and truncate at the end; epiphallus about as long as the penis, slender anteriorly, the penial retractor inserted on it a short distance from its entrance in the penis; albumen gland large; reproduction oviparous. Babrakzai, Miller, and Ward (1975) found a large number of submetacentric chromosomes and a haploid chromosome nnumber of $n = 32$ to be characteristic of *Radiocentrum.*

The few-whorled, radially costulate protoconch is the only diagnostic conchological character. The shells are otherwise much like *Oreohelix,* depressed-helicoid to lenticular in shape, the periphery ranging from rounded, through obtusely subangular, to distinctly carinate.

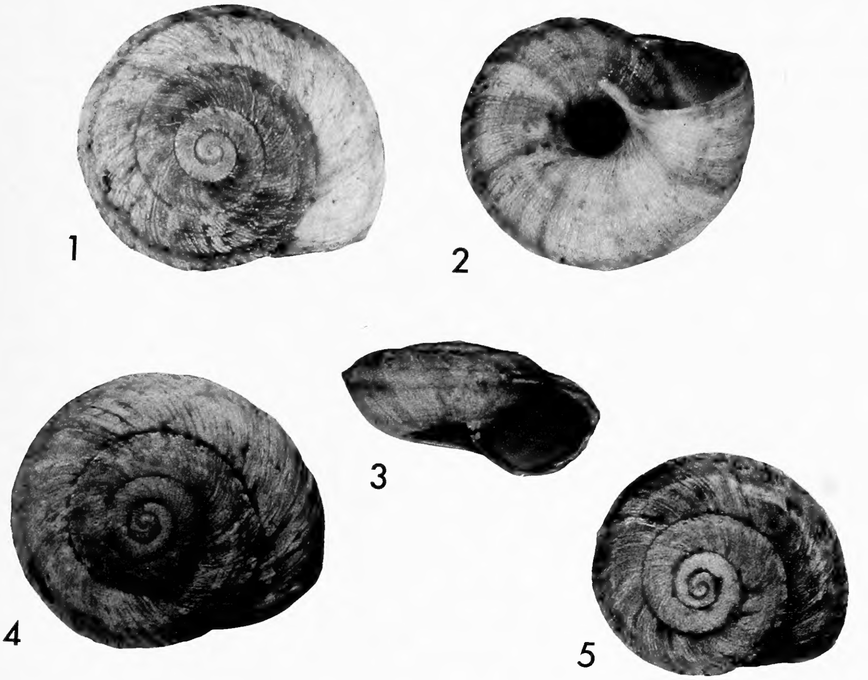
Remarks.—The endemic North American pulmonate family Oreohelicidae consists of two genera: *Oreohelix* Pilsbry, 1905, and *Radiocentrum,* the latter originally proposed as a subgenus of the former.

Conchologically, *Radiocentrum* has a distinctive, radially ribbed 1.5-whorled embryonic shell. Living *Radiocentrum* deposit eggs, whereas Recent *Oreohelix* are ovoviviparous. On the basis of reproductive characters and chromosome data, Babrakzai, Miller, and Ward (1975) elevated *Radiocentrum* to full generic status.

Radiocentrum avalonense (Hemphill in Pilsbry, 1905)
(Figs. 1–6)

Pyramidula hemphilli Newcomb (in part), Stearns 1902:62.

Oreohelix (Radiocentrum) avalonensis Hemphill, *in* Pilsbry 1905:283–284, pl. 11, figs. 4–7.—Cockerell 1905:71.—Pilsbry 1916:341, 354.—Berry 1931a:73.—



Figs. 1–5. *Radiocentrum avalonense.* 1–2, Lectotype, ANSP 86671a; top and basal views; diameter 11.2 mm. 3, 5, SBMNH 33997, live-collected specimen from south-facing slope approximately 4 km south of Avalon, Santa Catalina Island, Calif., B. Roth coll. 5 January 1982; apertural and top views; diameter 9.9 mm. 4, SBMNH 33998, from same locality, F. G. Hochberg coll. 4 December 1978; top view; diameter 12.3 mm.

Berry 1931b:115.—Pilsbry 1934:408.—Keep 1935:312, fig. 329.—Pilsbry 1939: 552–553, fig. 367.—Miller 1973:333–334.

Helix var. *avalonensis* Hemphill 1911:104–106, pl. 4.

Helix avalonensis Hemphill, Orcutt 1915:159.

Oreohelix avalonensis "Hemphill" Pilsbry, Cockerell 1938:11.—Ingram 1946: 89.—Baily 1953:22.—Baker 1962:4.—Smith 1970:42.—Roth 1972:11.—Bequaert and Miller 1973:32, 35.

Radiocentrum avalonense Hemphill in Pilsbry, Coan, and Roth 1987:325.

Type material.—Lectotype (designated herein): ANSP 86671a. Santa Catalina Island, California, H. Hemphill coll. Paralectotypes: ANSP 86671 (2 specimens). CAS 029012 (18) and 032996 (4). CM 6160 (3) (Brooks and Brooks 1931:248). SBMNH 33996 (9) and 34882 (2). SDMNH 1376 (5). SUPTC 6162 (51). UCM 20746 (8) and 21273 (4) (Wu and Brandauer 1982:29–30). USNM 174685 (6).

The data for the paralectotypes are the same as for the lectotype, except that later labels with CAS 032996 and SBMNH 33996 add "Avalon," SUPTC 6162 adds the date "1902," and SBMNH 33996 gives the date as "I-II-1902" (presumably January and February).

Referred material.—SBMNH 33997–34001, Santa Catalina Island, California, south-facing slopes approximately 4 km south of Avalon, elevation ca. 300–380 m, under *Opuntia* patches and in rock rubble areas around *Salvia,* F. G. Hochberg

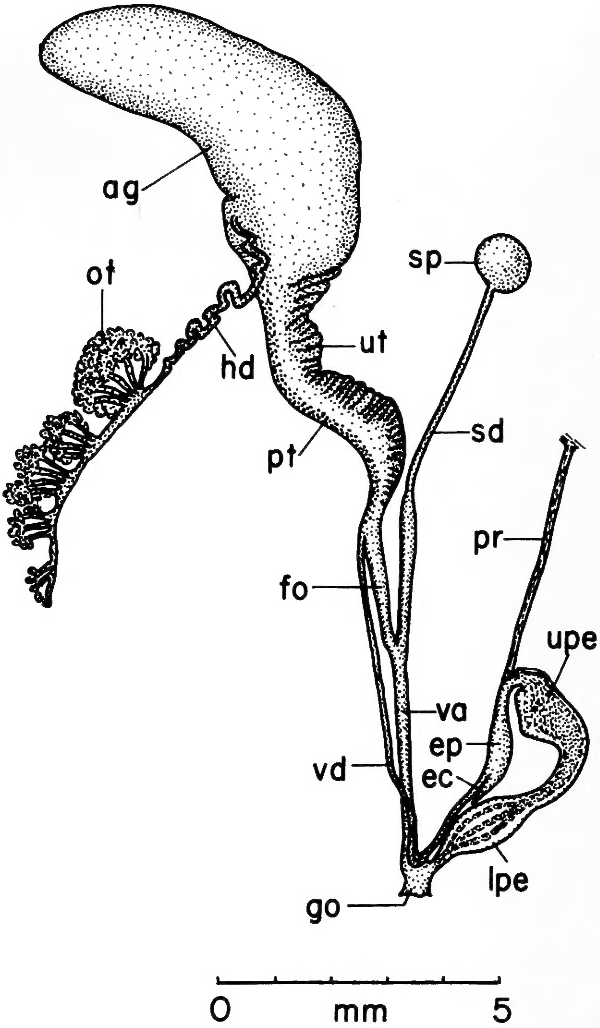


Fig. 6. Reproductive system of *Radiocentrum avalonense.* ag, albumen gland; ec, epiphallic caecum; ep, epiphallus; fo, free oviduct; go, genital orifice; hd, hermaphroditic duct; lpe, lower part of penis; ot, ovotestis; pr, penial retractor muscle; pt, prostate; sd, spermathecal duct; sp, spermatheca; upe, upper part of penis; ut, uterus; va, vagina; vd, vas deferens. Drawn from stained whole mount, WBM 7251.

and others coll., 1978, 1980, 1982, 1983, 1984. Specimens also in private collections of the junior authors (WBM 7251, BR 1347).

Description.—"'Whorls 4½, granulated above and below, the last one wide; aperture large. Alt. 6, diam. 11 mm.' (*Hemphill*)" (Pilsbry 1905:283).

> "The shell is lens-shaped, sharply carinate; umbilicus contained slightly more than 5 times in the diameter. Spire dull brown, the last whorl cream white with steaks of light brown and gray, and two pale brown bands, the upper one a short distance above, the lower immediately below the periphery. Embryonic shell of 1½ strongly convex whorls, the initial half turn smooth,

the following whorl with strong radial ribs with wider, smooth intervals. Later whorls with rough, irregular striation, irregularly cut into long granules by spiral impressions; base with irregular radial striae and fine, weak spiral striation, with about 5 stronger spirals at wide intervals. The last whorl is subangular in the middle of the upper surface, at least in front; and it does not descend to the aperture. The peristome is thin, its ends connected by a thin, rather long parietal callus.

"Height 6 mm., diameter 11.2 mm; 4½ whorls. Height 6.3 mm., diameter 11.4 mm; 4⅔ whorls. 'Height 8 mm., diameter 14 mm; 5 or 5½ whorls.' (Hemphill.)" (Pilsbry 1939:553).

Pilsbry (1905) quoted a brief diagnosis from an unpublished manuscript by Hemphill and illustrated shells, sufficient to validate the name six years before Hemphill (1911) published a full description. ANSP 86671a, which Pilsbry (1939) and Baker (1962) referred to as "the type," is hereby designated lectotype of the species (Figs. 1, 2). Paralectotypes CAS 029012 are accompanied by a label in Hemphill's handwriting in ink, "H. var. avalonensis/Hemph/Santa Catalina Is./Cal." with a later addition in pencil, "Type lot." They range from juveniles 4.9 mm in diameter with 3.5 whorls to a single specimen 14.0 mm in diameter, 8.8 mm in height, with 5.5 whorls. This specimen, evidently the one Hemphill (1911) regarded as his "single mature shell," is slightly worn, the carina is obsolete on the last half of the body whorl, and the color ranges from flesh color on the spire to mottled cream white on the body whorl. The ribbed *Radiocentrum* embryonic shell is present. There seems to be no reason to doubt that this large shell came from the same source as the rest of Hemphill's material. The next largest specimens in the lot are 12.3 and 12.1 mm in diameter, both with 4.9 whorls. There is a tendency in all material we have seen for shells greater than about 11.3 mm in diameter to have inflated body whorls.

The newly collected specimens do not differ significantly in shell characters from the type material. The largest is 12.3 mm in diameter and has 5.0 whorls (Fig. 4). A dissected specimen 9.9 mm in diameter with 4.5 whorls was sexually mature.

Anatomy.—The reproductive system of *R. avalonense* (Fig. 6) has been critically compared with those of *R. chiricahuanum* (Pilsbry, 1905), *R. labrenanum* (Pilsbry, 1948), *R. clappi* (Ferriss, 1904), *R. exorbitans* (Miller, 1973), and *R. discus* Christensen and Miller, 1976. It is typical of the genus in the following aspects: the albumen gland is large, as in other oviparous genera (in *Oreohelix,* which is ovoviviparous, it is much reduced); the lower part (approximately one-third) of the spermathecal duct is swollen; the upper part of the penis is much enlarged and "hatchet-shaped." It differs, however, from other species of *Radiocentrum* in having a swollen lower part of the penis, containing three distinct longitudinal pilasters. This characteristic was observed in all adult specimens dissected.

Externally the animal is light tan, the mantle collar somewhat grayish. Specimens in terraria were active infrequently—far less than *Micrarionta* and *Xerarionta* kept under the same conditions. They were not observed to eat fresh lettuce but apparently fed on dead stems and leaf litter collected under *Salvia* clumps at their native locality.

Habitat.—All our collections of *R. avalonense* have been made in a limited area near the southeast end of Catalina Island (Fig. 7), near the top of steep, south-

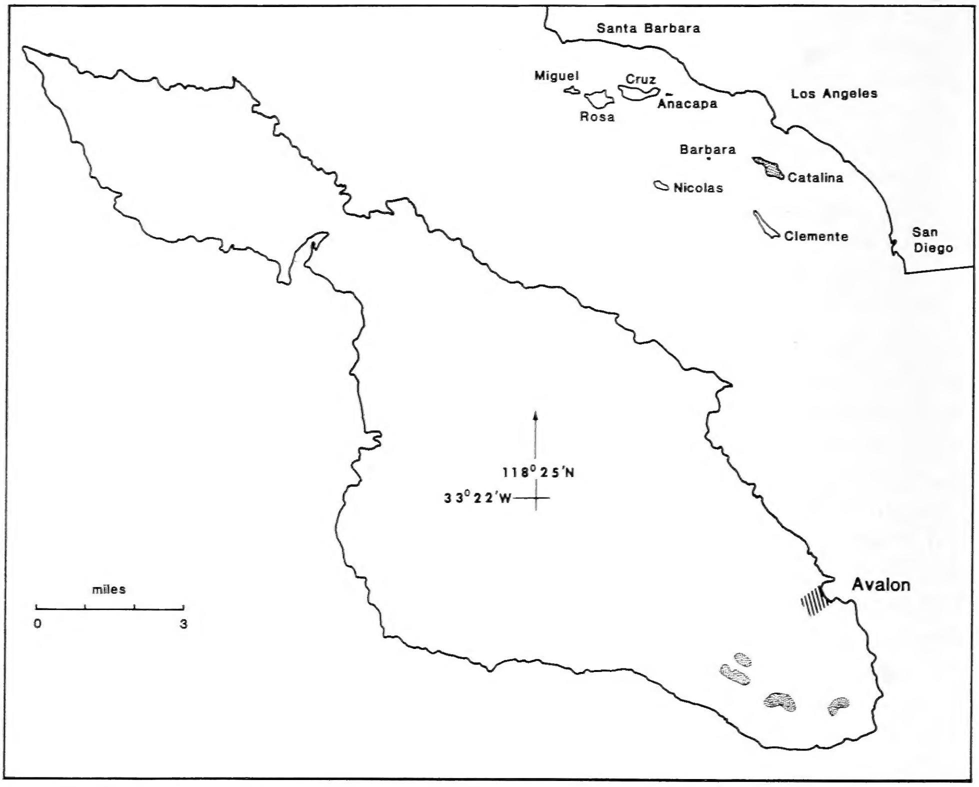


Fig. 7. Map of Santa Catalina Island, Calif., showing generalized distribution of *Radiocentrum avalonense* (stippled).

facing slopes sparsely covered with coastal sage scrub vegetation. The dominant plants are black sage (*Salvia mellifera*) and prickly-pear cactus (*Opuntia littoralis*). Sclerophyll shrubs such as lemonade berry (*Rhus integrifolia*) and toyon (*Heteromeles arbutifolia*) are also present (Figs. 8, 9). Few herbaceous plants occur on these upper slopes, probably because of persistent grazing by feral goats, whose trails, bare of vegetation, crisscross the slopes. The vegetation is less dense and arborescent than that on north-, east-, or west-facing slopes in the same area.

Living specimens were first discovered early on 5 January 1982, after a night of drenching rain that continued into the morning. They were on a slope that, the day before, had yielded only a few empty shells. At 10:00 A.M. the snails were all active, quite turgid, and crawling either on stems or on the ground around the edge of *Salvia* clumps, or in one case on a stone deep in a patch of *Opuntia*. The helminthoglyptid snails *Xerarionta kelletti* (Forbes, 1850) and *Micrarionta beatula* Cockerell, 1929, were relatively common in the same area. One of the living *R. avalonense* was observed to be rasping the bark of a *Salvia* twig, and the first feces of specimens in captivity were grayish brown, the same color as the *Salvia* stems and leaf litter.

The breakage pattern on some of the empty shells, body whorl broken from the side and spire decollated, suggests predation by small mammals such as mice.

A field survey of the land mollusks of Catalina Island organized by the Santa

Figs. 8–11. 8, *Radiocentrum avalonense* habitat: slope with coastal sage scrub vegetation. Low plant cover predominantly *Salvia mellifera* and *Opuntia littoralis*; larger shrubs are mainly *Rhus integrifolia*. 9, *R. avalonense* shells among litter of *Salvia mellifera*. 10, Avalon, Santa Catalina Island, looking northwest, about 1903; photograph courtesy of Catalina Island Museum. Vegetation on distant slope largely coastal sage scrub. 11, Similar view in 1983. Note increase in density of large chaparral shrubs, principally *Rhus integrifolia*, on distant slope.

Barbara Museum of Natural History has not found *R. avalonense* elsewhere on the island. The eastern part of Catalina that includes Avalon Canyon is more completely dissected by canyons than any other sector of equivalent size. The bedrock is an intrusive dacite porphyry of Miocene age, which, however, also extends a considerable distance to the west (Platt 1976: fig. 3). This eastern sector also contains the largest uninterrupted area of coastal sage scrub on the island (Minnich 1980: fig. 2). Beyond these general observations on exposure, vegetation, and topography, we have been unable to correlate the distribution of *R. avalonense* with any more specific environmental factors.

