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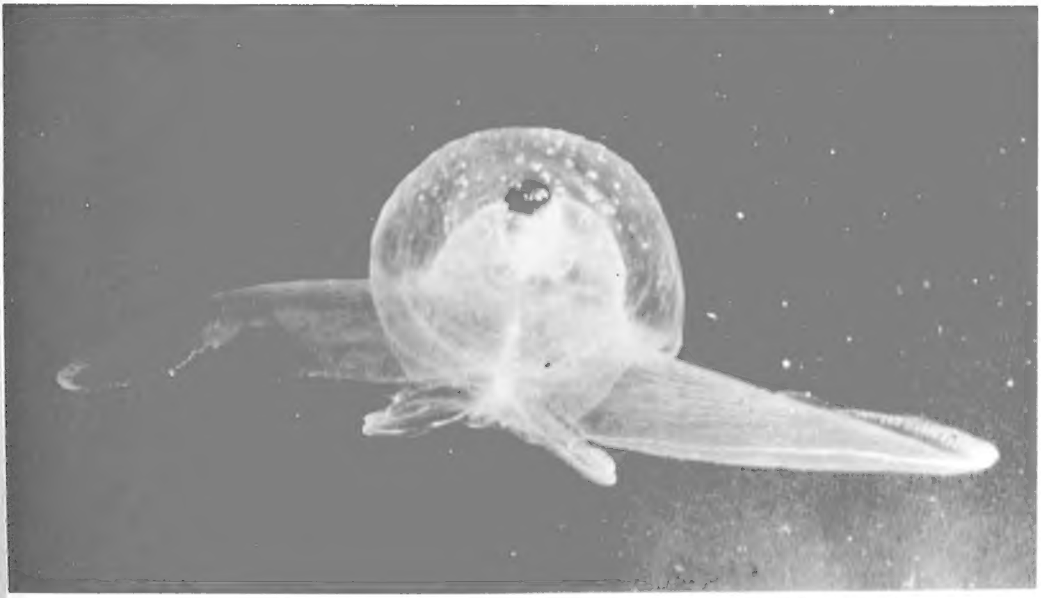

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The Taxonomy of Some Neotropical *Hylaeus* and Descriptions of New Taxa (Hymenoptera: Colletidae)

Roy R. Snelling

Abstract.—The taxonomy of some neotropical *Hylaeus* and descriptions of new taxa (Hymenoptera: Colletidae) by Roy R. Snelling. *Bull. Southern California Acad. Sci.*, 81(1):1–25, 1982. All previously described *Hylaeus* from Mexico and Central America are placed within existing subgenera and some new synonymies are proposed. The following species are placed in the subgenus *Prosopis*: *H. aztecus* and *H. transvittatus*. Species placed in the subgenus *Hylaeopsis* are: *H. callosulus* (=*H. callosa* =*H. monacha*), *H. dubiosus*, *H. gracillimus* (=*H. gracillinea*), *H. grossus* (=*H. maculata*), *H. gualanicus* (=*H. ruficollis* =*H. albifrontella*), *H. maculipennis*, *H. maculosus*, *H. mexicanus*, *H. opaciventris*, *H. subgriseus*, *H. titanius*, *H. vigilans* (=*H. trepandus*) and *H. zamoranicus*. The following are assigned to the subgenus *Hylaeana*: *H. costaricensis*, *H. knabi*, *H. panamensis* (=*H. aztecus* of previous authors), *H. quadratiferus*, *H. rufoclypeatus* and *H. trivittatus*. *Prosopis crenulata* and *P. howardiella*, both described as hylaeines, are an andrenid and colletid, respectively.

Four new species in the subgenus *Hylaeana* are described from Jamaica, French Guiana and Trinidad. A new subgenus is described to accommodate *H. cruentus*, *H. orbicus* and a new species from Bolivia.

Introduction

Up to the present time, about two dozen species of *Hylaeus* have been described and recorded from Central America. The first of these were named by F. Smith. Subsequently, others were added by Cresson, Cockerell, Friese, and Michener. Most of these have been known only from the descriptions and the appropriate type specimens.

I have been able to examine most of the types. Notes on those described by F. Smith were provided for me, and I am now able to assign each species to a subgeneric category and to propose some synonymy. More detailed treatment of these and other Mesoamerican *Hylaeus* must remain for a future paper.

The opportunity is taken to describe a few new species so that their names may be made available to other researchers.

Terminology

For the most part, morphological terminology used herein is that of my earlier papers on *Hylaeus* (e.g., Snelling 1966b, 1970a). In the latter paper, I suggested a tentative terminology for puncture sizes; it has since proven unsatisfactory, and a new system is here proposed:

Ultraminute—average diameter less than 0.010 mm.
Minute—puncture diameter 0.010–0.019 mm.

Fine—puncture diameter 0.020–0.035 mm.
Moderate—puncture diameter 0.036–0.055 mm.
Coarse—puncture diameter 0.056–0.070 mm.
Very coarse—puncture diameter over 0.070 mm.

Similarly, a system for expressing degree of closeness of punctures was developed:

Contiguous—punctures crowded, often deformed, interspaces sharp-edged. At its extremes, this may be termed rugosopunctate or reticulopunctate when punctures no longer have the appearance of punctures.

Subcontiguous—interspaces more or less flat-topped, interval between them up to about 0.25 times a puncture diameter.

Dense—more or less flat-topped interspaces, averaging about 0.3–0.7 times a puncture diameter.

Close—intervals between punctures averaging between 0.7–1.5 times a puncture diameter.

Sparse—intervals between punctures averaging between 1.5–3.0 times a puncture diameter.

Scattered—intervals between punctures greater than 3.0 times a puncture diameter.

Puncture size and density, on a given segment, often vary and an appropriate combination of the above terms can be used to express such diversity.

Some descriptive terms have been abbreviated as follows:

ASD—Antennal socket diameter. The maximum diameter, between outer margins, perpendicular to the longitudinal axis of the head.

BCW—Basal clypeal width. The distance between the subantennal sutures along the basal margin of the clypeus.

COD—Clypeocular distance. Distance from laterobasal angle to nearest point on eye margin.

CL—Clypeal length. The maximum length of the clypeus, from basal margin to its anteriormost extremity.

CW—Clypeal width. The maximum width of the clypeus near its lowermost point.

FSW—Frontal shield width. The width of the frontal shield at its upper termination on the frons.

HL—Head length. Maximum length between highest point of the vertex and lowermost extremity of the clypeus.

HW—Head width. Maximum width of the head, across the eyes.

IAD—Interantennal distance. The minimum distance between the antennal sockets.

LFW—Lower facial width. The minimum distance between the eyes at their lower end. This term is utilized in its relationship with UFW (q.v.) to express degree of convergence of the inner eye margins: *weakly convergent*—UFW 1.01–1.29 times LFW; *moderately convergent*—UFW 1.30–1.49 times LFW; *strongly convergent*—UFW 1.50–1.70 times LFW; *very strongly convergent*—UFW more than 1.70 times LFW.

OD—Ocellar diameter. Transverse diameter of anterior ocellus.

SL—Scape length. The usual method, length of scape shaft, exclusive of basal condyle.

TL—Total length. This is the least satisfactory of the measurements used; it is certainly the least exact. The method used here differs from the conventional but seems less subject to the vagaries resulting from wide variations in death posture of the specimen. TL is the sum of the following: HL + thoracic length (in dorsal view, from anterior margin of pronotal collar to posterior extremity of propodeum) + length of first tergum (dorsal view, along midline with the summit of the anterior or basal face just occluding the basal attachment) + length of second tergum (along midline, from gradulus to apical margin).

UFW—Upper facial width. The minimum distance between the upper ends of the eyes, at about the level of the anterior ocellus, not at a point of greatest width as Houston (1975) has it; consistent with my use of the term in earlier papers (e.g., 1970).

WL—Wing length. The length of the anterior wing from margin of tegula to apical extremity.

The specimens examined are in the collections of the American Museum of Natural History (AMNH), the Museum of Comparative Zoology (MCZ), the Natural History Museum of Los Angeles County (LACM), and the University of Kansas (UKAN).

Previously Described Species

Of the 27 names previously ascribed to the hylaeine fauna of Central America, 25 are placed in their respective subgenera in the following list; 2 are non-hylaeines and are treated in the following section. Most names are new combinations within those subgenera. New synonymy proposed below is based on a study of the relevant types.

There are numerous undescribed species in Central America, but an effort to describe these would be premature.

Subgenus *Prosopis* Fabricius

Prosopis Fabricius 1804:293. Type species. *Sphex signata* Panzer 1798 = *Mellinus bipunctatus* Fabricius 1804; designation of Morice and Durant 1914.
aztecus (Cresson). Mexico.
  Prosopis azteca Cresson 1869:272. ♀.
transvittatus (Cockerell). Mexico; southeastern Arizona.
  Prosopis transvittata Cockerell 1917:437–438. ♂♀.
  Hylaeus (*Prosopis*) *transvittatus*: Snelling 1966a:2, 3, 16. ♂♀.

Subgenus *Hylaeopsis* Michener

Hylaeus, subg. *Hylaeopsis* Michener, 1954:27. Type species: *Prosopis mexicana* Cresson 1869; original designation.
callosulus Friese. Costa Rica
  Prosopis callosa Friese 1921:82. ♀. Preoccupied.
  Hylaeus callosulus Friese, *in* Meade-Waldo 1923:31. New name.
  Prosopis monacha Warncke 1970:747. New name, NEW SYNONYMY.
dubiosus (Cresson). Mexico.
  Prosopis dubiosa Cresson 1869:272. ♂.

gracillimus (Schrottky). Brazil; Panama.
Prosopis gracillinea Schrottky 1903:340; pl. 2, fig. 1. ♀. Schrottky 1906:16.
Prosopis gracillima Schrottky 1906:16. (emend.)
Hylaeus gracillimus Michener 1954:27–28. ♀.
grossus (Cresson). Mexico; Costa Rica.
Prosopis grossa Cresson 1869:273. ♂.
Prosopis maculata Friese 1921:81. ♂. NEW SYNONYMY.
gualanicus (Cockerell).Guatemala; Costa Rica; Honduras.
Prosopis gualanica Cockerell 1912:565. ♂.
Prosopis ruficollis Friese 1921:82. ♂. NEW SYNONYMY.
Prosopis albifrontella Cockerell 1949:432. ♂. NEW SYNONYMY.
maculipennis (F. Smith). Mexico.
Prosopis maculipennis F. Smith 1879:23. ♂.
maculosus Friese. Costa Rica.
Prosopis trivittata var. *maculosa* Friese 1921:81. ♀.
mexicanus (Cresson). Mexico.
Prosopis mexicana Cresson 1869:272. ♀ only, not ♂.
Hylaeus (*Hylaeopsis*) *mexicana*: Michener 1954:27.
opaciventris (Friese). Costa Rica.
Prosopis opaciventris Friese 1925:2. ♂♀.
subgriseus (Cockerell). Mexico.
Prosopis subgrisea Cockerell 1918:424. ♀.
titanius (Friese). Costa Rica.
Prosopis titania Friese 1925:2. ♀.
vigilans (F. Smith). Mexico.
Prosopis vigilans F. Smith 1879:22. ♀.
Prosopis trepanda F. Smith 1879:23. ♀.
Hylaeus trepandus: Moure 1960:64, 66. ♀. Note: Moure (1960) correctly observed that *vigilans* and *trepanda* were conspecific. He chose to use the latter name, even though *vigilans* has strict page priority. My preference is to use *vigilans* not only because of page priority but also because the type of *trepanda* lacks the abdomen.
zamoranicus (Cockerell). Honduras.
Prosopis zamoranica Cockerell 1949:433. ♂.

Subgenus *Hylaeana* Michener

Hylaeus, subg. *Hylaeana* Michener 1954:28. Type species: *Hylaeus panamensis* Michener 1954, original designation.
costaricensis (Friese). Costa Rica.
Prosopis costaricensis Friese 1916:301. ♂.
knabi (Cockerell). Guatemala; Mexico.
Prosopis knabi Cockerell 1918:425. ♂.
panamensis Michener. Panama to southwestern United States.
Hylaeus aztecus: Cockerell 1924:530. Misidentification.
Hylaeus panamensis Michener 1954:28–30. ♂.
Hylaeus (*Hylaeana*) *aztecus*: Snelling 1968:4; figs. 2, 3. ♂ ♀. Misidentification.
Hylaeus (*Hylaeana*) *panamensis*: Snelling 1975:8.
quadratiferus (Cockerell). Guatemala.

Prosopis quadratifera Cockerell 1912:566. ♂.
rufoclypeatus (Friese). Costa Rica.
Prosopis rufoclypeata Friese 1916:301. ♀♂.
trivittatus (Friese). Costa Rica.
Prosopis trivittata Friese 1921:81. ♀.

Species Incorrectly Described as *Prosopis*

Prosopis crenulata Cockerell 1905:200. ♂. Described from Medellin, Vera Cruz, Mexico. Placed in *Panurginus* by Cockerell 1941:510. According to Timberlake (1973:17), this is a *Pseudopanurgus* (Andrenidae, Panurginae).

Prosopis howardiella Cockerell 1918:423. ♂. Described from Oaxaca, Mexico. According to Snelling (1970b), this is a synonym of *Chilicola ashmeadi* (Crawford) (Colletidae, Xeromelissinae).

Descriptions of New Taxa

In the descriptions that follow, when a range is indicated for a given measurement, the figure in parentheses is the measurement for the holotype (or allotype, if appropriate).

Hylaeus (*Hylaeana*) *rawi* new species
Figures 1, 4–7

Diagnosis: Separable from known *Hylaeana* species by the following combined characteristics. Basal area of propodeum not rugulose; metapleuron discretely punctate. *Male:* supraclypeal mark absent or minute; FSW less than ASD: scape yellow beneath. *Female:* upper end of facial fovea well removed from eye margin; clypeus ferruginous; first tergum without apicolateral fringe.

Description: *Male, measurements (mm):* HL 1.03–1.10 (1.05); HW 1.03–1.10 (1.07); WL 2.4–2.6 (2.5); TL 3.2–3.5 (3.3).

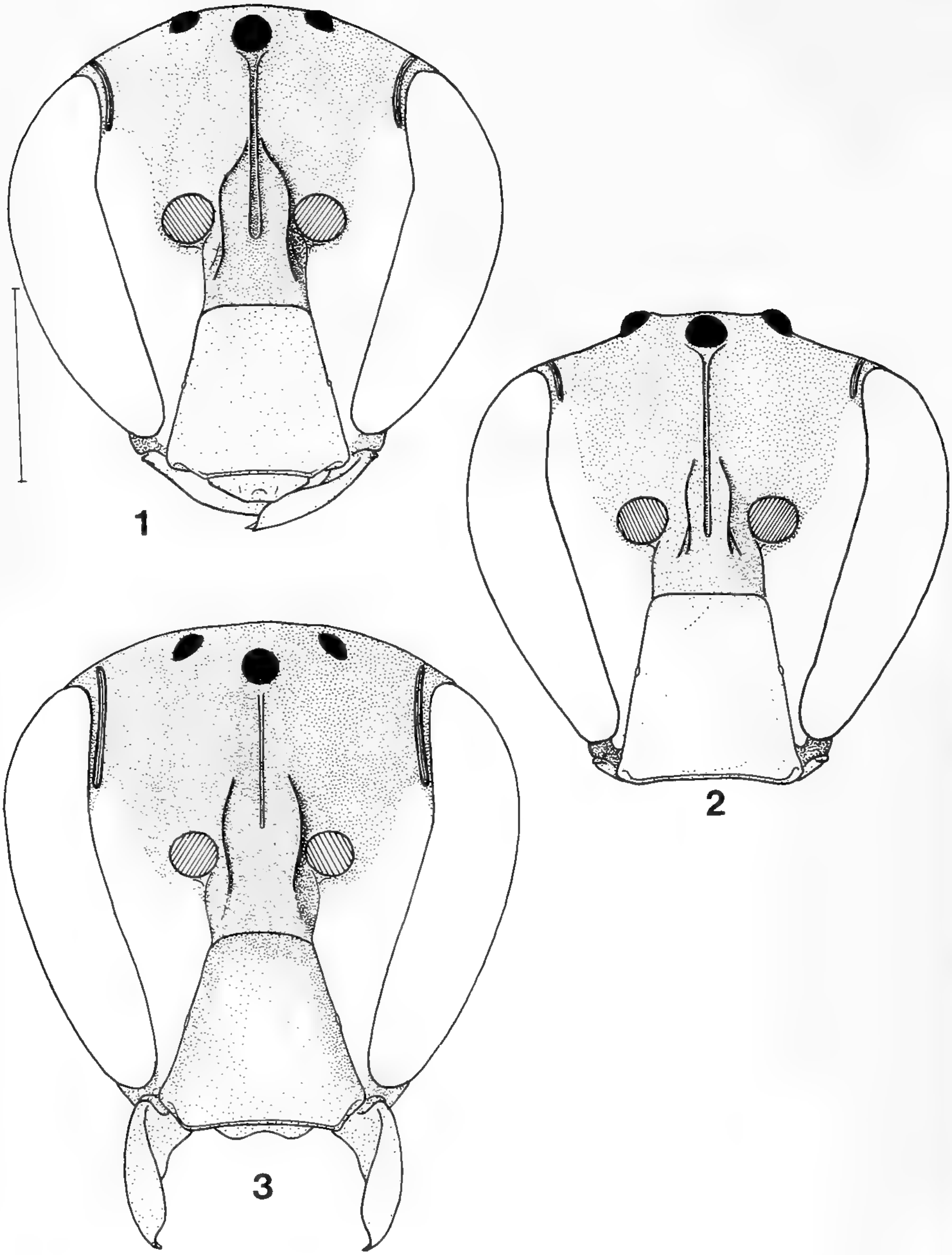
Head.—Moderately broad, HW 1.00–1.03 (1.02) × HL. Scape quite short, SL 0.19–0.21 (0.19) × HL; stout, SL 1.78–2.00 (1.89) × SW; first two flagellar segments much broader than long, first shorter than second; third segment a little longer than second, subequal to pedicel. Eyes very strongly convergent below, UFW 1.80–2.07 (2.07) × LFW.

Clypeus narrow, CW 0.79–0.80 (0.79) × CL; BCW 0.46–0.48 (0.46) × CW, 0.80–0.87 (0.80) × IAD, 1.20–1.44 (1.20) × ASD, 0.92–0.93 (0.92) × COD. Frontal shield about twice longer than wide, apex narrow, FSW 0.70–0.80 (0.80) × ASD. Interocellar distance about 1.5 × OD, distinctly greater than ocellocular distance.

Clypeus and supraclypeal area slightly shiny between close to sparse, fine punctures; maculate side of face similar, but punctures dense to close; frontal shield on either side with a row of fine, contiguous punctures, otherwise longitudinally microlineolate with occasional ultraminute punctures; face and vertex moderately shiny between fine, contiguous to subcontiguous punctures; gena moderately shiny, microlineolate between subcontiguous to dense, minute to fine punctures.

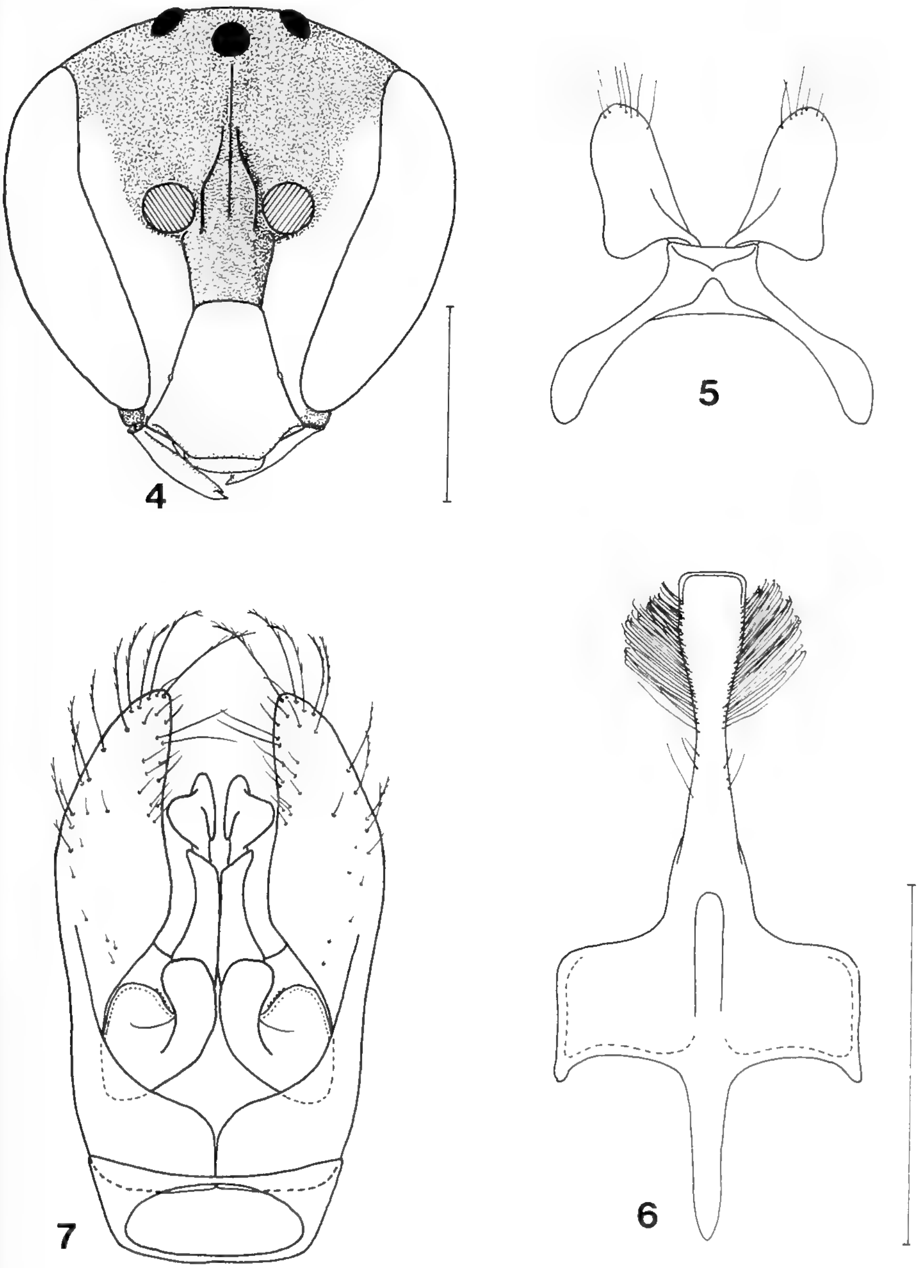
Thorax.—Mesoscutum 1.3–1.4 times wider than long; scutellum flattened, about 0.4 times length of mesoscutum; metanotum flattened.

Mesoscutum moderately shiny between dense, fine punctures; scutellum mod-



Figs. 1–3. *Hylaeus* (*Hylaeana*) spp., frontal view of female heads: 1, *H. rawi*; 2, *H. extrinsecus*; 3, *H. dictyotus*. Scale line = 0.50 mm.

erately shiny, punctures fine and quite variably spaced, from subcontiguous to sparse; metanotum slightly shiny between minute to fine, subcontiguous to dense punctures; mesopleuron moderately shiny between dense, fine punctures, metapleuron moderately shiny between subcontiguous to dense punctures. Side, disc,



Figs. 4–7. *Hylaeus* (*Hylaeana*) *rawi*, male: 4, frontal view of head; scale line = 0.50 mm. 5, sternum eight; 6, sternum nine; 7, genitalic capsule, ventral view; scale line = 0.25 mm.

and stigmatal area of propodeum moderately shiny to shiny between subcontiguous to dense, fine punctures; basal area moderately shiny and with scattered minute punctures.

Abdomen.—Disc of first tergum moderately shiny, transversely microlineate, and with scattered ultraminute punctures; disc of second tergum moderately shiny, transverse microlineation less sharp, punctures close to sparse, ultraminute to minute.

Pilosity.—First tergum without apicolateral hair patch.

Color.—Blackish. The following yellow: mandible, except reddish teeth and upper margin; labrum except reddish margins; clypeus, except reddish apical margin; lateral face mark, ending on eye margin at level about midway between antennal socket and anterior ocellus; scape, except large, brownish dorsal blotch; pronotal collar, broadly interrupted in middle; pronotal lobe; tegular spot; protibia; mesotibia, except external, preapical brown blotch; basal half of metatibia and apical annulus; all tarsi. Flagellum brown above, paler beneath. Wings clear, very faintly brownish, veins and stigma brown.

Female, measurements (mm): HL 1.15; HW 1.17; WL 3.0; TL 3.7.

Head.—Moderately broad, HW 1.01 × HL. Scape short, SL 0.26 × HL; slender, SL 3.13 × SW; first flagellar segment distinctly longer than second or third; second plus third subequal to pedicel. Eyes moderately convergent below, UFW 1.54 × LFW.

Clypeus slender, CW 0.85 × CL; BCW 0.62 × CW, 1.31 × IAD, 2.10 × ASD, 1.40 × COD. Frontal shield about one-third longer than greatest width, apex narrow, FSW 0.80 × ASD. Interocellar distance about twice OD, distinctly greater than ocellocular distance.

Clypeus and supraclypeal area slightly shiny, appearing granulose, between close to sparse, minute to fine punctures; lateral facial area similar but punctures dense, slightly larger; frontal shield slightly shiny with subcontiguous, fine punctures on either side; face and vertex slightly shiny between subcontiguous, fine punctures; gena moderately shiny between subcontiguous to dense, fine punctures, which tend to be in rows.

Facial fovea ending about about one-third of distance between eye and lateral ocellus.

Thorax.—Mesoscutum about 1.3 times wider than long; scutellum flat, about 0.4 times length of mesoscutum; metanotum flat.

Mesoscutum slightly shiny between subcontiguous to dense, fine punctures; scutellum shinier, punctures fine, subcontiguous in middle, becoming close laterad; metanotum slightly shiny between dense to close, minute punctures; mesopleuron moderately shiny between dense, minute to fine punctures; metapleuron moderately shiny between close, fine punctures. Side, disc, and stigmatal area of propodeum slightly to moderately shiny between contiguous to subcontiguous, fine punctures; basal area slightly shiny and irregularly roughened, more strongly so in middle.

Abdomen.—Disc of first tergum transversely microlineate, slightly shiny, and with a few widely scattered ultraminute punctures; disc of second tergum similar but a little shinier, microlineation less defined.

Pilosity.—First tergum without apicolateral hair patch.

Color.—Blackish. The following ferruginous: mandible; labrum; clypeus; scape; underside of flagellum; most of legs. The following yellow: narrow stripe on mandible; lateral face mark to lower end of fovea; pronotal collar, narrowly interrupted in middle; pronotal tubercule; tegular spot; incomplete stripe on protibia; basal spot on mesotibia; basal half of metatibia. Metabasitarsus yellowish white. Wings clear, slightly brownish, veins and stigma brown.

Type material: Holotype male, allotype, 2 male paratypes: cemetary, Port Royal, St. Andrew, JAMAICA, 9 Apr. 1972 (A. W. Raw); paratype male, same data, except 15 Apr. 1972; paratype male, same data, except 11 Mar. 1971. Holotype, allotype, 1 paratype in LACM; 2 paratypes in collection of A. W. Raw.

Etymology: This species is dedicated to the collector of the only known series, A. W. Raw.

Discussion: See Discussion under *H. dictyotus* below.

Hylaeus (*Hylaeana*) *phaeoscapus* New species

Figures 8–11

Diagnosis: Separable from known *Hylaeana* species by the following combined characteristics. *Male:* Supraclypeal area and entire scape dark; first tergum without apicolateral hair patch; FSW = ASD. *Female:* unknown.

Description: *Male, measurements (mm):* HL 0.90; HW 0.93; WL 2.4; TL 2.8.

Head.—Moderately broad, HW 1.04 × HL. Scape short, SL 0.22 × HL; stout, SL 2.14 × SW; first flagellar segment broader than long, conspicuously shorter than second or third segments, latter longer than pedicel. Eyes very strongly convergent below, UFW 2.26 × LFW.

Clypeus narrow, CW 0.79 × CL; BCW 0.59 × CW, 1.44 × ASD. 0.93 × IAD, 1.30 × COD. Frontal shield a little longer than greatest width, apex broad, FSW = ASD. Interocellar distance more than twice OD, distinctly greater than ocellocular distance.

Clypeus slightly shiny between sparse, fine to minute punctures; supraclypeal area slightly shiny, with subcontiguous, minute punctures on either side; lateral facial area slightly shiny, with subcontiguous, fine punctures; frontal shield dull, with contiguous, fine punctures on either side of midline; face and vertex dull, contiguously and finely punctate; gena moderately shiny between subcontiguous, minute punctures.

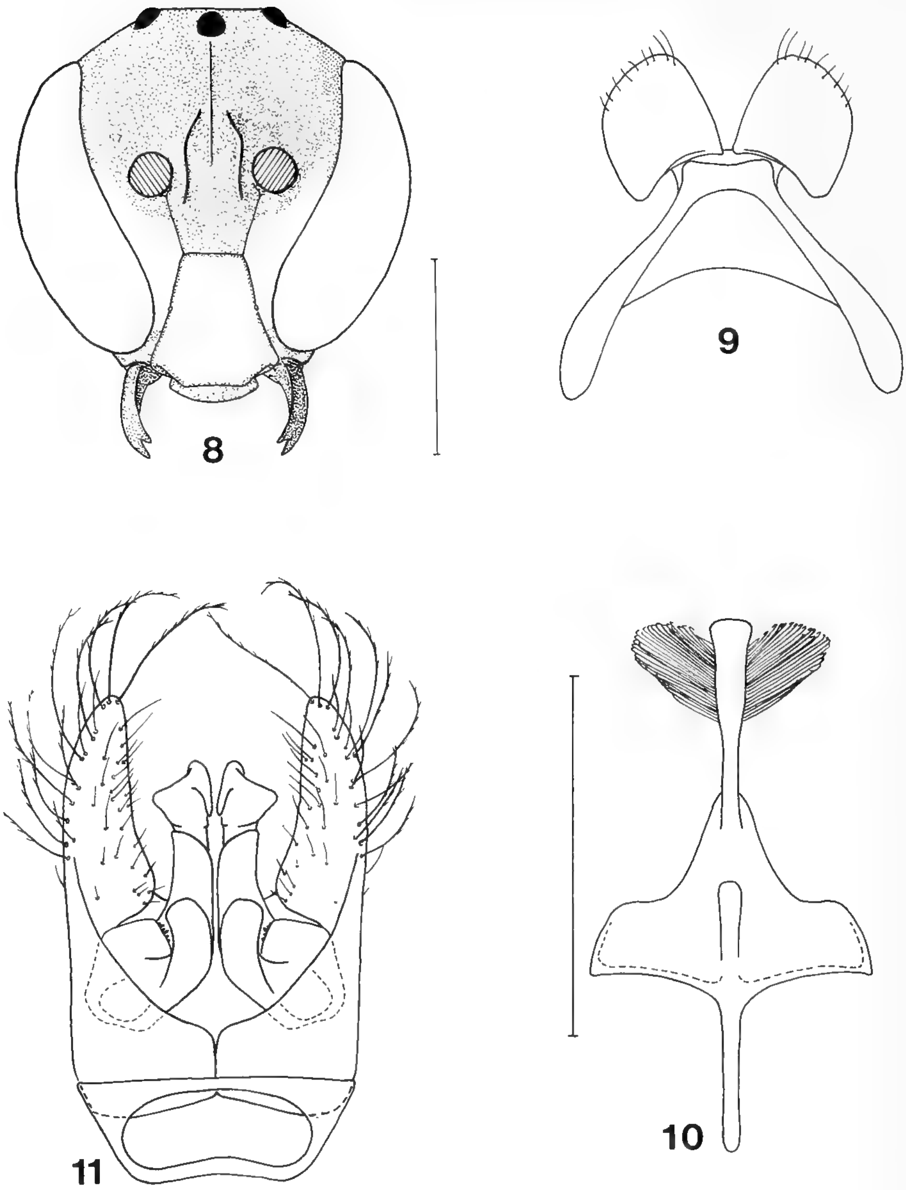
Thorax.—Mesoscutum 1.3 times wider than long; scutellum flattened, about 0.4 times length of mesoscutum; metanotum flattened. Basal face of propodeum as long as scutellum.