In order to be able to collect over 100 specimens, most apparently live-taken, of a species that we found rare and difficult to locate, Hemphill must have encountered more populous colonies, perhaps nearer to the town of Avalon. Historical photographs show that around Avalon, upon release from grazing pressure, a landscape of sparse grass, prickly-pear cactus, and open chaparral in the 1880s developed rapidly into coastal sage scrub by 1900. Thereafter, chaparral species such as *Rhus integrifolia* invaded at a slower pace (Minnich 1980) (Figs. 10, 11). The scrub has now been protected from brush fires for many years and in consequence is very mature and woody. Young or fire-renewed scrub would yield more soft litter and perhaps support a denser snail population like that which Hemphill may have found. There is also the possibility, hinted at by Smith (1970), that Hemphill over-collected the species and that the effects are still being felt today. Intemperate collecting by early naturalists was an important factor in the

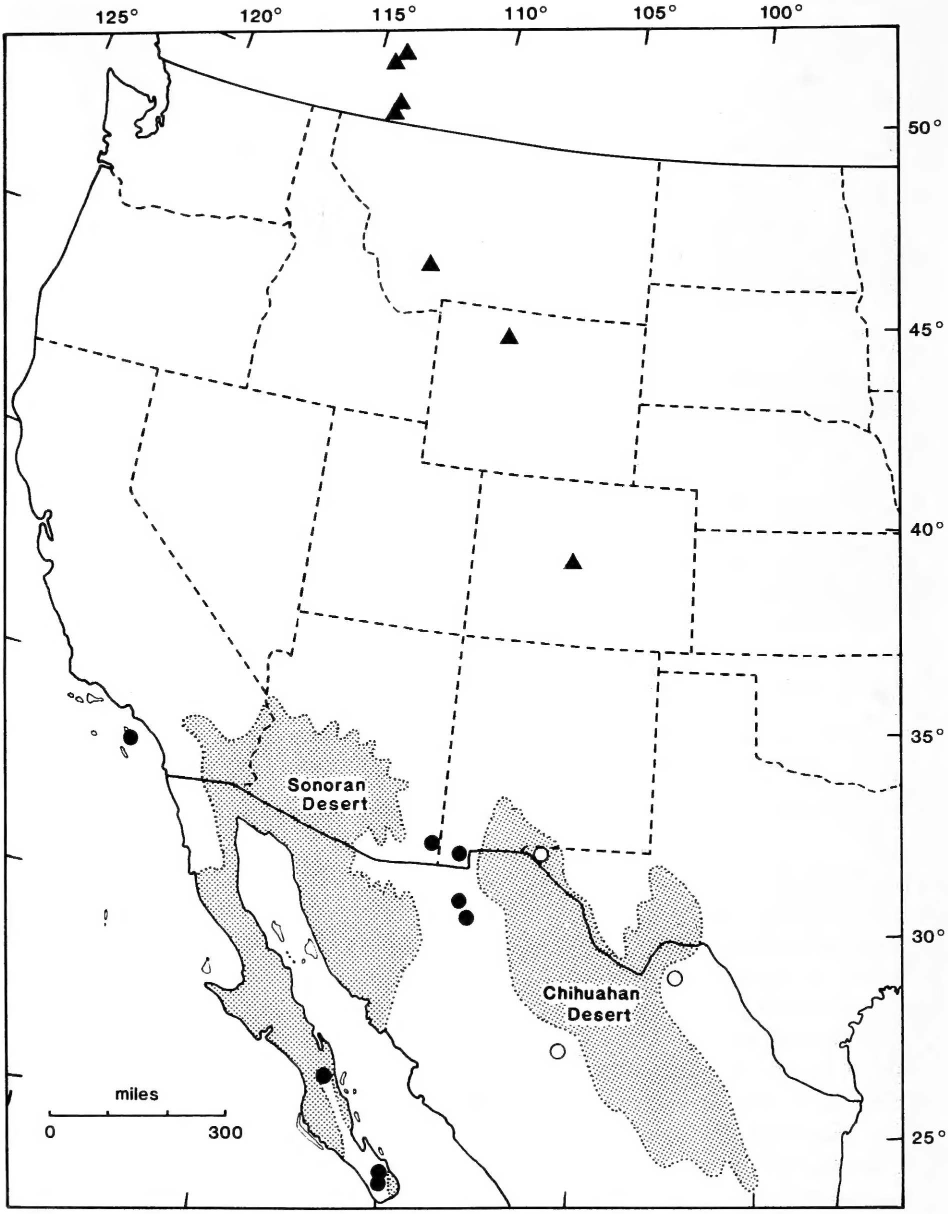


Fig. 12. Map of western North America showing Recent and fossil ditribution of genus *Radiocentrum*. Solid circles, living; open circles, Quaternary (Pleistocene or early Holocene); triangles, upper Cretaceous through Oligocene occurrences. Stippled areas, approximate limits of Sonoran and Chihuahuan deserts (after Axelrod 1979).

decline of the slow-maturing *Achatinella* snails on Oahu (Hadfield and Mountain 1980). Without comparable data on reproductive rate in *R. avalonense* we cannot automatically rule out the effects of early collecting.

Biogeography.—The Pleistocene to Holocene distribution of *Radiocentrum* (Fig. 12) includes the following taxa:

Southern New Mexico
  R. hachitanum hachitanum (Pilsbry, 1905)
  R. h. cadaver (Pilsbry, 1915)
  R. ferrissi ferrissi (Pilsbry, 1915)
  R. f. morticinum (Pilsbry, 1915)
Southern Arizona
  R. clappi clappi (Ferriss, 1904)
  R. c. cataracta (Pilsbry and Ferriss, 1910)
  R. c. emigrans (Pilsbry and Ferriss, 1910)
  R. chiricahuanum chiricahuanum (Pilsbry, 1905)
  R. ch. obsoletum (Pilsbry and Ferriss, 1910)
  R. ch. percarinatum (Pilsbry and Ferriss, 1910)
Chihuahua
  R. caenosum (Pilsbry, 1948)
  R. labrenanum (Pilsbry, 1948)
  R. almoloya (Drake, 1949)
Northern Coahuila
  R. orientalis Metcalf, 1980, probably Pleistocene
Franklin Mountains, El Paso County, Texas
  R. ferrissi ferrissi, late Pleistocene fossils (Metcalf and Johnson 1971)
Baja California Sur
  R. exorbitans (Miller, 1973)
  R. discus Christensen and Miller, 1976
Santa Catalina Island
  R. avalonense (Hemphill, in Pilsbry, 1905).

In addition to the species assigned a Pleistocene age, *R. almoloya, R. hachitanum cadaver,* and *R. ferrissi morticinum* are known from their empty shells only and may represent extinct colonies.

Tozer (1956) found *Oreohelix angulifera* (Whiteaves, 1885) from the St. Mary River and Edmonton Formations, upper Cretaceous of western Alberta, and *O. thurstoni* (Russell, 1926) from the Paskapoo, Porcupine Hills, and Willow Creek Formations, Paleocene of western Alberta, to have regular costae on the embryonic whorls, strongly suggestive of *Radiocentrum.* Two undescribed species of *Radiocentrum* occur in the Bozeman Group, Eocene and/or Oligocene, of Broadwater and Gallatin counties, Montana (D. W. Taylor *in* Robinson 1963:68, table 4; Taylor 1975:209; where cited as *Oreohelix* n. sp.; Roth, in press). Additional fossil oreohelicids probably assignable to *Radiocentrum* include *R. grangeri* (Cockerell and Henderson, 1912) from the Eocene of Park County, Wyoming, and *R. hendersoni* (Russell, 1938) from the Oligocene of Colorado. Cockerell (1914) assigned *Helix nacimientensis* White, 1886, from the Paleocene of New Mexico, to *Radiocentrum*; Taylor (1975), however, regarded this species as probably helminthoglyptid.

These Cretaceous and early Tertiary species are all north of the present range of the genus, along the eastern Cordillera (Fig. 12). The northernmost occurrences are the oldest: late Cretaceous and Paleocene. Eocene and Oligocene localities are somewhat farther south. The genus has evidently undergone a southward restriction or displacement of range since Paleogene time.

Evidence from paleobotany, oceanic foraminifera, and fossil vertebrates (Savin 1977; Wolfe 1978; Lillegraven 1979) indicates progressive cooling through the

Tertiary Period, a steepening latitudinal temperature gradient, and restriction of tropical and subtropical biota to lower latitudes. Over the same interval, precipitation in the western interior has become largely confined to the winter months (Axelrod 1979). The extinction of *Radiocentrum* in the northern regions from present-day Alberta to Colorado probably accompanied a climatic change from tropical to temperate and from summer-wet to summer-dry.

The Quaternary range of *Radiocentrum* includes two significant disjunctions, across the Sonoran and Chihuahuan deserts (Fig. 12). The Sonoran Desert is interposed between *R. avalonense* on Santa Catalina Island and the Baja Californian and the Arizona-New Mexico-Chihuahuan groups of species. The main mass of the Chihuahuan Desert separates the latter group from the Pleistocene *R. orientalis* in Coahuila; the occurrence of *R. ferrissi ferrissi* in the Franklin Mountains of west Texas (where it is apparently extinct) is about 180 km east of the living *R. ferrissi* of New Mexico and separated by a tongue of Chihuahuan Desert.

Many trans-Sonoran disjunctions are recognized among plants, including woody species of the woodland and chaparral vegetation of southern California and Arizona (Axelrod 1979: fig. 4, table 1) and unique taxa of the insular flora of southern California with their closest allies in the Sierra Madre of Mexico (Axelrod 1979: fig. 6). According to Clements (1936), the disjunct woodland and chaparral taxa imply a former continuity over the area at a time when temperatures were much milder and annual rainfall was near 500 mm at a minimum. Studies of late Pleistocene plant remains (summarized by Axelrod 1979:9) indicate that oak-conifer woodland covered much of the Sonoran Desert in Arizona and also the northern Chihuahuan Desert as recently as 10,000–12,000 years ago. Some of the component taxa persist now as relicts in the desert ranges, where they retreated as aridity increased after the last pluvial stage. Similarly, the arid environment of the Chihuahuan Desert separates the montane woodland of the eastern and western cordilleras of north-central Mexico.

The emergence of the Sonoran Desert as an environment of regional extent dates from the latest Cenozoic; its current broad area, the maximum ever achieved, is a post-Wisconsinan feature (Axelrod 1979).

The disjunct type of distribution shown by *Radiocentrum* is what one would expect of a formerly widespread taxon now persisting as relicts in scattered enclaves of favorable habitat. The fact that several taxa are known only from empty shells may indicate that recent extinction of localized populations is still taking place—consistent with Axelrod's timetable of modern desert development. *Radiocentrum avalonense* is thus probably a relict outlier of a once more continuously distributed genus that has undergone its most severe fragmentation during the late Cenozoic. Another molluscan taxon that may have had a similar history yet gone all the way to extinction on the Pacific Coast is the urocoptid genus *Holospira.* The present westernmost range of *Holospira* is in eastern Arizona and Sonora (Bequaert and Miller 1973: fig. 6), but Gregg (1944) reported fossils apparently referable to *Holospira* from the late Pleistocene deposits of Rancho La Brea in Los Angeles, California.

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Memorial Garden and Foundation) for identification of island plants and for partial funding support, and Patricia Moore (Catalina Island Museum) for use of historical photographs housed at the Museum. Field trip participants include Robert Given (Catalina Marine Science Center); Paul Scott, Eve Shipp, and Jim Shipp (SBMNH); Timothy Pearce (University of California); Betty Sue Miller, Jane Deisler, Edna Naranjo Garcia, Bob Carey, Russel Duncan, Jim Hoffman, Jennifer Titley, and Diana Warr (University of Arizona). Robert Robertson and Mary Garback (ANSP) loaned type specimens; Harald Rehder and the late Joseph Rosewater helped locate material at the USNM. The late S. Stillman Berry provided access to his bibliographic file and specimens in his collection. Carl Christensen and Art Metcalf critically reviewed the manuscript.

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Distribution and Stability of Grasslands in the Los Angeles Basin

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Abstract.—Present grassland distribution (as of 1980) was mapped from modern aerial photographs for 21 7.5 minute quadrangles in the Los Angeles Basin. These patterns were compared with the distribution of grasslands mapped from aerial photographs from 1928 to 1936. Grasslands increased in all but three quadrangles, the greatest increases being in the northwestern portion of the basin. Vegetational changes, however, were not unindirectional as shrubland, notably coastal sage scrub, replaced grassland in sections of nine quadrangles. In general, areas subject to frequent fires and grazing moved from shrubland to grassland while grassland areas with infrequent disturbance were invaded by shrubs. An intensive study was undertaken in a quadrangle in which vegetation had changed in both directions. Nine islands of coastal sage scrub surrounded by grassland were selected for study. Vegetation pattern was not dictated by topographic position or soil charateristics. Density of seedlings was high within patches of mature shrubs but seedlings were largely absent outside their boundaries. Shrub sizes in transects across the ecotone suggested that in eight of the nine coastal sage scrub patches shrubland was not invading grassland. Recent burning (within 10 years), coupled with intensive grazing, appears to inhibit the invasion of shrubs into adjacent grasslands. We hypothesize that the vegetation of the Los Angeles Basin is a mosaic of community types differing in their tolerances to disturbance.

Annual grasslands are a major vegetation type in California. Throughout much of their range they are dominated by non-native species and the vegetation composition prior to the introduction of these exotic species in the late 18th century is unknown. One hypothesis is that these grasslands were originally dominated by native bunchgrass species, notably *Stipa pulchra.* An alternative is that these regions were originally brush covered.

Clements (1934) noted that certain grassland areas contained isolated patches of *Stipa pulchra* which he interpreted as "relicts" of a previous native grassland. It has been suggested that these native grasslands succumbed to competition with annual exotics during periods of intensive grazing and drought in the mid 19th century (Heady 1977). Alternatively, Cooper (1927) noted what he interpreted as "relict" stands of brush in grassland areas and hypothesized that early settlers cleared brushlands by repeated fires. Since brush species are intolerant of repeated fires they were replaced by the exotic annual species which are good colonizers.

Wells (1962) suggested that the present annual grasslands were not derived from grasslands dominated by native perennial bunchgrasses on deep clay soils, but were derived from woody sage and chaparral vegetation on shallow rocky soils.

Today, areas dominated by native grasses are invariably on fine-textured substrates. Attempts to regenerate native grass species off such soils have largely failed (Kay et al. 1981). Although the theory of widespread native grasslands is based largely on "presumed relicts" of *Stipa pulchra* and other native grasses, the alternative theory is based on "known relicts" of chaparral. Documents show that many grassland areas once were covered by brush. Land managers have long used repeated prescribed fires to clear brush and Zedler et al. (1983) have shown this can result from frequent wildfires.

Annual grasslands are widely distributed throughout the Los Angeles Basin. The purpose of this study was to determine the distribution and stability of these grasslands and to identify the factors responsible for their formation. A major focus was to document present grassland distribution and determine if any distributional changes had occurred in the last 50 years by comparisons with early aerial photographs. A second focus was to examine site characteristics in a grassland area containing patches of coastal sage scrub. Demographic trends of shrubs at the grass : sage interface were examined in order to evaluate the stability of such zonation patterns.

Sites and Methods

Present and Past Grassland Distribution

Twenty-one 7.5-minute USGS quadrangles were selected for study. These included the most extensive grasslands in the Los Angeles Basin (Fig. 1) excluding the Santa Monica Mtns. where grassland distribution has been studied by Goode (1981) and Hobbs (1983). USGS quadrangle maps were used as a starting point for outlining the present-day grassland distribution. These maps give vegetation types, although in many cases they are out of date. Therefore, 1974–1976 aerial photographs were obtained for all quadrangles and used to update vegetation distribution. Updated maps were further checked by on-site inspection of most areas in 1979–1980. The historical record for these areas was constructed by examination of 1928–1936 aerial photographs from the Fairchild Collection at Whittier College, Whittier, California. Interpretation of these photographs was aided by vegetation maps produced by Wieslander circa 1930 (available at the Rancho Santa Ana Botanic Garden). USGS topographic maps were also a source of historical data since vegetation types were mapped, but often not updated for over 25 years. All historical vegetation data were mapped on acetate sheet overlays of the 7.5-minute topographic maps. From the present-day vegetation maps and historical overlays, the total area of vegetation change was estimated to the nearest hectare.

Data on the fire history were gathered from county, state, and federal agencies for areas where such data were available. For various reasons the area under study has very incomplete data on fire history. USDA soil survey maps were consulted for areas for which they were available.

Localized Patterns at the Grass : Sage Ecotone—Intensive Site

The intensive study site was the Calabasas Quadrangle between Palo Comado and Cheeseboro Canyons, 3–5 km N of Hwy 101. This area contains a mosaic of grasslands with patches of coastal sage scrub. Nine sites were selected; each included one scrub patch plus adjoining grassland.

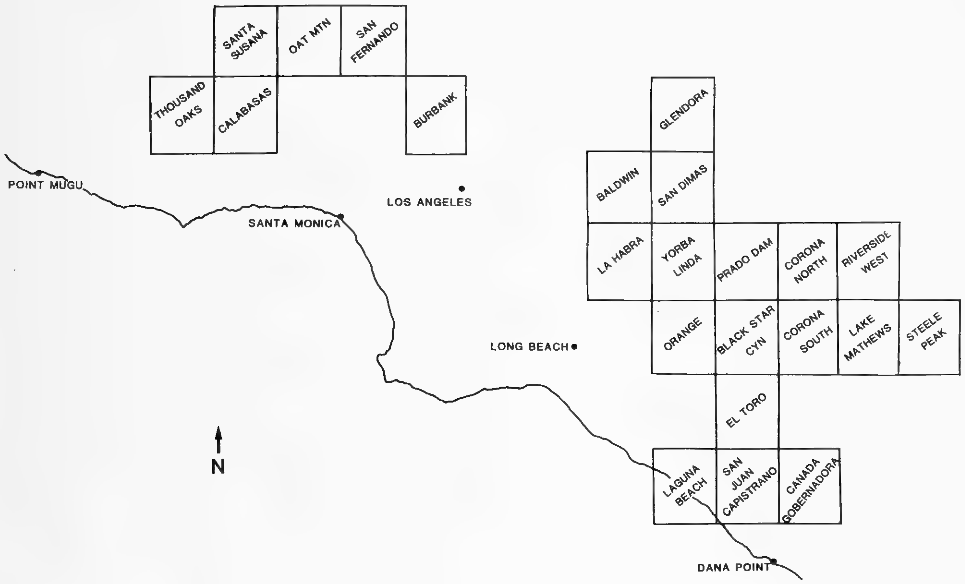

Fig. 1. Los Angeles Basin 7.5 minute quadrangles included in this study.

Slope aspect and inclination were recorded for each site. Soil samples from 0–15 cm depth were taken from the shrub stand and adjoining grassland, in most cases on two sides. For each soil sample, pH, organic matter content and soil texture were determined according to procedures in Cox (1980).

Vegetation at each site was sampled in spring 1982 by recording height and foliage diameter of all shrub species in 3.5 × 4.0 m quadrats placed contiguously from grassland through the coastal sage scrub patch and into the grassland on the other side.

Results

Grassland Distribution

During the past 50 years, vegetation has changed throughout the Los Angeles Basin (Table 1). Since urbanized areas and other human artifacts such as agricultural land have been excluded from this analysis, decreases in one vegetation represent an increase in another vegetation type. Grasslands have increased or decreased in many areas. Quantitatively, the major change has been an increase in grasslands at the expense of coastal sage scrub and chaparral. A brief description of the changes observed in each quadrangle follows.

Northwestern Los Angeles Basin

In the Thousand Oaks Quadrangle, coastal sage increased extensively at the expense of grassland over the past 40 years. This is evident in a comparison of 1936 aerial photos with the 1952 USGS topographic map. Further increases in coastal sage scrub were seen in the 1976 aerial photo. Except for a small fire around Medea Creek in 1970, this region had not burned since 1910. The area burned in 1970 was grassland in 1976. In general, grasslands predominated on

Table 1. Grassland distribution changes in the Los Angeles Basin between 1928 and 1980.

Quadrangle	Area changed (ha)	Area subject to change (ha)	% change	Grasslands	
				Increase	Decrease
Northwestern:					
Thousand Oaks	400	8000	5	X	X
Calabasas	700	12,000	6	X	X
Santa Susana	1000	12,000	8	X	
Oat Mountain	300	12,000	3	X	
San Fernando	1100	8000	14	X	
Burbank	50	8000	>1	X	
Northeastern:					
Glendora	400	15,000	3		X
San Dimas	500	8000	6	X	X
Baldwin Park	0	1700	0		
La Habra	300	4000	8	X	
Yorba Linda	200	23,000	2	X	
Prado Dam	250	10,000	2		X
Corona North	20	1500	>1	X	
Riverside West	100	1500	6	X	
Southern:					
Steele Peak	600	8000	8	X	X
Lake Mathews	1500	12,000	13	X	X
Corona South	100	12,000	>1	X	
Black Star Canyon	100	12,000	3		X
Orange					
El Toro	150	8000	7	X	
Canada Gobernadora	500	16,000	2	X	X
San Juan Capistrano	100	16,000	>1	X	
Laguna Beach	900	9000	10		X

soil such as Linne silty clay (30–50% slope), Rincon silty clay loam (2–9% slope) and Cropley clay (2–9% slope). Coastal sage tended to predominate on Calleguas shaley loam (30–50% slope). However, field examination detected numerous exceptions.

In the Calabasas Quadrangle, grassland has increased substantially, particularly in Las Virgenes, Cheeseboro, and Palo Comado Canyons. Increases were evident from 1928 to 1952, and from 1952 to 1976. Most of this area burned in 1970 and is now grazed by cattle. A small area in the southern portion showed an increase in coastal sage scrub over grassland, however.

The Santa Susana Quadrangle was dominated by grasslands in 1930. Since then, these grasslands have expanded at the expense of coastal sage scrub along Chivo, Gillibrand, Windmill, and Meier Canyons. The last known fire in this area was in 1970, 10 years prior to these observations. Today this area is heavily grazed by cattle. An area within a fenced-in water tank remained coastal sage while grassland replaced coastal sage outside. A 1-ha area of grassland, which appeared to be under cultivation in 1928, was coastal sage scrub in 1980.

Grasslands increased substantially on the south-facing slopes of the Santa Susana Mountains in the Oat Mountain Quadrangle. However, a few patches of

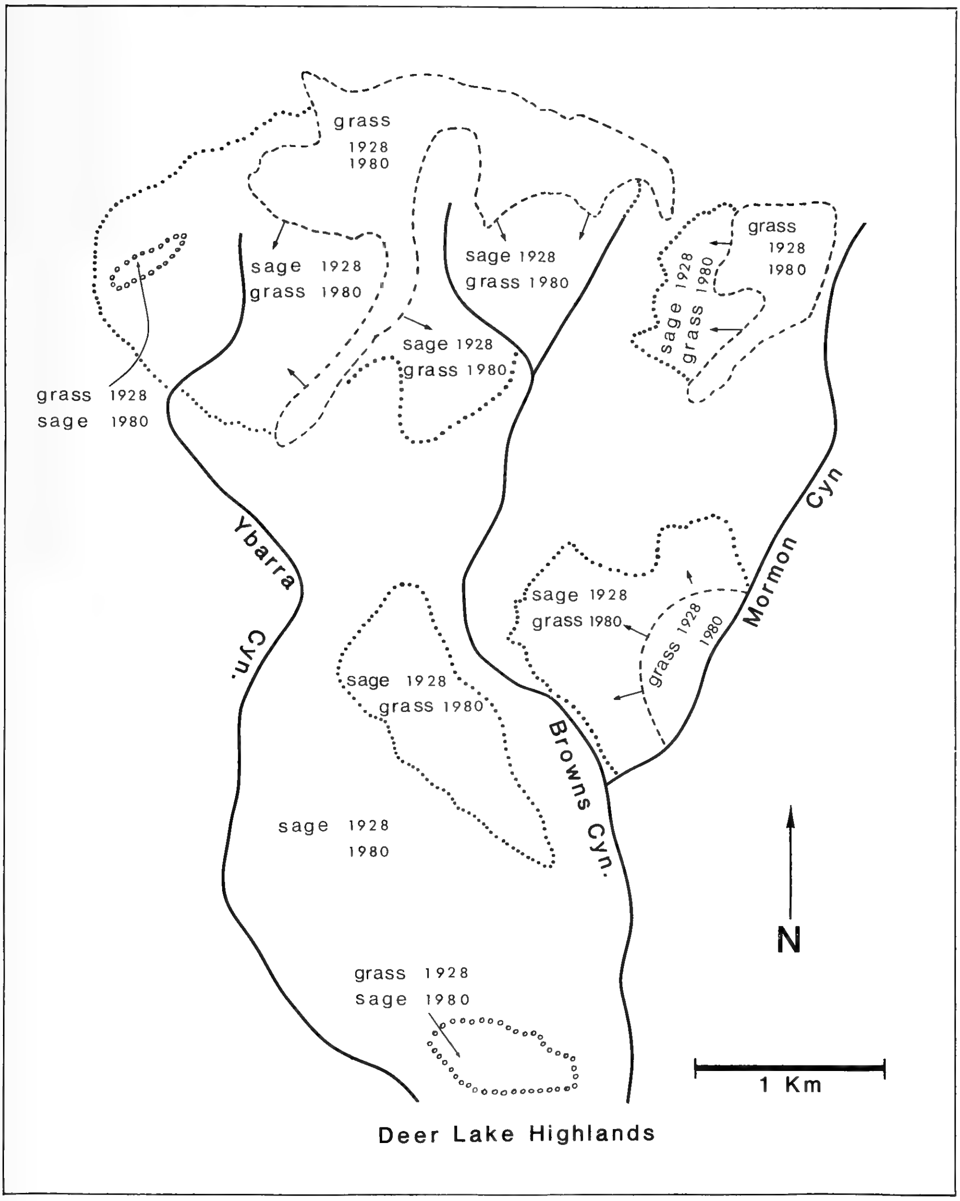

Fig. 2. Historical and present day vegetation patterns (as of 1980) on a portion of the Oat Mountain Quadrangle.

coastal sage scrub appeared in 1980 in areas that were grassland in 1928. These changes are illustrated in Fig. 2. Parts of this area burned in either 1969 and/or 1970. Most of this area is currently grazed by cattle.

In the San Fernando Quadrangle, grassland has increased markedly since a fire in 1975. Shrub resprouts were most evident on north-facing slopes and ravines, however, and the entire area is likely to return to the dense chaparral recorded on the 1966 USGS map.

The vegetation of the Verdugo Mountains within the Burbank Quadrangle has remained unchanged, although the density of chaparral between Elmwood and Stough Canyons has increased since 1928.

Northeastern Los Angeles Basin

Glendora Quadrangle includes the USDA San Dimas Experimental Forest. A large section of chaparral in this area was converted to grassland as part of a type-conversion experiment.

Within the San Dimas Quadrangle there have been diverse changes. Three hectares on the south facing slope of Buzzard Peak were coastal sage or chaparral in the 1928 aerial photo and Wieslander's 1930 vegetation map. On the 1964 USGS map they were sparse shrub-grassland and in the 1975 aerial photo and 1980 field checks they had progressed to pure grassland at the lower elevations and open grass-shrubland higher on the slope. Several areas in this quadrangle had changed from grassland or sparse shrub cover circa 1930 to dense brush in 1980; e.g., east of Diamond Bar, within the Puddingstone Reservoir State Recreation Area and northeast of Tonner Canyon.

The Baldwin Park Quadrangle has remained relatively stable. Wieslander mapped this area in 1930 and much of his grassland-coastal sage scrub mosaic was still evident in the 1976 aerial photo. Much of this area burned in 1976.

In La Habra Quadrangle grassland increased somewhat at the expense of coastal sage scrub or chaparral, especially in the proximity of oil fields which were not present in 1928.

Parts of the Puente and Chino Hills, included in the Yorba Linda Quadrangle, have remained quite stable over the past 50 years despite the considerable mosaic of vegetation. Aerial photos showed that from 1928 to 1975 the density of scrub oak chaparral increased between Soquoel and Telegraph Canyons. An area along Brea Canyon Road burned in 1970, and the 1975 photo showed no change in vegetation since 1928 other than more open chaparral due to incomplete recovery from the fire. Soil maps for the San Bernardino section of this quadrangle showed that both grasslands and shrublands occurred on Fontana clay loam and Gaviota rock outcrop complex soils.

The vegetation in the Prado Dam Quadrangle has remained relatively stable over the past 50 years. One obvious change is a decrease in live oak (*Quercus agrifolia*) density in this region. The soils of the San Bernardino County portion of this quadrangle have been mapped and no obvious correlation exists between soil type and vegetation; scrub, grasses, and oak trees were found on Alo clay and Fontana clay loam as well as on the Gaviota rock outcrop complex. Topography seemed to be important since coastal sage scrub was concentrated on steep slopes, grassland on valley floors, oak woodland on gentle slopes and stream floodplains.

The Corona North Quadrangle was dense coastal sage scrub in 1931; however, the 1967 USGS map indicated it was $<25\%$ shrub cover and in 1980 it was still sparse coastal sage scrub. This may derive from a fire which covered most of the area in 1959.

Three hectares on the north facing slope of Arlington Peak in Riverside West Quadrangle were dense coastal sage scrub in the 1975 photos but burned in 1978. Field observations in 1980 indicated that these areas were predominantly grass covered.

In 1931, the Pedley Hills were covered by coastal sage which was denser on north-facing than on south-facing slopes. This area burned in 1970 and in 1975 was covered by a mixture of grass and sage.

Southern Los Angeles Basin

Steele Peak Quadrangle has had several changes in the valleys. An area adjacent to the Galvian Mine was partially cultivated and entirely grassland in 1930; however, the eastern three quarters of the valley was sage in 1980. Many of the other valleys covered by grassland in 1930 are now orchards and not considered in the estimates in Table 1. Several areas of rugged terrain southwest of Steele Peak were covered with sage in 1931 but were dominated by grassland in 1980. In general this replacement of coastal sage scrub by grassland did not occur on north-facing slopes. Between 1960 and 1979 there were at least five fires in various parts of this region.

In the Lake Mathews Quadrangle large areas that were grassland in 1930 are now coastal sage scrub. This area was heavily grazed in the 1930's and before. In the 1950's, as part of the Lake Mathews Reservoir project, a chain-link fence was constructed around much of the area. This fence bounds the area which has gone from grass to shrubland, possibly due to the elimination of grazing plus the fact that there have been no recorded fires since 1910. A small area outside this fence site, which was dense coastal sage scrub in 1974, burned in 1978. In 1980 it was still dominated by grasses and a few resprouting shrubs. Another site was dense coastal sage in 1930, burned in 1957, and was still sage in 1974.

The Corona South Quadrangle showed some expansion of grassland at the expense of coastal sage scrub.

In the Black Star Canyon Quadrangle some area has gone from woodland to grass and several hectares of grassland have been invaded by coastal sage scrub. In the northern half of the quadrangle the chaparral vegetation has become noticeably sparser since 1931. This area burned in 1948 and 1967. The chaparral east of Black Star Canyon has not burned since 1914 and is considerably denser than in 1931. A grassland area north of Fresno Canyon to the Santa Ana River burned in 1928, 1958, and 1967 and was still grassland in 1975.

The Orange Quadrangle was largely grassland in 1928 and remains so today. Riparian woodland has declined in the Peralta Hills and sage scrub is less extensive along the lower hills around Chapman Ave.

The hills above Rattlesnake and Siphon Reservoirs in the El Toro Quadrangle were sage in the 1931 photo and grassland in the 1974 photo. These areas burned in 1948 and 1967. The coastal sage on the hills between Williams and Silverado Canyons was denser in 1974 than in 1931.

Within the Canada Gobernadora Quadrangle pockets of coastal sage surrounded by grassland were evident in 1929. By 1974 the coastal sage had expanded and dominated the area, particularly the region west of Trampas Canyon. The scrub cover was also denser in 1929 than in 1974. A similar pattern was evident along the eastern wall of Bell Canyon. In 1958 wildfire burned from Canada Chaquita east into the Cleveland National Forest. An area near Trampas Canyon that escaped this fire showed an increase in density of scrub.

Much of the open area within the San Juan Capistrano Quadrangle has remained grassland over the past 50 years. This area has been cultivated and grazed heavily.

A 1-ha patch on the western bank of Arroyo Trabuco was coastal sage in 1929 and grassland in 1974.

In the Laguna Beach Quadrangle many localities changed from grassland in 1931 to sparse coastal sage scrub in 1964, and to dense coastal sage scrub in 1980: e.g., Emerald, Laguna, East Moro and Los Trancos Canyons, and the southwest-facing slopes of Mustard Hill. The 1964 USGS indicated that the San Joaquin Hills had <25% coastal sage coverage, whereas the 1974 photos and 1980 field checks showed this area to be dense coastal sage scrub. Today most grasslands are on 9–50% slopes on Alo clay or Balcom clay loam. Much of the coastal sage is on 30–75% slopes on Cieneba rock outcrop complex and Callegaus clay loam. However, there were numerous exceptions. These areas have not burned since 1931. This quadrangle was heavily grazed by sheep in the late 1800's and early 1900's (Fusch 1968) but is no longer being grazed.

Localized Patterns at the Intensive Study Site

The study area was in the Calabasas Quadrangle and had not burned for 10 years as indicated by ring counts of *Salvia leucophylla* shrubs. This corresponds to the Clampitt Fire of 1970. This area has been intensively grazed in recent years.

The nine patches of coastal sage scrub were distributed on a range of slope aspects and inclinations (Table 2). Observations of these and other sage patches confirmed that they are not related to topographic position. Soils data likewise suggest that they are not distributed according to soil differences. Grassland soils tended to be more similar to those of adjacent sage stands than to those of other grassland areas (Table 2).

A reasonable hypothesis is that the mosaic of coastal sage patches in grassland is a dynamic system controlled by disturbance. If the boundaries between these communities are changing, then in what direction? Is coastal sage invading grassland or vice versa? Leak and Graber (1974) suggested a technique for determining the direction in which a shrubland-grassland boundary is moving. Their theory suggests that if sage scrub species are advancing into grassland, one should find an advancing front of young plants. On the other hand if the grasslands are gradually replacing the sage, perhaps due to disturbance such as frequent fires, the sage plants along the margins should be as old as those throughout the stand. A rough test of this prediction was made by examining the distribution of shrub heights, as height and age are related in these shrub species.

Figure 3 shows such a height profile for a belt transect 4 m wide through Site 1. In this stand *Salvia leucophylla* was the dominant shrub (Table 3). It is clear that the distribution of size classes is not greatly different in the border areas as compared to within the stand itself; mature shrubs occurred in the ecotone as well as within the stand. Seedlings (plants <25 cm high) were abundant (Table 3) within the stand but not at the advancing front. Seven of the other eight sites showed a pattern broadly similar to Site 1.

Site 2 was co-dominated by *Salvia leucophylla* and *Artemisia californica* (Table 3). One difference from the Site 1 pattern was that while seedlings were not found outside the boundary of the stand, there was an area within the stand devoid of mature shrubs (possibly from disturbance) but with abundant seedlings and "saplings." This area extended for three quadrats (out of 22) and had 1.9 seedlings/m^2 compared to $<0.1/\text{m}^2$ in all other plots.

Table 2. Slope aspect and inclination for each coastal sage patch studied and soil characteristics within each stand and in the adjacent grassland in the Calabasas Quadrangle.

					Soil characteristics				
						Texture (%)			
Site	Area	Aspect	Inclination (°)	pH	Organic matter (% dry weight)	Clay	Silt	Sand	Gravel
#1	Upper grass	N	20	6.5	6.7	15	11	74	1.1
	Shrubs			7.5	8.9	10	14	76	7.1
	Lower grass			7.8	7.9	6	17	77	6.1
#2	Upper grass	WNW	30	6.5	7.3	11	11	78	0.2
	Shrubs			6.7	6.2	9	12	79	0.5
	Lower grass			7.6	8.8	11	12	76	3.4
#3	Upper grass	NNW	35	6.8	7.5	11	13	76	2.0
	Shrubs			6.9	7.9	10	13	77	2.9
	Lower grass			6.7	7.0	10	12	78	3.7
#4	Upper grass	NW	25	6.9	8.2	9	14	77	4.2
	Salvia			6.7	11.8	12	13	75	9.0
	Haplopappus			6.8	8.0	12	12	76	5.5
	Haplopappus		15	6.5	7.5	14	10	76	2.6
	Lower grass			6.4	7.0	13	13	74	6.5
#5	Upper grass	E	25	7.7	6.0	7	16	77	0.4
	Shrubs			7.2	6.2	9	11	80	1.5
#6	Upper grass	NW	40	6.7	6.9	11	10	79	0.1
	Shrubs			6.7	6.8	9	11	80	0.9
	Lower grass			6.9	6.9	8	13	79	3.6
#7	Upper grass	W	30	7.6	8.4	9	15	76	6.2
	Shrubs			7.5	9.1	8	14	78	5.0
#8	North grass	ESE	15	7.8	5.6	8	12	80	1.7
	Shrubs			7.8	6.3	7	15	78	3.2
	South grass			7.7	6.4	7	13	80	2.6
#9	Upper grass	N	30	6.5	6.8	11	11	78	1.0
	Shrubs			6.8	6.6	10	11	79	1.1
	Lower grass			6.6	6.4	8	13	79	7.5

Salvia leucophylla and *Artemisia californica* dominated Site 3. One variation from the pattern seen for Site 1 (Fig. 3) was that half of the site lacked seedlings altogether whereas the other half had a seedling density of 0.6/m^2.