Mesoscutum slightly shiny between subcontiguous to dense, minute punctures; scutellum a little shinier, punctures close to sparse, minute; metanotum slightly shiny between dense to close, minute punctures; mesopluron moderately shiny between close to sparse, minute punctures; metapleuron longitudinally roughened between dense, minute punctures. Side, disc, and stigmatal area of propodeum moderately shiny between close to sparse minute punctures; basal area moderately shiny, surface roughened but without rugulae.

Abdomen.—Discs of first and second terga transversely microlineate and without obvious punctures of any size, except laterad, where a few ultraminute punctures are present.

Pilosity.—First tergum without apicolateral pubescent patch.

Color.—Blackish. The following yellow: clypeus; lateral face mark to level, on eye margin, of upper margin of antennal sockets. Reddish yellow: most of protibia; basal spot and apical annulus on mesotibia; basal spot on metatibia; tarsi. Antenna brown, flagellum a little lighter beneath. Wings clear, veins and stigma brown.



Figs. 8–11. *Hylaeus* (*Hylaeana*) *phaeoscapus*, male: 8, frontal view of head; scale line = 0.50 mm. 9, sternum eight; 10, sternum nine; 11, genitalic capsule, ventral view; scale line = 0.25 mm.

Type material: Holotype male: Irish Town, St. Andrew, JAMAICA, 31 Jan. 1972 (A. W. Raw), in LACM.

Etymology: From Greek, *phaios* (dusky, brown) and *skapos* (stem), in allusion to the wholly brown scape.

Discussion: The type is in poor condition. The head and prolegs are detached, and the pronotum is entirely missing. The dark scape seems to be unique within

Hylaeana, and I have no doubt of the distinctness of this taxon. Other unusual features include the dark labrum, minutely punctate mesopleuron, and long basal area of the propodeum.

Hylaeus (Hylaeana) extrinsecus New species
Figure 2

Diagnosis: Separable from known *Hylaeana* species by the following combined characteristics. *Female:* Upper end of facial fovea close to inner eye margin; clypeus ferruginous; mesopleural punctures separated by more than a puncture diameter. *Male:* unknown.

Description: *Female, measurements (mm):* HL 1.13; HW 1.17; WL 3.10; TL uncertain (probably about 3.8–4.0).

Head.—Moderately broad, HW 1.03 × HL. Scape short, SL 0.24 × HL; slender, SL 2.63 × SW; first flagellar segment longer than second, subequal to third, which is distinctly shorter than pedicel. Eyes moderately convergent below, UFW 1.51 × LFW.

Clypeus slender, CW 0.80 × CL; BCW 0.73 × CW, 1.60 × IAD, 2.40 × ASD, 1.85 × COD. Frontal shield without sharp margins, about twice longer than greatest width, apex moderately narrow, FSW 0.90 × ASD. Interocellar distance about twice OD, distinctly greater than ocellocular distance.

Clypeus, supraclypeal area, and adjacent side of face slightly shiny, subgranulose, between sparse, minute, obscure punctures; frontal shield with a few obscure, subcontiguous, fine punctures along each side; face dull between contiguous minute punctures (shiny within) which become subcontiguous on vertex; gena slightly to moderately shiny and finely lineate between minute, dense punctures more or less in rows.

Facial fovea ending above very close to eye margin.

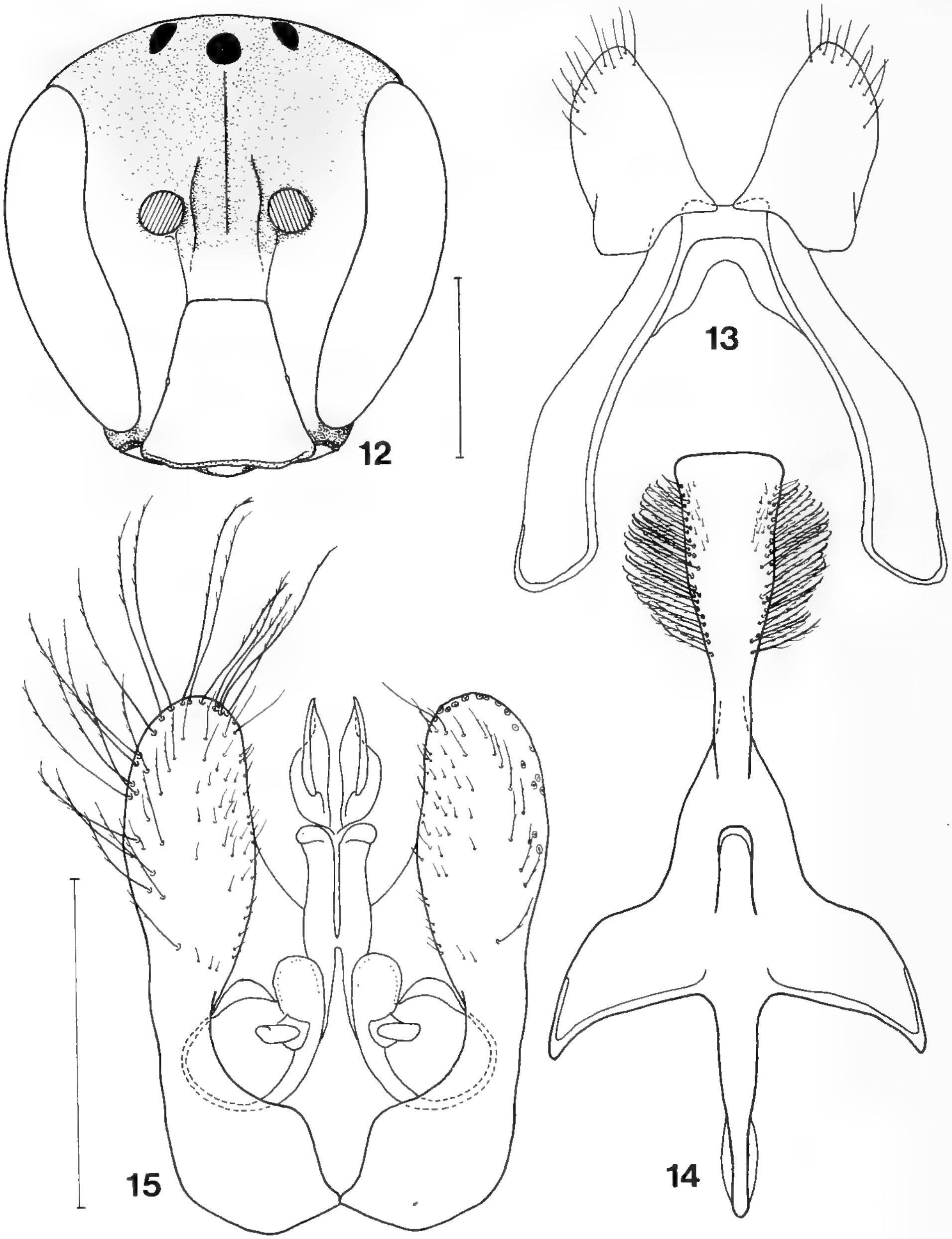
Thorax.—Mesoscutum about 1.3 times wider than long, posterior one-sixth abruptly sloping toward posterior margin; scutellum slightly flattened, about 0.3 times length of mesoscutum; metanotum flattened.

Mesoscutum slightly shiny between subcontiguous to dense, minute punctures; scutellum shinier, punctures dense to close, fine; metanotum weakly shiny between sparse, minute, obscure punctures; mesopleuron moderately shiny between close, minute punctures; metapleuron slightly shiny, irreguarly and longitudinally roughened. Side of propodeum moderately shiny, finely rugosopunctate; disc similar but more coarsely roughened; stigmatal area moderately reticulorugose; basal area weakly reticulorugose in front of shallow subbasal transverse impression.

Abdomen.—Missing from the one specimen available. Probably first and second terga transversely microlineate and with scattered minute or fine punctures.

Pilosity.—Shorter hairs of mesoscutum subappressed, abundant, longer than distance between them, those of posterior one-sixth directed cephalad.

Color.—Blackish. The following yellow: broad median clypeal stripe; lateral face mark to lower end of fovea; small spot on lower outer orbit; complete pronotal collar stripe; pronotal lobe; tegular spot; incomplete outer stripe on protibia; basal spot on mesotibia; basal half of metatibia. Mandible, clypeus (except median stripe), scape, underside of flagellum, most of tarsi reddish. Wings clear, slightly brownish, veins and stigma brown.



Figs. 12–15. *Hylaeus* (*Hylaeana*) *dictyotus*, male: 12, frontal view of head; scale line = 0.50 mm. 13, sternum eight; 14, sternum nine; 15, genitalic capsule ventral view; scale line = 0.25 mm.

Type material: Holotype female: Balaclava, JAMAICA (A. E. Wight), in MCZ.

Etymology: The specific name is a Latin word meaning "on the outside" and refers to the yellow spot on the lower outer orbit of the eye.

Discussion: It is unfortunate that the one available specimen lacks the gaster. By analogy with related species, TL should be 3.8–4.0 mm. The first two terga probably will be transversely microlineate (the first more sharply so), rendering a somewhat satiny or silky luster at lower magnifications. These segments should have scattered, obscure, minute punctures.

Possibly this is the female of *H. phaeoscapus*, described above, but dissimilarities of thoracic sculpture suggest otherwise.

Hylaeus (*Hylaeana*) *dictyotus* new species
Figures 3, 12–15

Diagnosis: Separable from known *Hylaeana* species by the following combined characteristics. Basal area of propodeum moderately rugulose in middle; first tergum with apicolateral hair patch. *Male:* supraclypeal area and stripe on scape yellow; UFW less than 1.75 × LFW. *Female:* facial fovea above ending very close to inner eye margin.

Description: *Male, measurements (mm):* HL 1.12–1.32 (1.20); HW 1.08–1.27 (1.17); WL 2.5–3.0 (2.8); TL 3.4–4.6 (3.7).

Head.—Head moderately broad, HW 0.95–1.03 (0.97) × HL. Scape short, SL 0.20–0.24 (0.21) × HL; thick, SL 2.00–2.67 (2.14) × SW; first and second flagellar segments broader than long, each shorter than pedicel; third flagellar segment subequal to pedicel. Eyes strongly convergent below, UFW 1.51–1.76 (1.61) × LFW.

Clypeus slender, CW 0.79–0.86 (0.83) × CL; BCW 0.40–0.48 (0.44) × CW, 0.83–1.00 (0.92) × IAD, 1.22–1.60 (1.22) × ASD, 0.76–1.00 (0.92) × COD. Frontal shield about one-third longer than greatest width, apex broad, FSW 0.88–1.00 (0.89) × ASD. Interocellar distance about 2 × OD, about equal to ocellocular distance.

Clypeus and other maculate areas slightly shiny between obscure, sparse to scattered, minute to fine punctures. Frontal shield slightly shiny and lineolate between subcontiguous fine punctures, median line impunctate. Face and preoccipital area slightly shiny between subcontiguous, fine punctures; interocellar and ocellocular areas similar but punctures dense to close; gena slightly shiny, punctures minute to fine, some elongate, subcontiguous to dense.

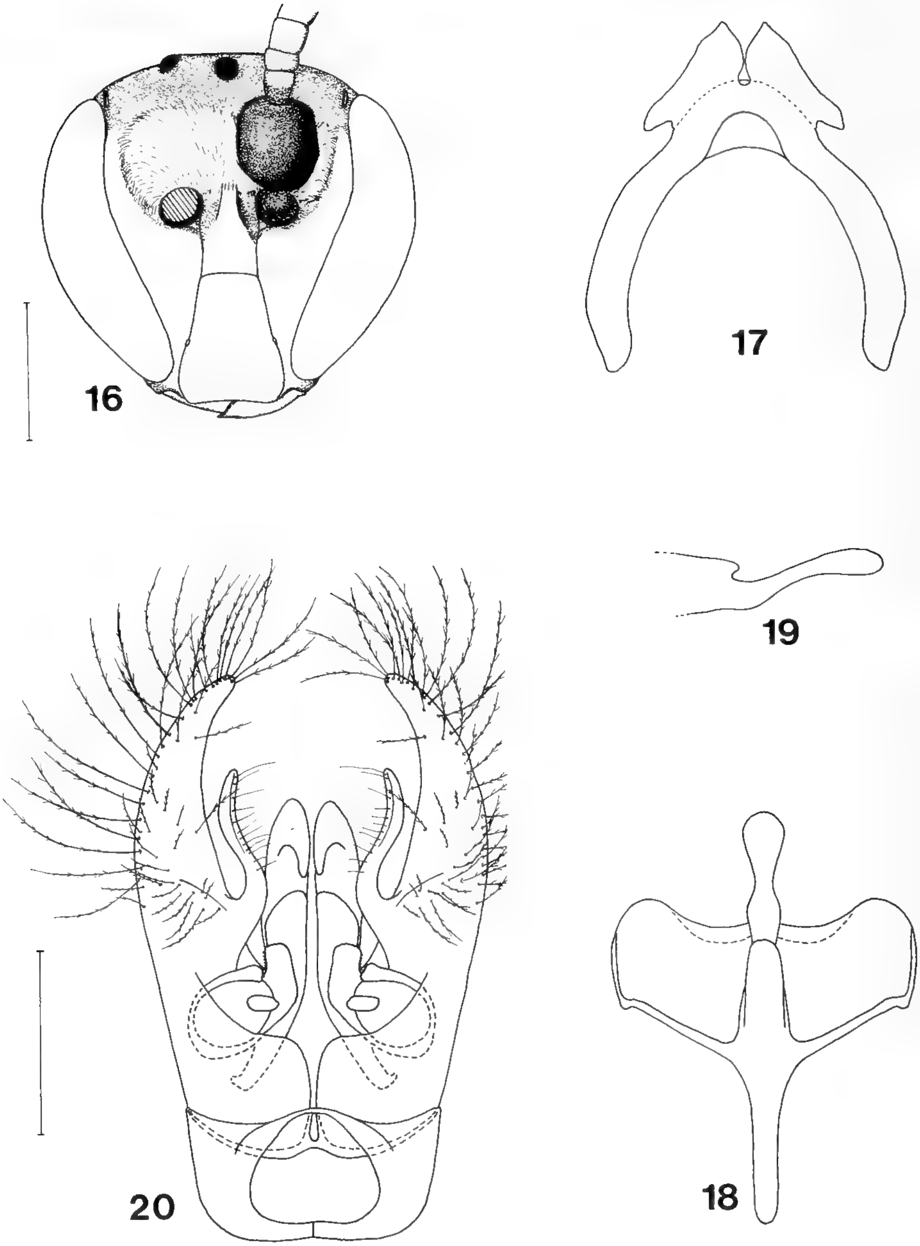
Thorax.—Mesoscutum 1.3–1.5 times broader than long; scutellum about 0.4 times length of mesoscutum, flattened; metanotum flattened.

Mesoscutum, scutellum, and metanotum slightly shiny between contiguous to subcontiguous, fine punctures; mesopleuron moderately shiny between subcontiguous to dense, fine punctures; metapleuron slightly shiny, finely rugosopunctate. Side of propodeum moderately shiny, punctures fine and irregularly spaced from contiguous to dense, becoming subcontiguous on stigmatal area and disc; basal area irregularly and moderately rugose in middle, becoming finely roughened laterad.

Abdomen.—Disc of first tergum slightly shiny, transversely microlineate, and with scattered minute punctures; disc of second tergum moderately shiny, less sharply transversely microlineate, punctures weak, ultraminute to minute, dense to sparse.

Pilosity.—First tergum with apicolateral patch of appressed white hairs.

Color.—Blackish. The following yellow: mandible, except reddish margins; large median spot on labrum; clypeus; supraclypeal area; lateral face mark, terminating on eye margin at level about midway between antennal socket and



Figs. 16–20. *Hylaeus* (*Gongyloprosopis*) *cruentus*, male: 16, frontal view of head; scale line = 0.50 mm. 17, sternum eight; 18, sternum nine; 19, profile of distal process of sternum nine; 20, genitalic capsule, ventral view; scale line = 0.25 mm.

anterior ocellus; lateral stripe on scape, extended mesad above; pronotal collar, broadly interrupted in middle; pronotal lobe; tegular spot; apical spot on all femora; outer face of pro- and mesotibia; basal half and apical annulus of metatibia. Tarsi reddish yellow except whitish meso- and metabasitarsi. Flagellum reddish brown, paler beneath. Wings clear, very weakly brownish, veins and stigma light brown.

Female, measurements (mm): HL 1.18–1.28 (1.25); HW 1.15–1.30 (1.25); WL 2.9–3.2 (3.2); TL 3.8–4.3 (4.3).

Head.—Moderately broad, HW 0.97–1.03 (1.00) × HL. Scape short, SL 0.24–0.27 (0.25) × HL; slender, SL 2.67–3.25 (3.17) × SW; first flagellar segment longer than second and third segments; third flagellar segment about half as long as pedicel. Eyes moderately convergent below, UFW 1.45–1.68 (1.50) × LFW.

Clypeus slender, CW 0.85–0.97 (0.91) × CL; BCW 0.56–0.62 (0.57) × CW, 1.21–1.50 (1.31) × IAD, 1.89–2.43 (1.89) × ASD, 1.22–1.50 (1.42) × COD. Frontal shield about one-third longer than greatest width, apex broad, FSW 1.00–1.29 (1.00) × ASD. Interocellar distance about twice OD, subequal to ocellocular distance.

Clypeus and supraclypeal area slightly shiny, surface appearing granulose between very obscure, sparse to scattered, fine punctures; lateral, maculate area similar but a little more shiny; frontal shield dull between contiguous, fine punctures, except along deeply impressed midline; face and preocciput slightly shiny between contiguous to subcontiguous, fine punctures; gena slightly shiny, irregularly lineate between sparse to scattered, minute to fine punctures; punctures of vertex fine, dense to close.

Facial fovea ending above very close to inner eye margin.

Thorax.—Mesoscutum 1.3–1.4 times wider than long; scutellum flattened, about 0.4 times length of mesoscutum; metanotum flattened.

Mesoscutum slightly shiny between subcontiguous, fine punctures; scutellum similar but a little shinier; metanotum moderately shiny between subcontiguous to dense, minute to fine punctures; mesopleuron moderately shiny between subcontiguous to dense, fine punctures; metapleuron weakly shiny, finely rugosopunctate. Side of propodeum, disc, and stigmatal area moderately shiny between contiguous to subcontiguous, fine punctures; basal area coarsely reticulorugose in center, roughened laterad, slightly shiny.

Abdomen.—Disc of first tergum with satiny luster from ultraminute transverse lineation, with scattered, obscure, ultraminute punctures; disc of second tergum similar but impunctate or with scattered, very obscure, ultraminute punctures.

Pilosity.—First tergum with apicolateral patch of appressed white hairs.

Color.—Blackish, clypeus largely suffused with reddish; mandible and labrum reddish; antenna reddish brown, flagellum paler beneath; scape paler externally. The following yellow: weak preapical clypeal spot (sometimes absent); lateral face mark, to lower end of fovea; pronotal collar, broadly interrupted in middle; pronotal lobe; tegular spot; outer stripe, incomplete, on protibia; basal half and apical annulus of metatibia; most of metabasitarsus. Mesotibia and tarsal segments reddish yellow. Wings clear, faintly brownish, veins and stigma medium brown.

Type material: Holotype male, allotype, 19 male and 13 female paratypes: Ile Royal, Iles du Salut, FRENCH GUIANA, 4 Mar. 1977 (C. D. Michener). Holotype, allotype, and most paratypes in UKAN; 5 male, 4 female paratypes in LACM.

Etymology: From Greek, *diktyotos* (reticulate or net-like), in reference to the distinctly sculptured propodeal base.

Additional material (not paratypes): *French Guiana:* 5 ♂♂, 2 ♀♀, 14 km SE Sinnamary, 7 Oct. 1976; 1 ♂, 6 ♀♀, Kourou, 28 Feb. 1977; 2 ♀♀, 7 km SW Kourou, 7 Oct. 1976 (all C. D. Michener; UKAN); 1 ♀, Montagne de Pere, Kourou, 10 Oct. 1976 (Otis, Winston, and Michener; UKAN); 1 ♀, 10 km NW Kourou, 10 Oct. 1976 (D. Roubik; UKAN); 1 ♂, Kourou, Beach NW, 21 Dec. 1976 (D. Roubik; UKAN). *Trinidad:* 1 ♂, no further locality (R. Thaxter; MCZ); 6 ♂♂, 5 ♀♀, Cumuto, 14 Feb. 1965 (J.G. Rozen; AMNH).

Discussion: The female of this species, as well as those of *H. rawi* and *H. extrinsecus* (and presumably that of *H. phaeoscapus*) will go to *H. cruentus* in the key by Moure (1960); *H. cruentus,* however, belongs to another subgenus (see below). These females differ from that of *H. cruentus* in that the sculpture of the propodeal triangle, when present, consists of fine, irregularly anastomosing rugulae. In *H. cruentus,* the propodeal triangle is crossed by a subbasal, transverse carina, anterior to which there are a few weak rugulae that define more or less quadrate areolae. Also, the first gastric tergite of *H. cruentus* is smooth and shiny between scattered minute punctures, rather than transversely microlineate as in the *Hylaeana* species.

Females of the three *Hylaeana* species described here are very similar to one another. In both *H. rawi* and *H. extrinsecus,* the basal area of the propodeum is without obvious rugulae; in *H. dictyotus,* the midbasal area is conspicuously, though finely, sculptured with a network of irregularly anastomosing rugulae, which occupy almost half the total area of the basal triangle. A distinct apicolateral patch of appressed plumose hairs is present on the first gastric tergum in *H. dictyotus.* Such a patch is not present in *H. rawi* and probably not in *H. extrinsecus.*

The females of *H. rawi* and *H. extrinsecus* are less easily separated, though the yellow mark on the lower outer orbit of *H. extrinsecus,* if consistent, would be useful. The clypeus of *H. rawi* is wholly ferruginous rather than conspicuously yellow-marked as in *H. extrinsecus.* Clypeal color is, however, unstable and should not be relied upon. The best feature to separate females of these two species would seem to be the punctation of the frons. In *H. rawi,* the punctures are distinctly separated; in *H. extrinsecus,* they are contiguous.

Although the subgenus *Hylaeana* is not a particularly large group, no key for the species can be attempted at this time. A large proportion of the species appear to be undescribed, and until these can be included, any key would be premature.

Gongyloprosopis NEW SUBGENUS

Diagnosis: Separable from New World subgenera by the following combined characteristics. Pronotal collar without transverse crest or ridge; first and second terga shiny between fine, scattered punctures; oblique and transverse propodeal carinae absent. *Male:* Scape bulbous in frontal view (Figs. 16, 21, 25); frons with densely matted, short, plumose hairs. *Female:* Frontal shield broad above; facial fovea nearer eye than lateral ocellus.

Description: *Male:* Mandible short, broad, lower margin straight for most of its length; preapical tooth present. Labrum broader than long, with shallow median depression between low, rounded submedian ridges. Clypeus longer than broad, narrowly separated from lower end of inner eye margin. Frontal shield reduced to a pair of short, obscure ridges between antennal sockets. Frons with dense, matted, short, plumose hairs between level of antennal sockets and anterior ocellus. Short fovea present on vertex between eye and lateral ocellus. In frontal view, scape bulbous; first flagellar segment shorter than second, both broader than long.

Pronotal collar without transverse crest or elevated ridge, lateral angles sharp in dorsal view. Lateral propodeal carina high and sharp, oblique and transverse carinae absent; basal area without rugulae behind transverse subbasal ridge, or entirely smooth (without subbasal ridge).

First and second gastric terga shiny between scattered, fine punctures; seventh tergum with distinct median emargination. Sternum eight with apical lobes oblique and simple (Fig. 17) or transverse and complex (Figs. 22, 26). Sternum nine with distal process either more or less hastiform in ventral view (Figs. 23, 27) or short and somewhat swollen at base and apex (Fig. 18). Gonocoxite, in ventral view, moderately stout, outer margin curved, apex subacute or narrowly rounded; beset with numerous long, barbulate to plumose setae (Figs. 20, 24, 29).

Female: Mandible short, broad, preapical notch distinct. Labrum broader than long, with a pair of low, rounded, submedian swellings. Clypeus longer than broad, narrowly separated from lower end of inner eye margin. Frontal shield sharply marginate, apex broad. Facial fovea ending above nearer to eye margin than to lateral ocellus. Preoccipital ridge sharp, extending to gular area.

Pronotal collar without transverse crest or elevated ridge; lateral angle, in dorsal view, sharp. Lateral carina of propodeum present, oblique and transverse carinae absent; basal area irregularly vermiculorugose and with more or less distinct transverse subbasal ridge.

First and second gastric terga shiny between scattered, fine punctures. Gradulus of tergum two very faint, almost absent, pregradular area not differentiated from postgradular area.

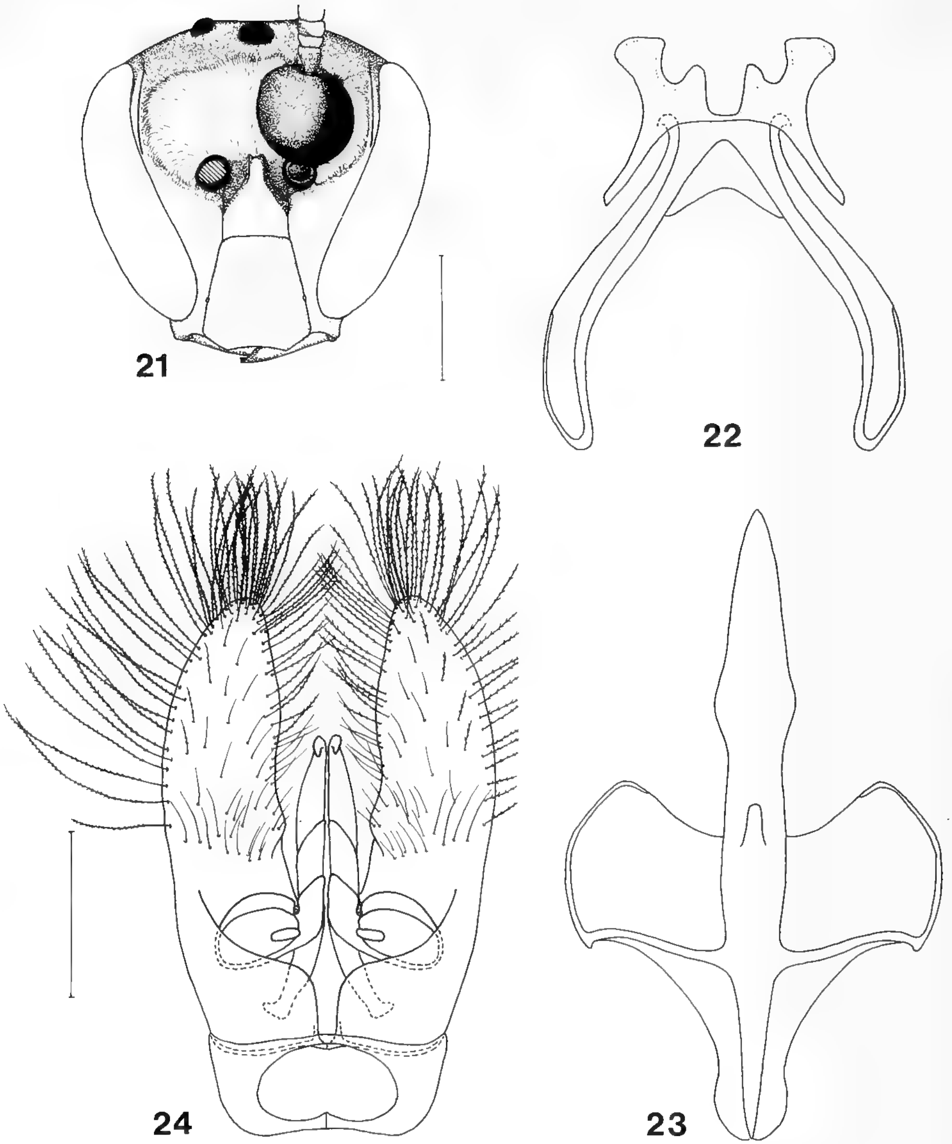
Type species: *Prosopis cruenta* Vachal, 1910.

Etymology: From Greek, *gongylos* (ball) and *Prosopis* (an old generic name for *Hylaeus*); in allusion to the shape of the male scape.

Discussion: In addition to the type species, *Gongyloprosopis* includes *H. orbicus* (Vachal) and *H. preposterosus,* described below.

Males of this subgenus are easily recognized by the greatly swollen scape and the dense mat of very short, plumose hairs covering most of the frons. In posterior view, the scape is more or less concave and with a transverse or oblique depression. In *H. cruentus,* there is a deep, reniform pit at about the middle of the posterior face and another, much smaller pit near the inner margin (Fig. 30). A small, oblique pit is present in *H. orbicus,* situated below the middle, near the inner margin (Fig. 31).

Females are, as usual in *Hylaeus,* much less readily characterized. Among the Neotropical subgenera, they may be separated by the lack of a crest on the pronotal collar and the lack of oblique and transverse propodeal carinae (unlike *Hylaeopsis*) and by the presence of a sharp lateral propodeal carina and the smooth first gastric tergum (unlike *Hylaeana*). In this sex, *Gongyloprosopis* is most like the Holarctic subgenus *Prosopis* and there is no clear distinction between the females of these subgenera.