Figure 4 shows the profile observed in Site 4 which showed the greatest deviation from the pattern noted at Site 1 (cf. Fig. 3). The area was dominated by *Haplopappus venetus.* The distribution was the closest example we observed of a shrub population expanding outward into the grassland.

Salvia leucophylla dominated Site 5 and all shrub seedlings were within the boundary of the largest shrubs.

Co-dominants at Site 6 were *Salvia leucophylla* and *Artemisia californica.* This stand had an abundance of seedlings which followed a pattern comparable to Fig. 3 although the greatest concentration of seedlings was in the center of the stand.

Site 7 was essentially pure *Salvia leucophylla* and no shrub <50 cm height occurred within 12 m of the outer boundary of the stand.

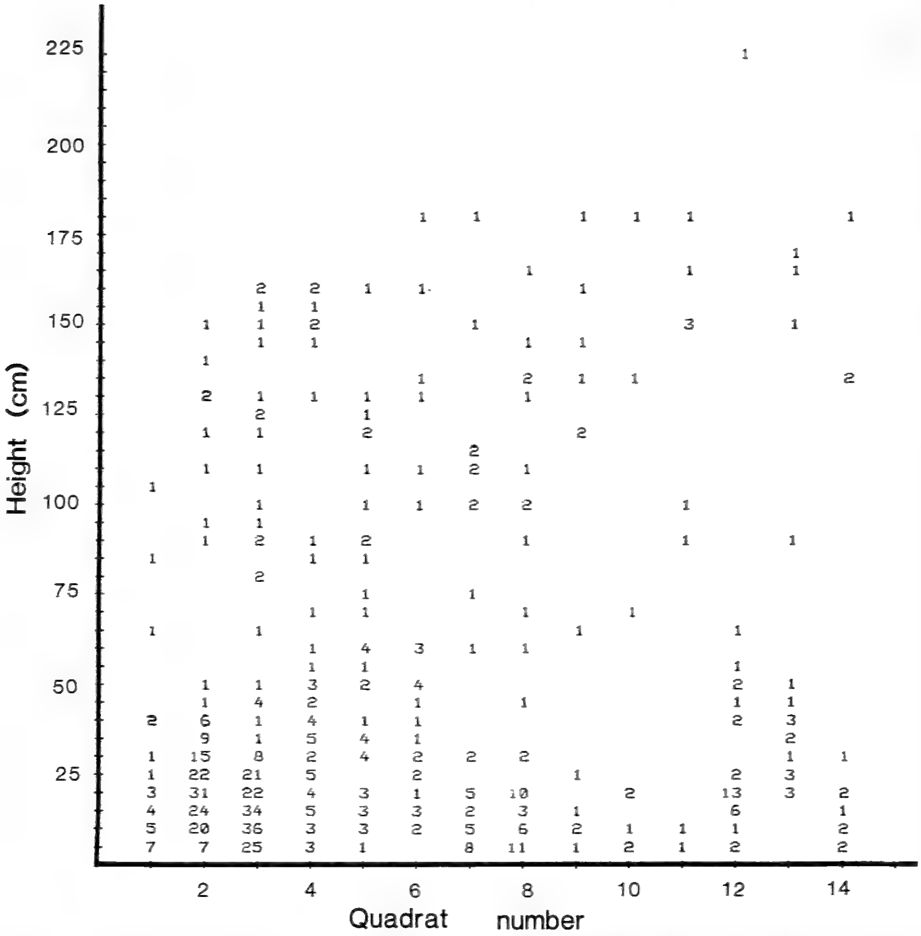

Fig. 3. Shrub height profile for 4 m wide 3.5 m deep contiguous quadrats through Site 1 in the Calabasas Quadrangle (number of individuals in 5 cm size class are plotted). Sampling began and ended in pure grassland although for presentation only the first and last quadrats with shrub species present are included.

Shrub height distribution at Sites 8 and 9 followed closely the pattern observed at Site 1 (Fig. 3).

Discussion

We believe that Well's (1962) model of grassland dynamics applies well to the Los Angeles Basin. He argued that the vegetation patterns in the coastal ranges of California are determined largely by different tolerances to disturbance and by different colonizing abilities. Grasslands represent the rapid-recovery extreme of a continuum of resilience. This community persists under intensive grazing and frequent fires. Coastal sage scrub, due to its subligneous character, falls between grassland and chaparral with respect to its resilience to disturbance. Coastal sage recovers rapidly after fire from resprouts, although seedling establishment is poor in the first post-fire season (Keeley and Keeley 1984). Fires in successive or

Table 3. Shrub density in nine coastal sage sites in the Calabasas Quadrangle.

	Relative density (%)								
Species Site:	1	2	3	4	5	6	7	8	9
Salvia leucophylla	92	60	85	26	85	82	99	79	5
Artemisia californica	1	35	14	3	2	18	1	6	67
Haplopappus venetus	5	4	1	71				15	28
Malacothamnus fasciculatum		1			13				
Eriogonum fasciculatum	2								
Shrub seedlings/m^2	2.1	0.3	0.3	13.5	<0.1	5.9	0.2	<0.1	2.9

alternate years are highly destructive to coastal sage scrub species (Zedler et al. 1983). Chaparral regenerates after fire with resprouts and seedlings but requires the longest fire-free period to maintain itself (Keeley 1981).

The Los Angeles Basin in prehistorical times was likely dominated to a great extent by ligneous formations such as chaparral and oak or walnut woodlands. Natural lightning fires were a source of wildfires although there is reason to believe the frequency of such disturbance was lower than at present (Keeley 1982). Even then, boundaries between communities were probably dynamic, due to the random nature of wildfires or disturbances from the large grazing fauna (Stock 1956). Grasslands at that time may have been dominated by *Stipa pulchra,* particularly on heavier clay soils, although annuals were undoubtedly important components (Wester 1981, Bartolome and Gemmill 1981). Early human occupation of coastal California was accompanied by an increase in fire frequency (Knowles 1953) and a concomitant shift in the dominant vegetation (Aschmann 1959, Heusser 1978).

When the first Europeans entered California, grasslands were noted and it appears from diaries such as Fray Juan Crespi's that they were commonly in close proximity to Indian Villages and maintained through frequent Indian burning (Bolton 1927; Timbrook et al. 1982).

With European occupation came most of the annual grasses and forbs which now dominate the grasslands. These species were adapted to frequent disturbances such as fires and grazing through millenia of selection under such conditions in mediterranean Europe (Naveh 1967). Not only were these species resilient to disturbances, they were aggressive colonizers of such sites (Stebbins 1965). As land use intensified (Mooney and Dunn 1972) grasslands expanded. In the Los Angeles Basin during the second half of the 19th century, demand for grazing sites increased resulting in the conversion of brush covered sites to herbaceous vegetation (Burcham 1957). Historically, type conversion of this sort has been achieved by repeatedly burning coastal sage or chaparral (Sampson 1944; Arnold et al. 1951). These sites are readily colonized by grassland species and with successive fires their dominance increases. The process begins as a gradual thinning due to the fact that a portion of the resprouting shrub population, for all resprouting species, is killed in each successive fire and obligate seedling species require a decade or more to reach reproductive age (Keeley and Zedler 1978).

In the past 50 years land use practices have changed; in some areas grazing is less extensive and fire protection more effective. These changes have resulted in shrub reestablishment. Initially, coastal sage species are favored over chaparral

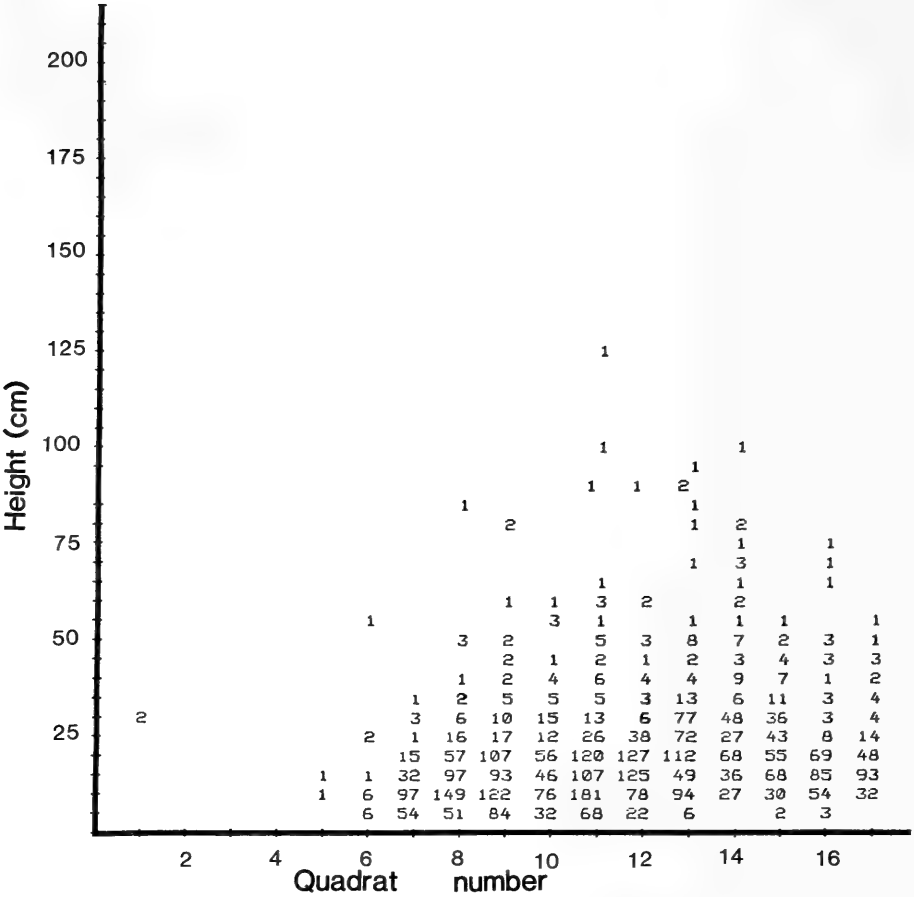

Fig. 4. Shrub height profile for Site 4 in the Calabasas Quadrangle.

species due to their higher dispersability (Wells 1962) and seeds which germinate readily without fire (Keeley and Keeley 1984). Such patterns of coastal sage invasion into grasslands following reduced disturbance were evident in several quadrangles (e.g., Thousand Oaks, Lake Mathews, and Laguna Beach) and similar patterns have been described by others (Haines 1966; McBride 1974; Westman 1976; Oberbauer 1978). The detailed studies of coastal sage demography patterns in the Calabasas Quadrangle (Fig. 3) suggest that a 10 year fire frequency, coupled with intensive grazing, are sufficient to inhibit sage invasion into grassland.

The hypothesis that disturbances such as grazing inhibit shrub invasion is at odds with the opinion of some (e.g., Dodge 1975 and others), who have suggested that grazing has enhanced coastal sage scrub invasion into grasslands in Southern California. Oberbauer (1978), however, points out that this opinion is based on extrapolation from other ecosystems such as desert grasslands where it has been demonstrated that grazing favors the spread of unpalatable spiny shrubs. Indeed, Oberbauer (1978) argues that one should not expect the same effect in coastal sage : grassland areas since the shrub species are not as noxious as thorny desert shrubs. Wells (1962) provided good evidence of the inhibitory effect of grazing on coastal sage scrub and suggested that factors other than direct predation of seedlings could be involved, e.g., soil compaction and trampling. McBride and Heady (1968) also demonstrated that grazing inhibits the invasion of scrub vegetation into annual grasslands. Cessation of grazing and fires in their Berkeley Hills sites resulted in a return of scrub vegetation and a concomitant reduction in those grasslands. Similar conclusions were reached for Point Reyes Peninsula in northern California by Elliot and Wehausen (1974), for Santa Cruz Island by Brumbaugh (1980), and for the Santa Monica Mountains in southern California by Hobbs (1983).

Certain parts of the Los Angeles Basin, possibly due to increased population density, have experienced increased fire frequency. Here, grasslands have expanded at the expense of brush (particularly evident in Oat Mtn—Fig. 2, Calabasas, and Santa Susana quadrangles).

The patterns and processes involved in the vegetation mosaic in the Los Angeles Basin today are not unlike those in primeval times. The extent of grasslands has undoubtedly increased and the species composition has changed. The concept of a climax vegetation in this instance must be tempered with a recognition of the dynamic nature of the vegetations. Even so, successional patterns will be influenced to varying extents by species tolerances to such site characteristics as elevation, topography, aspect and substrate.

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A New Species of Hippolytid Shrimp from the West Coast of Mexico

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Abstract.—*Thor algicola* n. sp. is described from the Gulf of California and southwestern Mexico. Related to *T. manningi* and *T. floridanus* of the warmer western Atlantic, *T. algicola* can be distinguished by the spines on its first pereopods and its larger size. *T. algicola* usually lives on rocky bottoms, often among algae.

Species of *Thor* are shallow-water hippolytid shrimps living in warm-temperate and tropical marine areas. During studies of the caridean fauna of the Gulf of California, a common species of *Thor* was found among algae. Chace (1972) reported *T. manningi* from the eastern Pacific, but the species from western Mexico was considerably larger than *T. manningi* and had a more robust rostrum. I originally identified the species as *T. paschalis* (Heller) (Wicksten, 1983). Further study of the eastern Pacific species, *T. manningi,* and *T. paschalis* indicated that the eastern Pacific species was in fact undescribed. The new species is described herein.

Thor algicola new species
Figs. 1–3

Thor manningi.—Chace, 1972:137 (part: the Islas Tres Marías specimens).—?Ríos and Carvacho 1982:459.
Thor paschalis (Heller): Wicksten 1983:24–25. (Not *Hippolyte paschalis* Heller 1862).

Diagnosis.—Small hippolytid shrimp lacking supraorbital spine. Anterior margin of carapace with antennal spine only, rounded elsewhere. Spine at base of stylocerite. Ischium of first pereopod bearing small spine on distal flexor margin, two small spinules on flexor margin of merus. Dactyl of third pereopod bearing two stout claws and 3–4 spinules, merus with one stout distal spine. Merus of fourth pereopod with one stout subdistal spine, merus of fifth pereopod with one or no stout subdistal spine. Free-living, not commensal with cnidarians.

Description.—Rostrum at most barely reaching anteriorly as far as distal margin of first segment of antennular peduncle, reaching pigmented area of eye, armed with one spine on dorsal midline of carapace and 3–6 spines on dorsal surface of rostrum proper, one ventral spine on rostrum in line with tip, giving rostrum bifid appearance. Rostrum of larger females slightly arched over eye, deeper than rostrum of males or immature females. Spacing of rostral teeth variable.

Eyes large, pigmented; with ocellus.

Carapace with prominent antennal spine, otherwise rounded on anterior margin.

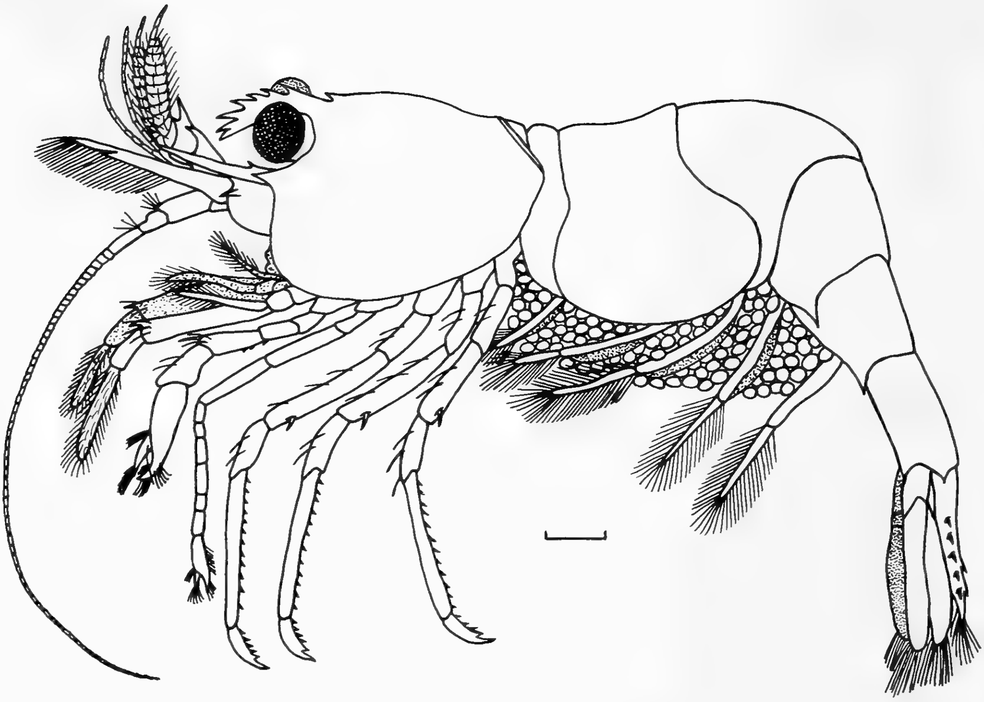

Fig. 1. *Thor algicola* n. sp. Female in lateral view. Carapace length 5.1 mm. Specimen from Bahía Bocochibampo, Mexico. Scale in all figures is 1 mm.

No supraorbital spine or prominence, but slight supraorbital ridge visible in largest individuals.

Pleura of abdominal segments 1–3 rounded, those of fourth and fifth segments with posterolateral points, sixth segment with distolateral point. Sixth segment longer than fifth. Telson with 4–5 pair prominent posterolateral spines, 3 pair terminal spines and long setae.

Stylocerite nearly as long as third segment of antennular peduncle, with curved spine at base. First segment of antennular peduncle with spine on ventromesial margin, setae at distal margin, about 0.66 × length of stylocerite. Statocyst obsolescent. Second segment of antennular peduncle with sharp distolateral spine. Third segment with subtriangular dorsal scale. Dorsolateral flagellum stout and heavily setose, ventromesial flagellum thin and whip-like.

Second antenna with sharp distolateral spine on basicerite. Carpocerite less than 0.5 × length of antennal scale. Antennal scale broad, about 3 × as long as wide, blade greatly exceeding tooth.

Mandibles asymmetrical. Molar process swollen, armed with numerous teeth; incisor process narrow, armed with 5 teeth. First maxilla with slender lower endite, broad upper endite and bilobed palp. Second maxilla with large scaphognathite, well developed palp, bilobed upper endite and small lower endite. First maxilliped with exopod, two-jointed palp, and bilobed epipod. Second maxilliped with exopod, podobranch, and epipod. Third maxilliped with setose terminal segment, ending in sharp dark spines. Penultimate segment about 0.4 × length of ultimate,

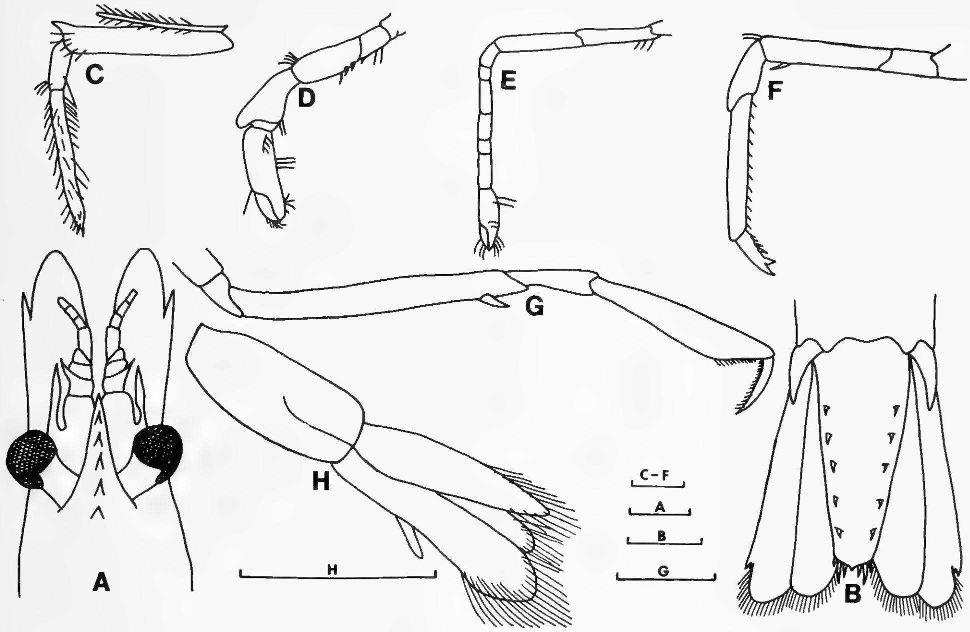

Fig. 2. *Thor algicola* n. sp. A, frontal region of female in dorsal view; B, telson and uropods; C, third maxilliped; D, first pereopod; E, second pereopod; F, third pereopod of female; G, third pereopod of functional male; H, second pleopod of male.

with tuft of setae on mesial distal margin. Antepenultimate segment with tooth and stiff setae on distal margin, about equal to ultimate segment. Exopod and small epipod present.

First pereopod stout, chelate. Dactyl about 0.4× length of propodus, with tuft of setae at end. Fixed finger with tufts of setae, row of setae on outer proximal margin of propodus. Carpus about 0.5× length of propodus. Merus shorter than propodus, with 2 small spines on proximal flexor margin. Ischium about 0.5× merus, with small distal spine on flexor margin. No epipod or exopod.

Second pereopod slender, chelate. Fingers of chelae with tufts of setae. Dactyl about 0.3× length of propodus. Carpus of 6 divisions, the sixth the longest. Merus shorter than carpus, ischium shorter than merus. No epipod.

Third pereopod of female with slender dactyl, 3× as long as wide; tip with two stout darkly pigmented claws, that on flexor margin the broader, and 3–4 spines on flexor margin. Propodus 4× length of dactyl, with 10–14 spinules occurring singly or in pairs on flexor margin, tufts of setae on extensor margin. Carpus about 0.3× length of propodus. Merus about equal to propodus, with prominent distolateral spine. Ischium about 0.4× length of merus. Third pereopod of male prehensile, subchelate, barely overreaching scaphocerite. Dactyl with bifid tip and 9 closely appressed spines on flexor margin. Propodus 3× length of dactyl, distal third of flexor margin converging toward extensor margin, armed with spinules; carpus about 0.5× propodus, merus 1.5× propodus, with distolateral spine, ischium without spine. No epipod in either sex.

Fourth and fifth pereopods similar to third of female in both sexes. Fourth pereopod with one meral spine, fifth pereopod with one or no meral spine.

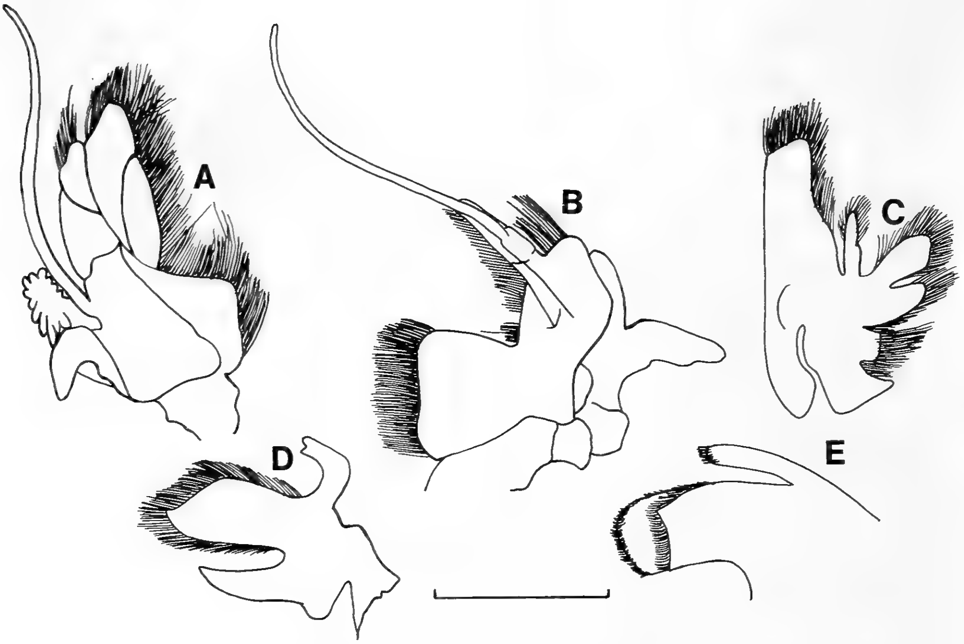

Fig. 3. *Thor algicola* n. sp. A, second maxilliped; B, first maxilliped; C, second maxilla; D, first maxilla; E, mandible.

Female with appendix interna on second pleopod. Male with first pleopod smaller than other pleopods. Male second pleopod with setose appendix masculina.

Uropods longer than telson, fringed with setae. Outer branch of uropod with small distolateral tooth and movable spine.

Holotype.—Female, ovigerous, total length in millimeters 18.4, carapace length 5.1. Bahía Bocochibampo, Guaymas, Sonora (27°57′N, 111°02′W), 5 m, among *Sargassum* sp., 19 June 1978, Alex Kerstitch, Allan Hancock Foundation (University of Southern California) type number 786.

Paratypes.—Cholla Bay, Sonora, on sand, 16 Aug. 1966, Tom and Beatrice Burch, 2 specimens.—S. shore, Isla Tiburon, Gulf of California, shore, among shingle, 25 Jan. 1940, *Velero III* sta. 1045-40, 2 specimens.—Isla San Nicolas, Sonora, 20 m, rubble, 2 July 1978, Alex Kerstitch, 1 specimen.—Isla San Pedro Nolasco, Sonora, 10 m, rocks, 23 Dec. 1978, A. Kerstitch, 1 male.—Punta Doble, Sonora, 25 m, under rock, 25 June 1983, Alex Kerstitch, 1 specimen (dissected).—Isla Candelero, Sonora, 20 m, among rocks, 2 Jan. 1984, Alex Kerstitch, 1 specimen, California Academy of Sciences.—Bahía San Carlos, Sonora, 20 m, rocks and sand, 28 Dec. 1982, A. Kerstitch, 1 specimen.—Bahía Bocochibampo, Guaymas, 5 m, 19 June 1978, A. Kerstitch, 4 ovigerous females in addition to holotype.—Bahía San Gabriel, Isla Espíritu Santo, Gulf of California, shoal, among coral, 14 Feb. 1940, *Velero III* sta. 1110-40, 2 females.—Bahía San Gabriel, Isla Espíritu Santo, 2 m, coral, 15 March 1949, *Velero IV* sta. 1737-49, 36 specimens, 1 of them male.—Zihuatanejo, Guerrero, shore, among rocks, 11 June 1979, R. C. Brusca, 4 specimens.—Bahía Santa Lucia, Acapulco, Guerrero, 2–8 m, mud and sand, 1–2 Feb. 1954, *Velero IV* sta. 2596-54, 15 specimens, 2 of them males.—San Lorenzo Rocks, Acapulco, 0–4 m, rocks, 30 Jan. 1954, *Velero IV* sta. 2591-54, 15 specimens.—Islas Tres Marías, Mexico, 1927, 4 specimens, United States National Museum (USNM).—Bahía Piñas, Panamá, 4–7 m, coral, 29 Jan. 1935, *Velero III* sta. 444-35, 1 ovigerous female (USNM).—Bella Vista, Panamá, shore, rock, 2 Feb. 1935, *Velero III* sta. 445-35, many specimens (USNM). Except as noted, all specimens are in the collection of the Allan Hancock Foundation, University of Southern California.

Size range.—Total lengths 8–18.4 mm, carapace lengths 1–5.9 mm. Males with prehensile third pereopods: carapace lengths 1–2.4 mm. Ovigerous females: carapace lengths 1.6–5.9 mm.

Color in life.—Mottled with brown and white, closely resembling algae in the habitat. Lines of chromatophores on carapace. Tail fan with white stripe across proximal dorsal surface. Legs banded with brown and white. Very small individuals translucent.

Etymology.—The specific epithet means "dwelling in algae," referring to the common habitat of the shrimp.

Remarks.—*Thor algicola* resembles seven other species of *Thor* in lacking supraorbital spines. Unlike *T. paschalis,* it has a proximal tooth on the stylocerite. In *T. intermedius* Holthuis, there is only one pair of minute dorsal spines on the telson; *T. algicola* usually has five pair. *Thor marguitae* Bruce has three–four meral spines on the third pereopod; *T. algicola* has only one spine. *Thor dobkini* Chace has one or two spines on the distal half of the flexor margin of the merus of the first pereopod, *T. algicola* has at most two spinules on the proximal margin of the merus of the first pereopod. *Thor amboinensis* (De Man), a commensal of cnidarians, can be distinguished easily from *T. algicola* in life by its distinctive pattern of large spots, as well as by the angular anterolateral margin of its carapace and the relatively shorter dactyls of its third-fifth pereopods. Of these related species, only *T. amboinensis* has been reported from the eastern Pacific (Abele and Patton 1976).

Thor algicola is most closely related to *T. floridanus* Kingsley and *T. manningi* Chace. Neither of these species has two spinules on the merus of the first pereopod. In *T. algicola,* the distal claws of the dactyl of the third pereopod of the female are stronger and the claw on the flexor margin tends to be broader than in the other two species, the merus of the third pereopod does not bear more than one spine, the distal margin of the antepenultimate segment of the third maxilliped often bears a stout tooth, the telson often bears five, not three or four, pair of dorsolateral spines, and the cornea and eyestalk are relatively smaller, not equal in length to more than half the length of the entire carapace. However, both the spinules of the merus of the first pereopod and other distinguishing features tend to be missing or difficult to see in smaller animals.

The major difference between *Thor algicola* and the two most nearly related species is size. Chace (1972) gave a carapace length for females of *T. floridanus* of up to 2.3 mm and *T. manningi* of at most 2.5 mm. The majority of ovigerous females of *T. algicola* are over 3.0 mm long, with 16 of those examined over 4.0 in carapace length. Males also are larger: Chace (1972) reported the males of *T. floridanus* as measuring 1.3–1.6 mm and the majority of functional males of *T. manningi* in the carapace length range of 0.9–1.4 mm, while in *T. algicola,* func-

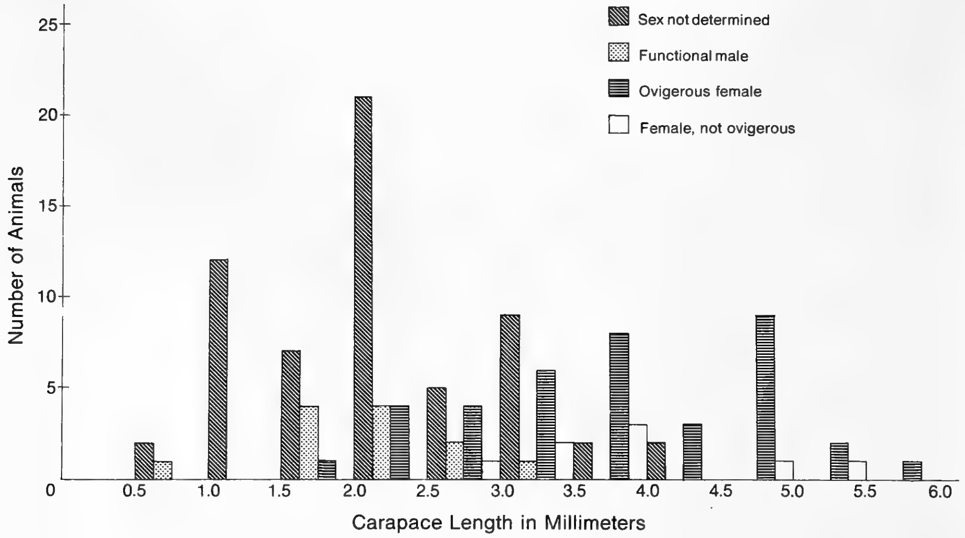

Fig. 4. Size distribution of specimens of *Thor algicola,* by carapace lengths.

tional males range from 1.0–2.6 mm in carapace length, with only one animal with a length less than 2.5 mm. The distribution of all of the specimens of *T. algicola* is given in Fig. 4.

Like *T. manningi, T. algicola* may be an imperfect protandric hermaphrodite, with males occurring only in the smallest size ranges. Sexing of the majority of small specimens was not attempted in this study, so males without prehensile third pereopods were not distinguished from females at smaller sizes.

Chace (1972) and Ríos and Carvacho (1982) reported *T. manningi* from the eastern Pacific. I examined the specimens from Mexico which Chace (1972) assigned to *T. manningi.* I consider these specimens to fall within the variation for *T. algicola.* I suspect that the specimens taken by Rios and Carvacho also belong to *T. algicola,* although I have not had the opportunity to examine material from their area of study.

It is difficult to distinguish specimens of *T. manningi,* known from the Caribbean and western Atlantic, from smaller individuals of *T. algicola,* the eastern Pacific species. The two populations of shrimp, however, have been isolated from each other since the closing of the Panamic seaway, about 3.1–3.5 million years ago (Glynn and Wellington 1983). The differences in the sizes of the animals and slight differences in morphology suggest genetic change on either side of the Panamic land mass. Further studies of the genetics, behavior and color patterns of these shrimp would be useful in determining how closely related these seeming "sibling species" are to one another.

Acknowledgments

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Population Genetics of an Introduced Species: *Bairdiella icistius* in the Salton Sea

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Abstract.—The bairdiella, *Bairdiella icistius* (Jordan and Gilbert), in the Salton Sea are the progeny of a successful introduction made in the 1950's. They form a central link in a productive and heavily utilized sportfishery. Genetic variability at 56 enzyme and protein loci was studied by means of starch and polyacrylamide gel electrophoresis. Eight loci were polymorphic, and all polymorphic loci were close to Hardy-Weinberg equilibrium. Average heterozygosity per locus was 0.043, which is within the typical range for marine fish species. There appeared to be fewer rare alleles than expected in a population at equilibrium. The Salton Sea habitat is harsh and changing. The amount of genetic variability present in the bairdiella is an indication of the ability of this population to adapt to environmental change.

Any introduction of a species into a new habitat constitutes an experiment on the significance of the founder effect. The introduction of the bairdiella, *Bairdiella icistius* (Jordan and Gilbert), into the Salton Sea is an example of a successful founder event. From an initial population of 67 individuals, the population rapidly increased into the millions. The case of the bairdiella is particularly amenable to study because the population has been well documented since its inception. The date, number, and point of origin of the founders is well known, and the course of development of the population has been followed regularly up to the present.

The bairdiella is a small fish of the family Sciaenidae. The fish is abundant in the Gulf of California, where it is fished commercially (Berdegue 1956). Two introductions of bairdiella were made into the Salton Sea. In 1950, 57 fish were transplanted from San Felipe, Baja California, Mexico, and in 1951, an additional 10 fish were taken from the same location (Whitney 1961). These 67 fish represent the total known introduction. Whitney estimated that juvenile fish that were spawned from the first planting reached reproductive maturity within two years, and that the population of bairdiella was several million by 1954.

The bairdiella is currently one of the most abundant species in the Salton Sea. It not only supports a major sportfishery itself, but is the main forage fish for the larger introduced game fishes (e.g., orangemouth corvina, *Cynoscion xanthulus,* Walker et al. 1961). The Salton Sea contains a simplified and truncated food web, with a few species dominating. The total biomass in the lake is large, and supports an active sportfishery. The number of angler hours and the catch per unit effort are among the highest of any inland body of water in California (Black 1983).