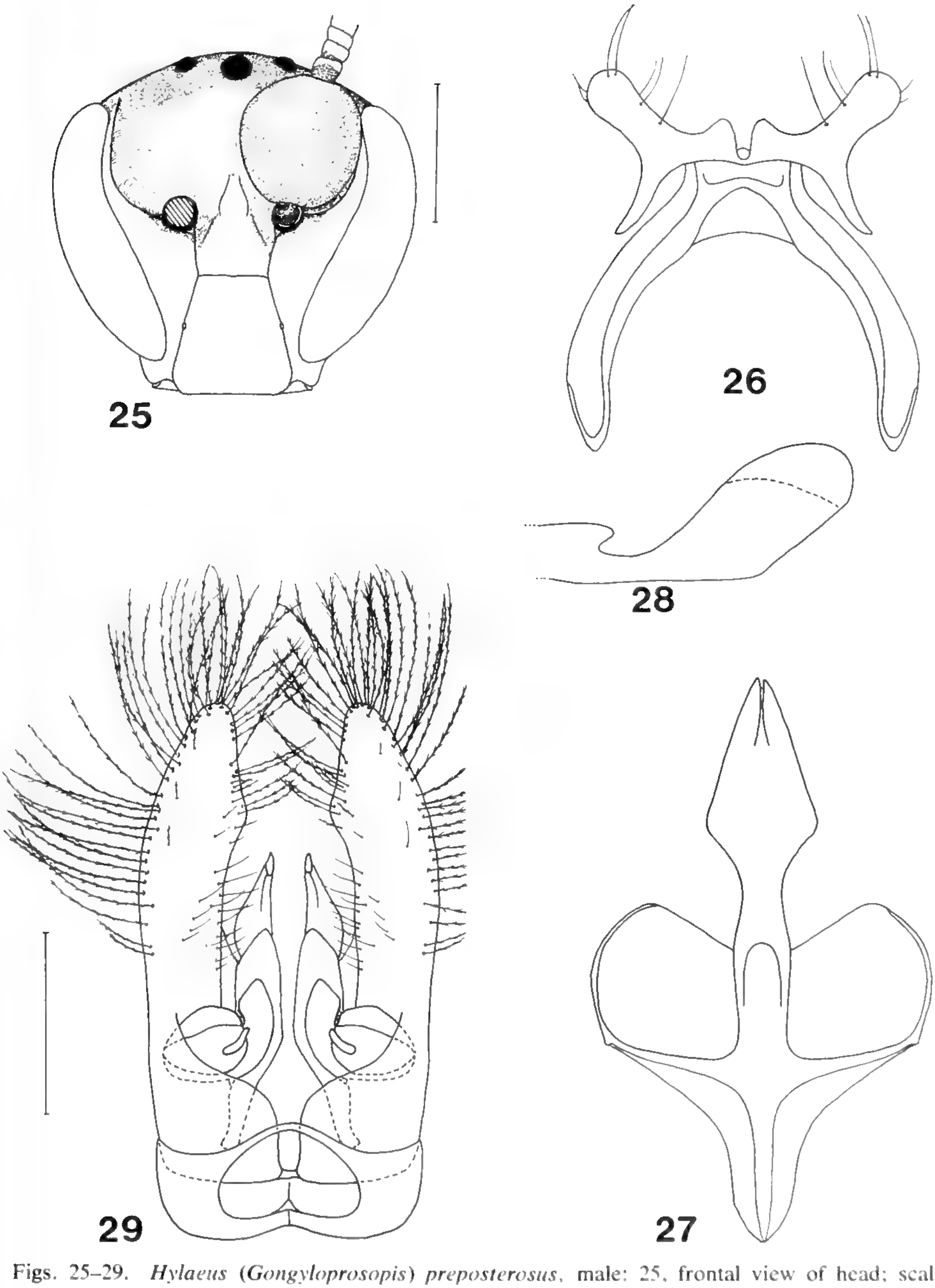


Figs. 21–24. *Hylaeus* (*Gongyloprosopis*) *orbicus*, male: 21, frontal view of head; scale line = 0.50 mm. 22, sternum eight; 23, sternum nine; 24, genitalic capsule, ventral view; scale line = 0.25 mm.

Hylaeus (*Gongyloprosopis*) *cruentus* (Vachal)
Figures 16–20, 30, 32

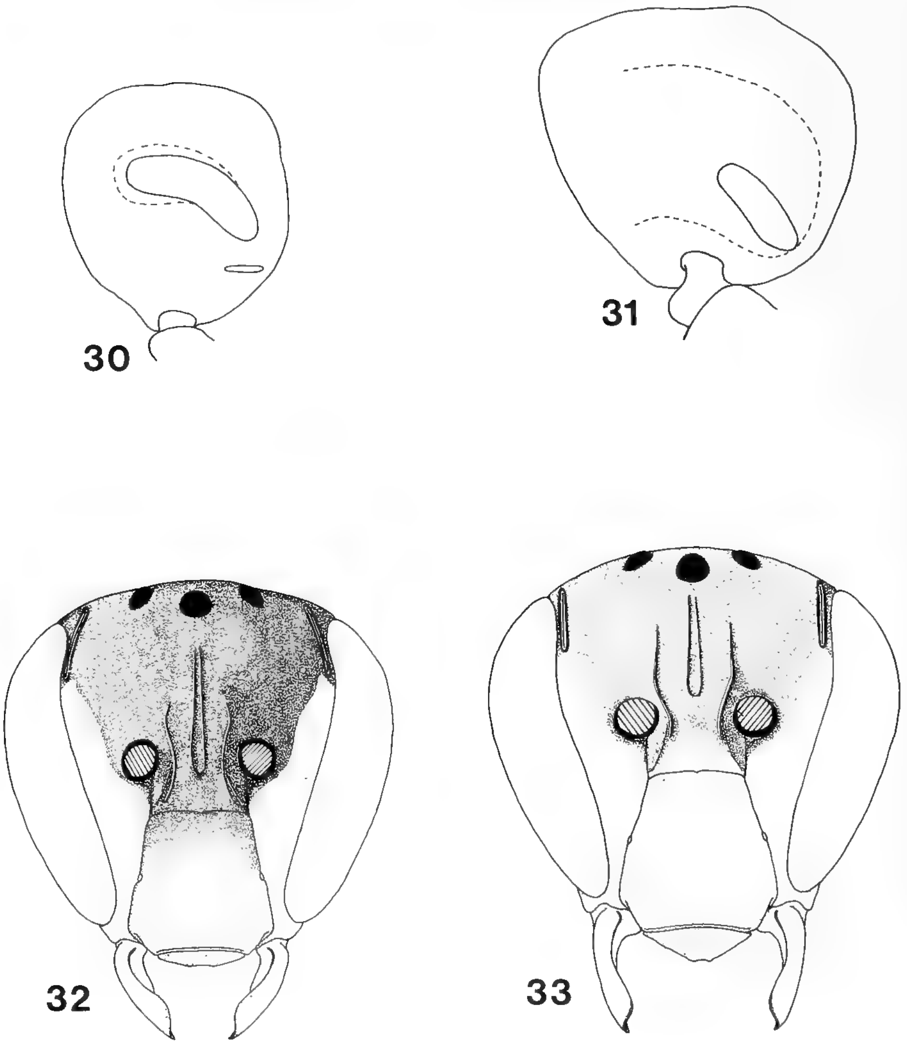
Specimens examined: *French Guiana:* 15 ♂♂, 10 ♀♀, Ile Royal, Iles du Salut, 4 Mar. 1977 (C. D. Michener; UKAN).

Discussion: *Prosopis cruenta* was based on a single female from an unknown locality in British Guiana (Guyana). Moure (1960) redescribed the type, which is in the Paris Museum. The females I have seen agree closely with that redescrip-



Figs. 25–29. *Hylaeus* (*Gongyloprosopis*) *preposterosus*, male: 25, frontal view of head; scale line = 0.50 mm. 26, sternum eight; 27, sternum nine; 28, profile of distal process of sternum nine; 29, genitalic capsule, ventral view; scale line = 0.25 mm.

tion. The amount of ferruginous on the clypeus is variable; in some specimens, the clypeus is almost wholly reddish and, in others, it is largely blackish. The first gastric tergum is mostly bright ferruginous but with considerable blackish along the posterior margin and in the middle. Sublateral patches of appressed



Figs. 30–33. *Hylaeus* (*Gongyloprosopis*) spp. 30, posterior view of male scape, *H. cruentus*; 31, same, *H. orbicus*. 32, frontal view of female head, *H. cruentus*; 33, same, *H. preposterosus*.

white hairs are present on the apical margins of the first and second gastric terga, though worn off in some specimens (including the type).

Although Moure (1960) thought that *H. cruentus* might prove to be the female of *H. orbicus*, the males here associated with the *H. cruentus* females are clearly distinct from *H. orbicus*. The association is based largely on the similarity in the sculpture of the basal area of the propodeum. These males also differ from those of *H. orbicus* in the less swollen scape, the entirely yellow clypeus, and the distinctive genitalic structure.

In the males here presumed to be those of *H. cruentus*, there is a peculiar, inner, ventral process arising near the base of the gonocoxite (Fig. 20). This structure is unique among the Neotropical *Hylaeus* I have studied. The form of the genitalia and associated structures is very different from that of the other two species here placed in *Gongyloprosopis*. The temptation to propose another subgenus for *H. orbicus* and *H. preposterosus* is strong, but there are so many other similarities among these three species that they are best left together for the present. When the Neotropical *Hylaeus* are better known, this conclusion can be reconsidered if necessary.

Hylaeus (Gongyloprosopis) orbicus (Vachal)
Figures 21–24, 31

Specimens examined: *French Guiana:* 3 ♂♂, Ile Royal, Iles du Salut, 4 Mar. 1977 (C. D. Michener; UKAN).

Discussion: This species was based on a single male from an unknown locality in British Guiana (Guyana). The type is in the Paris Museum and was redescribed by Moure (1960). The three specimens I examined agree well with Moure's redescription except that in two there is no yellow on the clypeus. Instead, a broad median area is very light ferruginous.

The female is unknown but probably is very similar to that of *H. cruentus*. The basal area of the propodeum might differ from that of *H. cruentus* in lacking a distinct subbasal ridge.

Hylaeus (Gongyloprosopis) preposterosus new species
Figures 25–29, 33

Diagnosis: Separable from *H. cruentus* and *H. orbicus* by the following combined characteristics. *Male:* Face marks whitish; scape brown; basal area of propodeum roughened behind transverse subbasal ridge; first and second terga with apicolateral hair patches; sternum eight with setae. *Female:* Lateral face marks pale yellowish; metanotal punctures close; apicolateral hair patch of third tergum as dense as that of second.

Description: *Male, measurements (mm):* HL 1.35; HW 1.36; WL 3.5; TL 3.1.

Head.—Moderately broad, HW 1.01 × HL. Scape short, SL 0.36 × HL, bulbous in frontal view, SL 1.03 × SW; first two flagellar segments transverse, subequal in length, third segment slightly broader than long. Eyes very strongly convergent below, UFW 1.80 × LFW.

Clypeus narrow, CW 0.86 × CL; BCW 0.60 × CW, 1.15 × IAD, 1.50 × ASD, 1.07 × COD. Frontal shield very short, consisting of a pair of weakly bowed, subparallel ridges between antennal sockets, apex narrow, FSW 0.40 × ASD. Interocellar and ocellocular distances subequal, about 2 × OD.

Punctures of clypeus, supraclypeal area, and paraocular area fine, dense to close on clypeus and supraclypeal area, close to sparse on paraocular area, interspaces slightly shiny. Front face of scape with sparse, fine punctures. Gena slightly shiny and microlineolate between somewhat elongate, dense punctures.

Thorax.—Mesoscutum about 1.4 times wider than long; scutellum flattened, about 0.4 times length of mesoscutum; metanotum flattened.

Mesoscutum slightly shiny between fine, subcontiguous to dense punctures; scutellum similar, but punctures more separated in center; metanotum slightly shiny between fine, contiguous punctures; mesopleuron slightly shiny, punctures fine, contiguous to subcontiguous; metapleuron dull, finely rugosopunctate. Side of propodeum slightly shiny, finely rugosopunctate; stigmatal area and disc similar but moderately rugosopunctate; basal area with a thin transverse subbasal ridge, anterior to which are a number of coarse, irregular areolae; behind subbasal ridge, a few irregular rugulae and areolae.

Abdomen.—Disc of first tergum shiny between sparse to scattered, fine, and interspersed minute, punctures; disc of second tergum less shiny, obscurely lineolate between sparse, minute punctures.

Pilosity.—First two gastric terga with apicolateral patches of appressed white hair.

Color.—Blackish. The following whitish: large inverted triangle on clypeus; supraclypeal area; paraocular area, including narrow extension along inner orbit to top of eye; narrow line on either side of pronotal collar; margin of pronotal lobe. The following ferruginous: mandible; labrum; malar area; clypeus, except as noted above; flagellum, darker above; tibiae, except dark irregular blotches; tarsi; tegula. Scape brown. Wings strongly transparent brownish; veins and stigma dark brown. First gastric tergum bright ferruginous with brownish margin in middle.

Female, measurements (mm): HL 1.32–1.43 (1.43); HW 1.38–1.50 (1.50); WL 3.3–3.7 (3.7); TL 4.4–4.8 (4.8).

Head.—Moderately broad, HW 1.05 × HL. Scape moderately long, SL 0.30–0.36 (0.36) × HL; slender, SL about 4 × SW; first three flagellar segments subequal in length, each shorter than pedicel. Eyes moderately convergent below, UFW 1.54–1.58 (1.54) × LFW.

Clypeus slender, CW 0.86–0.87 (0.86) × CL; BCW 0.69–0.71 (0.69) × CW, 1.29–1.33 (1.29) × IAD, 2.22–2.44 (2.44) × ASD, 1.66–1.69 (1.69) × COD. Frontal shield about one-third longer than greatest width, apex broad, FSW 1.56–1.89 (1.89) × ASD. Interocellar distance less than twice OD, subequal to ocellocular distance.

Clypeus, supraclypeal area and paraocular area slightly shiny between close, minute punctures; frontal shield with fine, longitudinal rugulae separated by rows of fine to moderate punctures, which are shiny within; frons slightly shiny between fine, subcontiguous punctures; vertex similar but duller, punctures becoming less distinct on preocciput; gena slightly shiny, finely lineolate between dense to close, fine punctures.

Facial fovea ending above about one-fourth of distance between eye and lateral ocellus.

Thorax.—Mesoscutum 1.3–1.4 times wider than long; scutellum flat, about 0.4 times length of mesoscutum; metanotum weakly convex.

Mesoscutum slightly shiny, punctures fine, subcontiguous at sides, becoming dense to close in posteromedian area, punctures obscured by distinct transverse lineation; scutellum slightly shinier, lineation less sharp, punctures fine, dense to close; metanotum dull, with subcontiguous minute to fine punctures; mesopleuron dull, appearing almost granulose, between fine to moderate, subcontiguous to dense punctures; metapleuron and side of propodeum weakly shiny, finely to moderately rugosopunctate; stigmatal area and propodeal disc moderately rugosopunctate; basal area as in male.

Abdomen.—Disc of first tergum shiny, polished between minute, sparse to scattered punctures; disc of second tergum shiny, slightly roughened, between scattered, ultraminute punctures.

Pilosity.—First three terga with apicolateral patches of appressed white hairs.

Color.—Blackish. The following pale yellowish: lateral face mark, ending broadly at lower end of fovea; dorsal stripe on either side of pronotal collar; much of pronotal lobe; tegular spot; basal spot on each tibia. The following ferruginous: mandible; labrum; malar area; all or most of clypeus. First gastric tergum bright ferruginous. Dull ferruginous mark present or absent on supraclypeal area. Antenna reddish brown, lighter beneath; legs light reddish brown with irregular darker blotches on femora and tibiae. Wings as in male.

Type material: Holotype male: 20 km W Laranjeiras, Dept. Beni, BOLIVIA, 3–5 Aug. 1954 (J. K. Bouseman and J. Lussenhop). Allotype: Rio Itenez, Pampa de Meio, Dept. Beni, BOLIVIA, 11–13 Sept. 1954 (J. K. Bouseman and J. Lussenhop). Paratype female: Rio Itenez at mouth of Rio Baures, Dept. Beni, BOLIVIA, 30 Sept. 1954 (J. K. Bouseman). Holotype and allotype in AMNH, paratype in LACM.

Etymology: From Latin, *praeposterus* (absurd).

Discussion: The male of this species is similar to that of *H. cruentus* in propodeal structure, but its genitalic features are more like those of *H. orbicus,* with which it also agrees in having a partially ferruginous clypeus. The maculate portion of the upper inner orbit is elevated and visible in lateral view; its inner margin is abrupt and extends as a sharply cariniform ridge which turns mesad to the lower margin of the antennal socket. A raised cariniform ridge is present also in male *H. orbicus* but is parallel with the inner eye margin and fades away at about the level of the lower margin of the antennal socket.

The female of *H. preposterosus* is very similar to that of *H. cruentus*. In *H. cruentus* females, the punctures of the frons, above the frontal shield, are not in definite rows separated by fine ridges, and the metanotal punctures are sparse to scattered. The metapleuron and side of the propodeum in *H. cruentus* have numerous very short, plumose, subappressed hairs, which do not conceal the surface. In *H. preposterosus,* the hairs are longer and denser so that the surface is partially obscured.

The following key will separate those species currently placed in *Gongyloprosopis*.

1a. Antenna 12-segmented (female) 2
b. Antenna 13-segmented (male) 3
2a. Punctures of frontal shield and middle of frons in rows separated by fine, raised, subparallel ridges; metanotal punctures subcontiguous; integument of side of propodeum partially concealed by subappressed plumose pubescence .... *preposterosus*
b. Punctures of frontal shield and middle of frons irregularly spaced and not separated by distinct raised ridges; metanotal punctures sparse to scattered; side of propodeum with very short, subappressed, plumose hairs, which do not conceal integument .... *cruentus*
3a. Basal triangle of propodeum with transverse subbasal ridge, behind which surface is finely and irregularly rugulose 4
b. Basal triangle without transverse subbasal ridge and without network of fine rugulae .... *orbicus*
4a. Clypeus entirely yellow; scape width 0.33–0.35 times face width at level of ocular sinuation; gonocoxite with digitiform ventral process .. *cruentus*

b. Clypeus partially ferruginous; scape width 0.47 times face width at level of ocular sinuation; gonocoxite without digitiform ventral process .... *preposterosus*

Acknowledgments

I am very much indebted to D. C. Rentz, who loaned the types of Cresson's Neotropical species, thus enabling me to settle some important questions regarding the status of these species. Notes on the F. Smith types were generously provided by I. H. H. Yarrow.

A. W. Raw sent material from his Jamaican collection. Institutional specimens were sent by H. E. Evans (MCZ), C. D. Michener (UKAN) and J. G. Rozen, Jr. (AMNH).

Literature Cited

Cockerell, T. D. A. 1905. American Hymenoptera: new bees and a new proctotrypid. Ann. Mag. Natur. Hist. (ser. 7), 15:200–204.

———. 1912. Descriptions and records of bees.—XLIV. Ann. Mag. Natur. Hist. (ser. 8), 9:554–568.

———. 1917. Descriptions and records of bees.—LXXVIII. Ann. Mag. Natur. Hist. (ser. 8), 19: 436–441.

———. 1918. Descriptions and records of bees.—LXXXI. Ann. Mag. Natur. Hist. (ser. 9), 1:418–425.

———. 1924. Expedition of the California Academy of Sciences to the Gulf of California in 1921. The bees (II). Proc. Calif. Acad. Sci. (ser. 4), 12:529–560.

———. 1941. Descriptions and records of bees.—CLXXII. Ann. Mag. Natur. Hist. (ser. 11), 8: 504–510.

———. 1949. Bees from Central America, principally Honduras. U.S. Natl. Mus. Proc., 98:429–490.

Cresson, E. T. 1869. Description of North American bees. No. 2. Boston Soc. Natur. Hist. Proc., 12:269–273.

Friese, H. 1916. Zur Bienenfauna von Costa Rica (Hym.). Stettiner Entomol. Zeit., 77:287–350.

———. 1921. Nachtrag zur Bienenfauna von Costa Rica. Stettiner Entomol. Zeit., 82:74–98.

———. 1925. Neue neotropische Bienenarten, zugleich, II. Nachtrag zur Bienenfauna von Costa Rica (Hym.). Stettiner Entomol. Zeit., 86:1–41.

Meade-Waldo, G. 1923. Fam. Apidae, Subf. Prosopidinae. *In* P. Wytsman, Genera Insectorum, Brussels, fasc., 18:1–45.

Michener, C. D. 1954. Bees of Panamá. Amer. Mus. Natur. Hist. Bull., 104:1–176.

Moure, J. S. 1960. Os tipos das especies Neotropicais de *Hylaeus* do colecáo Vachal no Museu de Historial Natural de Paris (Hymenoptera-Apoidea). Mus. Parense E. Goeldi Bol., 27:1–104.

Schrottky, C. 1903. Ensaio sobre as abelhas solitarias do Brasil. Mus. Paulista Rev., 5:330–613.

———. 1906. Contribución al conocimiento de las Himenópteros del Paraguay. Cient. Paraguayos An. (ser. 1), 6:1–32.

———. 1907. A contribution to the knowledge of some South American Hymenoptera, chiefly from Paraguay. Smithsonian Misc. Coll., 48:259–274.

Smith, F. 1879. Descriptions of new species of Hymenoptera in the collections of the British Museum. British Museum (Natural History), London, 240 pp.

Snelling, R. R. 1966a. Studies on North American bees of the genus *Hylaeus* 1. Distribution of the western species of the subgenus *Prosopis* with descriptions of new forms (Hymenoptera: Colletidae). Contrib. Sci. Los Angeles County, 98:1–18.

———. 1966b. Studies on North American bees of the genus *Hylaeus*. 3. The Nearctic subgenera (Hymenoptera: Colletidae) So. Calif. Acad. Sci. Bull., 65:164–175.

———. 1968. Studies on North American bees of the genus *Hylaeus*. 4. The subgenera *Cephalylaeus, Metziella* and *Hylaeana* (Hymenoptera: Colletidae). Contrib. Sci. Los Angeles County, 144:1–6.

———. 1970a. Studies on North American bees of the genus *Hylaeus*. 5. The subgenera *Hylaeus*, s. str. and *Paraprosopis* (Hymenoptera: Colletidae). Contrib. Sci. Los Angeles County, 180: 1–59.

———. 1970b. A new synonymy in the genus *Chilicola* (Hymenoptera: Colletidae). So. Calif. Acad. Sci. Bull., 70:52.

———. 1975. Taxonomic notes on some colletid bees of western North America with descriptions of new species (Hymenoptera: Colletidae). Contrib. Sci. Los Angeles County Mus. Natur. Hist., 267:1–9.

Timberlake, P. H. 1973. Revision of the genus *Pseudopanurgus* of North America (Hymenoptera, Apoidea). Univ. Calif. Publ. Entomol., 72:1–58.

Warncke, K. 1970. Beitrag zur Systematik und Verbreitung der Bienengattung *Prosopis* in der Westpaläarktis (Hymenoptera, Apoidea, Colletidae). Rech. agron. Gembloux Bull. (n.s.), 5: 745–768.

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Taxonomic Status of Some Neotropical Garter Snakes (Genus *Thamnophis*)

Robert G. Webb

Abstract.—Taxonomic status of some neotropical garter snakes (genus *Thamnophis*) by Robert G. Webb, *Bull. Southern California Acad. of Sci.* 81(1):26–40. Study of the black-necked garter snake, *Thamnophis cyrtopsis,* and of three other taxa of garter snakes from south of the Isthmus of Tehuantepec, Mexico, indicates that 1) *T. cyrtopsis collaris* (Jan) occurs in the Mexican state of Chiapas and in Guatemala, 2) *T. cyrtopsis* var. *fulvus* (Bocourt) is a valid species occurring in Chiapas, Guatemala, Honduras, and El Salvador, 3) *T. sumichrasti cerebrosus* Smith has been incorrectly referred to the species *sumichrasti* and *cyrtopsis,* and seems to have affinities with *T. marcianus,* and 4) *T. sumichrasti salvini* Smith, Nixon and Smith is a synonym of *T. cyrtopsis collaris.*

This study is the result of an attempt to ascertain the status of the black-necked garter snake, *Thamnophis cyrtopsis,* south of the Isthmus of Tehuantepec. A previous study of this widespread, polytypic species (Webb 1966) indicated the occurrence of the tropical, southernmost subspecies, *T. c. collaris,* in the Mexican state of Chiapas. In addition to *T. c. collaris,* the taxonomic status of three other named kinds of garter snakes that have been associated with *T. cyrtopsis* was investigated—1) *fulvus* Bocourt 1893; 2) *cerebrosus* Smith 1942; and 3) *salvini* Smith, Nixon, and Smith 1950. This paper, in anticipation of prior publication, was referenced as "in press" and some of the conclusions were included in a review of *T. cyrtopsis* (Webb 1980).

Methods and Materials

Only external morphological features are used to assess taxonomic status. Emphasis is placed on numbers of supralabials, dorsal scale rows, ventrals and subcaudals, and on aspects of pattern. The Dowling method (1951) is employed to count ventral scales (for types the maximum number is also indicated, e.g. 142+2). The following acronyms (cited in text) indicate the location of preserved specimens in museums as listed by Duellman et al. (1978): AMNH, BM, CAS, FMNH, KU, LACM, LSUMZ, MCZ, MNHP, MVZ, TCWC, UA, UIMNH, UMMZ, USNM, UTA; the acronym UTEP indicates Laboratory for Environmental Biology, University of Texas at El Paso.

Thamnophis cyrtopsis collaris (Jan)

The trans-isthmian specimens of *T. c. collaris* from Chiapas and Guatemala do not differ appreciably from those described elsewhere in Mexico (Webb 1966).

Color and pattern: The nuchal blotches are fused to form a black collar, indented posteriorly where the vertebral stripe terminates. The vertebral stripe is distinct, contrasting with the dark background, is usually confined to the vertebral row, and extends the length of the body and tail. The pale lateral stripe on the second and third dorsal scale rows is either ill-defined or absent with the first three scale rows whitish. Small black marks on edges of scales are either scattered on the first three scale rows or are virtually absent. The largest ventrolateral markings are those regularly spaced and overlapping the first scale row and adjacent edges of the ventral scales; often there is slightly darker pigment between these dark markings that suggests an indistinct pale brown stripe. These lateral black marks are most prominent, forming spots (mostly on first scale row), on the neck. The dark dorsolateral areas masque alternating black blotches that are most evident anteriorly; small scattered black specks (as well as white marks) are especially evident when scales are spread. The black suture marks between the supralabials are absent between infralabials (except posteriormost suture). The ventral surfaces are immaculate, although scattered black marks may occur laterally on the anterior edges of some ventrals. The tongues are red with black tips. A skull of a female from Guatemala (MCZ 64098) has 27 maxillary teeth. A Chiapan specimen of *Thamnophis cyrtopsis collaris* is photographed in Fig. 1.

Scutellation: Dorsal scale rows are invariable 19-19-17. There are eight supralabials; the only variant combination of 8–9 occurs in four of 25 specimens. Ventrals in nine males average 152.2 (150–154), and in 11 females 147.3 (136–151). Subcaudals in seven males average 94.4 (90–97), and in six females 89.2 (86–92); one unsexed snake, probably female, has 85 subcaudals.

Distribution: South of the Isthmus of Tehuantepec, *Thamnophis cyrtopsis collaris* is known only from the Mexican state of Chiapas, and Guatemala (Fig. 4). Generally a lowland species, *T. c. collaris* penetrates into pine-oak forest to elevations as high as 2042 m (6700 ft, UA 26572, 26576). The distribution of *T. c. collaris* seems to fit the "subhumid corridor" distributional pattern described by Stuart (1954a). Specimens examined are documented in the section Locality Records.

Status of Taxon *Fulvus* Bocourt

Eutaenia cyrtopsis var. *fulvus* Bocourt 1893:777. Type-locality, "dans le département de la Haute Vera Paz (Guatemala)." Holotype, male, MNHP 94. Stuart (1948:9) mentioned that such labeled specimens are probably from the vicinity of Cobán.

Description of holotype: My observations generally agree with Bocourt's description of the holotype (1893:777–778) and his accompanying illustrations (Pl. LVII, Fig. 2). The non-colored illustrations (Figs. 2–2d) depict dorsal view of head-neck (2), side of head-neck (2a), ventral view of head-neck (2b), nasal scale (2c), and rostral scale (2d). The male (tail dissected) has 19-19-17-15 dorsal scale rows, 8-8 supralabials, 149+2 ventral scales, 67 subcaudals (tail incomplete), and is about 451 (body 348, tail 103) mm in total length. The vertebral stripe is ill-defined anteriorly, otherwise virtually absent. The dorsolateral areas are patternless. Dark nuchal blotches and spots on neck (first dorsal scale row) are indistinct. Unsloughed dorsal scales are brownish.

Description. Color and pattern: The nuchal blotches are blackish, or are ill-defined owing to non-contrast with dark brown dorsolateral areas, or to many scales of blotch being brown. The vertebral pale stripe is usually expanded anteriorly (about two and one-half or three scales wide) between the dark nuchal blotches. The nuchal blotches of some specimens have attenuated posterior ex-

Fig. 1. *Thamnophis cyrtopsis collaris,* UIMNH 6328, from Chiapas, showing prominent vertebral stripe.

tensions. The buffy vertebral stripe, mostly confined to the vertebral row, is not sharply defined, and may be virtually absent (UMMZ 106739). The vertebral stripe is most distinct anteriorly, at least on neck, and is absent (or very indistinct) posteriorly, but an indistinct stripe may extend the length of body (absent on tail). The indistinct pale lateral stripe (unsloughed scales), which may be scarcely evident, covers parts of the second and third dorsal scale rows; the first dorsal row is pale brown and slightly darker than the pale stripe, but the first row is slightly paler than the dorsolateral areas. The brown pigment of the first dorsal row encroaches ventrad covering the lateral edges of the ventral scales. The dorsolateral areas vary from olive brown to fulvous brown and are patternless except for black spotting anteriorly on the neck; rarely, spotting is evident the length of body (KU 94136). The anteriormost neck markings vary in size and in extent posteriorly, and may be partly joined forming vertical linear marks that encroach on the vertebral stripe. In juveniles the upper rows of black spots on either side may be confluent forming partial crossbands (FMNH 64715, Fig. 2). Distinct, and rather large, black spots usually occur in the neck region on the first scale rows (also covering adjacent parts of scales of second row and ventrals). Posteriorly the patternless dorsolateral areas may have black specks (confined to edges of scales); white flecks are evident when scales are spread, and black markings are intensified when scales are sloughed. The top of the head is brownish and about the same color as the dorsolateral areas. Black markings may occur on top of the head; these markings may be extensive forming a definite pattern (e.g., CAS 66976; FMNH 64715, 167114; MVZ 109363, 109424). Paired parietal spots, which may be partly encircled in black, may be absent. The black markings on the supralabial sutures are reduced to narrow lines. One specimen (UMMZ 106739) with an extensive dorsal head pattern also has abnormally thick, dark markings

Fig. 2. *Thamnophis fulvus*, showing characteristic dorsal pattern of adult, CAS 66974 (above), and occasional juvenile pattern, FMNH 64715 (below).

on the supralabial sutures. Infralabial black markings on sutures are lacking (occasional on posteriormost suture). Scales in the temporal regions are usually devoid of pattern, but may be partly black or have black margins, or have varying development of a thick barlike mark that crosses the anterior part of the anterior temporal (e.g., FMNH 30434, 64715, 167114; UMMZ 106739; MVZ 109363, 109424). Some of these extensive dorsal and lateral head patterns are illustrated in Fig. 3. The ventral surfaces are immaculate, but often the anterior margins of the ventral scales are narrowly blackened with the pigment thicker laterally form-

Fig. 3. Ornate head patterns of specimens of *Thamnophis fulvus*—A, FMNH 167114; B, MVZ 109363; C, MVZ 109424.

ing small spots, or the belly may have small diffuse, dusky markings, which may form a midventral stripe (UTA 7088). The tongues are entirely black (dark gray, slate, MVZ 130822; UMMZ 119759, N = 2; UMMZ 98288; UTA 6080, 7092). A skull of a Guatemalan specimen (UMMZ, S-1347) has 28 maxillary teeth.

Scutellation: The dorsal scale rows are characteristically 19-19-17; 21 scale rows may occur in the neck region, and 15 (11%) or 13 (0.4%) rows in front of anal plate. Supralabials usually number eight with the combination 8-8 most frequent (81%); less frequent combinations are 7-8 (10%), 8-9 (4%), 7-7 (3%), 6-6, 6-8, 9-9, and 9-10. Ventrals in 101 males average 145.1 (136–154), and in 113 females 141.4 (132–150). Subcaudals in 64 males average 70.3 (63–80), and in 97 females 62.6 (56–72).

Distribution: *Thamnophis fulvus* is confined to highland pine-oak forests in Chiapas (Central Highlands and Sierra Madre), Guatemala (Guatemalan Highlands, Sierra de Chuacús-las Minas, and Sierra de los Cuchumatanes-Alta Verapaz Highlands), and western Honduras and northern El Salvador (Fig. 4). The recorded elevations range from 1636 to 3353 m (5369 to 11,000 ft). Specimens examined are documented beyond in the section Locality Records.

Status: Smith (1942:112) referred to the taxon as *Thamnophis sumichrasti fulvus*. Rossman (1965) discussed the involved taxonomic history of the name *sumichrasti,* which is now regarded as the valid name for a distinct, monotypic species occurring in highland areas of eastern Mexico. The highland populations of garter snakes across the Isthmus of Tehuantepec are currently referred to as *Thamnophis cyrtopsis fulvus* (Rossman 1965:243, 1971:2), a name-combination first employed by Stuart (1954b:59). Garter snakes referable to Bocourt's *fulvus* bear a general resemblance to *T. cyrtopsis* in having a narrow vertebral stripe, the pale lateral stripe on the second and third scale rows, and in having dark nuchal blotches.

The contrasting striped pattern (distinct vertebral stripe length of body) and black collar easily distinguish *Thamnophis cyrtopsis collaris* from *Thamnophis fulvus*. *Thamnophis c. collaris* has a much longer tail than *T. fulvus*; the range of variation in subcaudal counts for the few Chiapan and Guatemalan specimens of *T. c. collaris* (seven males, 94.4, 90–97; six females, 89.2, 86–92) does not approach that of specimens of *T. fulvus* (64 males, 70.3, 63–80; 97 females, 62.6, 56–72) regardless of sex. If data from a larger sample, based on other Mexican specimens of *T. c. collaris* (Webb 1966:60), is utilized for comparison (28 males, 97.5, 77–109; 39 females, 88.7, 76–103) the significance of relative tail length is maintained. *Thamnophis fulvus* also differs from *T. c. collaris* in having a completely black tongue.

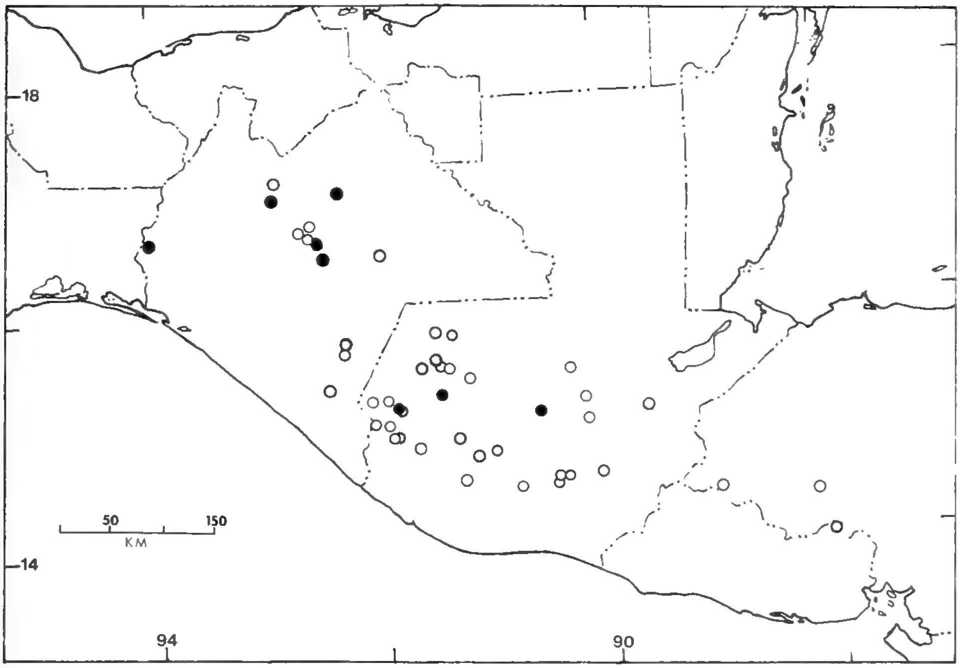

Fig. 4. Map of southern Mexico and northern Central America showing distribution of *Thamnophis cyrtopsis collaris* only in Chiapas and Guatemala (solid circles), and known distribution of *Thamnophis fulvus* (open circles).

The two taxa also differ in hemipenial morphology. The hemipenis in both *Thamnophis fulvus* and *Thamnophis cyrtopsis collaris* is bilobed with a nude apex and a simple straight sulcus spermaticus, and has differentiated spinose ornamentation with enlarged basal hooks (terminology of Dowling and Savage 1960). The proximal and distalmost spines are smallest and grade into an area of slightly larger and more dispersed spines just distal to the enlarged hooks. The basal area in the vicinity of the sulcus and hooks is mostly bare, relatively devoid of small spines (but spines dense on asulcate side). Both taxa have two pair of enlarged basal hooks on either side of the sulcus with the medial pair smaller than, and slightly distal to, the lateral pair. There is no further modification of this groundplan in *T. fulvus* (Fig. 5A). The drawing of the hemipenis of *fulvus* is based on an examination of the everted hemipenes of 16 specimens (UMMZ 91050, 94636, 98288, 98290, 98294–96, 100513, 106738; UTA 2462, 2465, 2467, 5544, 5721, 6604, 6611), all of which are consistent in the above-mentioned features, except for two specimens—the right organ of UMMZ 98288 has only one enlarged medial hook (left organ has two medial hooks), and the left organ of UTA 2467 has only one medial hook, which is as large as either lateral hook (right organ has two medial hooks). The size of the medial hooks in *T. fulvus* seems to vary slightly relative to that of the lateral hooks.

In *Thamnophis cyrtopsis collaris* a smaller hook (but larger than surrounding spines) occurs between and slightly laterad to the two large lateral hooks (Fig. 5B, left). The individual hooks seem to be longer and more slender than those of

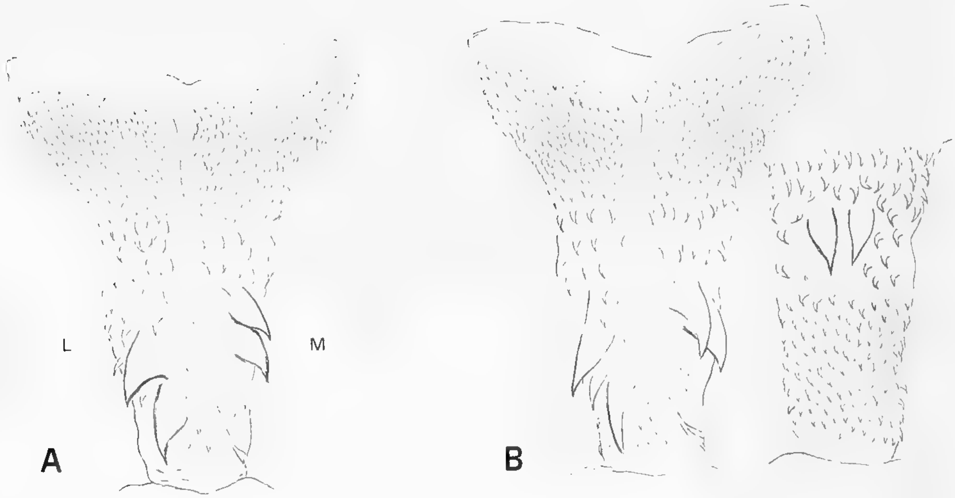

Fig. 5. Sulcate view of right hemipenis (L indicates lateral, M medial) of *Thamnophis fulvus* (A) and *Thamnophis cyrtopsis collaris* (B, incomplete drawing at right showing asulcate pair of hooks).

T. fulvus. In addition, the hemipenis of *T. c. collaris* is adorned with another pair of enlarged hooks (about size of medial pair) more distal than the other pairs of hooks and on the asulcate side (Fig. 5B, right). The drawing of the hemipenis of *T. c. collaris* is based on an examination of three specimens (UTEP 3390–92) from Durango-Sinaloa, Mexico, all of which agree in the above-mentioned features; presumably these features obtain in specimens of *T. c. collaris* from Chiapas and Guatemala. Of interest is the hemipenis of *T. cyrtopsis cyrtopsis* (UTEP 1701–02, 2889 from New Mexico and Texas) that resembles that of *T. c. collaris* in having two medial and three lateral basal hooks, but differs in lacking the distal asulcate pair. The hemipenial morphology of taxa of *Thamnophis* seems to vary primarily in the number, relative size and shape, and arrangement of the enlarged hooks. However, the significance of the differences noted between *T. fulvus* and *T. c. collaris* is uncertain, since the degree of variation within and between taxa of *Thamnophis* is unknown.

Recorded elevations indicate an overlap in the altitudinal range of *Thamnophis cyrtopsis collaris* and *Thamnophis fulvus*. *Thamnophis c. collaris* occurs at relatively low elevations, but is reported as high as 2042 m (6700 ft) in Chiapas (UA 26572, 26576); elsewhere in Mexico the subspecies was reported near 2134 m (7000 ft) by Webb (1966:62). *Thamnophis fulvus* is a highland species with the lowest elevation recorded as 1636 m (5369 ft, KU 95786). Specimens of the two species are not recorded from the same locality, but are closely approximated in the vicinity of San Cristóbal de las Casas, Chiapas, and Tejutla, Guatemala (see specific localities for specimens of each species in section Locality Records). None of the specimens is intermediate or perplexing in combining features of both species.

All of these data suggest that the taxon *fulvus* is not conspecific with *Thamnophis cyrtopsis*. South of the Isthmus of Tehuantepec the two species are easily distinguished as follows:

T. fulvus: Vertebral stripe indistinct posteriorly, absent on tail; paired black nuchal blotches separated by vertebral stripe; tongue entirely black; tail short, number of subcaudals not greater than 80.

T. cyrtopsis collaris: Vertebral stripe distinct and contrasting for length of body, extending on tail; black nuchal blotches fused to form collar; tongue red, black-tipped; tail long, number of subcaudal scales rarely fewer than 80.

Thamnophis fulvus may be distantly related to *Thamnophis sumichrasti*. Some variant features of pattern of *T. fulvus* are shared with *T. sumichrasti*—the indistinctness or absence of vertebral stripe, and the occasional dark vertebral markings, dark ornate head patterns, and elongate nuchal blotches. These pattern features are best observed in juveniles. Note the general resemblance of pattern features of juveniles of *T. fulvus* illustrated in Figs. 2 (bottom) and 3, and those of *T. sumichrasti* illustrated by Taylor (1940, as *Thamnophis halophilus*), Rossman (1965, 1966) and Conant (1965). *Thamnophis fulvus* also resembles *T. sumichrasti* in the relatively short tail. Dr. Douglas A. Rossman kindly provided data on subcaudal counts of *T. sumichrasti*, which in 12 males average 71.3 (67–79) and in 10 females 63.4 (57–68). The corresponding data for *T. fulvus* is 64 males averaging 70.3 (63–80) and 97 females 62.6 (56–72). Both taxa occur in highland pine-oak forest. Their respective ranges, however, are separated by the unsuitable lowlands of the Isthmus of Tehuantepec.

Status of Taxon *Cerebrosus* Smith

Smith (1942) described *Thamnophis sumichrasti cerebrosus* on the basis of three specimens from Guatemala—the holotype (USNM 12734) and one paratype (USNM 12735) from Escuintla, the other paratype (FMNH 410) without precise locality data (invoice data indicates "no locality, probably Guatemala"). To my knowledge there is no published information on specimens referred to *cerebrosus* other than the type-material. The name has been generally regarded as invalid and a synonym of the taxon hitherto treated as *T. cyrtopsis fulvus* (Stuart 1963: 126, Peters and Orejas-Miranda 1970:302). But more recently Rossman (1971:2) alluded to *cerebrosus* as a highland race of *T. cyrtopsis*. A comparison of features of the holotype of *T. s. cerebrosus* with descriptive comments provided by Rossman (1971) suggests affinity with *Thamnophis marcianus*.

Description: The holotype is described in some detail by Smith in the original description (1942:111). Characteristics of the holotype that facilitate comparison with neotropical populations of *Thamnophis marcianus* are mentioned below. The female holotype has 19-19-17 dorsal scale rows, 7-7 supralabials (third and fourth entering orbit); 1-1 preoculars, 142+2 ventrals, 67 subcaudals (tip of tail barely incomplete; 55 or 56 subcaudals excludes a loosely attached part of tail that may ultimately become detached), and is approximately 835 mm (body 650, estimated complete tail 185) in total length, or tail as percentage of total length, 0.22. Maxillary teeth are difficult to count but seem to be about 22. In dorsal pattern the wide vertebral stripe (covering vertebral and halves of adjacent rows) is distinct on most of the body but is less contrasting posteriorly and on the tail. The dorsolateral areas (scales somewhat spread) consist of a distinct checkerboard pattern of dark blotches that is gradually reduced posteriorly to small flecks on the tail. None of the black blotches of the lowermost row have extensions to the venter, and none of the blotches of the uppermost row encroach on the

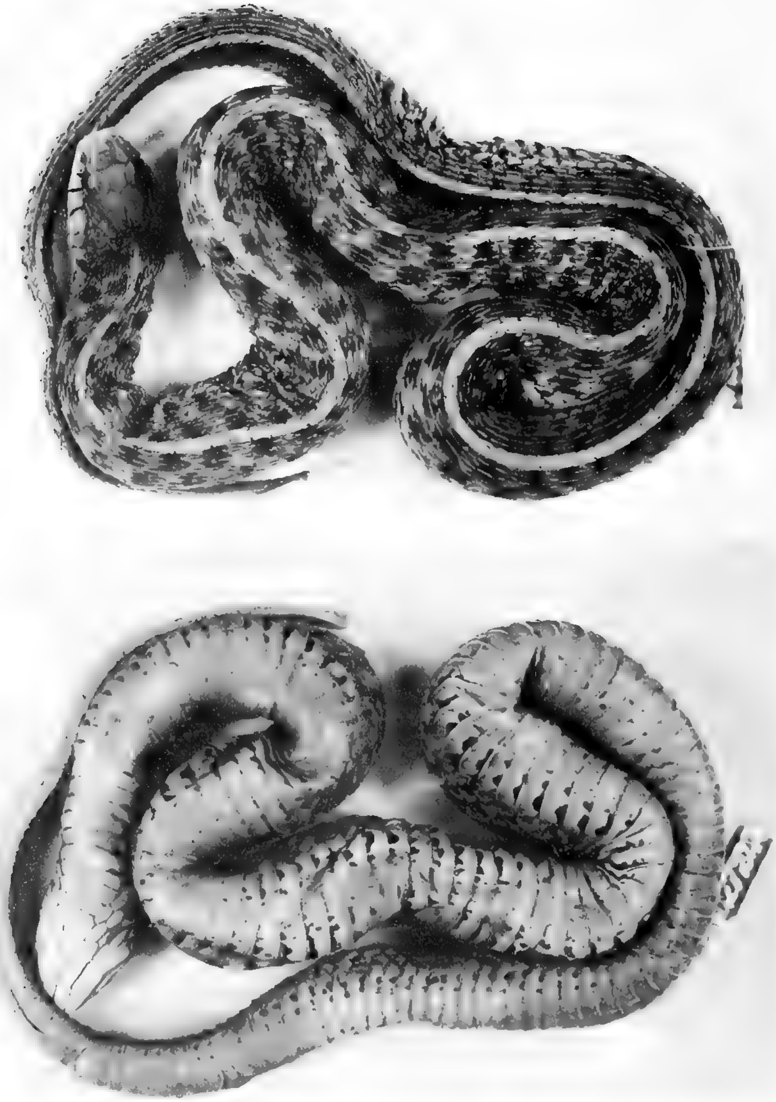

Fig. 6. Dorsal and ventral views of holotype of *Thamnophis sumichrasti cerebrosus* Smith, USNM 12734, from Escuintla, Guatemala.

straight-margined vertebral stripe. The pale lateral stripe is not recognizable. The first three scale rows are unicolor and paler than the rest of the ground color, and are adorned with scattered black marks, mostly on adjacent margins of scales; in some places they are arranged to form short jagged vertical or diagonal lines. Black nuchal blotches are mostly interrupted by the vertebral stripe. Black supralabial markings are reduced; those of any consequence are narrow, occurring only on the two sutures that flank the fifth supralabial. Pale crescent-shaped marks behind the last supralabials are not evident (skin torn on right side of neck). A

Fig. 7. Dorsal view of paratopotype of *Thamnophis sumichrasti cerebrosus* Smith, USNM 12735.

pair of pale parietal spots is present. Ventral scales have roundish black spots laterally that are arranged to form longitudinal rows. Each lateral black spot may be expanded medially to form a barlike mark, which in turn may be crescentic or interrupted to form two spots; some ventrals have indistinct and sparse pigment medially along the anterior margins (between lateral black spots). Unsloughed belly scales are pale orangish. Black markings are absent on the underside of the head and tail. The partly extruded tongue is pale (red) with a black tip. The dorsal and ventral patterns of the holotype are photographed in Fig. 6.

The male paratopotype (USNM 12735) has 19-19-17 dorsal scale rows, 6-6 supralabials (fourth and fifth fused left side), 1-1 preoculars, 75 subcaudals, and 149+2 ventral scales. Black nuchal blotches are divided by the vertebral stripe, which is mostly confined to the vertebral row and emphasized by having mostly continuous black borders; the vertebral stripe is absent on the tail. The characteristic "*marcianus*" head pattern is lacking, although there is an indistinct narrow pale line bordering the side of the black collar. Most body scales are sloughed off. A pale lateral stripe is not evident. The dorsolateral areas are patternless except for scattered small black flecks. Black supralabial markings are virtually absent except for indistinct marks flanking the fifth supralabial. The dorsal pattern is illustrated in Fig. 7. The belly is immaculate with very few small scattered (most laterally) spotlike marks; the anterior margins of some scales are narrowly blackened laterally.

The other male paratype (FMNH 410), from "probably Guatemala," has 19-19-17 dorsal scale rows, 7-7 supralabials, 1-1 preoculars, 79 subcaudals and 164+3 ventral scales. Black nuchal blotches (separated by vertebral stripe) are ill-defined. Parietal spots are indistinct under fluid. Remnants of the characteristic *marcianus* head pattern seem to occur on each side of the head with indistinctly darkened sixth and seventh supralabials, darkened upper margins of supralabials two to five, the fifth supralabial having an inverted horseshoe-shaped mark, and with pale vertical bars on preoculars and parts of the two lowermost postoculars. A pale crescent-shaped mark behind the last supralabial is absent. The wide vertebral stripe, covering the vertebral row and halves of adjacent rows, is evident on the tail. A pale lateral stripe involves the second and third scale rows. Unsloughed scales of the dorsolateral areas are brown. Black spots anteriorly in the dorsolateral areas are relatively large, and some have lateral extensions to the ventral scales (crossing pale lateral stripe). Posteriorly small dark marks are arranged in checkerboard fashion; some of these black spots encroach on the vertebral stripe. The lateral ends of the ventrals tend to have small roundish black spots, especially on the right side.

Discussion

The holotype lacks the characteristic *marcianus* head pattern of contrasting pale-dark and boldly marked supralabials, and pale crescent-shaped marks behind the last supralabials. However, the distinctness of this pattern seems to be variable in view of two small Chiapas specimens of *T. marcianus* (from Aguacate, USNM 108598–99, paratypes of *Thamnophis rozellae*) that have reduced black supralabial markings and non-contrasting pale-dark supralabials. The variant number of seven supralabials (instead of the usual eight for *T. marcianus*) occurs in the type-material of *cerebrosus* (abnormally 6-6 in paratopotype) as well as in some Chiapas specimens of *T. marcianus* (USNM 108597, 108599). The other features of the holotype do not differ from those of specimens of *T. marcianus* from south of the Isthmus of Tehuantepec (Rossman 1971). The holotype of *cerebrosus* is regarded as representative of *T. marcianus*. The wide vertebral stripe and ventral pattern would seem to ally the holotype most closely with *T. m. preocularis,* although the ventral pattern tends toward *T. m. bovallii*.

The two paratypes of *T. s. cerebrosus* do not agree in general features of pattern with the holotype, but they share in having rows of black lateral belly spots (reduced in USNM 12735), and in lacking the *marcianus* head pattern. The paratopotype differs most markedly from the holotype in the narrower vertebral stripe, and the reduced pigmentation of the venter and dorsolateral areas. The FMNH paratype is peculiar in the high number of ventral scales, and in its striped appearance with a pale lateral stripe on the second and third dorsal scale rows. However, a lateral stripe is reported for a *T. marcianus* from Veracruz by Rossman (1972), and some specimens of *T. marcianus* from Nicaragua (KU 174386–88 of a large series from Masaya, Laguna Tisma) have indistinct pale lateral stripes (best developed posteriorly) on the second and third scale rows. The status of the two paratypes requires further study.

Rossman (1971:2) declared *cerebrosus* a highland race of *Thamnophis cyrtopsis,* which would seem incongruous with the general lowland habitat of *T. marcianus*. Escuintla, the type-locality and only known locality for *cerebrosus,* is in the Pacific coastal foothills at an elevation less than 500 m (1640 ft). Smith (1942: 112, account of *T. s. fulvus*) notes that *cerebrosus* is a lowland and foothill subspecies, and Smith, Nixon, and Smith (1950:579) report *cerebrosus* as "from Pacific slopes."

Status of Taxon *Salvini* Smith, Nixon, and Smith

Smith, Nixon, and Smith (1950) described *Thamnophis sumichrasti salvini* on the basis of two females from Guatemala. The holotype, BM 1869.2.22.3, has

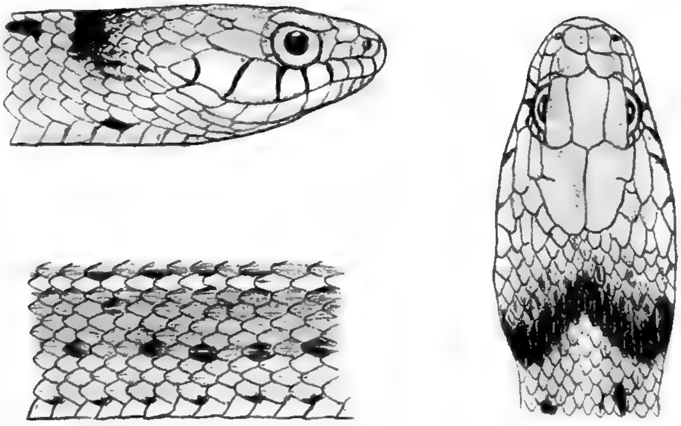

Fig. 8. Pattern on side and top of head, and posterior section of body (near level of ventral 115 owing to folding of skin and sloughing of scales elsewhere) of holotype of *Thamnophis sumichrasti salvini* Smith, Nixon, and Smith, BM 1946.1.23.62 from Río Chixoy below Cubulco, Baja Verapaz, Guatemala.

been re-registered as 1946.1.23.62; the type-locality "Rio Chixoy, below the town of Cubules (? Cubilquitz)" was amended to the town of Cubulco by Stuart (1963). The paratype, BM 1860.12.1.24, re-registered as 1946.1.23.63, lacks precise locality data. Descriptive remarks in the original description do not differ from features ascribed to *Thamnophis cyrtopsis collaris*, and my examination of the two specimens verifies this association. The holotype with 19-19-17 dorsal scale rows and 8-8 supralabials (eighth on both sides seems irregularly divided) has 79 subcaudals (but tail incomplete) and 148+3 ventrals. The paratype has 136+3 ventrals and 92 subcaudals; the dorsolateral areas are liberally black-spotted owing to spreading of scales. Aspects of scutellation and pattern of the holotype are illustrated in Figure 8. There is no hesitation in regarding *Thamnophis sumichrasti salvini* Smith, Nixon, and Smith 1950 as a junior synonym of *Tropidonotus collaris* Jan 1863.

Acknowledgments

I am grateful to the curators and their assistants for the loan of specimens or for permission to examine specimens during visits to some museums. Persons helpful in locating obscure place-names are mentioned in the section Locality Records under the appropriate specimens examined. Special thanks are extended to George R. Zug and Hymen Marx for the loan of type-material, and to Byron Alexander for the illustrations reproduced as Figure 8. Finally I thank The American Philosophical Society, Johnson Fund (Grant No. 1077) and The University of Texas at El Paso (Cotton Trust Funds) for partial defrayment of expenses incurred during visits to museums in Paris and London.

Locality Records

Specimens examined: *Thamnophis cyrtopsis collaris* (25): MEXICO: *Chiapas*: Fénix, 3 mi NW Monserrate (UIMNH 6328; symbol for this locality misplaced on map by Webb 1966); 2 mi E El Phenix, ca. 45 mi NW Arriaga (UMMZ 102241);

2.5 km S Jitotol (KU 58135); 6.4 mi E Teopisca (UTA 5764–65); 52.5 km NE jct. with Mex. hwy 190 on road to Ococingo (AMNH 114854); 13 mi SE San Cristóbal de las Casas (UA 26576); 12 mi SE San Cristóbal de las Casas (UA 26572). GUATEMALA: *Baja Verapaz*: Río Chixoy, below Cubulco (BM 1946.1.23.62; holotype of taxon *salvini*). *Huehuetenango*: Malacatancito (MCZ 64098, ca. 8 km SW Huehuetenango). *San Marcos*: Tejutla (UMMZ 98297). *Department unknown*: BM 1946.1.23.63; MNHP 85, 91–92, 93 (N = 5), 7781 (N = 3), 6609; USNM 25225.

Thamnophis fulvus (241): MEXICO: *Chiapas*: 3 km NW Pueblo Nuevo Solistahuacán (UTEP 3388–89); Finca Patichuix, ca. 33 mi NE Las Margaritas (UA 26578); Chamula, 9 mi NE San Cristóbal de las Casas (MVZ 99542); 8.2 mi E San Cristóbal de las Casas (UMMZ 119759, N = 2; UMMZ 119760); 7.5 mi SE San Cristóbal de las Casas (UMMZ 94635–37); 6 mi SE San Cristóbal de las Casas (UMMZ 118791); 5 mi SE San Cristóbal de las Casas (KU 37914–16); 5 mi N San Cristóbal de las Casas (AMNH 91488; specimen not examined, data from Douglas A. Rossman); 4.5 mi W San Cristóbal de las Casas (UMMZ 119766); "Tzontihuetz" (KU 94136; probably Cerro Zontehuitz, ca. 10–15 km N San Cristóbal de las Casas, Joseph T. Collins, pers. comm.); Mt. Paschtal (UMMZ 87631–34, location unknown); "Saxchamel" (UMMZ 94638; probably Cerro Saxchanal, 13 km N Ovando, Gary Breitenbach, pers. comm.); Siltepec (UMMZ 94639); Cerro Mozotal, near Siltepec (UMMZ 128389); Chicomuselo (UMMZ 94640); Rancho Nuevo (UIMNH 6534-57, location unknown); "Region Soconusco" (UIMNH 33665, restricted to vicinity of Finca La Esperanza by Bumzahem and Smith 1954:61). GUATEMALA: *Alta Verapaz*: Finca Chichén (UMMZ 91049–51); vicinity of Cobán (MNHP 86–87, 94 [holotype]). *Baja Verapaz*: 3 mi S Purulha (MVZ 109363); Plantación Santa Teresa, 7.7 km SSE Purulha (UTA 6198, 6204, 6270–71, 6460–76, 7091); La Union Barrios (UTA 7090); Cerro Verde (UTA 6550, 7085–86, 7092); Cerro Quisis, Hacienda Vieja (UTA 7087–89); Cerro Quisis, Río Chipilin (UTA 7093) [three last mentioned localities within five mile radius Union Barrios, Jonathan A. Campbell, pers. comm.]. *Chimaltenango*: Santa Elena, near Tecpán (FMNH 1926, 30432–34); Chichavac, 5 mi N Tecpán (FMNH 20261–62, 20275; CAS 66974–82); ca. 13 km N and 6.5 km W Patzún (MVZ 109424). *El Quiche*: Nebaj (UMMZ 89203, 89205); Salquil Grande (UMMZ 89204). *Guatemala*: 11 km E San José Pinula (UMMZ 100513); Granja Los Ocales, 10 km SE Guatemala City (UMMZ 100514); 10 mi SE Guatemala City (UTA 2267); Parque San Jorge Muxbal, ca. 15 mi S Guatemala City (UTA 1993, 2462–67, 4922, 5541–44, 5721–22, 6070–80, 6264, 6320, 6602–11, 6886–87, 7151–55). *Huehuetenango*: San Mateo Ixtantán (MCZ 25212); Cerro Chemal (LACM 39975–76); Barillas (LACM 40045); Todos Santos (UMMZ 89206, 89207 [N = 2], 89208–12); 3 km E San Juan Ixcoy (UMMZ 128372–74, 124352). *Jalapa*: Soledad Grande (UMMZ, S-1347, skeletal parts including skull). *Progreso*: Finca Bucaral (UMMZ 106738–39). *Quezaltenango*: Volcán Chicabel, 3.0–4.5 km S and 1.0–2.5 km W San Martín Sacatepéquez (MVZ 109418). *Sacatepéquez*: Dueñas (BM 1860.12.1.28–29); Finca El Potrero, Volcán Agua (CAS 66973); San Antonio (CAS 66983–98); path up Volcán Agua from Santa Maria de Jesus (MVZ 131727). *San Marcos*: Tacaná (UMMZ 88335, 98288–92); 1 km NW Ixchiguán (UMMZ 98294); Ixchiguán (UMMZ 98293); below Tejutla along Río Molino (UMMZ 98296); 3 km E Tejutla (UMMZ 98295); Finca El Porvenir, Volcán Porvenir, Volcán Tajumulco (UMMZ 107123–

27); Km 11–12 on road from San Marcos to Tejutla (UMMZ 137368); ca. 2 km W El Rincón (MVZ 104409, 130822–23); Finca Insula, 14 road km W San Marcos (MVZ 104415–16); 5.5 km W and 0.5–1.0 km S San Marcos (MVZ 104712–13); 4.3 km N Toquián Grande (KU 58134). *Solola*: Finca Olas de Moca, near Guatalón (MCZ 31938–39); 1 km E Panajachel (KU 95786); Panajachel (UMMZ 122701, 137566); along tributary Río Panajachel (UMMZ 126428). *Totonicapán*: 1.5 mi S and 5 mi E Totonicapán (TCWC 17189); 6 mi ESE Totonicapán (KU 42291). *Zacapa*: Santa Clara, Sierra de las Minas (FMNH 64714–18, 167113–14). *Department unknown*: BM 1860.12.1.28–29; MNHP 7783. HONDURAS: *Intibuca*: 3 mi NNE La Esperanza (LSUMZ 23834); La Esperanza (LSUMZ 23835). *Ocotepeque*: 12.5 mi E Nueva Ocotepeque (LSUMZ 23832–33).