Since the Salton Sea was formed in 1904–1907, the level of the lake has fluctuated considerably. The salinity has increased to a present level of 38 parts per

Table 1. Enzymes, electrophoretic buffers, tissue source, and number of loci scored for *Bairdiella icistius*. Buffer systems: POUL = discontinuous Borate-Tris-citrate, "Poulik" (Selander et al. 1971); TC 7 = Tris-citrate-EDTA, pH 7.0 (Ayala et al. 1973); TC 8 = Tris-citrate, pH 8.0 (Selander et al. 1971, electrode buffer diluted 1/5); TBE 9.2 = Tris-borate-EDTA, pH 9.2 (Ayala et al. 1973); EBT = Tris-borate-EDTA, pH 8.6 (Whitt et al. 1976); Acryl = acrylamide gel (see Methods). Tissue sources: B = brain, E = eye, H = heart, L = liver, M = muscle.

Enzyme	Locus abbreviation	E.C. number	Buffer	Tissue source
Adenylate kinase	*Ak-A*	2.7.4.3	TC 7	M
Alcohol dehydrogenase	*Adh-A*	1.1.1.1	EBT	L
Aldolase	*Ald-A*	4.1.2.13	TC 7	M
Aspartate aminotransferase	*S-Aat-A*	2.6.1.1	TC 7	L
	M-Aat-A			L
Creatine kinase	*Ck-A*	2.7.3.2	TC 7	M
	Ck-B			B
Esterase	*Est-1*	—	Acryl	L
	Est-2			L
	Est-3			L
	Est-4			L
	Est-5			L
	Est-6			H
	Est-7			H
	Est-8			H
Fumarase	*Fum-A*	4.2.1.2	TBE 9.2	L
General proteins	*Gp-1*	—	Acryl	M
	Gp-2			M
	Gp-3			M
	Gp-4			M
	Gp-5			M
	Gp-6			H
	Gp-7			H
	Gp-8			H
	Gp-9			H
	Gp-10			H
	Gp-11			H
	Gp-12			H
	Gp-13			H
	Gp-14			H
Glucosephosphate isomerase	*Gpi-A*	5.3.1.9	POUL	L
	Gpi-B			M
Glucose-6-phosphate dehydrogenase	*G6pdh-A*	1.1.1.49	TC 8	L
	G6pdh-B			L
Glyceraldehyde-3-phosphate dehydrogenase	*Gapdh-A*	1.2.1.12	EBT	M
	Gapdh-B			H
Glycerol-3-phosphate dehydrogenase	*G3pdh-A*	1.1.1.8	TC 8	M
	G3pdh-B			L
Hexokinase	*Hk-A*	2.7.1.1	TC 8	L
L-Iditol dehydrogenase	*Iddh-A*	1.1.1.14	TC 8	L
Isocitrate dehydrogenase	*S-Icdh-A*	1.1.1.42	TC 7	L
	M-Icdh-A			M
Lactate dehydrogenase	*Ldh-A*	1.1.1.27	POUL	M
	Ldh-B			H
	Ldh-C			E
Malate dehydrogenase	*S-Mdh-A*	1.1.1.37	TC 7	L
	S-Mdh-B			M

Table 1. Continued.

Enzyme	Locus abbreviation	E.C. number	Buffer	Tissue source
Malic enzyme	*S-Me-A*	1.1.1.40	TC 8	M
Mannosephosphate isomerase	*Mpi-A*	5.3.1.8	TC 8	H
Peptidase	*Pep-A*	—	EBT	B
	Pep-B			L
	Pep-C			L
	Pep-D			L
Phosphoglucomutase	*Pgm-A*	2.7.5.1	POUL	M
	Pgm-B			L
Phosphogluconate dehydrogenase	*Pgdh-A*	1.1.1.43	TC 7	L
Superoxide dismutase	*Sod-A*	1.15.1.1	TBE 9.2	L
Xanthine dehydrogenase	*Xdh-A*	1.2.1.37	TC 7	L

thousand (ppt) total dissolved solids, and there are continuing inputs of pesticides and fertilizers from the surrounding agricultural land. The latter inputs, coupled with high temperatures in summer, result in periods of anoxia and fish kills. Several fishes are still reproducing in the Salton Sea at this time, but it is not clear what the time course or significance of continued environmental change will be. There are presently several plans under consideration for the management of the Salton Sea, as a result of which salinity could remain constant or rise as high as 88 ppt (Black 1983). Salinities in excess of 50 ppt are considered to be harmful to the continued reproduction of fishes in the Salton Sea.

The Salton Sea is a harsh and changing environment. Knowledge of the genetic structure of the bairdiella can help predict the likely consequences of continued environmental degradation on a major resource. One possible consequence of a founder event or any population bottleneck is the loss of genetic variation from the population. It is this reservoir of genetic variability that provides the material upon which selection operates, as the population adapts to environmental change. Allozyme electrophoresis can be used to examine genotypes and allele frequencies for a large number of loci that encode for enzymatic or structural proteins. Even if these loci are not themselves significant for adaptation to environmental changes, they are the best estimate of variation in the whole genome, including those loci that can respond to selection.

Methods

Both starch and polyacrylamide gel electrophoresis were used to examine enzyme or protein variation. A total of 24 enzyme or protein stains were used, which resolved the products of 56 loci. The enzymes examined, the electrophoretic conditions, the number of loci resolved and their abbreviations are given in Table 1. Starch gel enzyme electrophoresis followed Selander et al. (1971) with the following exceptions: The stains for ADH, AK, CK, FUM, GAPDH, LDH, and MPI were from Allendorf et al. (1977). Peptidase staining and nomenclature followed Frick (1983). The ALD stain was from Shaw and Prasad (1970), the AAT stain from from May et al. (1979), and the ME stain was from Ayala et al. (1973). All stains that used G6PDH as an intermediate were modified after Buth

Table 2. Allele frequencies, sample sizes and mean heterozygosities per locus (H) for eight polymorphic loci of *Bairdiella icistius* from the Salton Sea. Alleles are named in terms of increasing anodal mobility.

	Locus and sample size							
	Est-3	*Est-6*	*Gp-12*	*S-Icdh-A*	*Ldh-C*	*S-Mdh-B*	*Pep-D*	*Pgm-B*
Allele	100	102	102	102	101	100	101	99
1	0.140	0.039	0.069	0.020	0.149	0.385	0.574	0.338
2	0.860	0.794	0.931	0.980	0.851	0.615	0.426	0.662
3		0.167						
H	0.242	0.342	0.128	0.039	0.254	0.476	0.491	0.450

and Murphy (1980). The agar overlay method of Brewer (1970) was used for all stains that included an enzyme intermediate. Starch gels were 10% (w/v) Sigma starch.

Polyacrylamide gel electrophoresis was used to resolve esterases and general proteins. Esterases were run on 6% (w/v) acrylamide in the TBE buffer of Maniatis et al. (1982) and stained after Selander et al. (1971) using beta-napthyl acetate as the substrate. General proteins were run on split gels (4–8% w/v) using the discontinuous buffer system of Laemmli (1970) without SDS, and stained with Coomassie Blue.

Data analysis was done with the aid of the BIOSYS-1 package of computer programs (Swofford and Selander 1981).

Fish were collected by gill-net from two locations on the north side of the Salton Sea (North Shore Marina and Bombay Beach), with the cooperation of the California Department of Fish and Game. Fish were packed on dry ice and transported to the laboratory, where they were stored whole at −20°C until used for electrophoresis.

Results

There is substantial genetic variability in the Salton Sea population of bairdiella. Eight loci are polymorphic: *Est-3, Est-6, Gp-12, S-Icdh-A, Ldh-C, S-Mdh-B, Pep-D,* and *Pgm-B.* Allele frequencies for these loci are given in Table 2. The average heterozygosity per locus is H = 0.043 ± 0.016 (S.E.). To put this in perspective, Winans (1980) reviewed the literature on natural populations of 82 species of fishes, for which the mean H was 0.048. Data from two other sciaenids, *Genyonemus lineatus* and *Seriphus politus,* can also be compared at 33 loci studied in common (Beckwitt 1983). The H estimates are 0.030, 0.043 and 0.046 for *Genyonemus, Seriphus,* and *Bairdiella* respectively. All polymorphic loci are close to Hardy-Weinberg equilibrium (Table 3), implying that inbreeding or differential survival of genotypes is not now a significant factor.

Although the average heterozygosity per locus is typical for a fish, the pattern of allele frequencies is not. There are only two loci at which there are rare alleles (frequency less than 0.05). Typically this class is more numerous (Nei 1975). In a sample of 100 diploid individuals, the probability of finding an allele is 0.99 if its true frequency is 0.05; if the true frequency is 0.01, the probability is 0.87. Thus, all but the rarest alleles have been well sampled.

The average number of all alleles per locus is 1.16. Using an analysis similar

Table 3. Exact test of goodness of fit to Hardy-Weinberg equilibrium.

Locus	Common homozygotes	Common/rare heterozygotes	Other genotypes	Probability
Est-3	75	22	3	0.339
Est-6	64	34	4	1.000
Gp-12	89	12	1	0.380
S-Icdh-A	98	4	0	1.000
Ldh-C	73	26	2	1.000
S-Mdh-B	39	45	16	0.673
Pep-D	31	54	16	0.419
Pgm-B	42	47	10	0.656

to Bryant et al. (1981), one can estimate the expected number of alleles per locus in a population at equilibrium. This estimate is highly dependent on the value used for N_ev (N_e = effective population size, v = mutation rate per gene per generation). This value can not be directly estimated from the data, but is likely to be about 0.1 (Nei 1975). Under those conditions, the expected number of alleles in a sample of 100 fish is 1.57. Although this estimate is not likely to be very accurate, it does suggest that alleles could have been lost during the founder event.

One can also compare the pattern of heterozygosity per locus with the expected pattern for a large population at equilibrium. When the data for the bairdiella are compared to the theoretical distribution obtained by Fuerst et al. (1977), there is no significant difference (Kolomogorov-Smirnov test, $P > 0.2$). One cannot exclude the null hypothesis that the Salton Sea population is at equilibrium.

The data are consistent with the known facts of the introduction of the bairdiella into the Salton Sea. The founding population was relatively large (67 individuals) and the bottleneck was of short duration—there were at least 1,000,000 fish in reproductive condition within 3 years. Under these conditions, one would expect the new population to retain nearly all of the heterozygosity of the parent population, but to lose a large number of rare alleles.

Discussion

The founder effect has been discussed at some length in the literature of theoretical population genetics. It is often cited as an important mechanism for speciation (see Carson and Templeton 1984 for review). When a founder population is subject to a severe bottleneck in numbers, there is a chance for the loss or alteration of genetic variability. Nei et al. (1975) discussed the genetic consequences of a population bottleneck. They showed that there will be a decrease in heterozygosity that is dependent not only on the size of the bottleneck, but also on the rate of population growth after the bottleneck. They also showed that the loss of neutral alleles from the population is more dependent on the size of the bottleneck and less so on its duration. These results have since been extended and generalized by Chakraborty and Nei (1977), Sirkomma (1983), and Maruyama and Fuerst (1984).

There have been few explicit tests of the genetic consequences of a population bottleneck. Several studies have observed decreased genetic variability in peripheral or relict populations, and inferred a bottleneck or founder event as the cause

(Avise and Selander 1972; Kat 1982; Larruga et al. 1983). One striking example is the elephant seal, hunted to near extinction and now without any genetic variation demonstrable by enzyme electrophoresis (Bonnell and Selander 1974).

Introduced species have been studied as examples of founder events. Bryant et al. (1981) studied the face fly, an introduced pest. They found a non-significant decrease in heterozygosity at 14 electrophoretic loci between North American and European populations, but a loss of up to 50% of the alleles in the introduced populations. Turner (1984) examined artificial refugium populations of the desert pupfish, and showed little difference from the parent populations, in terms of heterozygosity or number of alleles.

The bairdiella of the Salton Sea harbor considerable genetic variability, equal to most natural populations of marine fishes. Thus, there is considerable potential for adaption to environmental change. However, the possibility that rare alleles are lacking from the Salton Sea population may be important. If the bairdiella are called upon to adapt to radically changing physical factors, some rare allele could be vital. Such speculation can only be verified with data from the parent population.

Acknowledgments

I would like to thank personnel of the VANTUNA Research Group, particularly M. Matsui and S. Smith, as well as G. Black of the California Department of Fish and Game for help in collecting fishes. M. Matsui also contributed her considerable knowledge of the natural history of the Salton Sea. I would also like to thank D. Buth for advice on enzyme nomenclature. This study was performed under contract from Southern California Edison Company, and is a contribution of the VANTUNA Research Group, Occidental College, Los Angeles, California.

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The Chiton Fauna of Cocos Island, Costa Rica (Mollusca: Polyplacophora) with the Description of Two New Species

Antonio J. Ferreira

We regret to announce the death of Antonio J. Ferreira on 19 May 1986. Inquiries and requests for his scientific work may be sent to the Department of Invertebrate Zoology and Geology, California Academy of Sciences, San Francisco, California 94118.

Abstract.—Six species of chitons are here recognized at Cocos Island, Costa Rica, including two new species, an *Ischnochiton* and an *Acanthochitona.* The reported presence on the island of *Chiton goodallii* and *Acanthochitona hirudiniformis* has not been corroborated.

Cocos Island lies at 5°32′N, 87°04′W, some 500 kms (300 miles) southwest of Punta Arenas, Costa Rica, 600 kms (350 miles) northeast of the Galápagos Islands. At the eastern edge of the Indo-Pacific, in the path of the North Equatorial Countercurrent, and within the reach of currents from western American shores, the fauna of Cocos Island is of particular interest. Although Cocos is considered to be part of the Panamanian Province (Briggs 1974), its marine fauna has a considerable admixture of Indo-West Pacific species. With respect to mollusks, Hertlein (1963) found that among 88 species recorded at the island, 88% are Panamic, 6% Indo-Pacific, and 6% endemic; Emerson and Old (1964), Montoya (1983), and Shasky (1983, 1985), reported comparable observations.

This report on the chiton fauna of Cocos Island is based mostly upon material obtained by Donald R. Shasky (DRS) (Apr. 1983; Mar. 1984; May, 1985) and myself (AJF) (Nov. 1984), from aboard the schooner VICTORIA; additional material was found in the collections of the California Academy of Sciences, San Francisco, California (CAS), U.S. National Museum of Natural History, Washington, D.C. (USNM), and the Los Angeles County Museum of Natural History (LACM).

Six species of chitons are here recognized at Cocos Island, Costa Rica, two new to science:

Chiton stokesii Broderip, 1832
Placiphorella blainvillii (Broderip, 1832)
Stenoplax boogii (Haddon, 1886)
Lepidozona rothi Ferreira, 1983
Ischnochiton victoria Ferreira, spec. nov.
Acanthochitona shaskyi Ferreira, spec. nov.

The reported presence of two other species at Cocos Island—*Chiton goodallii* Broderip, 1832, and *Acanthochitona hirudiniformis* (Sowerby, 1832)—are considered to be either misidentifications, or represent such rare and unlikely occurrences that they cannot be accorded permanent status in the chiton fauna of the island.

Systematic Treatment

Polyplacophora Gray, 1821
Order Neoloricata Bergenhayn, 1955
Suborder Ischnochitonina Bergenhayn, 1930
Family Ischnochitonidae Dall, 1889
Ischnochiton Gray, 1847a

Type species: *Chiton textilis* Gray, 1828, by subsequent designation (Gray 1847b).

Ischnochiton victoria Ferreira, spec. nov.

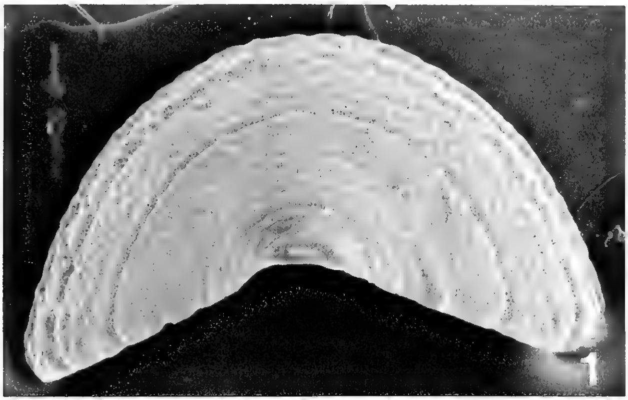
Figs. 1–7

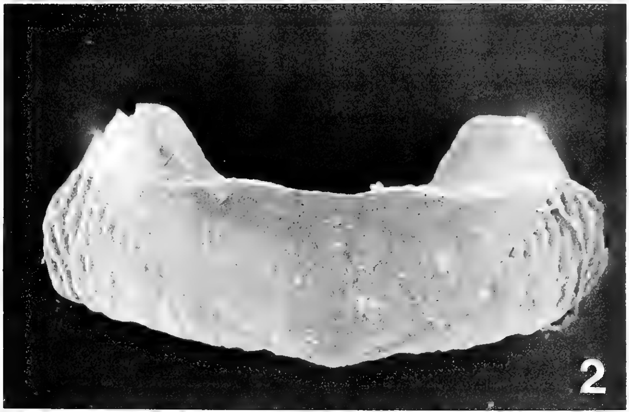
Diagnosis: Very small chitons, up to 3.5 mm long. Valves brightly colored in reddish tones, often with touches of brown or blue; round-backed, not carinate, not beaked; posterior valve remarkably inflated, mucro central, inconspicuous, postmucro convex, at sharp slope. Articulamentum white; sutural laminae sharp, small, separated by wide sinus; teeth small, sharp; slits 9/10-1-9/10. Girdle scales small (up to 100 μm) with 12–14 striations. Radula major lateral teeth tricuspid.

Type material and locality: Holotype (CAS 061096), entire specimen, off Roca Sucia, near Wafer Bay, Cocos Island, Costa Rica (5°33′N, 87°02′W) at 24 m; 17 loose valves (CAS 061097; LACM 2124; D. R. Shasky Colln.) designated as paratypes, 16 found at same locality as holotype, in sand, at 18–34 m, 1 also found in sand, 1.5 km NE of Manuelita Id., off Cocos Island, at 91–95 m.