Eleven specimens of *Thamnophis* in the MNHP are tagged 94–85, 94–86, 94–87, 94–91, 94–92, 94–93 (N = 5), and 94-94; the holotype of *T. fulvus*, 94-94, was so cited by Stuart (1963:120). Specimens 86 and 87 are also referable to *T. fulvus*, are listed in the MNHP catalog as *Tropidonotus* (*Eutaenia*) *ordinatus*, var *sumichrasti* from Haute Vera Paz, Bocourt, and are probably the basis for Bocourt's description of *Eutaenia cyrtopsis* var. *sumichrasti* (1893:775–777), who indicated the locality as "les environs de Coban (Haute Vera Paz)." Specimens 85, 91, 92, and 93 (N =5) are referable to *T. cyrtopsis collaris*, are cataloged as *Tropidonotus* (*Eutaenia*) *ordinatus* var. *eques* with data no more precise than "Guatemala, Bocourt" and are probably the specimens Bocourt described as *Eutaenia cyrtopsis* (1893:774–775).

Meyer and Wilson (1971:112, as *Thamnophis cyrtopsis*) reported *T. fulvus* from Honduras, based on the above-mentioned LSUMZ specimens (three TCWC specimens from La Esperanza mentioned by them not examined by me). Other Honduran specimens referred to *T. cyrtopsis sumichrasti* by Neill and Allen (1961) were reallocated to *Thamnophis marcianus* by Rossman (1971:11). The basis for Stebbins' (1966:172) report of "*cyrtopsis*" from El Salvador is unknown; however, Hidalgo (1981:67) discussed three specimens of *T. fulvus* from Cantón El Zancudo, 12 km NE Perquín, Departamento de Morazán, El Salvador (locality indicated on map, Fig. 4). The first Chiapas specimen of *T. fulvus* was briefly mentioned by Smith and Burger (1955). Slevin (1939, as *Thamnophis eques*), Smith, Nixon, and Smith (1950), and Stuart (1943, 1948, 1950, 1951, 1954b, 1963) identified or mapped many of the above-mentioned place-names and/or provided scutellation and life history data for Guatemalan specimens of *T. fulvus*. In addition Stuart provided photographs of the general habitat of *T. fulvus* near Finca Chichén (1950) and Tejutla (1951).

Literature Cited

Bocourt, M. F. 1893. Mission scientifique au Mexique et dans l'Amerique Centrale . . . recherches zoologiques. Part 3, Sect. 1. Études sur les reptiles. Livr. 13, pp. 733–780, pls. 52–57. Paris.

Bumzahem, C. B., and H. M. Smith. 1954. Additional records and descriptions of Mexican frogs of the genus *Plectrohyla*. Herpetologica, 10:61–66.

Conant, R. 1965. Miscellaneous notes and comments on toads, lizards, and snakes from Mexico. Amer. Mus. Novitates, 2205:1–38.

Dowling, H. G. 1951. A proposed standard system of counting ventrals in snakes. Brit. J. Herpetol., 1(5):97–99.

———, and J. Savage. 1960. A guide to the snake hemipenis: A survey of basic structure and systematic procedure. Zoologica, 45(1):17–28.

Duellman, W. E., T. Fritts, and A. E. Leviton. 1978. Museum acronyms. Herp. Review, 9(1):5–9.

Hidalgo, H. 1981. Additions to the snake fauna of El Salvador. Herp. Review, 12(2):67–68.

Meyer, J. R., and L. D. Wilson. 1971. Taxonomic studies and notes on some Honduran amphibians and reptiles. Bull. So. California Acad. Sci., 70:106–114.

Neill, W. T., and R. Allen. 1961. Colubrid snakes (*Tantilla, Thamnophis, Tropidodipsas*) from British Honduras and nearby areas. Herpetologica, 17(2):90–98.

Peters, J. A., and B. Orejas-Miranda. 1970. Catalogue of the neotropical Squamata: Part I. Snakes. Bull. U.S. Natl. Mus., 297:vii+347.

Rossman, D. A. 1965. Identity and relationships of the Mexican garter snake *Thamnophis sumichrasti* (Cope). Copeia, 1965(2):242–244.

———. 1966. Evidence for conspecificity of the Mexican garter snakes *Thamnophis phenax* (Cope) and *Thamnophis sumichrasti* (Cope). Herpetologica, 22(4):303–305.

———. 1971. Systematics of the neotropical populations of *Thamnophis marcianus* (Serpentes: Colubridae). Occas. Pap. Mus. Zool. Louisiana State Univ., 41:1–13.

———. 1972. An unusual specimen of *Thamnophis marcianus* from Veracruz, Mexico. Herp. Review, 4(5):169.

Slevin, J. R. 1939. Notes on a collection of reptiles and amphibians from Guatemala I. Snakes. Proc. California Acad. Sci., Ser. 4, 23:393–414.

Smith, H. M. 1942. The synonymy of the garter snakes (*Thamnophis*) with notes on Mexican and Central American species. Zoologica, 27:97–123.

———, and W. L. Burger. 1955. Range extensions of certain amphibians and reptiles of southern Mexico. Herpetologica, 11:75–77.

———, C. W. Nixon, and P. W. Smith. 1950. Mexican and Central American garter snakes (*Thamnophis*) in the British Museum (Natural History). Linnean Soc. J. Zool., 41:571–584.

Stebbins, R. C. 1966. A field guide to western reptiles and amphibians. Houghton Mifflin Co., Boston, xiv + 270 pp.

Stuart, L. C. 1943. Comments on the herpetofauna of the Sierra de los Cuchumatanes of Guatemala. Occas. Pap. Mus. Zool. Univ. Michigan, 471:1–28.

———. 1948. The amphibians and reptiles of Alta Verapaz, Guatemala. Misc. Publ. Mus. Zool. Univ. Michigan, 69:1–109.

———. 1950. A geographic study of the herpetofauna of Alta Verapaz, Guatemala. Contrib. Lab. Vert. Biol., 45:1–77.

———. 1951. The herpetofauna of the Guatemalan Plateau, with special reference to its distribution on the southwestern highlands. Contrib. Lab. Vert. Biol., 49:1–71.

———. 1954a. A description of a subhumid corridor across northern Central America, with comments on its herpetofaunal indicators. Contrib. Lab. Vert. Biol., 65:1–26.

———. 1954b. Herpetofauna of the southeastern highlands of Guatemala. Contrib. Lab. Vert. Biol., 68:1–65.

———. 1963. A checklist of the herpetofauna of Guatemala. Misc. Publ. Mus. Zool. Univ. Michigan, 122:1–150.

Taylor, E. H. 1940. Two new snakes of the genus *Thamnophis* from Mexico. Herpetologica, 1: 183–189.

Webb, R. G. 1966. Resurrected names for Mexican populations of black-necked garter snakes, *Thamnophis cyrtopsis* (Kennicott). Tulane Stud. Zool., 13:55–70.

———. 1980. *Thamnophis cyrtopsis*. Cat. Amer. Amphib. Rept.: 245.1245.4.

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Salt Marsh Algal Mat Composition: Spatial and Temporal Comparisons

Joy B. Zedler

Abstract:—Salt marsh algal mat composition: spatial and temporal comparisons by Joy B. Zedler, *Bull. Southern California Acad. Sci.*, 81(1):41–50. Diatoms, filamentous algae, and green algae form thick algal mats on the soil surface of a southern California salt marsh. Algal composition in four habitats (including three elevations and four marsh vegetation types) differed both spatially and temporally during 1977. Of the most frequently occurring species (32 diatoms, 4 bluegreen algae, and 2 green algae), 37 were non-randomly distributed in space, and 36 were non-random in seasonal occurrence.

Shifts in species composition, measured by similarity of the consecutive sampling periods, occurred in spring and fall, with bluegreen algae more frequent in warm seasons and diatoms and green algae more frequent in cool seasons.

Introduction

Algal mats found beneath the canopies of salt marsh vegetation can be very important to ecosystem functioning (e.g. Zedler 1980), yet little is known of their community structure or factors influencing species distribution. Sullivan (1975, 1977, 1978) examined salt marsh diatoms in Delaware, New Jersey, and Mississippi and found rather high similarities among the communities studied. This led him to propose that further work "may reveal the existence, within as yet undefined limits, of a single basic edaphic diatom community indigenous to Atlantic and Gulf Coast salt marshes" (Sullivan 1978, p. 473). Further study of the Mississippi salt marsh (Sage and Sullivan 1978) suggested that bluegreen algal communities were even more similar than diatoms. They state that, "the existence of a single, ubiquitous, temperate North Atlantic bluegreen algal association . . . appears to be strengthened by our findings" (Sage and Sullivan 1978, p. 336).

Since no comparable work has been done along the Pacific Coast of North America, the geographic extent of these communities is not known. The arid environment and wetland vegetation of southern California differ greatly from coastal marshes elsewhere. Vascular plant canopies are more open; seasonal droughts occur, and interstitial soil water is frequently more saline than sea water (Zedler 1982). Hence it is likely that the algal communities are very different from those along the Atlantic and Gulf of Mexico coasts. On a smaller scale of comparison, it is also likely that algae beneath different canopy types differ more within an arid region marsh, because of salinity differences imposed by extreme desiccation at high but not low elevations.

This paper provides basic information concerning the algal communities of the Tijuana Estuary salt marsh in southern California. Species composition in four habitats, which differ in light penetration and in elevation, was examined to develop hypotheses concerning the factors which influence algal distributions. The total diatom species list is compared with those of eastern wetlands.

Study Area and Methods

The Tijuana Estuary salt marsh (34°N, 117°7'W) has been the site of several investigations of wetland structure and function (Zedler 1977, Zedler, Winfield and Mauriello 1978, Zedler, Winfield and Williams 1980, Winfield 1980). This study was carried out simultaneously with an examination of salt marsh algal mat productivity. In both investigations, spatial and temporal patterns were sought, and environmental data appear in Zedler (1980). Four sampling stations were established to allow comparison of algal mats at three different elevations and under two types of overstory; these were named for their vascular plant dominants: *Spartina* (tall dense canopy of *S. foliosa* Trin. at low elevation, 162 cm above MLLW), *Jaumea* (open succulent canopy of *J. carnosa* (Less.) Gray, at the same low elevation), *Batis* (open succulent canopy of *B. maritima* L. at intermediate elevation, 169 cm above MLLW), and *Monanthochloe* (mixed grass and succulent cover dominated by *M. littoralis* Engelm. at high elevation, 180 cm above MLLW).

Algal mats were sampled biweekly in 1977 within each 6 m diameter station. Five algal mat cores (8.3 cm diameter) similar to one another in macroscopic appearance, were chosen for use in analyzing algal mat productivity, and one of these was selected at random for composition study. This core was placed into a 1 cm deep petri dish and frozen for later subsampling. Because the productivity study required collection of algal mats of equal cover for light and dark chambers, the cores were not collected randomly. However, previous collection areas were not resampled, so the year's data drew from the entire station. Bias in sampling the algal composition is unlikely, since species were not recognizable in the field.

In order to sample both filamentous and unicellular species, species abundances were measured as frequency of occurrence (as in McIntire 1968 and Sage and Sullivan 1978), rather than counts of individuals. Replicate microcores were taken from each petri dish sample using a 1 mm diameter capillary tube pressed 5 mm into the mat. Each of the four stations was sampled with 20 microcores on 24 dates during 1977. Loss of 12 petri dishes during storage reduced the total data set to 1680 microcores.

Each microcore was spread on a glass slide (wet mount) and the entire contents were examined under phase contrast. Only species which appeared to have been alive at the time of sampling were recorded as present (empty frustules were ignored). Diatoms were identified by acid cleaning subsamples for comparison with the wet mount forms. Since counts of frustules were not made, it was not essential to identify each cell encountered, but only to determine whether or not a species was represented at least once in the wet mount. While some rare species may have been missed, this was not a problem in describing the general species composition nor in examining distributions of the most common species.

Results

Spatial and temporal patterns of algal community composition were examined with similarity analysis and comparisons of the distributions of the common species by station and season of occurrence. The complete data set included 7 species of bluegreen algae, 2 species of green algae and 74 species of diatoms. Of these, 33 species occurred in more than 5% of the 1680 microcores and the remaining 45 species were rare.

Table 1. Percent similarity of algal mats among four sampling stations. Data were combined for all 1977 sampling dates before calculating similarity. The four stations (*Spartina* and *Jaumea* at 162 cm MLLW, *Batis* at 169 cm MLLW, and *Monanthochloe* at 180 cm MLLW) are referred to by their first letter.

Stations Compared	All Species Included (83 species)	Diatoms Only (74 species)	Bluegreen Algae Only (7 species)	Green Algae Only (2 species)
S × J	68	67	70	67
S × B	59	59	71	28
S × M	55	47	69	19
S × B	67	67	36	19
J × M	65	63	88	7
B × M	70	68	86	68
$\bar{x}$	64	62	78	35

Spatial patterns. To compare the algal mats from the four stations, the year's data were summed. Similarity between stations was then calculated on the basis of species occurrences in 380–440 microcores from 19–22 cores/station using Sørensen's index [200w/(a+b), where w = the shared occurrences for two stations, and a and b are the respective total occurrences per station (Mueller-Dombois and Ellenberg 1974)].

On the average, stations were 64% similar (Table 1). Stations at equal elevation (*Spartina* and *Jaumea*) were 68% similar, while the two upper stations (*Batis* and *Monanthochloe*) were 70% similar. The lowest similarity (55%) was between the two grass dominated stations (*Spartina* and *Monanthochloe*) which occurred at opposite ends of the elevation gradient. Factors which differ with elevation appear to be important in influencing species composition.

The results of Sullivan (1978) and Sage and Sullivan (1978) suggest that diatoms are more sensitive to habitat differences than are bluegreen algae. They found that bluegreen algae of five habitats within their Mississippi marsh were more similar than the diatoms. The same was true at the Tijuana Estuary salt marsh ($\bar{x}$ = 78% and 62%, Table 1). Low similarity among diatoms could be caused by chance occurrences of the many rare species. However, in the Tijuana Estuary data, exclusion of rarer species from calculations did not cause much change in the mean similarity among stations ($\bar{x}$ = 67% for 38 species over 5% frequency; $\bar{x}$ = 67% for 17 species over 20% frequency). Hence, differential occurrences of common species are indicated, and further analysis is used to reveal the source of community differences.

To determine which species showed spatial patterns, each of the 38 common species was examined with a 2 × 4 contingency table (presence and absence in four stations) and deviations from expected occurrences were detected with Chi square (Zar 1974). Only one of these species, *Nitzschia obtusa* var. *nana*, failed to show spatial pattern ($P > 0.05$). All others had highly significant patterns ($P < 0.01$); that is, the species did not occur at random among the four stations. To determine for which station(s) the probability of encountering a species was greater than or less than expected, the contingency tables were subdivided and retested with Chi square (Zar 1974), and results are indicated with symbols in Table 2.

The spatial patterns were varied, both in strength (number of habitats with non-

Table 2. Percent frequency of the 38 common species by station and season. Data for all 1977 sampling dates were summed for comparison by station; data for all stations were summed for comparison by season. Contingency tables were used to identify spatial and temporal patterns; symbols after the frequencies indicate where observed and expected occurrences differed significantly (as determined with Chi square). Species are arranged in order of decreasing occurrence in 1680 microcores. Sample sizes and total number of species encountered are given below.

		Stations				Seasons			
Rank	Species	*Spartina*	*Jaumea*	*Batis*	*Monanthochloe*	Winter	Spring	Summer	Fall
1	*Trachyneis aspera* (Ehr.) Cl.	59.1<	80.4	85.2	78.7	79.9	81.9>	67.4<	73.9
2	*Denticula subtilis* Grun.	14.3<	44.8<	84.3>	86.8>	68.4>	54.2	51.9	53.7
3	*Microcoleus lyngbyaceus*[b] (Kütz.) Crouan	70.2>	51.6	49.0	52.1	22.8<	57.9>	86.2>	49.3<
4	*Nitzschia vermicularis* (Kütz.) Grun.	58.9>	65.4>	39.3<	28.2<	39.4<	58.1	67.4>	54.3
5	*Diploneis smithii* (Bréb. *ex* W.Sm.) Cl.	16.4<	72.3>	60.2>	71.3>	64.7>	56.0	48.1	51.3
6	*Nitzschia incrustans* Grun.	71.6>	68.2>	21.7<	42.9<	33.4<	57.7>	60.2>	50.4<
7	*Navicula ramosissima* (Ag.) Cl.	37.3<	49.5>	55.5>	19.2<	9.7<	27.9	12.1	18.7
8	*Achnanthes* #1	36.4>	26.6<	46.0>	22.1<	25.3<	42.5>	49.8>	13.0<
9	*Mastogloia exigua* Lewis	29.5	33.2	43.8>	19.5<	50.0>	20.2<	11.2<	50.0>
10	*Nitzschia subtilis* Grun.	35.2>	53.0>	9.5<	24.2<	25.6<	46.9>	42.9>	7.2<
11	*Amphora turgida* Greg.	21.1<	33.2<	43.3>	24.7<	35.9>	16.2<	11.0<	60.0>
12	*Rhizoclonium riparium*[g] (Roth) Harvey	6.6<	1.6<	46.4>	69.5>	45.6>	30.2	16.2<	29.6
13	*Schizothrix mexicana*[b] Gom.	11.8<	32.3	32.1	27.6	9.1<	29.2	32.9	27.6
14	*Gyrosigma obliquum* (Grun.) Boyer	58.6>	22.0<	5.2<	1.3<	18.4<	25.6>	35.0>	11.5<
15	*Schizothrix arenaria*[b] (Berk.) Gom.	12.3<	22.0	29.8>	25.3	2.2<	25.2>	41.0>	15.7<
16	*Nitzschia obtusa* v. *nana* Grun.	21.4	22.5	23.6	15.5	28.7>	15.4<	19.8	22.2
17	*Surirella fastuosa* (Ehr.) Kütz.	0.7<	10.2<	15.7	61.1>	38.1>	18.1	15.7	15.4
18	*Diploneis interrupta* (Kütz.) Cl.	0.0<	9.5<	4.8<	70.8>	25.0>	21.0	16.4	17.6
19	*Navicula mollis* (W.Sm.) Cl.	22.7	4.1<	23.6	22.4	9.7<	27.9>	12.1<	18.7>
20	*Schizothrix calcicola*[b] (Ag.) Gom.	7.7	23.6>	9.8	30.0>	3.4<	26.9	32.9	3.3
21	*Nitzschia longissima* (Bréb. *ex* Kütz.) Ralfs	27.3>	5.2	31.2>	2.6	10.6<	32.1>	17.9>	4.6<
22	*Nitzschia punctata* v. *coarctata* (Grun.) Hustedt	27.5>	16.6	6.4<	16.3	12.5	31.5>	13.8	7.4<
23	*Achnanthes* #2	8.0	20.7>	29.8>	8.4	24.7	21.0	21.7	2.6<
24	*Nitzschia fonticola* Grun.	16.4	5.5<	24.5>	21.6	23.1>	6.5<	4.3<	34.3>
25	*Achnanthes brevipes* Ag.	11.4	8.0<	15.7	32.6>	19.1	14.2	3.6<	28.5>
26	*Nitzschia fasciculata* Grun.	0.0<	26.4>	15.2	18.9	8.7<	0.0<	26.9>	24.1>

Table 2. Continued.

Rank	Species	Stations				Seasons			
		Spartina	*Jaumea*	*Batis*	*Monanthochloe*	Winter	Spring	Summer	Fall
27	*Caloneis westii* (W.Sm.) Hendey	8.2<	23.0>	15.2>	5.3<	13.7	11.5	5.0<	22.0>
28	*Amphora exigua* Greg.	7.3<	3.2<	14.8>	23.9>	12.2	11.7	10.0	13.5
29	*Navicula digito-radiata* (Greg.) Ralfs	14.3>	4.1<	21.0>	7.1<	23.4>	11.5	11.7	3.7<
30	*Rhopalodia musculus* (Kütz.) O. Mull.	3.9	0.2<	38.3>	2.1	12.2	11.5	11.7	9.6
31	*Nitzschia angularis* W. Smith	16.1>	17.5>	0.5<	5.3<	17.2>	10.4	15.5>	0.0<
32	*Amphora coffaeformis* (Ag.) Kütz.	6.8<	2.7<	13.3>	17.4>	15.9	10.6	0.7<	12.8
33	*Enteromorpha clathrata* v. *crinita*[g] (Roth) J. Ag.	4.8	5.9	23.8>	1.3<	15.0>	14.2>	0.0<	7.8<
34	*Pinnularia ambigua* Cl.	5.2	6.4	8.8	11.6>	33.4>	4.0<	1.4<	0.0<
35	*Nitzschia obtusa* v. *scapelliformis* Grun.	1.8<	4.1<	11.2>	13.7>	5.0	2.9	1.7<	19.1>
36	*Diploneis bombus* Ehr.	0.7	2.3	1.7	21.6>	10.9>	11.2>	2.1<	0.9<
37	*Nitzschia acuminata* (W. Sm.) Grun.	2.0<	7.0>	12.4>	1.6<	12.5>	4.4	1.9<	6.3
38	*Diploneis lineata* (Donk.) Cl.	8.9>	4.5	1.9<	4.5	6.6>	10.0>	1.0<	2.4<
Sample size:	number of microcores	440	440	420	380	320	480	420	460
	number of petri dish cores	22	22	21	19	16	24	21	23
Number of species encountered		75	71	75	71	77	75	57	74

[b] Blue green alga; [g] Green alga; all others are diatoms.

random occurrences) and type. Most unexpected was the pattern shown by *Surirella fastuosa* and *Diploneis interrupta*. Both species seemed favored by the highest, driest site (Table 2). Several species were more prevalent in both the intermediate and highest sites (*Denticula subtilis, Rhizoclonium riparium, Amphora exigua, A. coffaeformis, Nitzschia obtusa* v. *scapelliformis*), while others occurred most frequently in the two low elevation sites (e.g. *Nitzschia vermicularis, Ni. incrustans, Ni. subtilis, Ni. angularis*). Factors correlating with elevation (salinity, inundation) may play a role in these species' distributions. At the low elevation, several species responded to differences associated with the dense *Spartina* compared to the open *Jaumea* canopy (e.g. *Diploneis smithii, Gyrosigma obliquum,* Table 2), and light penetration may influence their occurrence.

That so many species showed highly significant spatial patterns suggests that most algal mat species are sensitive to environmental differences present within the salt marsh. Community differences clearly result from a broad spectrum of species responses to environmental conditions, and experimental studies are encouraged to understand how these spatial patterns arise.

Temporal patterns. For each station the similarities of consecutive biweekly sampling dates were calculated to detect when shifts in composition occurred (Fig. 1). The similarity index was used in two ways: first with w, a, and b calculated on the number of occurrences within the 20 microcores for each date, and second with w, a, and b calculated on the presence (i.e. species list occurrence ≥ 1) for a sampling date. A shift in community composition is indicated by a low similarity value between sequential sampling dates. If the shift is due more to changes in abundance of the species present, then only the first index would be low (lines in Fig. 1); if the shift is due mainly to disappearances and appearances of species, then only the second index would be low (dots in Fig. 1). If both features are changing, both indices would be low.

In general, the species did not show any abrupt changes in species composition which would indicate a bloom of a single species or simultaneous die-off or appearance of several species. Community composition was most stable in the summer, when date-to-date similarity was high. Shifts in composition were noted between April and May and August and September, as well as later in the year. The spring shifts in composition were the result of both abundance and species list differences. They coincide with a period of low algal productivity and a time of desiccation stress (Zedler 1980).

To determine which species were responsible for these temporal patterns, I analyzed the data further, using contingency tables and Chi square as in the spatial comparisons. The data for all four stations were summed within the traditional four seasons, providing a sample of 320–480 microcores from 16–24 petri dish cores per season. Occurrences were tallied in 2 × 4 tables (presence and absence in four seasons). Seasons for which the probability of encountering a species was greater or less than expected are indicated next to the observed frequencies of occurrence (Table 2).

Two of the diatom species were random in occurrence (*Amphora exigua* and *Rhopalodia musculus*), one showed significant pattern ($P < 0.05$) and all others were highly significant in temporal pattern ($P < 0.01$). There was a tendency for bluegreen algae to be more frequent in summer (e.g. *Microcoleus lyngbyaceus*

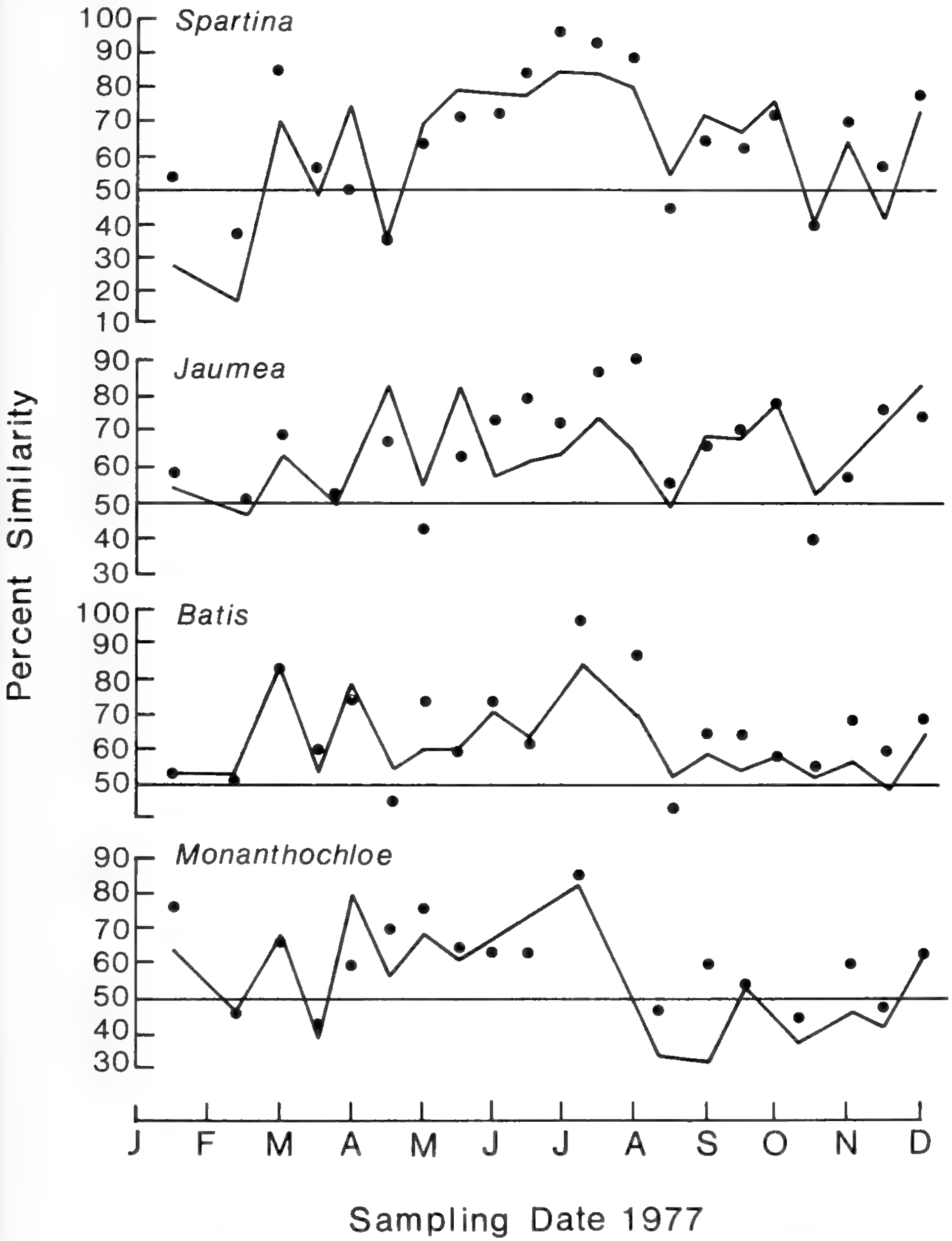

Fig. 1. Similarity of algal mat samples between successive sampling dates for four salt marsh habitats. Lines are drawn where the similarity index [200w/(a+b)] is based on percent frequency of species, while dots are provided where the index is based on species lists only.

and *Schizothrix arenaria*), while green algae and diatoms were not. The high frequencies of bluegreen algae through the summer (Table 2) gave stability to the community and led to high similarities between summer sampling dates (Fig. 1).

Green algae and diatoms were generally more abundant in cooler seasons. The spring declines and fall increases of several species caused the low similarities in Figure 1. Only six diatoms in Table 2 were more frequent than expected in summer, while 25 of the rare diatom species disappeared entirely in the summer samples, leading to the low number of species for that season (Table 2). However, most of the common species were found throughout the year and the temporal patterns consisted mainly of changes in frequency. The temporal separation of bluegreen algae and diatoms is similar to that found by Sullivan (1975) as well as patterns in phytoplankton communities, where negative interactions between these species groups are sufficient to cause seasonal changes in dominants (Keating 1978).

Discussion

Both spatial and temporal patterns exist in the algal communities of the Tijuana Estuary marsh. However, overall similarity of stations and seasons failed to suggest an abrupt change in composition through space or time. No station or season was consistently dissimilar to the others. Nor was any station or season considered "best" for algal occurrence, as each had about the same number of species which occurred there more often than expected (Table 2).

The responses of individual species to environmental conditions were identified using contingency tables. Nearly every common species exhibited highly significant pattern in relation to both sampling station and season. Several of the spatial patterns correlated with elevation and others with overstory type. Most of the temporal patterns correlated with warming or cooling weather. These findings, in conjunction with our other studies of the marsh, suggest the following generalizations.

1. Algal distributions are less restricted than are vascular plants in the intertidal environmental gradients. Stations at low and high elevations had algal communities of 55% similarity, while vascular plants differed completely (Zedler 1977). While factors which correlate with elevation (desiccation, inundation) appear responsible for several of the distributional patterns seen, the effect was rarely strong enough to eliminate any algal species entirely. All but two of the common species (*Diploneis interrupta* and *Nitzschia fasciculata*) were found in all four habitats.

2. Shade produced by vascular plants significantly influences the understory algal mats. The algal mats under *Spartina* and *Jaumea* were 63% similar, and several algal species had differential distributions in relation to these two canopy types (Table 2). Algal productivity also differed between the two stations, with the more open *Jaumea* canopy allowing significantly higher productivity (Zedler 1980).

3. Bluegreen algae and diatoms differ in the response to environmental conditions. Spatial and temporal differences were generally greater among diatom species. The larger size, filamentous form, and mucilaginous sheaths may allow the bluegreen algae to occupy a broader range of microhabitats in the salt marsh, while the small, unicellular diatoms would be more readily eliminated from the less favorable sites. In addition, there may be negative interactions between the diatoms and bluegreen algae. The high biomass of bluegreen algae may have both competitive and allelopathic effects on diatoms, much as Keating (1978) found

between planktonic species in Linsley Pond, Connecticut. The reduced occurrences of several common diatoms and elimination of many rare diatoms in summer coincided with increased frequency of the bluegreen algae in the Tijuana Estuary salt marsh.

4. Algal mat composition changes in both species abundance and presence through the year. In comparison to the vascular plant overstory, the algal mat composition is more dynamic through time but more similar through space. These traits correlate with size and life span of plants and are reminiscent of differences between forest canopies and their understory herbaceous vegetation. Species with short life spans tend to be widely dispersed but temporally separated, while larger species are often longer lived and their communities are more stable in time, of lower diversity, and of narrower distribution.

Geographic comparisons.—Is there a universal community of salt marsh edaphic algae? It depends on one's definition, i.e. how similar two samples must be to be considered representatives of the same community and what features of the community (e.g. density, frequency) should be assessed to measure similarity. For Sullivan (1978, p. 473), the predominance of the same kinds of taxa (pennate diatoms and filamentous bluegreen algae) at both Tijuana Estuary and eastern marshes would support the idea of a universal community. However, it would seem more fruitful to compare the magnitude of differences between sampling locations rather than draw an arbitrary conclusion.

Although edaphic algae are widely dispersed, it is likely that the distance between sites plays a role in determining their similarity. If so, species lists should decrease in similarity with distance between sampling locations. To test this idea, the diatom species lists (the taxonomic group for which the most data are available) from four locations (Sullivan 1975, 1977, 1978; this study) have been compared with the $200w/(a+b)$ index. Abundance of each species has been ignored, since density and frequency data are not comparable. Even species lists are not directly comparable where different size areas have been searched and where taxonomic biases may exist. Hence the following values should be considered general indicators, rather than absolute differences.

The two closest salt marshes, Delaware and New Jersey, had diatom lists that are 44% similar. The Mississippi list is 41% similar to each of the Atlantic Coast marshes, and the California list is 10–15% similar to the three eastern marshes. On a geographic scale, the similarity of species lists decreases with distance between sampling locations. However, this is a very general relationship, since some species which co-occurred in distant locations, such as Delaware and Mississippi, were not found in Delaware and New Jersey. A thorough understanding of salt marsh algal communities awaits further study at the microhabitat through geographic scales.

Acknowledgments

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Literature Cited

Keating, K. I. 1978. Bluegreen algal inhibition of diatom growth: transition from mesotrophic to eutrophic community structure. Science 199:971–973.

McIntire, C. D. 1968. Structural characteristics of benthic algal communities in laboratory streams. Ecology 49:520–537.

Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and methods of vegetation ecology. Wiley, New York.

Sage, W. W. and M. J. Sullivan. 1978. Distribution of bluegreen algae in a Mississippi Gulf Coast salt marsh. J. Phycol. 14:333–337.

Sullivan, M. J. 1975. Diatom communities from a Delaware salt marsh. J. Phycol. 11:384–390.

———. 1977. Edaphic diatom communities associated with *Spartina alterniflora* and *S. patens* in New Jersey. Hydrobiologia 52:207–211.

———. 1978. Diatom community structure: Taxonomic and statistical analyses of a Mississippi salt marsh. J. Phycol. 14:468–475.

Winfield, T. P., Jr. 1980. Dynamics of carbon and nitrogen in a southern California salt marsh. Ph.D. Dissertation, San Diego State University and University of California, Riverside.

Zar, J. H. 1974. Biostatistical analysis. Prentice-Hall, Englewood Cliffs.

Zedler, J. B. 1977. Salt marsh community structure in the Tijuana Estuary, California. Est. Coast. Mar. Sci. 5:39–53.

Zedler, J. B. 1980. Algal mat productivity: comparisons in a salt marsh. Estuaries 3:122–131.

Zedler, J. B. 1982. The ecology of southern California coastal salt marshes: a community profile. U.S. Fish and Wildlife Service, Biological Services Program, Washington, D.C. FWS/OBS-81/54. 110 p.

Zedler, J., T. Winfield, and D. Mauriello. 1978. Primary productivity in a So. California estuary. Coastal Zone '78, Vol. II: 649–662. Am. Soc. Civil Engr., New York.

Zedler, J. B., T. Winfield and P. Williams. 1980. Salt marsh productivity with natural and altered tidal circulation. Oecologia 44:236–240.

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McWilliams, K. L. 1970. Insect mimicry. Academic Press, vii + 326 pp.
Holmes, T. Jr., and S. Speak. 1971. Reproductive biology of *Myotis lucifugus*. J. Mamm., 54:452–458.
Brattstrom, B. H. 1969. The Condor in California. Pp. 369–382 *in* Vertebrates of California. (S. E. Payne, ed.), Univ. California Press, xii + 635 pp.

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CONTENTS

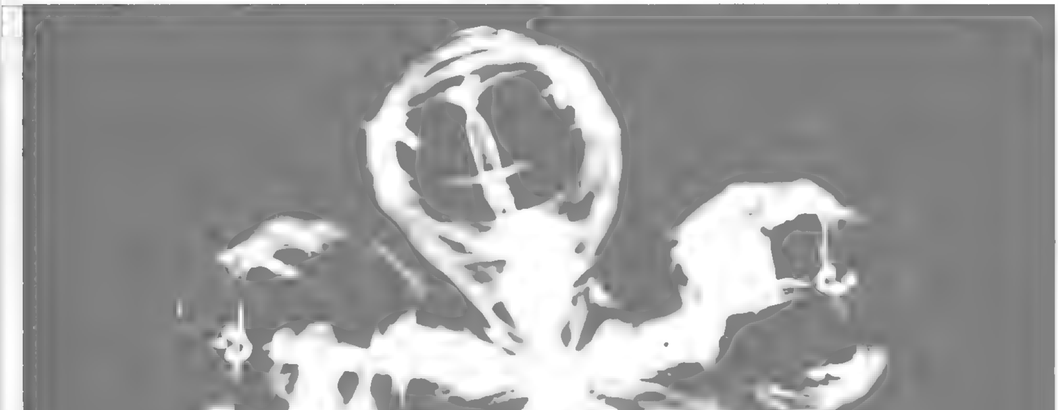
COVER: Sea Butterfly (*Corolla spectabilis*) is related to the snail. The foot has evolved into gelatinous wings whose swirling movement is controlled by long slender muscles seen as parallel white lines in the wings.

This is the second picture of our series on UFOS (Unfamiliar Fauna of the Open Seas) photographed by Jonathan Trent, graduate student at Scripps Institute of Oceanography.

SOUTHERN CALIFORNIA ACADEMY OF SCIENCES

BULLETIN

Volume 81 Number 2



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Status of Sea Turtle Nesting in Southern Baja California, México

Thomas H. Fritts, Margery L. Stinson, and Rene Márquez M.

Abstract.—Status of sea turtle nesting in southern Baja California, México by Thomas H. Fritts, Margery L. Stinson, and Rene Márquez M. *Bull. Southern California Acad. Sci.*, 81(2):51–60, 1982. A paucity of data on nesting by sea turtles on beaches in Baja California, México exists. Terrestrial and aerial surveys of coastal Baja California Sur between Punta Marques on the outer coast and La Paz on the gulf coast in August and September 1978, located nesting beaches presumably frequented by *Lepidochelys olivacea.* Successful oviposition by these turtles is apparently dependent upon beach configuration and recent rainfall patterns that affect the friability of the sand. A high percentage of open nest holes were found in sand too friable to maintain its shape during construction of nest chambers.

Reports from local residents of southern Baja California suggest that leatherback turtles (*Dermochelys coriacea*) nest in southern Baja California from October through March. The carapace of a female leatherback killed while nesting near Cabo Falso substantiates oral reports of other nestings in 1976–1978.

Caldwell (1962) reviewed the sea turtles of Baja California and pointed out the fragmentary data on the nesting of sea turtles in the Gulf of California and the outer coast of Baja California. The presence of significant populations of sea turtles in the waters of Baja California has led to much speculation on the location of nesting beaches of these turtles, but few areas have been documented as known sea turtle rookeries (Carr 1967; Parsons 1962). Townsend (1916) mentioned reports of turtles nesting near the mouth of the Colorado River in the Gulf of California. Both McGee (1896) and Dawson (1944) suggested that *Chelonia mydas* nested on the beaches on Sonora near El Infiernillo. Both apparently assumed that *Chelonia* nested in the area on the basis of the local abundance of turtles and their importance as a food item of the Seri Indians. Carr (1961b) recorded sparse nesting of *Lepidochelys* on the west coast of México only as far north as Mazatlán, Sinaloa. Townsend (1916) and Van Denburgh (1922) suggested that green turtles (*Chelonia*) nested in Bahia San Bartolome during April and May, but neither mentioned the basis of these remarks. Similarly the localities suggested by Caldwell (1962) as potential turtle rookeries remain unconfirmed in the scientific literature.

Although most of the attention of Caldwell (1962) and other authors has focused on identifying rookeries of *Chelonia* in the Gulf of California, a large mass of data gathered along the western coast of mainland México by the Instituto Nacional de Pesca suggests that nesting by *Chelonia* is much more common along the southern Pacific coast of México and decreases markedly from Michoacan north to Mazatlán (Márquez 1976a). Although *Chelonia mydas* is one of the most commonly encountered turtles in the waters of the Gulf of California, other less conspicuous turtles nest in Baja California. The present report describes nesting activities by turtles presumed to be *Lepidochelys olivacea* and *Dermochelys coriacea.*

Carr (1961a, 1961b) suggested that *Lepidochelys olivacea* nest on beaches in the southeastern Gulf of California (i.e. Sinaloa). Márquez, Villanueva, and Peñaflores (1976) indicated nesting beaches for the same species between Punta Conejo and Todos Santos on the outer coast of Baja California Sur, based on interviews with local residents. In conjunction with other field investigations Fritts and Stinson visited these areas and made observations on nests during August and early September 1978.

Materials and Methods

Sea turtle nesting in Baja California Sur was investigated 6–12 August and 26 August–5 September 1978. During this period we concentrated our efforts on the outer coast of the peninsula between Punta Conejo (24°5′N, 111°00′W) in the north and Cabo San Lucas (23°52′N, 109°56′W) in the south (Fig. 1). We interviewed local beach residents, fishermen, and other persons with knowledge of the area and of sea turtle nesting. The beaches south of Punta Conejo are largely steep and shallow beaches composed of coarse sand and are backed by dunes 10–30 m high. The sand beaches between Punta Conejo and Cabo San Lucas are interrupted in only a few areas by rocky bluffs, which project into the sea. A road paralleling the coast between Punta Conejo and Todos Santos allowed terrestrial access to about 110 km of sandy beaches where Márquez et al. (1976) had considered nesting by *Lepidochelys olivacea* to occur. Beaches south of Todos Santos were more broken by bluffs and often further from roads. As a result this area was less uniformly studied.

Beaches were walked in search of turtle crawls, old nests, and egg shells as evidence of turtle nesting. Following the discovery on 28 August of recent nests and crawls near Punta Marques, we made an aerial survey of the coastal areas between Punta Conejo (24°05′N, 111°00′W) and Las Cruces (24°12′N, 110°06′W) via Cabo San Lucas on 30 August 1978, using a chartered Cessna 172 flying at an altitude of approximately 100 m with an airspeed of 90–110 knots. A second aerial survey made on the outer coast between Cabo San Lucas and Punta Marques with a twin engine Cessna on 5 September 1978 was less productive due to a faster airspeed and decreased visibility from the cockpit. Observations during aerial surveys were recorded on a battery-powered cassette tape recorder and later transcribed. Some of the crawls and nests identified during aerial surveys were subsequently examined on the ground.

Results

Collapsed and desiccated eggshells identifiable as those of marine turtles were found at several sites between La Salina (23°45′N, 110°35′W) and Las Piedritas (23°02′N, 110°06′W) 8–12 August 1978. The shells were occasionally associated with depressions in the sand up to 0.5 m deep and 1 m in diameter. We encountered no recent nests before 28 August 1978, despite direct examination of about 40 km of beach on foot. One nest was reported to have been poached from the beach near Rancho Las Piedritas, south of Todos Santos on 11 August 1978. Recent turtle crawls were noted on beaches from 28 August until 5 September when observations were terminated.

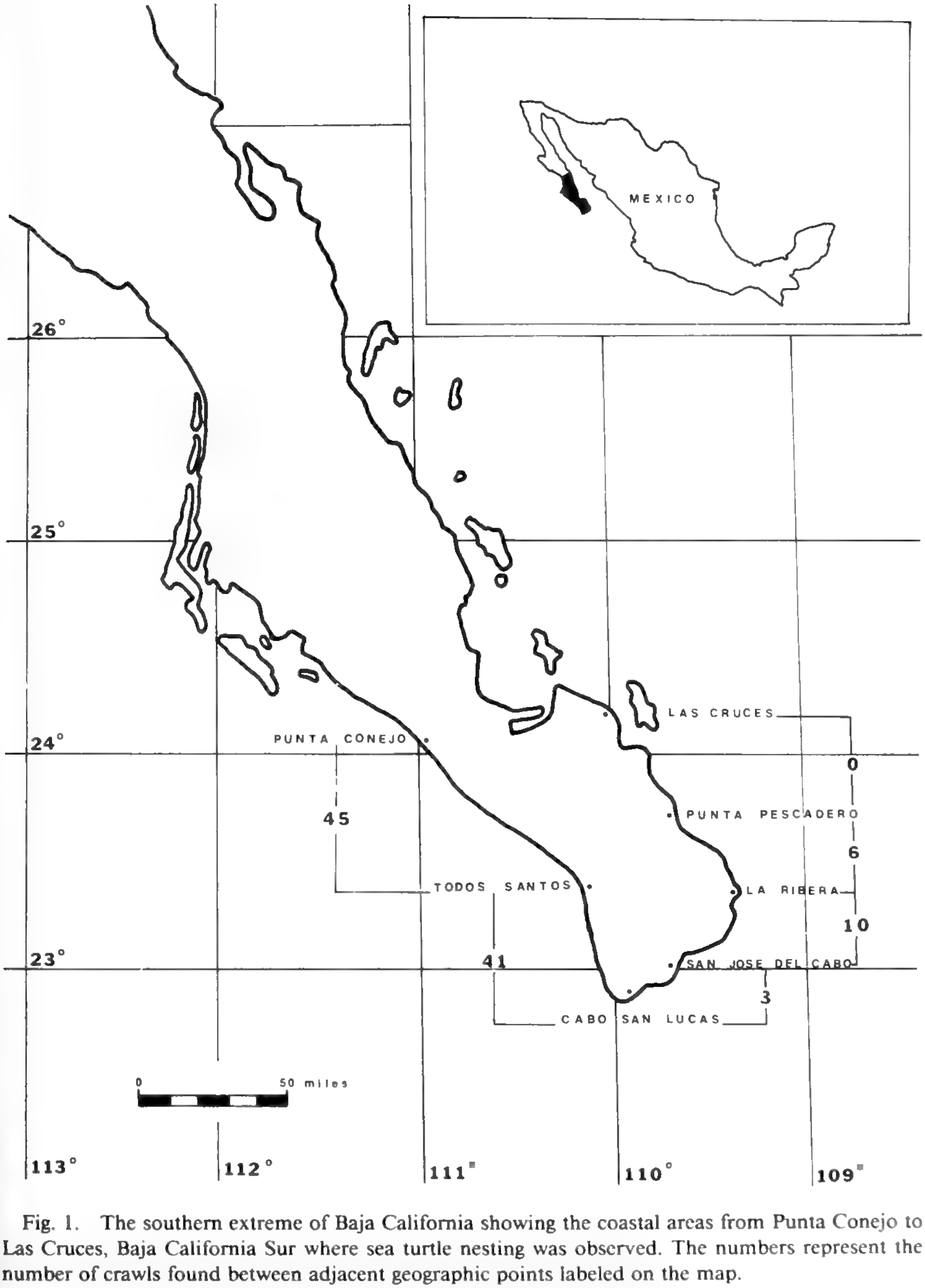

Fig. 1. The southern extreme of Baja California showing the coastal areas from Punta Conejo to Las Cruces, Baja California Sur where sea turtle nesting was observed. The numbers represent the number of crawls found between adjacent geographic points labeled on the map.

Lepidochelys olivacea (Eschscholtz)—Olive Ridley Turtle

On the basis of direct examination of beaches, aerial reconnaissance of the coast between approximately 23° and 24°N latitude, and interviews with local residents, nesting by marine turtles in southern Baja California is a widespread and regular

Table 1. Characteristics of 21 turtle crawls found at Punta Marques (north) and 12 crawls at Cabo Falso (south) Baja California Sur on 28–29 August and 31 August–1 September 1978, respectively.

	North	South
Width of crawl	.60–.95 m ($\bar{x}$ = .85; N = 5)	.64–.93 m ($\bar{x}$ = .78; N = 10)
Distance from first hole or nest to high tide level	7–39 m ($\bar{x}$ = 21.6; N = 13)	27–63 m ($\bar{x}$ = 47.4; N = 11)
Distance from first hole or nest to vegetated zone[a]	(−8)–(+14 m) ($\bar{x}$ = 3.8; N = 13)	(−15)–(−60 m) ($\bar{x}$ = −30; N = 6)
Number of crawls per kilometer	.76 (16 km)	1.20 (10 km)
Number of open holes per crawl	0–9 ($\bar{x}$ = 3.3; N = 21)	0–1 ($\bar{x}$ = .25[b]; N = 12)

[a] Negative numbers represent distances to seaward edge of vegetated zone for crawls that did not reach vegetated area. Positive numbers represent distances to seaward edge of vegetated zone for crawls that entered vegetated area.

[b] All three open holes were attributed to poaching of the nests by man.

occurrence in August and September. At least 86 turtle crawls were observed on beaches between Punta Conejo and Cabo San Lucas during an aerial survey on 30 August 1978. Of the 27 crawls subsequently examined on the ground, all were made by turtles employing an alternate gait of the forelimbs. An additional 19 turtle crawls were seen east and northeast of Cabo San Lucas on the gulf side of the peninsula as far north as Punta Pescadero (23°49′N, 109°42′W), but were not examined on the ground (Fig. 1).

The amount of data collected on each crawl seen during aerial surveys depended upon several factors and was variable. A total of 105 crawls were seen during aerial reconnaissance between Punta Conejo and Punta Colorado on 30 August 1978. Of these crawls 22 were judged to have normal body pits with indications of a completed nest on the beaches; 28 crawls had open holes visible near the landward side. The remainder of the crawls were not classed. Of the crawls with open holes, 18 had 1–8 holes visible ($\bar{x}$ = 2.2 holes/crawls). Of the crawls with the inland terminus visible from the air, 30 did not reach the vegetated areas of the beach whereas 16 reached shrubs. Because both open holes and normal body pits were more difficult to view where the crawl reached a vegetated area, no quantification of nesting success in vegetated and open areas can be made from our aerial data. However, on the basis of terrestrial beach surveys, a turtle that entered the vegetated area of the beach was more likely to dig multiple nest holes and leave such holes open than a turtle that attempted to dig in open sand. Since all turtles coming ashore had to pass through open sand, it is possible that vegetated areas are entered only if nest conditions in open areas are unsuitable. Several turtle species are known to shove the snout in beach sand during nesting forays and such behavior may function in selection of the nest site.

Of the 21 crawls examined on the ground in a 16 km length of beach near Punta Marques on 28–29 August 1978, only three were judged to have resulted in successful deposition of eggs (Table 1). Twenty-one crawls had 0–9 ($\bar{x}$ = 3.3) open holes near the inland terminus of the crawls. One crawl ended near a steep bank and had no evidence of digging activity. The open holes were within 7–39 m ($\bar{x}$ =21.6) of the high tide level. Fourteen crawls were noted to reach the vegetated area inland from the open sand of the beach and three crawls did not enter vegetated areas. Of the latter three crawls, two were evidently successful nesting attempts and another ended in an open hole on a sand ridge between the ocean and an estuary which lacked vegetation. Ten eggs extracted from a nest containing a much larger number near Punta Marques on 28 August 1978 were 39–44 mm in diameter ($\bar{x} = 40.9$ mm).

On the basis of observations on a beach north of Cabo Falso near the southern tip of the peninsula on 31 August and 1 September 1978, nesting success was much improved over that occurring further north. Of 12 turtle crawls examined in a span of beach about 10 km long, only three (25%) had open holes. Each of the three crawls with open holes had human footprints and tire tracks of a dune buggy in proximity, and nests were judged to have been opened and poached by humans. The remaining nine crawls had normal body pits and appeared to represent successful nesting attempts. Nest sites were within 27–63 m ($\bar{x} = 47.4$ m) of the high tide level. None of the crawls reached vegetated areas; six crawls were within 15–60 m ($\bar{x} = 30$ m) of vegetated areas (Table 1). Thus, oviposition occurred in only 14% of the crawls in the north, and in at least 75% (possibly 100%) of those in the south.

In contrast to the beach near Punta Marques, the beach at Cabo Falso was relatively flat with only a slight crest 1 m high near the high tide level and an interval of 30–100 m of open sand between the surf and vegetated areas. Beaches near Punta Marques were steeper and more variable in width, but consistently had vegetated areas closer to the surf zone.

Soil moisture also appeared to differ between the two sites. Attempts by THF to excavate a nest-like hole adjacent to open holes near Punta Marques resulted in collapse of the adjacent sand and produced an open funnel-shaped depression similar to those abandoned by turtles. In contrast, artificial nest chambers dug by THF near one successful nest near Punta Marques and several nests near Cabo Falso did not collapse. The sand near successful nests was sufficiently moist to retain its form when a hole 40 cm deep was dug. On the basis of the friable sand near open holes, all such holes lacking signs of humans or other egg predators were judged to be unsuccessful nest attempts resultant from dry substrate conditions.

Some of the crawls with open holes and evidence of multiple nesting attempts were complex trajectories through vegetated areas of the beach. It is possible that successful nests completed after one or more open holes were abandoned could have been overlooked. However, in most crawls with open holes, it was possible to determine that oviposition had not occurred anywhere along the length of the crawl.

The higher success of nesting attempts on southern beaches possibly reflects differences in rainfall for the 150 km distance in a NW–SE direction. However, it is possible that such differences in soil moisture are related to beach profiles. Subsequent measurements of environmental variables and nesting success in these areas will allow rejection of one or both of these hypotheses.

Residents of southern Baja California repeatedly remarked that sea turtles often construct false nests. Egg poachers often attribute such open nests to an attempt to camouflage the actual site with eggs. These false nests are probably the open holes resulting from attempts to nest in dry sand which collapses.

We found signs of humans walking or riding on horseback in search of turtle nests on approximately 60% of the beaches that we visited. The actual number of nests poached during the study period was difficult to determine because of the large number of open holes abandoned by turtles. A man who had removed 103 turtle eggs from a nest near Rancho Las Piedritas on 11 August allowed examination of the 20 eggs that remained in his possession on 12 August.

Dermochelys coriacea—Pacific Leatherback Turtle

Nesting of the leatherback turtle on the Pacific coast of México has been reported from Jalisco (Pritchard 1971) and other states further south (Márquez 1976a). However, on the basis of repeated and independent reports of nesting by this distinctive turtle of Baja California, it is now possible to extend the known breeding range over 500 km to the northwest. Nesting of *Dermochelys* in Baja California Sur is based on the following observations by residents of beach areas.

1. Mr. and Mrs. Jack Morgan, who reside on the beach 6 km N of Todos Santos, Baja California Sur, noted two turtle crawls and presumed nest sites on a beach near their home on 29 January 1977. On 15 February 1977, during a period of high surf conditions, some of the eggs from one or both nests were uncovered by wave action. The Morgans described the tracks on the beaches as exceeding 1.5 m in width and the eggs as being of various sizes with some much larger than egg shells of a turtle presumed to be *Lepidochelys olivacea* shown to them by THF.

2. According to Sr. Arturo Cota, a resident of Rancho Las Playitas, 3 km N of the Morgan residence and 9 km N of Todos Santos, a large turtle in the process of nesting was killed on the beach near the ranch by local residents in January 1976. The turtle was locally known as a "*tres filos*" and was too large for four men to move without the aid of a tractor. Sr. Cota also recalled finding the tracks of another large turtle of an unidentified species 200 m N on the same beach the same day.

In a letter dated 31 October 1978, the same observer described the discovery of six turtle crawls on 29 October on the beach adjacent to Rancho Las Playitas. Only one of the six crawls had been present on 26 October when Cota's brother had traversed the beach. The crawls were within a 4 km stretch of beach and separated by intervals of 400–1500 m ($\bar{x} = 750$).

Despite active search by Cota, no eggs were found in the area. According to Cota, the crawls were 1.85, 1.6, 1.6, 1.5, and 1.1 m wide. Cota expressed a belief that the five widest crawls were made by *Dermochelys,* but that the narrowest crawl might represent another species of turtle.

3. Sr. Gonzalvo Garstelo Victoria, a resident of Rancho El Cardonal, reported that a very large turtle nests in large numbers on the beaches north of Cabo Falso, Baja California Sur during November–February. He knew the turtle as "*la golfina*" (a name normally applied to *Lepidochelys olivacea*), but described it as a large turtle with eggs as large as oranges and fewer in number than the "*prieta*" nesting on the same beach June–September. The eggs of the large turtle were buried at a greater depth than those of the smaller species. Apparently, he was describing *Dermochelys* as "*la golfina*" and *Lepidochelys* as "*la prieta,*" whereas these names are normally associated with *Lepidochelys olivacea,* and *Chelonia mydas,* respectively. Garstelo reported finding 30 nests on the beach near his house in the winter of 1977–1978. Garstelo's father confirmed his son's descriptions indicating that

the large species was also known as "*siete filos*" and was known to nest on various beaches in southern Baja California.

4. Sr. José Agúndez Ochoa, a resident of Rancho Los Meganos, 3 km NW of Rancho El Cardonal showed one of us (THF) a carapace of a leatherback which was killed while nesting on a beach nearby on 7 February 1977. The carapace measured 132 cm in length along a paravertebral furrow. Sr. Agúndez reported the nests of *Dermochelys* to measure up to 1 m in depth and the crawls up to 2 m in width. He has lived on the beach for 10 years and recalled up to 100 nests on the beach at one time.

In a letter dated 6 November 1978, Sr. Agúndez informed THF that five nests of the "*siete filos*" had been laid in recent days near Cabo Falso.

5. A rancher residing at Rancho El Tomate, about 15 km S Punta Marques, described the discovery of a large turtle known to him as "*tres filas.*" He had killed the turtle when it crawled onshore to nest, but did not recall the date.

6. Biologist Jorge Sepulveda of Todos Santos, B.C.S. saw a crawl and presumed nest of a turtle near Punta Gasparino, south of Todos Santos, in February 1976. He considered it to represent the nesting signs of a leatherback on the basis of the extremely wide crawl.

7. THF examined a carapace of *Dermochelys* with a length of 139 cm on 3 September 1978, on a beach near Todos Santos. According to Biologist Jorge Sepulveda, the turtle was an adult female with mature eggs, which had been caught in open water and subsequently butchered by fishermen on 1 September 1978.

8. Mr. Tom Rutherford of Todos Santos reported numerous comments made by local fishermen as to the seasonal abundance of leatherback turtles and that more had been seen in 1976–1978 than in previous years.

The leathery carapace with distinct longitudinal ridges and the large size of *Dermochelys coriacea* make this species readily identifiable to nearly all observers. In addition the greater width of crawls by *Dermochelys,* the larger size of eggs, and the deeper excavations are also characteristics facilitating identification of leatherback nests.

The name "*siete filos*" which refers to the seven ridges running the length of the carapace is the most common name used to describe the species by fishermen in Baja California. However, the variants of "*siete filas,*" "*tres filos,*" "*tres filas,*" and "*la golfina,*" and "*laud*" are also encountered in conversations with fishermen and ranchers. On the basis of the above reports, the composite nesting season for *Dermochelys* in Baja California appears to extend from October through March and is later than the seasons given by Márquez (1976a) for Michoacan (August–October). However, the Baja California nesting season appears to concur with that given by Pritchard (1971) for Jalisco (October–March), and Márquez (1979) for Tierra Colorada, Guerrero (October–April).

Discussion

The nests and crawls encountered were thought to represent reproductive efforts by *Lepidochelys olivacea.* The alternate gait and narrow width of crawls were consistent with those of *Lepidochelys olivacea* and *Eretmochelys imbricata.* Neither crawl width or egg size is adequate to distinguish these species in the absence of other data.

From a biogeographic viewpoint the nesting beaches reported herein (whether *Lepidochelys olivacea* or *Eretmochelys imbricata*) in southern Baja California are significant in being near the northern limits of the nesting range of the species in the eastern Pacific. Other than the nesting areas in Baja California described herein, the closest area with significant nesting by *Lepidochelys* is an area near Mazatlán, Sinaloa, being studied by Biol. Daniel Ríos Olmeda. The Mazatlán rookery is at the mouth of the Gulf of California and is bounded by waters that are warmer than those of the outer coast of Baja California, especially during the warmer months of the year (Robinson 1973). Significant commercial exploitation of *Lepidochelys olivacea* previously occurred in waters offshore from Sinaloa and Baja California Sur (Márquez 1976b), but at present is much less because of decreased numbers of turtles and protective legislation of the Méxican government. Caldwell (1962) reported numerous records of *Eretmochelys* in waters of southern Baja California. To date no rookery is known in the peninsula for this species.