Description: Holotype about 3.5 mm long, elongate, round backed; valves very thin, not carinate, not beaked, posterior edges straight. Tegmentum in reddish tones mottled with white, particularly on valve v, with dark brown and blue markings on pleural areas. Anterior valve broken, 1/3 missing. Sculpture of anterior valve and lateral areas of intermediate valves limited to 6–8 coarse concentric rugosities (Figs. 1 and 2); lateral areas hardly elevated; central areas uniformly sculptured with minute, roundish pits, 7–8 μm in diameter, close together (Fig. 3). Posterior valve very elevated, inflated (Fig. 4 and 5); mucro inconspicuous, about central; postmucro sloping sharply, convex, with vague concentric rugosities. Articulamentum translucent, colors of tegmentum showing through; sutural laminae short, very thin, sharp; sinus very wide; relative width of sinus on valve viii (width of sinus / width of sutural laminae), 1.2; insertion teeth short, sharp; slits 8-1-10. Girdle dorsal surface covered with imbricate, flat scales, up to 110 μm long, with 12–14 striations (Fig. 6A); girdle ventral surface with transparent, rectangular scales, 30 × 15 μm (Fig. 6B), arranged in columns. Radula (Fig. 7) 1.3 mm long comprising some 35 rows of mature teeth; median tooth 11 μm wide at anterior blade, narrowing posteriorly; first lateral teeth about 38 μm long, widely concave at outer border, with prominent knob at antero-lateral corner; spatulate teeth, simple, 55 μm long; major lateral teeth with tricuspid head, 25 μm wide; outer marginal teeth 30 × 30 μm.

Paratypic material consists of 17 loose valves found in sand ("grunge") mostly from 18–34 m at Roca Sucia (DRS): 4 anterior, 2 intermediate, and 11 posterior valves. Tegmental color variegated from cream to red. Largest posterior valve 1.1 mm long, 1.6 mm wide. Slit formula 9/10-1-10/12.





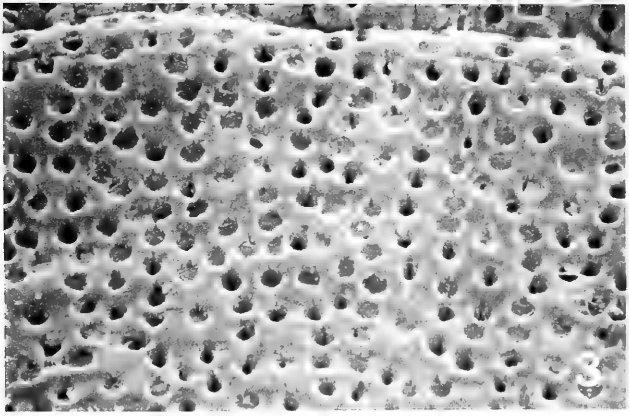
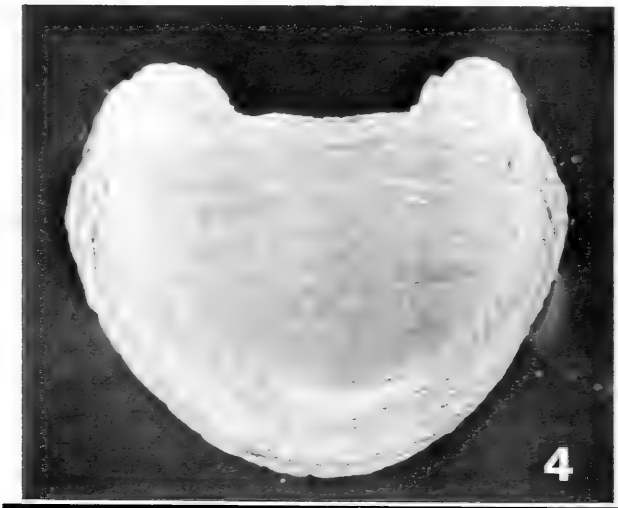


Fig. 1. *Ischnochiton victoria* Ferreira, spec. nov. Paratype (CAS 0610979): Anterior valve, dorsal surface. SEM micrograph, courtesy of Terrence Gosliner.

Fig. 2. *Ischnochiton victoria* Ferreira, spec. nov. Holotype (CAS 061096): Intermediate valve, dorsal surface. SEM micrograph, courtesy of Terrence Gosliner.

Fig. 3. *Ischnochiton victoria* Ferreira, spec. nov. Holotype (CAS 061096): Intermediate valve, close-up of central area (×400). SEM micrograph, courtesy of Terrence Gosliner.



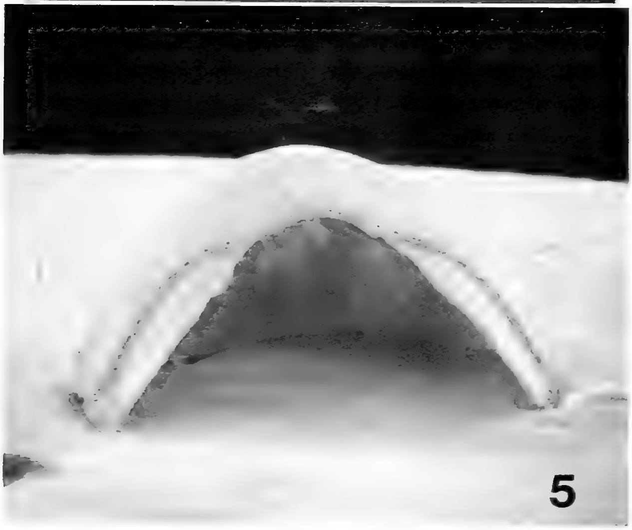


Fig. 4. *Ischnochiton victoria* Ferreira, spec. nov. Paratype (CAS 061097): Posterior valve, dorsal surface. SEM micrograph, courtesy of Terrence Gosliner.

Fig. 5. Same specimen as in Fig. 4: Frontal view of posterior valve. SEM micrograph, courtesy of Terrence Gosliner.

Distribution: *Ischnochiton victoria* is known only from Cocos Island, Costa Rica.

Remarks: The single entire specimen of *Ischnochiton victoria* was obtained through a unique method in chiton collecting: ". . . I was determined to spend most of the dive [at Roca Sucia, Cocos Island] just shaking coral slabs [into the collecting bag] . . . After returning to the boat I [poured] the contents of the bag into a basin of water and washed out the interior of the bag in the basin. I then put the material through screens and saved everything except the silt. What I saved was then dried and bagged for examination under the microscope . . . and

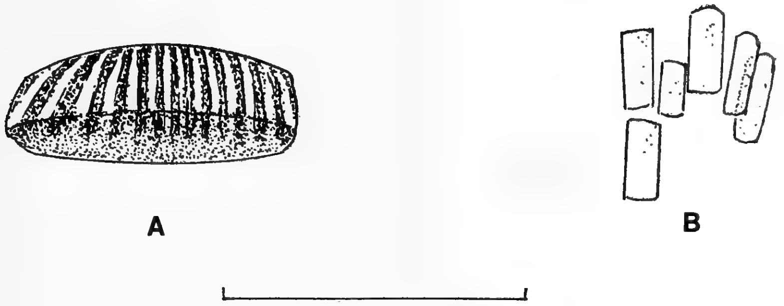


Fig. 6. *Ischnochiton victoria* Ferreira, spec. nov. Holotype (CAS 061096): Girdle elements: A—Scale of upper surface; B—Scales of undersurface. Camera lucida drawing. Bar = 100 μm.

it was from this grunge that the live specimen of the *Ischnochiton* [*victoria*] was found." (Donald R. Shasky, in litt., 3 Sept. 1985).

For its color (? with bright blue spots), elongate body, minute, striate girdle scales, and radula with tricuspid major lateral teeth, *I. victoria* may be confused with *I. rugulatus* (Sowerby 1832). The differential diagnosis between the two species is important since *I. rugulatus,* although not found at Cocos, has a range—along the western American coast from Malarrimo Point, Baja California, Mexico (27°04′N) to Isla Lobos de Afuera, Peru (6°57′S), as well as Galápagos Islands, Revillagigedo Islands, and Hawaii (Ferreira 1983)—which could well include Cocos Island. *Ischnochiton victoria* differs from *I. rugulatus* not only in the smaller size of its specimens and subtle distinctions in the tegmental sculpture, but clearly in 1) peculiarly "inflated" posterior valve, almost defining a perfect fourth of a hollow sphere, 2) convex postmucro, and 3) very wide sinus.

Noteworthy is the fact that *I. victoria* is quite similar to *I. pseudovirgatus* Kaas,

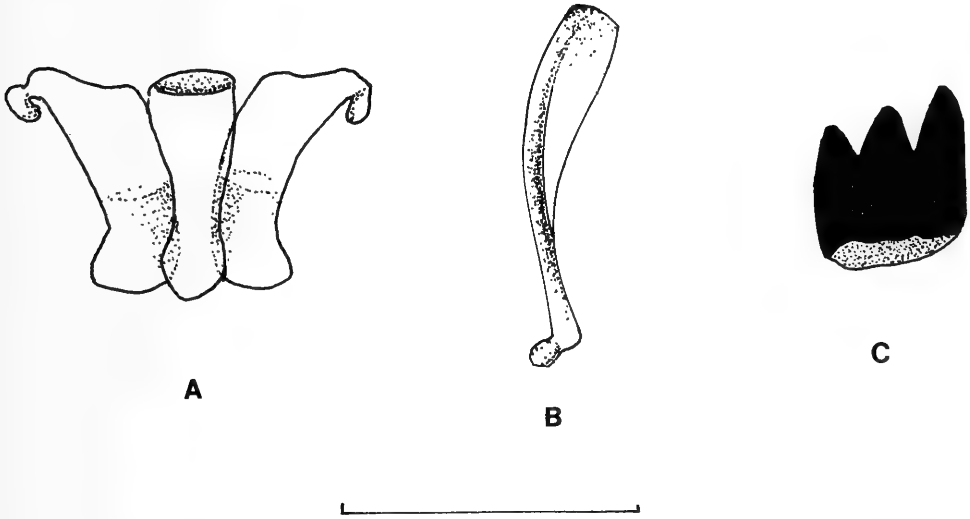


Fig. 7. *Ischnochiton victoria* Ferreira, spec. nov. Holotype (CAS 061096): Radula: A—Median and first lateral teeth; B—Spatulate tooth; C—Head of major lateral teeth. Camera lucida drawing. Bar = 50 μm.

1972, a tropical western Atlantic species known at Curacao, Trinidad, Florida, and Barbados (Ferreira 1985). Specimens of both species are very small, elongate, parallel-sided, colored often with brown designs and blue spots, valves thin and roundbacked, very wide sinus, sharp insertion teeth, small, striated girdle scales, and radula with tricuspid major lateral teeth. Morphologically, *I. victoria* and *I. pseudovirgatus* may be considered sibling species. However, they differ in 1) the tegmental surface (dull, micro-pitted in *I. victoria*; smooth, almost shiny in *I. pseudovirgatus*), and 2) the posterior valve (elevated, inflated, convex postmucro in *I. victoria*; not elevated or elevated, concave postmucro in *I. pseudovirgatus*). Likely the two species share a not too distant ancestor, perhaps having been separated by the rise of the Isthmus of Panama.

The species is named *victoria* [a noun in apposition] after the schooner VICTORIA and her crew who made possible these collecting trips to Cocos Island.

Lepidozona Pilsbry, 1892

Type species: *Chiton mertensii* Middendorff, 1847, by original designation.

Lepidozona rothi Ferreira, 1983

Lepidozona rothi Ferreira, 1983:316–317, figs. 19–22.

Material examined: 3 specimens, 10.8 mm, 6.1 mm, 4.8 mm long (including girdle), dredged at Chatham Bay, at 46–53 m (DRS); 1 intermediate valve dredged at 91–95 m, 1 mile NE of Isla Manuelita (DRS).

Remarks: The specimens are in reddish brown tones, one maculated with cream on pleural areas. Their identification was confirmed by examination of the mounted girdle scales and radula.

Lepidozona rothi was previously recognized at Cocos Island, at Chatham Bay, 70–110 m, and off Nuez Id., at 55–90 m, (Ferreira 1983).

Stenoplax Dall, 1879

Type species: *Ischnochiton limaciformis* Sowerby, 1832, by original designation.

Stenoplax boogii (Haddon, 1886)

Ischnochiton boogii Haddon, 1886:15–16.
Stenoplax boogii: Ferreira, 1985:197–199, fig. 9.

Material examined: 5 specimens collected with SCUBA at 10–20 m, on Chatham Bay, largest 15.3 mm long (AJF 857; AJF 859); 3 specimens collected at 20–30 m, off Manuelita Id. (AJF 858; AJF 861); 2 specimens dredged at 46–53 m on Chatham Bay (DRS); 3 loose valves dredged at 18–61 m on Waifer Bay, Ulloa Id., and Roca Sucia (DRS).

Mopaliidae Dall, 1889

Placiphorella Dall, 1879

Type species: *Placiphorella velata* Dall, 1879, by original designation.

Placiphorella blainvillii (Broderip, 1832)

Chiton blainvillii Broderip *in* Broderip and Sowerby, 1832:27.
Placiphorella blainvillii: Dall, 1908:357; 1909:246—Hertlein, 1963:243—Smith and Ferreira, 1977:88–89, fig. 12.

Placiphorella blainvillii was reported by Dall (1908) dredged at 120 m "near Cocos Island." The single specimen (USNM 122968) was previously examined and illustrated (Smith and Ferreira 1977).

Family Chitonidae Rafinesque, 1815
Chiton Linnaeus, 1758

Type species: *Chiton tuberculatus* Linnaeus, 1758, by subsequent designation (Dall 1879).

Chiton stokesii Broderip, 1832

Chiton stokesii Broderip *in* Broderip and Sowerby, 1832:25–26—Thorpe *in* Keen, 1971:864, Polyplacophora, sp./fig. 5.

Material examined: 25 specimens, largest 73 mm long, collected at Chatham Bay, in the intertidal zone, exposed on large boulders (AJF 856).

Remarks: *Chiton stokesii* is very abundant at Cocos Island, on top of large boulders in the intertidal zone. The species has been reported at Cocos by several authors (Biolley 1907; Dall 1908; Tomlin 1927; Hertlein 1963; Emerson and Old 1964; Montoya 1983). Largest specimen reported at the island, 110 mm long (Biolley 1907).

Chiton goodallii Broderip, 1832

Chiton goodallii Broderip *in* Broderip and Sowerby, 1832:25—Thorpe *in* Keen, 1971:864, Polyplacophora, sp./fig. 4.

Reports of *Chiton goodallii* at Cocos (Martens 1902; Boone 1933) have not been corroborated; very likely, these reports represent misidentifications for *C. stokesii.* The species is only known at the Galápagos Islands (Smith and Ferreira 1977).

Suborder Acanthochitonina Bergenhayn, 1930
Family Acanthochitonidae Pilsbry, 1893
Acanthochitona Gray, 1821

Type species: *Chiton fascicularis* Linnaeus, 1767, by monotypy.

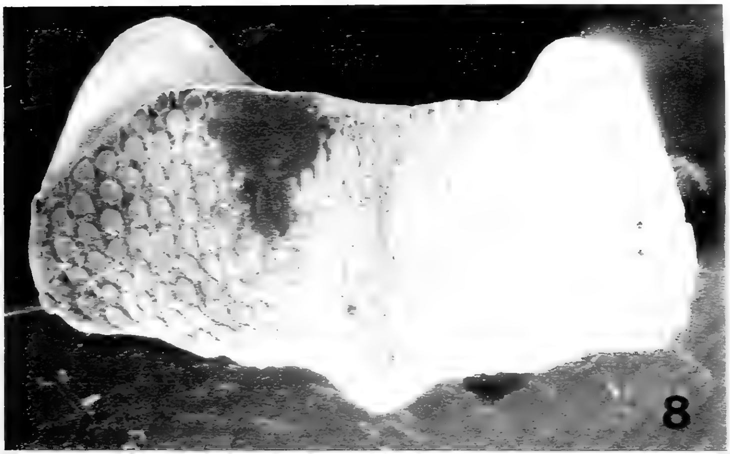
Acanthochitona hirudiniformis (Sowerby 1832)

Chiton hirudiniformis Sowerby *in* Broderip and Sowerby, 1832:59.
Acanthochitona hirudiniformis: Hertlein, 1963:242—Thorpe *in* Keen 1971:866–868, Polyplacophora, sp./fig. 13—Smith and Ferreira 1977:92–93, fig. 17—Montoya 1983:345.

The single report of *Acanthochitona hirudiniformis* at Cocos Island (Hertlein 1963) has not been corroborated; Hertlein's (op. cit.) material has not been found in the CAS chiton collection.

Acanthochitona shaskyi Ferreira, spec. nov.
Figs. 8–12

Diagnosis: Small (up to 6 mm long) *Acanthochitona,* valves all yellow, all white, or maculated cream with red; girdle banded cream and red. Jugal area much wider in front, with microgranules defining irregular longitudinal striae. Latero-pleural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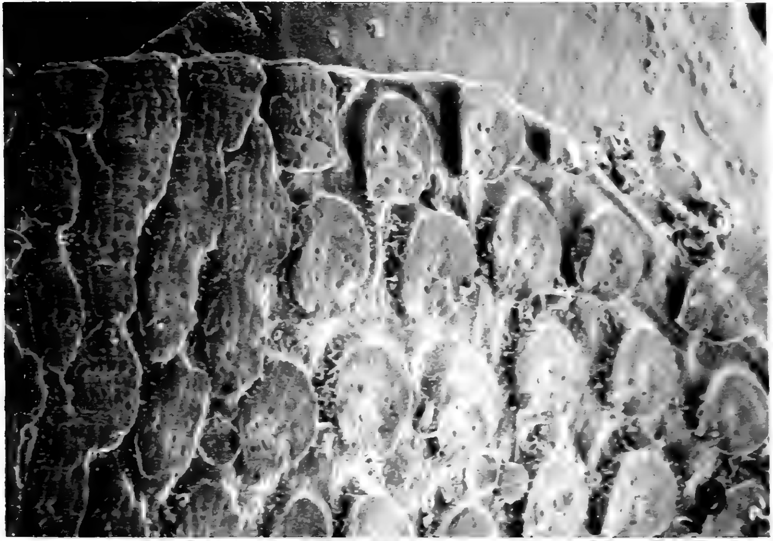

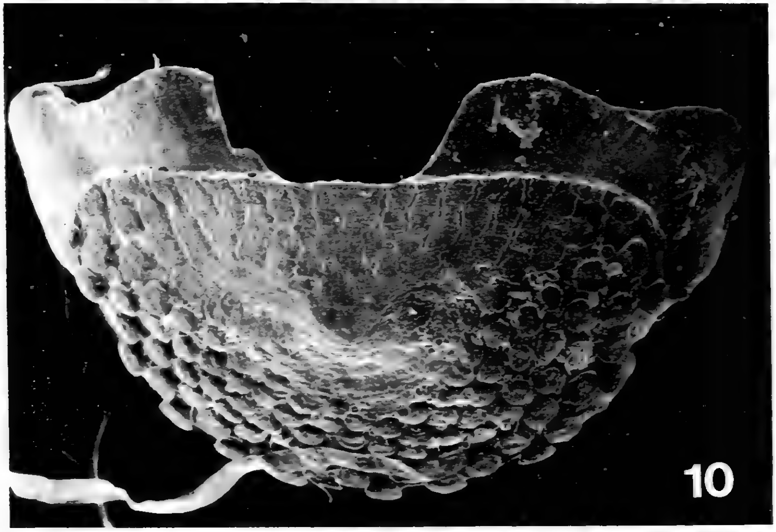
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areas with round, flat-topped pustules. Mucro central or slightly anterior, not prominent. Girdle covered with small, spiculoid elements; tufts with relatively short (up to 0.5 mm long), glassy, white spines. Conspicuous marginal fringe of white and reddish spicules. Radula with tricuspid major lateral teeth.