Further observations are needed in Baja California to determine if nest collapse due to dry sand conditions is common and a potential limiting factor to nesting. Since August and September are months during which *chubascos* are frequent, the success of nest excavation may depend largely on the rainfall patterns in preceding weeks. The problem of nest collapse is not unique to turtles in Baja California, but may be exaggerated by the tendency of both potential species to dig a shallower body pit than other marine turtles. The distances from the high tide level to the nests observed in northern sites were comparable to those recorded by Casas-Andreu (1978) in Oaxaca. Nests near Cabo Falso were farther from the high tide line.

The actual number of turtles nesting on beaches in southern Baja California is obscured by the high incidence of unsuccessful nesting emergences during the period of observation. Since crawls examined on the ground on 28 and 29 August were visible during an aerial survey on 30 August, it is likely that signs of nesting emergences persist in the absence of rain for several days. Thus, the 105 crawls seen on 30 August between Punta Marques and Punta Colorada possibly represent the additive nesting record for an unknown number of days. A rainstorm accompanied by strong winds on 1 September 1978 erased all signs of the crawls on the beach at Cabo Falso. Only three crawls were seen during an aerial survey from Cabo San Lucas to Punta Marques on 3 September 1978. Since none of the crawls present on 31 August were visible during the second aerial survey, it is probable that the three crawls seen were made on 1 or 2 September 1978. Although crawls having multiple nest holes were common, females which did not oviposit possibly returned to the surf and reemerged at some other site on nearby beaches. If multiple emergences are common, consideration of the number of crawls seen on a beach to reflect the number of nesting females would result in an overestimation.

Márquez et al. (1976) estimated the number of females of *Lepidochelys olivacea* nesting in Baja California to be 1000–5000 on the basis of reports from local residents. Observations made over a longer period and under a variety of conditions are necessary to provide better estimates of the number of turtles nesting in Baja California, but available data suggest that sparse nesting occurs over a distance of approximately 300 km along the outer coast of Baja California. If nesting extends north of Punta Marques on the outer coast or Punta Pescadero on the gulf coast, a much larger span of beach may be involved.

The significance of nesting by *Dermochelys* in Baja California remains to be determined by direct study of the species. Pritchard (1971) considered the most northern nesting beach of this species to be Jalisco, México. Márquez (1979) reported 11 major turtle nesting beaches in the states of Oaxaca, Guerrero, Michoacan, Colima, and Jalisco with common incidences of *Dermochelys.* The nesting records detailed herein for Baja California extend the nesting range 520 km to the northwest.

The beaches where *Dermochelys* is reported to nest in Baja California are predominately steep beaches with coarse sand and relatively deep water near shore. All of these characteristics are ones mentioned by Pritchard (1971) as being present on leatherback rookeries in other areas of the world. Caldwell (1962) reported the discovery of a hatchling-sized leatherback in the northern Gulf of California and suggested that leatherbacks might nest in the northwestern Gulf. Although his remarks were directed to *Chelonia,* Caldwell also suggested that turtles hatched on the outer coast of Baja California might be carried south by Pacific currents and subsequently swept into the Gulf of California by strong tides. Biol. Daniel Ríos of Mazatlán recalled finding an extremely wide turtle crawl several years ago on a beach approximately 20 km N of Mazatlán during winter after all nesting by *Lepidochelys* had finished for the year. Although *Lepidochelys olivacea* is the predominate turtle nesting in the vicinity of Mazatlán, the large size of the turtle and its winter emergence suggest that it possibly was a leatherback. In October 1979, Ríos noted a leatherback nesting on the same beach. Thus, occasional nesting of leatherbacks occurs in other northern areas of western México.

It is noteworthy that the nesting season of *Dermochelys* in Baja California (October–March) spans a period when sea surface temperatures are lower than in preceding months when *Lepidochelys* seems to nest (July–October). Mean sea surface temperatures on the Pacific coast of southern Baja California are 24–28°C during July–October and 20–28°C October–March (Robinson 1973).

The two specimens of *Dermochelys* measured in Baja California support Pritchard's suggestion that leatherbacks from the eastern Pacific nest at a smaller size than those from the Atlantic. Both had curved carapace lengths smaller than all but the smallest individual of 192 nesting females measured by Pritchard (1971) in French Guiana.

On the basis of existing information, leatherback turtles and olive ridleys appear to nest on the same beaches between Punta Marques and Cabo San Lucas. Although crawls on the southern gulf coast of Baja California remain to be confirmed as those of *Lepidochelys,* and the presence of leatherback nests on the gulf coast is suggested by only a single oral report, it is possible that further investigations will confirm nesting by both of these species in the southwestern Gulf of California. The beaches on the outer coast of Baja California Sur to the north of Punta Conejo, and those north of La Paz on the gulf coast remain to be investigated in light of present knowledge of the nesting season and habits of sea turtles.

The failure to find evidence of nesting by *Chelonia mydas* during our study is additional weak evidence that the green sea turtles inhabiting the waters of Baja California nest farther to the south as implied by Carr (1961) and Márquez (1976a).

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Literature Cited

Caldwell, D. K. 1962. Sea turtles in Baja Californian waters (with special reference to those of the Gulf of California), and the description of a new subspecies of northeastern Pacific green turtle. Los Angeles Co. Mus., Contrib. Sci., (6):3–31.

Carr, A. 1961a. The ridley mystery today. Animal Kingdom 64:7–12.

———. 1961b. Pacific turtle problem. Nat. Hist. 70:64–71.

Carr, A. F. 1967. So excellent a fishe. The Natural History Press, Garden City, New York. 248 pp.

Casas-Andreu, G. 1978. Analisis de la anidación de las tortugas marinas del genero *Lepidochelys* en México. An. Centro Cienc. del Mar y Limnol. Univ. Nal. Quton México 5(1):141–158.

Dawson, E. Y. 1944. Some ethnobotanical notes on the Seri Indians. Desert Plant Life, 16(9):133–138.

Márquez M., R. 1976a. Reservas naturales para la conservation de las tortugas marinas en México. Inst. Nac. Pesca, INP/SI, i83:1–22.

———. 1976b. Estado actual de la pesqueria de tortugas marinas en México, 1974. Inst. Nac. de Pesca, Ser. Inf. INP/SI, i46:1–27.

———, A. Villanueva, and C. Peñaflores. 1976. Sinopsis de datos biologicos sobre la tortuga golfina, *Lepidochelys olivacea* (Eschscholtz, 1829). Inst. Nac. Pesca, INP Sinop. Pesca, (2):1–61.

———. 1979. Anidación de la tortuga Laud (*Dermochelys coriacea schlegelii*) en el Pacifico Mexicano Seminario Departamental, Escuela Nacional de Ciencias Biológicas, 10 pp.

McGee, W. J. 1896. The Seri Indians. Smithsonian Inst. Bur. Amer. Ethnol. Ann. Rept., 17(1):1–344.

Parsons, J. J. 1962. The green turtle and man. Univ. Florida Press, Gainsville. 126 p.

Pritchard, P. C. H. 1971. The leatherback or leathery turtle. Int. Union Conserv. Nat. Monograph No. 1, Morges, Switzerland. 39 pp.

Robinson, M. K. 1973. Atlas of monthly mean sea surface and subsurface temperatures in the Gulf of California, Mexico. Memoir, San Diego Soc. Nat. Hist., (5):1–19, 90 figs.

Townsend, C. H. 1916. Voyage of the "Albatross" to the Gulf of California. Bull. American Mus. Nat. Hist., 35:399–476.

Van Denburgh, J. 1922. The reptiles of western North America. Part II. Snakes and turtles. Occ. Pap., California Acad. Sci., 10:617–1028.

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Electrophoretic Evidence for Self-fertilization in Two Species of Spirorbid Polychaetes

Richard Beckwitt

Abstract.—Electrophoretic evidence for self-fertilization in two species of spirorbid polychaetes by Richard Beckwitt, *Bull. Southern California Acad. Sci.,* 81(2):61–68, 1982. The inheritance of electrophoretically detectable enzymatic variation was studied by means of laboratory culture of *Pileolaria pseudomilitaris* and *Janua brasiliensis.* These variants are inherited as simple Mendelian codominants in single-pair matings. A small percentage of progeny from single-pair matings of each species are produced by self-fertilization in these hermaphroditic worms. Isolated individuals of *P. pseudomilitaris* produced reduced numbers of progeny with genotypes that confirmed self-fertilization by the parent. Isolated individuals of *J. brasiliensis* did not reproduce in culture. The high degree of polymorphism at several loci suggests that self-fertilization is not a common occurrence in natural populations.

Introduction

Worms of the polychaete family Spirorbidae are small, sessile filter-feeders. They are often locally abundant, especially on harbor floats and ship hulls. Spirorbids are short-lived and easily cultured in the laboratory. All species of Spirorbidae that have been examined have proven to be hermaphroditic, with functional eggs and sperm present simultaneously (Gee and Williams 1965). Those species investigated have some capacity for self-fertilization (Potswald 1968). Fertilization is presumed to occur either as the eggs are being deposited or shortly after. Daly and Golding (1977) have demonstrated a sperm storage organ at the base of the tentacular crown. Sperm, released into the water, are apparently collected by the feeding apparatus of other individuals and stored.

Several species of spirorbids are commonly found in southern California. Among these, two of the most abundant are *Pileolaria pseudomilitaris* (Thiriot-Quievreux), and *Janua brasiliensis* (Grube). The latter species has been recently redescribed by Knight-Jones, Knight-Jones and Kawahara (1975). Both species are found together attached to *Mytilus edulis* shells on floating docks. In addition, *P. pseudomilitaris* is found attached to rocks in mid-intertidal pools.

Many aspects of reproductive biology, including self-fertilization, can be studied directly if there are genetic markers that allow the genotype of each individual to be determined. Enzyme electrophoresis provides a useful tool in such investigations, since several independent, polymorphic loci can be scored in a single individual. I have examined the inheritance of electrophoretic phenotypes (allozymes) in spirorbids reared in the laboratory. In this paper, I present data on the Mendelian inheritance of allozymes at seven loci, and also evidence for a small amount of self-fertilization in *Pileolaria pseudomilitaris.* Similar data are presented for three loci of *Janua brasiliensis.*

Materials and Methods

Laboratory Culture

Spirorbids were cultured using methods developed by Shisko (1975). Cultures were maintained at 16–18°C in aerated, non-circulating aquaria. Sea water was obtained from Marineland of the Pacific (this water was filtered through a coarse gravel filter). All cultures were started with newly settled juveniles. Larvae were allowed to settle in a covered plastic Petri dish (50 mm diameter), in about 5 ml of sea water. After settlement, the bottom half of the Petri dish was transferred to a one liter aquarium. Cultures were fed a suspension of the single-celled green alga *Dunaliella tertiolecta* and some finely ground Tetra-Min (Tetra KraftWerke, W. Germany), and the water changed every two weeks.

Electrophoresis

Horizontal slab starch gel electrophoresis was used exclusively. Individual worms were removed alive from their tubes, using fine jeweler's forceps and #0 insect pins. Each worm was placed in a small mortar and pestle and ground in 5 μl or less of deionized water with the aid of less than 1 mg of fine carborundum powder. Six enzyme stains were used: aspartate amino transferase (AAT, EC 2.6.1.1), a non-specific esterase (EST), glucosephosphate isomerase (GPI, EC 5.3.1.9), leucine amino peptidase (LAP, EC 3.4.11.1), malate dehydrogenase (MDH, EC 1.1.1.37), phosphoglucomutase (PGM, EC 2.7.5.1). Stain recipes were from Selander, Smith, Yang, Johnson and Gentry (1971). The stain and buffer combinations used are described in Beckwitt (1980).

Data were recorded for each band as distance traveled from the origin, divided by the distance traveled by the tracking dye, bromphenol blue, multiplied by 100. This relative mobility value allowed comparisons from one gel to another, even though the small amount of sample made it impossible to run any individual more than once. Alleles were named in terms of this mobility value (e.g., pgi^{20} is the allele of the PGI locus with a relative mobility of 20 units compared to bromphenol blue). Although no direct comparisons were possible, indirect comparisons using albumin and hemoglobin standards, as well as comparisons among individuals with a restricted number of known genotypes, and enzymes with little or no variability, showed relative mobility values to be similar from one gel to the next (±2 units). This degree of error was less than the usual difference between two alleles (it was about the same as the thickness of a single band). In cases where suspected alleles differed by distances of the same magnitude, they were treated as being the same.

Genetic Analysis

The genotypes of parents were compared with the genotypes of their F_1 offspring. Results were interpreted on the basis of a simple Mendelian model of multiple codominant alleles at a single locus. One or two larvae were allowed to settle in Petri dishes. These worms were reared in one liter aquaria as described above until they had produced one or more broods of offspring. The parents were then removed, and their genotypes determined for three enzymes. When a majority of the offspring had matured (determined by the production of F_2 offspring) they too were examined for genotypes at the same loci as their parents.

Sampling

Specimens of *Janua brasiliensis* used to initiate cultures were taken from *Mytilus edulis* shells attached to floating docks at Holiday Harbor Marina, San Pedro Harbor, Los Angeles County. Some specimens of *Pileolaria pseudomilitaris* used to initiate cultures were taken from Holiday Harbor Marina, others were taken from stones in mid-intertidal pools at Royal Palms Beach, Palos Verdes Peninsula, Los Angeles County.

Results

The results of all crosses between pairs of larvae of *Pileolaria pseudomilitaris* are given in Table 1. Cultures 1 through 11 in this table were started with a pair of larvae from Holiday Harbor (floating docks). Five additional cultures, 12 through 16, were started with one larva from Holiday Harbor and one from Royal Palms (intertidal habitat). For each culture, variation was scored for three enzymes: GPI, EST, and LAP or PGM, MDH, and AAT. In each case, the F_1 offspring are only those expected from the parental genotypes. Note that there is no evidence for reproductive isolation between the two populations from different habitat types.

Similar results were obtained for *Janua brasiliensis* (Table 2). In this case, two cultures were stained for the GPI locus and three for the PGM and MDH loci. Successful stain and buffer combinations for EST, LAP, and AAT were not discovered for this species.

In *Pileolaria pseudomilitaris,* there are multiple loci controlling PGM and EST expression. Large numbers of bands, of unequal intensity, are often closely spaced on a gel. Through formal genetic analysis, it was possible to assign bands to separate loci. For each enzyme system, one locus consistently stained more darkly. Only variation at this locus was scored. In addition, there are two loci with AAT activity that probably correspond to the mitochondrial and cytosolic forms in other animals. Both loci stain darkly and are well separated on a gel, so both loci were scored.

Variation at the MDH locus is rare for both species, as it is for AAT-1 and AAT-2 of *P. pseudomilitaris.* None of the rare alleles appeared in any culture tested. The allelic nature of variation at these loci can only be inferred from negative evidence: no alternate alleles appeared among progeny when they were absent from the parents.

Evidence for Self-fertilization

As Tables 1 and 2 show, certain offspring in some cultures of both *Pileolaria pseudomilitaris* and *Janua brasiliensis* could only have been produced by self-fertilization. There is evidence for self-fertilization in 8 of 16 *P. pseudomilitaris* cultures and in 1 of 5 *J. brasiliensis* cultures. For *P. pseudomilitaris,* GPI and EST were scored for the same individuals. Data from these two independent loci were consistent in indicating which progeny were produced by self-fertilization.

Some cultures of each species were attempted with single, newly settled larvae reared in isolation. Of these, no *J. brasiliensis* produced any offspring. Instead, worms produced three or more successive batches of embryos that were held in the brood chamber for up to one month, but never developed past the 32–64 cell stage. In one case, when a second immature worm was added to a Petri dish in

Table 1. Inheritance of allozymic variation: *Pileolaria pseudomilitaris.* F_1 genotypes given are only those found in that culture. Alleles are named in terms of their mobility relative to bromphenol blue. F_1 genotypes marked with an asterisk (*) are the product of self-fertilization; those marked with a dagger (†) are the product of cross-fertilization; the rest are unresolved.

Locus	Culture	P_1 Genotypes	F_1 Genotypes	Number
GPI	1	1/1 × 5/5	1/5	13†
	2	1/1 × 1/5	1/5	16
			5/5	4*
	3	1/1 × 1/5	1/1	10
			1/5	5
			5/5	4*
	4	1/1 × 1/5	1/1	12
			1/5	9
	5	−5/1 × 1/10	−5/1	3
			1/10	5
	12	1/1 × 20/20	1/20	9†
			20/20	4*
	13	−5/1 × 5/20	−5/5	5†
			−5/20	2†
			1/5	2†
			1/20	4†
			5/5	1*
			20/20	1*
	14	1/5 × 1/20	1/1	4
			1/20	4
			5/20	3†
	15	1/10 × 20/20	1/20	7†
			10/10	1*
			10/20	2†
	16	5/5 × 1/20	1/5	6†
			5/20	10†
PGM	6	50/50 × 46/54	46/50	9†
			50/50	1*
			50/54	8†
	7	46/50 × 46/50	46/46	10
			46/50	6
			50/50	3
	8	50/50 × 46/54	46/50	2†
			46/54	5*
			50/50	1*
			50/54	11†
			54/54	1*
	9	46/50 × 50/54	46/50	6
			46/54	4†
			50/50	8
			50/54	3
	10	46/46 × 46/54	46/46	22
			46/54	12
			54/54	4*
	11	40/40 × 40/40	40/40	14

Table 1. Continued.

Locus	Culture	P_1 Genotypes	F_1 Genotypes	Number
EST	1	52/56 × 52/56	52/52	4
			52/56	8
			56/56	2
	2	56/66 × 60/60	56/56	2*
			56/60	3†
			56/66	3*
			60/60	1*
			60/66	2†
			66/66	5*
	5	60/66 × 66/66	60/66	3
	12	56/60 × 56/60	56/56	3
			56/60	7
			60/60	3
	13	60/60 × 56/60	56/60	9
			60/60	6
	15	56/60 × 60/66	56/60	1
			56/60	3†
			60/60	2
			60/66	3
	16	60/60 × 60/66	60/60	9
			60/66	7
LAP	5	30/30 × 30/36	30/36	8
	12	30/30 × 30/36	30/30	3
			30/36	9
			36/36	1*
	13	27/27 × 30/30	27/30	13†
			30/30	2*
	16	30/30 × 36/40	30/36	8†
			30/40	8†

which the single individual had produced four aborted broods, both individuals subsequently produced normal broods that matured and reproduced as well.

Of eight attempted cultures of *P. pseudomilitaris* started with single individuals, three produced F_1 offspring; the others produced one to three aborted broods. None of the progeny produced by self-fertilization reached sexual maturity. In one case, a few immature individuals were used for electrophoresis. The parent was heterozygous at the GPI locus and offspring included both heterozygotes and homozygotes for the parental allozymes.

Fertilization in the field appears to be from at least a few neighboring individuals. Adults with broods of embryos ready to hatch were collected from the field, the offspring reared to maturity, and their genotypes compared to that of the parent. In all cases, all the offspring shared at least one allele with the parent. In one brood, four other alleles were also present at the GPI locus of the offspring, indicating fertilization by sperm from at least two other adults. At least one or two alleles not present in the known parent were always found in the offspring, indicating that self-fertilization does not play a major role in natural populations.

Table 2. Inheritance of allozymic variation: *Janua brasiliensis.*

Locus	Culture	P_1 Genotypes	F_1 Genotypes	Number
GPI	1	−4/1 × 1/1	−4/1	8
			1/1	11
	2	1/1 × 1/6	1/1	15
			1/6	5
PGM	3	36/42 × 36/42	36/36	4
			36/42	16
	4	32/36 × 32/42	32/32	3
			32/36	4
			32/42	14
			36/36	5*
			36/42	11†
	5	42/42 × 42/42	42/42	15

Discussion

Surveys of allozymic variation are becoming increasingly common in the literature of population genetics. Progeny testing is not often done prior to such surveys. Sometimes this is due to the technical difficulties of breeding a given species. Often, progeny testing is not considered necessary since the pattern of bands on electrophoretic gels appears to conform to a Mendelian interpretation. It is often assumed that different mobility classes of an enzyme can be translated directly into genotypes at the locus encoding for that enzyme. However, there are difficulties with this assumption. Johnson (1973) has discussed some of the problems that can confound interpretation of electrophoretic data. I have found the interpretation of data, especially from field samples, to be simplified greatly because of the results of progeny testing. In this way, the presence of two or more loci encoding for enzymes with similar activities can be detected, and the alleles more easily assigned to the correct locus. Proper interpretation of the results for the PGM and EST stains would not have been possible otherwise. Difficulties in the genetic interpretation of variation have been noted in studies of the eel *Anguilla rostrata* (Koehn 1972). Oxford (1975) showed that changes in diet induced phenocopies at an esterase locus in the snail *Cepaea nemoralis.* McGovern and Tracy (1981) were able to change the transferin and LAP "genotypes" of individual voles (*Microtus ochrogaster*) by holding them at different temperatures in the laboratory. Although such findings do not necessarily cast doubt on electrophoretic surveys done without the confirmatory evidence of progeny testing, they do suggest that progeny testing is highly desirable when possible.

Significance of Self-fertilization

A small but detectable amount of self-fertilization is present in laboratory cultures of both *Pileolaria pseudomilitaris* and *Janua brasiliensis.* This supports the earlier results of Gee and Williams (1965) and Potswald (1968) for some other species in the family. Neither previous study was entirely satisfactory. Gee and Williams (1965) used adult animals, collected from the field at a season when the animals were "entirely lacking in mature eggs and sperm." They were unaware of the presence of a sperm storage organ subsequently described by Daly and Golding (1977). Potswald (1968) used similar techniques, although he did rear a few isolated larvae to maturity and reproduction. In both studies, the progeny of self-fertilization were not held beyond metamorphosis and there was no indication that they were capable of reproduction. Although both studies adequately controlled for the presence of sperm from an outside source, there was no way for the investigators to prove that offspring were from self-fertilization, rather than parthenogenesis or some other process. I found that only a few *Pileolaria pseudomilitaris* reproduced successfully when reared entirely in isolation, and their progeny did not survive or grow well. Conclusive evidence that these progeny were the product of self-fertilization was provided by allozyme markers. In similar cultures of *Janua brasiliensis* survival and growth were even less.

In cultures initiated with pairs of worms, evidence from allozyme markers indicated that both species produced a small number of progeny by self-fertilization. Results of two cultures of *P. pseudomilitaris* are particularly informative: PGM culture 8 and EST cultures 2 (see Table 1). In each of these two cases, one parent is a heterozygote for two alleles that are not found in the other parent. Some individuals of the same heterozygous genotype are found among the F_1 offspring. These offspring can not be produced by any simple mechanisms of parthenogenesis except perhaps from diploid oocyctes. If parthenogensis were by diploid eggs, it is difficult to explain the presence of some homozygotes in the same cultures. A minimum estimate of the proportion of self-fertilization in culture can be made by summing all of the progeny known to be from self-fertilization and dividing by the total number of progeny from all cultures. This gives an estimate of 9.8% (22/276) of *P. pseudomilitaris* and 4.5% (5/111) for *J. brasiliensis* (based on data from the GPI and PGM loci). It is not possible to estimate the amount of self-fertilization that occurs in natural populations. Since natural populations are usually dense and water currents can easily carry sperm between neighbors, it is likely to be less than that in the laboratory.

Self-fertilization probably plays only a minor role in well-established *P. pseudomilitaris* populations. One brood from a single naturally fertilized parent often has three or more alleles at several loci. It is feasible that a single individual could found a new population, producing the first generation entirely by self-fertilization. Such an event can not be common since most natural populations are highly polymorphic, often with four or five alleles at each of several loci (Beckwitt 1980). As an event of evolutionary consequence, however, such a rare occurrence could be highly significant. It provides a way for spirorbids to colonize new habitats and may account in part for the degree of ecological speciation seen in the family.

Acknowledgments

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Literature Cited

Beckwitt, R. 1980. Genetic structure of *Pileolaria psudomilitaris* (Polychaeta: Spirorbidae). With appendix by R. Chakraborty. Genetics, 96:711–726.

Daly, J. M., and D. W. Golding. 1977. A description of the spermatheca of *Spirorbis spirorbis* and evidence for a novel mode of sperm transmission. J. Mar. Biol. Assoc. U. K., 57:219–227.

Gee, J. M. and G. B. Williams. 1965. Self- and cross-fertilization in *Spirorbis borealis* and *Spirorbis pagenstecheri*. J. Mar. Biol. Assoc. U.K., 45:275–285.

Johnson, G. G. 1973. Enzyme polymorphism and biosystematics: the hypothesis of selective neutrality. Ann. Rev. Ecol. Syst., 4:93–116.

Knight-Jones, P., E. W. Knight-Jones, and T. Kawahara. 1975. A review of the genus *Janua* including *Dexiospira* (Polychaeta: Spirorbidae). Zool. J. Linn. Soc., 56:91–129.

Koehn, R. K. 1972. Genetic variation in the eel: a critique. Mar. Biol., 14:179–181.

McGovern, M., and C. R. Tracy. 1981. Phenotypic variation in electromorphs previously considered to be genetic markers in *Microtus ochrogaster*. Oecologia, 51:276–280.

Oxford, G. S. 1975. Food induced esterase phenocopies in the snail *Cepaea nemoralis*. Heredity, 35:361–370.

Postwald, H. E. 1968. The biology of fertilization and brood protection in *Spirorbis* (*Laeospira*) *moerchi*. Biol. Bull., 135:208–222.

Selander, R. K., M. H. Smith, S. Y. Yang, W. E. Johnson, and J. B. Gentry. 1971. Biochemical polymorphism and systematics in the genus *Peromyscus* I. Variation in the old-field mouse (*Peromyscus polionotus*). Univ. Texas Studies in Genetics, 6:40–90.

Shisko, J. 1975. Life history of the annelid (Polychaeta: Spirorbidae) *Janua* (*Dexiospira*) *brasiliensis*. M.Sc. Thesis, Cal. State Univ. Long Beach., 81 pp.

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A Revision of the Honey Ants, Genus *Myrmecocystus*, First Supplement (Hymenoptera: Formicidae)

Roy R. Snelling

Abstract.—A revision of the honey ants, genus *Myrmecocystus,* first supplement (Hymenoptera: Formicidae) by Roy. R. Snelling, *Bull. Southern California Acad. Sci.,* 81(2):69–86, 1982. New distribution data are given for ten western species. Two new species are described: *M.* (*Eremnocystus*) *arenarius* is described from all castes; the type locality is Blow Sand Mts., Churchill Co., Nevada. *M.* (*M.*) *christineae* is described from all castes from the Ivanpah Mts., San Bernardino Co., California. New keys to the species of subgenera *Eremnocystus* and *Myrmecocystus* s. str. are provided and the two new species are appropriately illustrated.

Introduction

My revision of the honey ant genus *Myrmecocystus* was published in 1976. Since then, I have acquired interesting new distribution records for some species. Enough material of two undescribed species, then known from only a few specimens, is now available that these can be added to the known species.

The descriptive format is the same as that of my revision and figures in parentheses are those appropriate to the holotype or allotype, respectively.

New Records

All records, except as otherwise noted, are based on specimens in LACM. Specimens were collected by the author (RRS) or the author and C. D. George (CDG) unless otherwise noted.

Myrmecocystus (*Endiodioctes*) *intonsus* Snelling

Mexico, *Baja California Sur:* 51 km W La Paz, 274 m elev., 26 Aug. 1977 (RRS, No. 77-54); Estacion Microondas "Ligui," 425 m. elev., 48 km S Loreto, 25 Aug. 1977 (RRS, No. 77-50).

Myrmecocystus (*Endiodioctes*) *mendax* Wheeler

U.S.A., *California, Imperial Co.,:* Black Mtn. Rd., 1000′ elev., 4 rd mi SE Hwy. 78, 5 May 1978 (RRS & CDG, No. 78-24). *Inyo Co.:* Willow Cr., 2400′ elev., Inyo Mts., 17 Mar. 1976 (D. Giuliani); south Saline Range, 2500′ elev., 22 Apr. 1974 (D. Giuliani). *Riverside Co.:* Hidden Spgs., 2100′ elev., 24.5 rd mi WSW Wiley's Well, 25 Oct. 1978 (RRS, No. 78-135). *San Bernardino Co.:* Morningstar Mine Rd., 4200′–4260′ elev., Ivanpah Mts., 9.5 mi NNE Cima, 14 Apr. 1977 (RRS & CDG, No. 77-12).

Remarks

The collection at Morningstar Mine Rd. included alates of both sexes in the nest which was situated on a rocky slope. That at Black Mtn. Rd. was on an unusually arid ridge top in Cactus Scrub.

Myrmecocystus (*Endiodioctes*) *depilis* Wheeler

U.S.A., *Arizona, Yuma Co.:* Kofa Game Refuge, 3 Oct. 1978 (RRS & P. Mehlhop), in Creosote bush Scrub.

Myrmecocystus (*Endiodioctes*) *romainei* Cole

U.S.A., *California, San Bernardino Co.:* Morningstar Mine Rd., 4200′–4260′ elev., 13 Apr. 1977 (RRS & CDG, No. 77-5, 11, 13, 14, 15), in Joshua Tree Woodland.

Remarks

Nests were common in this area. Alates of both sexes were present in many nests.

Myrmecocystus (*Eremnocystus*) *colei* Snelling

U.S.A., *California, Los Angeles Co.:* Hwy. 138, 2700′ elev., 12.2 mi W Hwy. 14, 15 Sept. 1978 (RRS & CDG, No. 78-60, 61, 62).

Remarks

Previous records for this ant have been from coastal valley stations. The Mojave Desert samples are a little less pilose than those from coastal stations. Our samples were from the bed of a sandy wash dominated by *Salsola iberica* in rolling grassland which had been Joshua Tree Woodland until cleared.

Myrmecocystus (*M.*) *mexicanus* Wesmael

Mexico, *Baja California:* sand dunes, 8 km N Guerrero Negro, 8 Sept. 1977 (RRS, No. 77-71).

Remarks

Several colonies were found in this series of coastal dunes. Nest entrances were in the dune sand and lacked the conspicuous tumulus of coarse gravel characteristic of this species. Coarse gravel was not present in the area.

Myrmecocystus (*M.*) *navajo* Wheeler

Mexico, *Baja California:* 8 km N Punta Prieta, 300 m elev., 23 Aug. 1977 (RRS, No. 77-43).

Myrmecocystus (*M.*) *testaceus* Emery

U.S.A., *California, San Bernardino Co.:* Morningstar Mine Rd., 4100′–4200′ elev., 4.5 mi N Cima, 15 Apr. 1977 (RRS & CDG, No. 77-20).

Remarks

This is the first record for *testaceus* in the eastern Mojave Desert of California and is far removed from other Southern California localities. The site is Joshua Tree Woodland.

Myrmecocystus (*M.*) *ewarti* Snelling

U.S.A., *Nevada, Clark Co.:* 6 mi E Searchlight, 24 Nov. 1969 (G. & J. Wheeler, Nev. 590, in the collection of the Wheelers).