Type material and locality: Holotype (CAS 061094) and paratypes (CAS 061095; LACM 2125; SBMNH 34359; USNM 859008; D. R. Shasky Colln.; A. J. Ferreira Colln.); locality, Chatham Bay, Cocos Island, Costa Rica (5°33′N, 87°02′W) at 46–69 m.

Description: Holotype, intact, flat, preserved in alcohol, 48 mm long, 27 mm wide (including girdle but not the spicular fringe. Valves subcarinate, slightly beaked. Tegmentum cream colored maculated with reddish brown. Jugum much wider in front (Fig. 8); surface covered with minute granules, aligned longitudinally, defining about 10–12 fine striae. Pleurolateral areas covered with small, round, flat-topped pustules (Fig. 9); anterior valve and postmucro area of posterior valve similarly sculpture. Mucro anterior (Fig. 10); postmucro slightly concave. Girdle banded dark brown and cream, covered with very small, round elements; sutural tufts with relatively short, and sparse, transparent, sharp spines; marginal fringe of transparent, glassy spicules, about 300 μm long.

Paratypes do not differ significantly from holotype in general characteristics. Largest specimen 6.2 × 3.2 mm, smallest 2.8 × 1.7 mm; "average" specimen in the lot about 4 mm long. In alcohol preserved specimens, width/length, 0.55 (n = 12; SD = 0.027). Among 91 specimens in type lot, 74 (81%) are cream colored variously maculated with reddish brown, 16 (18%) uniformly bright yellow, 1 (1%) yellowish white.

Girdle uniformly paved with round to ovoid elements, about 5 μm in diameter, transparent or brown (Fig. 11A) as reflected in sharp white and brown banding seen in all specimens. Sutural tufts relatively inconspicuous; girdle pores 100–150 μm diameter, 400 μm apart, with straight, glassy spicules up to 500 μm long, 15 μm thick (Fig. 11B). Conspicuous marginal fringe of glassy, longitudinally striated spicules, up to 350 μm long, 35 μm thick (Fig. 11C), whitish or reddish corresponding to color of girdle. Girdle undersurface with transparent, lanceolate, somewhat imbricated scales, 40 × 10 μm (Fig. 10D).

Radula (of specimen 6 mm long) 1.8 mm long, 35 rows; median teeth 23 μm wide at anterior blade; first lateral teeth about 45 μm long (Fig. 12A); major lateral teeth with tricuspid head (cusps all about same size), 40 μm wide (Fig. 12B); outer marginal teeth 40 × 20 μm (length/width ratio, 2.0).

Distribution: *Acanthochitona shaskyi* is known only from the type lot.

Remarks: Given the usual difficulties in the differential diagnosis of species of *Acanthochitona, A. shaskyi* must be carefully distinguished from congenerics in

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Fig. 8. *Acanthochitona shaskyi* Ferreira, spec. nov. Paratype (CAS 061095): Intermediate valve, dorsal surface. SEM micrograph, courtesy of Terrence Gosliner.

Fig. 9. *Acanthochitona shaskyi* Ferreira, spec. nov. Paratype (CAS 061095): Same specimen as in Fig. 7. Close-up of latero-pleural areas (×170). SEM micrograph, courtesy of Terrence Gosliner.

Fig. 10. *Acanthochitona shaskyi* Ferreira, spec. nov. Paratype (CAS 061095): Posterior valve, dorsal surface. SEM micrograph, courtesy of Terrence Gosliner.

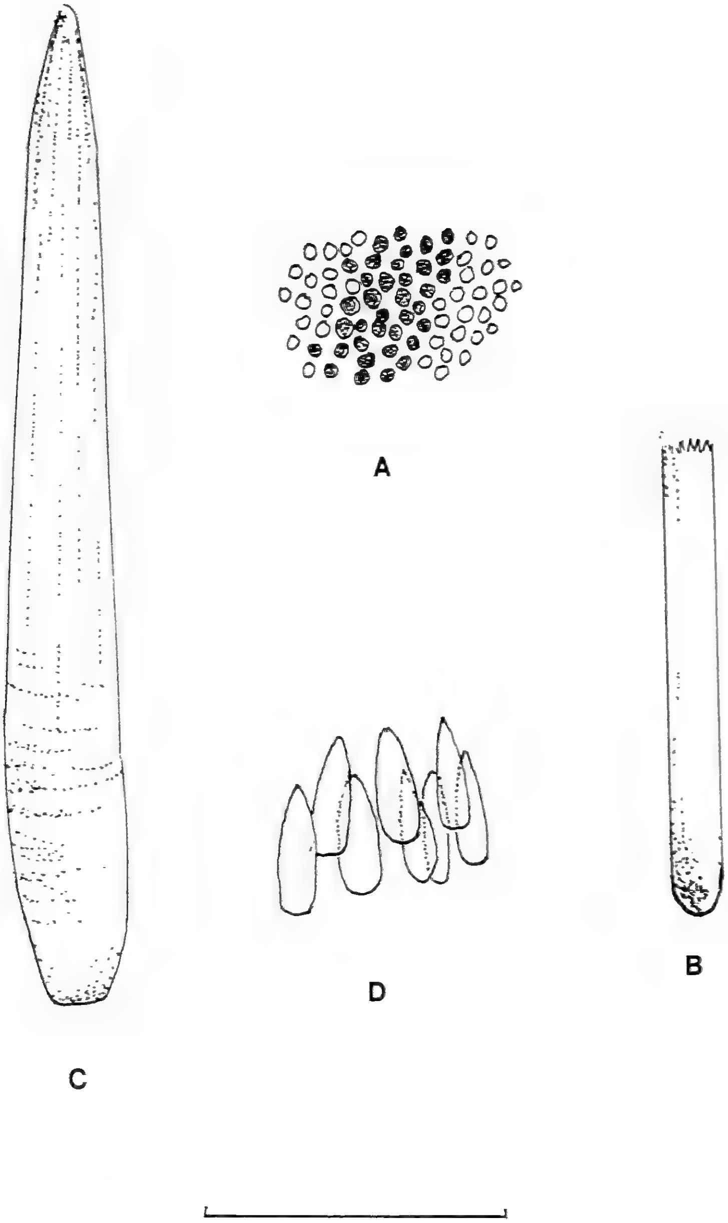

Fig. 11. *Acanthochitona shaskyi* Ferreira, spec. nov. Paratype (CAS 061095): Girdle elements: A—Scale-like elements of upper surface; B—Fragment of glassy spicule from sutural tuft; C—Spicule from marginal fringe; D—Scales of girdle undersurface. Camera lucida drawings. Bar = 100 μm.

the area, *A. hirudiniformis* (Sowerby, 1832), *A. arragonites* (Carpenter, 1857), *A. avicula* (Carpenter, 1864), and *A. jacquelinae* Smith and Ferreira, 1977.

Although *A. hirudiniformis* has been reported at Cocos (Hertlein 1963) the two species are too different in size, shape, color and sculpture of tegmentum, and girdle elements, to cause confusions in identification.

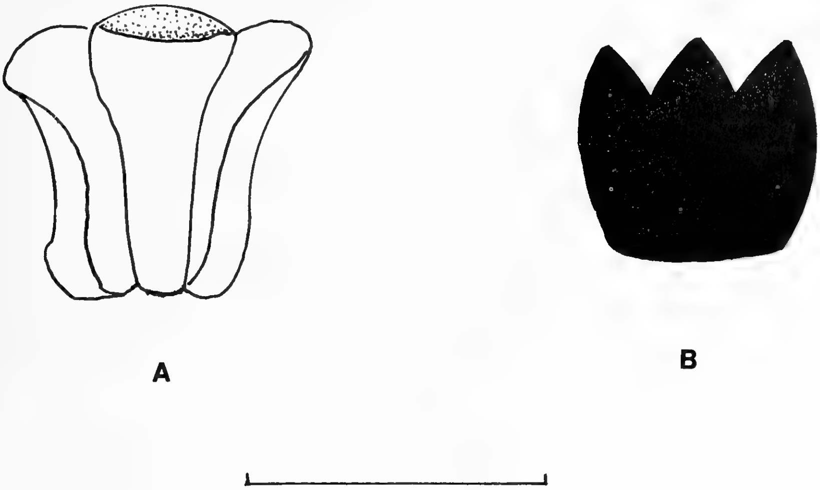

Fig. 12. *Acanthochitona shaskyi* Ferreira, spec. nov. Paratype (CAS 061095): Radula: A—Median and first lateral teeth; B—Head of major lateral tooth. Camera lucida drawings. Bar = 50 μm.

Unlikely to be confused, also, is *A. avicula* on account of its different size, and color; in addition the two species differ in the shape of the lateropleural areas pustules (tear-drop in *A. avicula*; round to suboval in *A. shaskyi*), and the mucro (prominent, central in *A. avicula*; subdued, anterior in *A. shaskyi*).

Acanthochitona arragonites, also quite small in size, and often with color patterns similar to those of *A. shaskyi,* may pose some difficulties in differentiation;

Table 1. *Acanthochitona shaskyi* Ferreira, spec. nov. *versus A. jacquelinae* Smith and Ferreira, 1977: Comparison of characters based on same size (about 6 mm long) specimens.

	A. jacquelinae (n = 41)	*A. shaskyi* (n = 91)
Specimens' color (%)		
Mottled cream-red	54	81
All yellow	37	18
All white	10	1
Specimen length (mm), max.	10	6
Jugal area	striated	striated
Lateropleural pustules top	flat to concave	flat
Diameter (μm), max.	80	80
Mucro, central	prominent	subdued
Postmucro slope	sharp	gentle
Girdle,		
Banding	inconspicuous	conspicuous
Pores diameter (μm)	300	150
Apart (μm)	200	450
Spicules in tufts		
Length (μm), max.	1500	500
Width (μm), max.	30	20
Radula, major lateral teeth tricuspid head, width (μm)	50	35

however, it suffices to point out that specimens of *A. arragonites* are clearly parallel-sided (i.e., not oval), with a distinctly elongate body, and a smooth jugal area.

However, the differential diagnosis between *A. shaskyi* and *A. jacquelinae* (endemic to the Galápagos Islands) must be carefully spelled out. Specimens of two species are about the same size, and color; in fact, both species take the same 3 color forms, cream mottled with brownish red, all-yellow, and all-white, albeit in possibly different proportions (Table 1). In addition, they have identical radulae, and rather similar girdle elements. They do differ, however, in 1) the spines at the sutural tufts (quite long, up to 1500 μm, in *A. jacquelinae*; short, up to 500 μm, in *A. shaskyi*), 2) the girdle pores (wide, 300–350 μm in diameter, 300–400 μm apart, in *A. jacquelinae*; narrow, 100–150 μm in diameter, 500–600 μm apart, in *A. shaskyi*), 3) the mucro (prominent in *A. jacquelinae*; subdued in *A. shaskyi*), and 4) the postmucro slope (sharp, near 90° in *A. jacquelinae*; gentle, near 45° in *A. shaskyi*).

Acknowledgments

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Research Note

Notes on Spawning of the Sharpchin Flying Fish, *Fodiator acutus* (Exocoetidae) from Peru

The sharpchin flying fish, *Fodiator acutus* is found from Mexico to Callao, Peru and in the Galapagos Islands and Hawaii (Chirichigno 1980). This report contains the first histological analysis of reproductively active females and males of this species. The purpose of this investigation was to obtain information on the spawning cycle of this species.

A total of 402 specimens of *F. acutus* (328 ♂ and 74 ♀) were purchased at the Mercado Pesquero Artesenal de Chorrillos, Lima, Peru (12°08′S, 77°02′W) between 11–16 January 1983. Fresh fish were weighed to the nearest g and measured to the nearest mm. Ovaries were preserved in 10% formalin and later weighed to the nearest 0.01 g. Gonosomatic indices (GSI = ovary weight/fish weight × 100) were then calculated. Ovaries were embedded in paraffin; sectioned at 8 μm and then stained with Harris' hematoxylin followed by eosin counterstain. Fish averaged 64 g body weight (range 49–91 g) and 164 mm standard length (SL) (145–179 mm). All specimens were reproductively active.

The ovaries of *F. acutus,* typical of teleosts, consist of paired fusiform organs attached at their posterior end by a mesentery. Eggs are grouped in fibrous masses. Within these masses the eggs are attached to each other by slender fibrils as reported for various members of the Exocoetidae by Bruun (1935). Histologically these fibrils appear as circular to oblong structures which are located between the zona radiata and theca externa. Breder (1928) reported that *F. acutus* deposited eggs with very long tendrils and that egg diameters averaged 1.53 mm.

We made use of the occurrence of hydrated eggs to identify fish in which spawning was imminent. In the process of hydration, the oocyte grows to as much as four times its original volume (Wallace and Selman 1981) making them readily distinguishable from unhydrated eggs. We also used the presence of postovulatory follicles as evidence of a recent spawning. These structures are remnants of the granulosa layer of the spawned eggs which undergo hypertrophy and form the convoluted postovulatory follicle. In *Engraulis mordax* spawned in captivity, the postovulatory follicle has a brief existence and is indistinguishable from atretic follicles after 48 hours (Hunter and Goldberg 1980). Yamamoto and Yoshioka (1964) also reported postovulatory follicles to be short-lived in the medaka, *Oryzias latipes.*

In our samples, three classes of ovaries were present: Class 1 pre-spawning, spawning imminent with hydrated eggs averaging 807 μm, but without postovulatory follicles; Class 2 post-spawning, with postovulatory follicles and occasional residual mature eggs; Class 3 consisted of eight females with hydrated eggs and postovulatory follicles in the same ovary. The presence of both hydrated eggs and postovulatory follicles in the same ovary suggests the fish were collected while spawning. Ovary weights and GSI data for Classes 1 and 2 are presented in Table 1. Student's t test was significant for differences in ovary weight ($t = 15.71$, $P < .001$) and GSI ($t = 17.96$, $P < .001$) between these two groups.

Table 1. Ovarian classes with mean ovary weights, gonosomatic indices (GSI) ± standard error of mean for Peruvian *Fodiator acutus* collected 11–16 January 1983.

Class 1 pre-spawning (hydrated eggs)			Class 2 post-spawning (postovulatory follicles)		
N	Ovary wt	GSI	N	Ovary wt	GSI
31	9.79 ± 0.39	14.76 ± 0.48	35	3.22 ± 0.13	5.23 ± 0.20

It is impossible to get a complete understanding of the *F. acutus* spawning cycle with only January data. Monthly samples will be required to know the duration of the spawning season as well as the number of times a female may spawn during the season. Nevertheless, some observations can be made from data on hand. The occurrence of two contrasting ovarian conditions (females contained either ripe ovaries with hydrated eggs or spawned-out ovaries with postovulatory follicles and residual oocytes) in samples collected during a five day period suggests that *F. acutus* is not a partial or fractional spawner that contains several modes of maturing eggs. Partial spawning is common in tropical and subtropical areas (Nikolsky 1963) and has been reported for California fishes (Goldberg 1981a, b, 1982).

Our data may have been collected near the end of the spawning season when the population is typically heterogeneous (Goldberg 1981b, c) with respect to its ovarian conditions. At this time it is common to find fishes with ovaries in spawning condition as well as those with regressed ovaries (breeding completed) in the same collection. We doubt that the *F. acutus* spawning season was coming to a close as no females were found with abundant atretic follicles. This condition is common at the close of the spawning season (Goldberg 1981a, b) when follicles that initiated but did not complete yolk deposition degenerate.

All 328 males examined contained enlarged testes. Histological examination of 30 fish confirmed that spermiogenesis was in progress. There was a preponderance of males in the collections we examined (328 ♂, 74 ♀). The chi-square value ($\chi^2 = 160$, df = 1) was significant ($P < .005$). Whether these data are indicative of sex ratios within the schools or reflect collection biases is not clear.

There is little information on spawning in other flying fishes. Fitch and Lavenberg (1971) reported that the California flying fish, *Cypselurus californicus* spawns from late June into September. As was the case for *F. acutus,* the eggs have long filaments attached over the egg surface. Tsukahara and Shiokawa (1957) found that off Japan, *Parexocoetus mento* has a long spawning season (May–September) with June–July peak. Most *P. mento* females die after a single spawning. Whether this occurs in *F. acutus* will require further study.

Acknowledgment

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SCAS ANNUAL MEETING
MAY 8–9, 1987
CALIFORNIA STATE UNIVERSITY
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The Academy's 1987 Annual Meeting will be held May 8 and 9 at California State University, Los Angeles. Dr. David L. Soltz, of the Department of Biology at Cal State L.A., is Program Chairman for the two-day event.

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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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CONTENTS

Research Note

COVER: Shell of the snail, *Radiocentrum avalonense,* from Santa Catalina Island, California. The species was rediscovered in 1978 after being "lost" for nearly 80 years. Drawn by Jamie Calhoun. Submitted by F. G. Hochberg, Jr., Curator of Invertebrate Zoology, Santa Barbara Museum of Natural History.