Myrmecocystus (*M.*) *pyramicus* M. Smith

U.S.A., *Nevada, Clark Co.:* 3 mi W Cottonwood Cove, 1200′ elev., 10 Dec. 1970 (G. & J. Wheeler, Nev. 1496, in the collection of the Wheelers).

Myrmecocystus (*Eremnocystus*) *arenarius* new species

Figures 1–6, 13, 15, 19, 21, 23

Diagnosis

Worker.—Scape, malar area and propodeum with abundant erect hairs; erect pronotal hairs abundant; pubescence of second tergum sparse to scattered. *Female* and *Male.*—Forewing without erect hairs on membrane.

Description

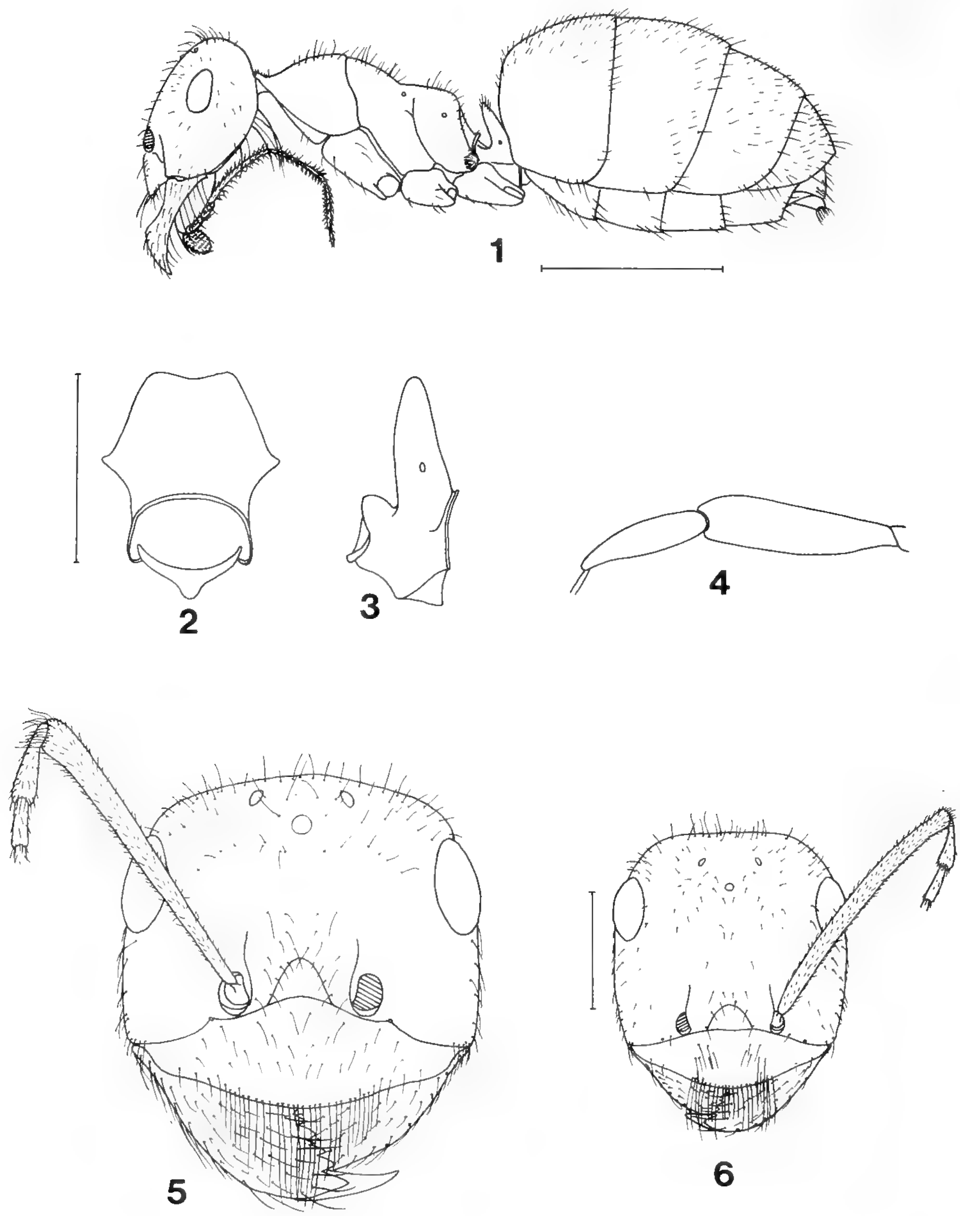
Worker.—Measurements: HL 0.65–1.02 (0.95); HW 0.58–0.90 (0.89); SL 0.66–1.07 (0.96); WL 0.83–1.40 (1.22); PW 0.42–0.63 (0.59).

Head: Longer than broad in all sizes, CI 105–119 (105); in full face view, malar margins nearly straight and convergent toward mandibles in smallest specimens, slightly convex in largest; occiput nearly flat in smallest workers, weakly convex in largest, sides broadly rounded; as long as, to a little shorter than, scape, SI 100–110 (101). Eye small to moderately large, EL 1.00–1.40 (1.31) × first flagellomere; OMD 1.17–1.54 (1.29) × EL. Mandible with seven teeth.

Thorax: Moderately robust, PW 0.43–0.52 (0.48) × WL. Mesonotum, in profile, nearly straight in smallest workers, broadly rounded into a sloping posterior face in largest specimens. Basal face of propodeum, in profile, short and broadly rounded into posterior face in small specimens, distinct, long, and abruptly rounded into posterior face in largest specimens.

Petiole: In profile, compressed and narrowly cuneate; spiracles distinctly projecting in larger specimens; crest broadly concave, in posterior view, in large specimens, flat or weakly notched in small individuals.

Vestiture: Pubescence scattered on head; long and dense, but not concealing surface, on thorax and first gastric tergum. Second tergum with scattered pubescence, usually more conspicuous (especially in larger individuals) along base, midline and at sides of disc. Erect hairs numerous on head; malar area with 5–11 suberect hairs; scape with sparse erect hairs and numerous shorter, decumbent to subdecumbent hairs; all surfaces of femora and tibiae with numerous erect and suberect hairs. Promesonotum with numerous erect hairs, the longest more than 0.5 × MOD; metanotum usually without erect hairs; dorsum of propodeum with 6 or more fine, short erect hairs. Petiolar scale with erect hairs on sides and crest. Terga with numerous discal hairs, becoming a little longer on succeeding segments.



Figs. 1–6. *Myrmecocystus arenarius.* 1, worker, lateral view, appressed pubescence not shown; scale = 1 mm. 2, 3, petiole of worker, posterior and lateral views; scale = 0.50 mm. 4, female, maxillary palp segments 4–6, vestiture not shown. 5, 6, female and worker head in frontal view, appressed pubescence not shown; scale = 0.50 mm.

Integument: Clypeus shiny, with scattered fine and coarse piligerous punctures; remainder of head subpolished, very weakly shagreened, with scattered piligerous punctures, frontal lobes virtually impunctate. Thoracic dorsum shiny, lightly shagreened. Gaster shiny, feebly shagreened.

Color: Medium to dark brown, appendages a little lighter; mandibles and apical part of clypeus yellowish brown, mandibular teeth dark red.

Female.—Measurements (mm): HL 1.36–1.38; HW 1.36–1.41; SL .36–.38; WL 2.51–2.78; PW 1.71–1.87.

Head: As broad as, or a little broader than, long, CI 95–100; in full face view, malar margin nearly straight or very weakly convex; distinctly longer than scape, SI 85–95. Eye small, EL 1.00–1.20 × first flagellomere; OMD 1.00–1.25 × EL. Mandible with seven teeth. Lateral ocelli slightly smaller than anterior ocellus, IOD 2.62–3.28 × OD; OOD 3.50–4.14. × OD. Fifth segment of maxillary palp broad at base, broadest near middle, distinctly narrowed distad; fourth segment narrowest at base, gradually broadened distad.

Thorax: Robust, PW 0.62–0.73 × WL. Posterior half of mesoscutum flattened; scutellum sloping and flat or very gently convex in profile. Basal portion of propodeum, in profile, sloping and abruptly rounded onto declivous face.

Petiole: Strongly compressed in profile, summit thin; in frontal view, sides a little convergent above; median emargination broad, deep, angulate; from above about 3 × wider than long.

Vestiture: Pubescence appressed, very scattered on head, most abundant (but still sparse) on lower malar area; appressed to subdecumbent on mesoscutum, scattered; longer, sparse, prostrate to suberect on sides of thorax, densest on pronotum and propodeum; appressed and scattered on tergal discs, becoming a little more abundant toward sides and apical margins.

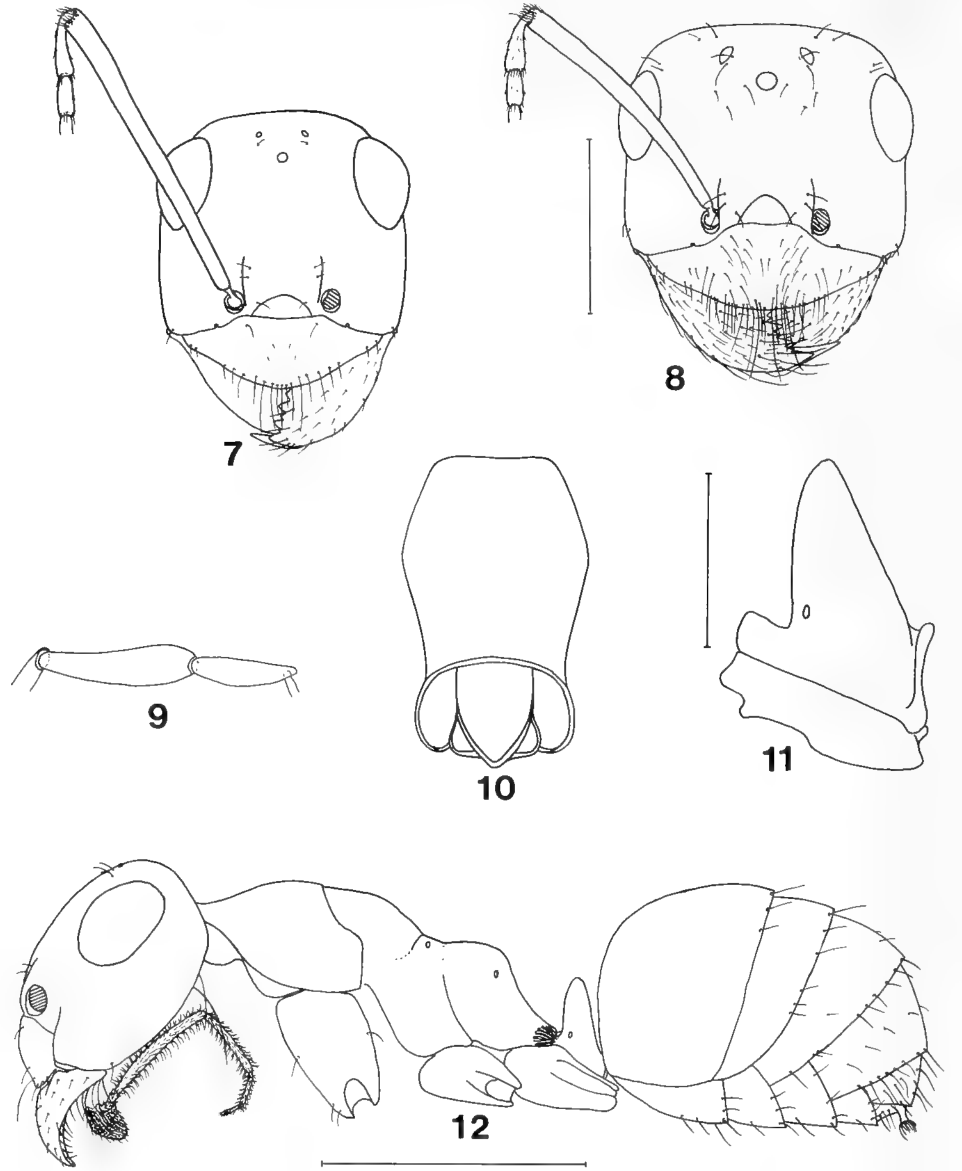
Scape with pubescence subdecumbent to suberect and with scattered fine, suberect hairs; femora and tibiae with abundant appressed to subdecumbent pubescence and numerous subdecumbent to erect hairs on all surfaces, least abundant on dorsal (extensor) femoral surfaces. Malar area, in frontal view, with 6–10 subdecumbent hairs; remaining frontal and dorsal head surface with rather sparse, short subdecumbent to erect hairs, longest hairs on occiput more than 0.5 × MOD. Scutum with sparse suberect to erect hairs, mainly peripherally, longest no more than 0.5 × MOD; scutellum with scattered suberect to erect hairs, longest more than MOD; pleura with scattered suberect to erect hairs, longest about 0.5 × MOD; propodeum with sparse erect hairs across base and at sides of declivity. Petiolar scale with a few short, erect hairs on sides and across summit. All terga with sparse, suberect to erect hairs, becoming longer and coarser caudad, longest on disc of second segment no more than 0.5 × MOD.

Membrane of forewing without obvious erect hairs at 45×; forewing without fringe hairs and hindwing with a very few on basal half of posterior margin.

Integument: Shiny and very weakly, or not at all, shagreened on most areas, including gastric terga; metapleuron and propodeum conspicuously duller.

Head generally with scattered minute punctures; clypeus with a few fine punctures. Mesoscutum with scattered fine punctures, middle of disc nearly impunctate; minute punctures even more scattered. Scutellum with sparse, fine setigerous punctures. Anepisternum for the most part with sparse to scattered fine and minute punctures; katepisternum similar but with posterior and posterodorsal zones of dense punctures; metapleuron and propodeum densely and finely punctate. Tergal discs with sparse to scattered minute to ultraminute punctures.

Color: Medium brown, sides and propodeum darker; appendages light brown. Wings hyaline, veins and stigma yellowish brown.



Figs. 7–12. *Myrmecocystus christineae.* 7, 8, worker and female head in frontal view, appressed pubescence not shown; scale = 1.0 mm. 9, female, maxillary palp segments 4–5, vestiture not shown. 10, 11, petiole or worker, posterior and lateral views; scale = 0.25 mm. 12, worker, lateral view; appressed pubescence not shown; scale = 1.0 mm.

Male.—Measurements (mm): HL 0.60–0.64 (0.64); HW 0.54–0.60 (0.60); SL 0.58–0.64 (0.64); WL 1.15–1.33 (1.33); PW 0.76–0.88 (0.76).

Head: Slightly to distinctly longer than broad, CI 104–117 (106), as long as, or longer than, scape, SI 94–100. In frontal view, margins distinctly convergent toward mandibular bases; occiput broadly convex, lateral angles broadly rounded. Eye large, OMD 0.47–0.65 (0.53) × EL; lateral ocelli slightly larger than anterior,

IOD 3.20–4.00 (3.75) × OD; OOD 2.75–3.25 (3.25) × OD. Mandible with distinct preapical cleft and one or two small teeth on cutting margin.

Thorax: Stout, PW 0.57–0.70 (0.57) × WL. Mesoscutum broad, vertical in front, posterior half flat or weakly concave; scutellum, in profile, with flat dorsal surface and abruptly sloping posterior face. Basal face of propodeum, in profile, narrow, convex and abruptly rounded into posterior face.

Petiole: Cuneate in profile, posterior face weakly convex, summit narrowly rounded; posterior view, crest straight or broadly and very shallowly concave.

Pilosity: Pubescence very fine, short, very scattered, most conspicuous on metapleuron and side of propodeum.

Scape with numerous very fine and short subdecumbent to suberect hairs; femora and tibiae with longer, coarser, sparse suberect hairs on all surfaces. Head and thorax with sparse to scattered subdecumbent to erect hairs, longest occipital hairs about 0.5 × MOD. Gastric terga with sparse, subdecumbent to erect hairs, longest on disc of second segment no more than 0.5 × MOD. Wings as in female.

Integument: Shiny and, at most, very weakly shagreened on most surfaces of head, thorax and gaster; metapleuron and basal face of propodeum moderately shiny, closely, though weakly, punctulate.

Color: Medium brown, occiput and thoracic dorsum a little darker, gaster a little paler. Appendages light brown. Wings hyaline, veins and stigma very pale brownish.

Terminalia: Figures 19, 21, 23.

Type material

Holotype worker, allotype and 211 worker, 8 female, 10 male paratypes: E end Blow Sand Mts., elev. 4600′, (T 15N, R 30E), Churchill Co., NEVADA, 14 Mar. 1979 (R. C. Bechtel and R. W. Rust). Additional paratypes: 173 workers, 4 females, 11 males, same locality, 4 Apr. 1979 (R. C. Bechtel and R. L. Bradley). Holotype, allotype and most paratypes in LACM; paratypes in AMNH, MCZ, USNM and collection of G. C. & J. Wheeler.

Additional Localities

Nevada, Churchill Co.: Sand Mountain, elev. 4000′, 1 July 1970 (G. C. & J. Wheeler, NEV. 1220); same locality, elev. 4200′, 14 Mar. 1979 (R. C. Bechtel and R. W. Rust). *Washoe Co.:* 6 mi N Nixon, elev. 4200′, 2 July 1977 (R. R. Snelling, G. C. & J. Wheeler; RRS No. 77-48, GJW No. NEV. 4191); same locality, 26 June 1965 (G. I. Stage); 2.8 mi W Wadsworth, 22 June 1963 (G. I. Stage).

Etymology

L., *arenarius* (pertaining to, or of, sand) because of the apparent preference of this ant for habitats of fine dune sand.

Distribution

At present known only from central Nevada, in areas of fine, drifting sand.

Discussion

The preeminent characteristic of this species is the great reduction of the appressed pubescence in all castes. In workers pubescence is abundant only on the dorsal surface of the first gastric tergum. Moderately dense pubescence is present only on the metapleuron, the base of the propodeum and, to a lesser degree, on the propodeal sides of the females and males.

Another unusual feature of this ant is shared by the sexual forms and is, as far as known, unique within this subgenus. Typically, within *Eremnocystus,* the membranes of the wings are beset with numerous fine, very short, subdecumbent to erect white hairs. These hairs are readily discernable at a magnification of 45×. In other subgenera the membrane is dotted with what appear to be, at 45×, minute papillae. In fact, they are hairs, but this becomes apparent only at high magnifications (see figure 33 of my 1976 revision). The wing membrane of *M. arenarius* is as it is in these other subgenera and thus atypical for a species of *Eremnocystus.*

While it might, perhaps, be argued that this represents a breakdown of an important characteristic separating *Eremnocystus* from *Endiodioctes* in particular, I do not think this is the case. The presence of hairs on the wing membrane seems to be a primitive feature retained within *Eremnocystus* generally, but modified in *Endiodioctes.* In other characteristics *Endiodioctes* is clearly the least advanced of the several subgenera of *Myrmecocystus.*

Within *Eremnocystus, M. arenarius* is a species with a number of derived character states. Chief among these are the great reduction of appressed pubescence, the fine and very scattered punctation (especially in the sexual forms) and the compressed petiolar scale of the worker. The isolation of this species from others within *Eremnocystus* is also an important factor. Only *M. hammettensis* is even geographically near *M. arenarius* and that is one of the most pilose of the *Eremnocystus.* It is highly improbable that there has been any genetic interchange between the two.

Females of *M. arenarius* are most similar to those of *M. tenuinodis,* another species in which the worker petiolar scale is compressed. This species, like *M. arenarius,* exhibits a preference for nest sites in fine sand which is prone to drifting. A third species whose worker possesses a compressed petiolar scale is *M. lugubris,* the female of which is unknown. If the female of *M. lugubris* is found to be sufficiently like those of *M. arenarius* and *M. tenuinodis,* and I predict that this will be so, we will have a complex of three species aligned along a roughly north-south axis with *M. lugubris* occupying the middle portion.

As I envision this particular complex, the protospecies once occupied a continuous range from what is now western and central Nevada to the head of the Gulf of Mexico and partway down either side of the Gulf. This protospecies may have been not very different from the present *M. yuma,* a species not particularly similar to those of the *lugubris* complex but nearer them than any others. During the Tertiary the three desert regions became sharply differentiated from one another; the Great Basin became higher and cooler, the Mojave and Sonoran lower and hot. Protospecies populations became isolated from one another and each developed along its own peculiar line in the absence of genetic moderation from other populations.

Ecology

The Wheelers and I were able to study this species briefly one day at a station six miles north of Nixon. This is an area of fine, drift-prone sand along the east side of Pyramid Lake. There was a sparse cover of *Salsola pestifer* and *Dalea polyadenia.* In one sector the annual, *Abronia turbinata,* was present and in bloom.

Two nests were situated in unstable sand with sparsely distributed *Salsola* and scattered *Dalea* plants. The third was in stabilized sand with denser cover, including *Abronia.* The only ant species common there was *Pogonomyrmex californicus* (Buckley). *Veromessor lariversi* M. Smith and *Conomyrma insana* (Buckley) were also present but uncommon.

Workers of *M. arenarius* were found foraging up to midmorning. Some were carrying miscellaneous fragments of other arthropods. A number of workers were also seen at nectaries of the *Salsola.* A single semireplete worker was recovered from one nest, but the unstable condition of the sand rendered deep excavation impractical.

The following key to species of *Eremnocystus* will replace that of my revision.

Key to Species of *Eremnocystus*

Workers

1. Antennal scape and dorsum of propodeum without fully erect hairs 2

– Antennal scape, usually, and dorsum of propodeum, always, with some fully erect hairs (propodeal hairs may be short and inconspicuous in *M. perimeces*; this species has an unusually elongate head, CI 70–81) 3

2. Pronotum and mesonotum with at least eight conspicuous, fully erect white hairs; petiolar scale strongly compressed in profile, crest distinctly notched .... *lugubris* Wheeler

– Pronotum and mesonotum each with no more than two fully erect hairs; petiolar scale not notably compressed, crest slightly concave or flat, but not conspicuously notched .... *creightoni* Snelling

3. Scape and/or tibiae, usually both, with conspicuous fully erect hairs; *or,* head moderately broad, CI 89 or more 4

– Scape and tibia without erect hairs and head unusually elongate, CI 70–81 .... *perimeces* Snelling

4. Scape with conspicuous erect or semierect hairs; femora and tibiae with abundant erect hairs, some present on dorsal femoral surfaces; petiolar scale variable, but often compressed with summit distinctly notched 5

– Scape with no erect hairs, except at apex; femora and tibiae with few erect hairs, none on dorsal femoral surface; petiolar scale thick in profile, crest flat or slightly convex .... *yuma* Wheeler

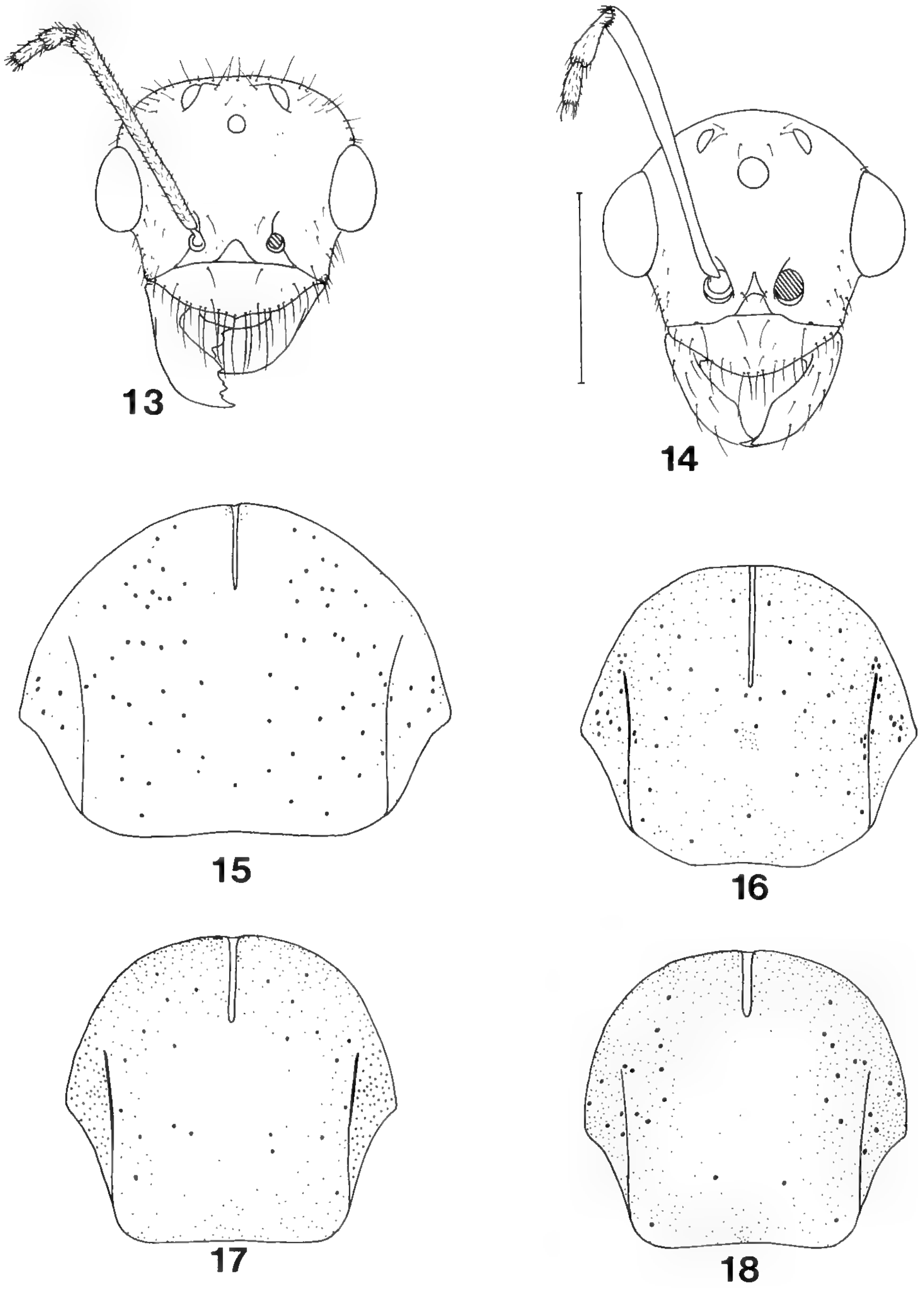
5. Scape with scattered erect and numerous suberect to subdecumbent hairs; malar area with fewer than 6 erect hairs in frontal view; if more, pubescence of second tergum much less dense than that of first 6

– Scape with numerous fully erect hairs; malar area with 10+ erect hairs in frontal view *and* second tergum fully as densely pubescent as first...... .... *hammettensis* Cole

6. Pubescence of second tergum as dense as that of first 7

– Pubescence of second tergum much sparser than that of first .... *arenarius* n. sp.

7. Appressed pubescence abundant on frons and third tergum; petiolar scale



Figs. 13–18. *Myrmecocystus* spp. 13–14, male, frontal view of head: 13, *M. arenarius* and 14, *M. christineae*; scale = 0.50 mm. 15–18, mesoscuta of females: 15, *M. arenarius*; 16, *M. christineae*; 17, *M. pyramicus*; 18, *M. ewarti*.

thick, at level of spiracle distinctly more than twice the length of the spiracle, crest flat or convex .... *colei* Snelling

– Appressed pubescence sparse on frons and third tergum; petiolar scale thin, at spiracle less than twice the length of spiracle, crest conspicuously notched .... *tenuinodis* Snelling

Females

1. Mesoscutum, finely, densely and uniformly punctate 2

– Mesoscutal punctation not uniform, punctures often of two sizes, with a large median impunctate area *or* with widely scattered punctures *or* with impunctate disc and median longitudinal punctate zone 3

2. Punctures subcontiguous on side of clypeus, very coarse, distinctly coarser than those of upper half of mesopleuron; occiput distinctly shiny, with scattered fine punctures; mid and hind femora without fully erect hairs except a few along lower side .... *creightoni* Snelling

– Punctures on side of clypeus distinctly separated, no coarser than on upper half of mesopleuron; occiput slightly shiny, densely shagreened, with fine obscure punctures; mid and hind femora with conspicuous fully erect hairs on all surfaces .... *colei* Snelling

3. Fourth segment of maxillary palp elongate-clavate, conspicuously broader at apex than at base; parapsis sparsely punctate, punctures irregular in size and spacing, but mostly separated by two or more puncture diameters ... 4

– Fourth segment of maxillary palp not clavate, about as broad in basal third as in apical third; parapsis with punctures uniform in size and spacing 6

4. Summit of first gastric tergum and much of discs of second and third shiny and polished, very nearly impunctate; scutellum with extensive nearly impunctate areas on either side of middle 5

– Summit of first gastric tergum and entire discs of second and third terga shiny between fine and evenly spaced piligerous punctures; scutellum with sparse, evenly spaced minute punctures .... *tenuinodis* Snelling

5. Fifth segment of maxillary palp uniformly broad, not conspicuously narrowed over apical one-half; forewing with numerous fringe hairs along costal margin .... *hammettensis* Cole

– Fifth segment of maxillary palp conspicuously narrowed over apical one-half (Fig. 4); forewing without fringe hairs on costal margin .... *arenarius* n. sp.

6. Face with abundant fine punctures between eyes and frontal lobes; clypeus shiny, polished; appressed gastric pubescence whitish; mesopleural hairs about as long as those of mesoscutum .... *yuma* Wheeler

– Face sparsely punctate between eye and frontal lobe; clypeus dull, densely sculptured; appressed gastric pubescence brownish; mesopleural hairs conspicuously longer than those of mesoscutum, little shorter than those of scutellum .... *perimeces* Snelling

Myrmecocystus (*Myrmecocystus*) *christineae* new species

Figures 7–12, 14, 16, 20, 22, 24

Diagnosis

Worker.—Erect hairs absent from malar area, scape tibiae and mesosomal dorsum; upper margin of eye little below occipital corner; basal face of propodeum flat or slightly rounded in profile. Female: Fifth segment of maxillary palp broadest in middle; OOD 1.8–2.5 × OD; scape, except at apex, with fine, appressed pubescence only; tibial hairs decumbent, sparse; mesoscutum, between parapsides, with sparse, fine punctures and scattered coarse punctures, center nearly impunctate. Male: Scape with appressed pubescence only, except at tip; tibiae with very short decumbent hairs; forewing with fringe hairs along apical margin, hindwing with fringe hairs along apical and posterior margins; forewing without discoidal cell; HL less than 0.8 mm.

Description

Worker.—Measurements: HL 0.77–1.13 (1.12); HW 0.63–1.03 (1.02); SL 0.97–1.33 (1.33); WL 1.03–1.63 (1.63); PW 0.43–0.72 (0.70) mm.

Head: Longer than broad, CI 75–94 (91), a little shorter than scape, SI 113–130 (119). In frontal view, sides of head nearly parallel in small workers, slightly convex in largest workers and widest at about midpoint of malar area. Occiput, in frontal view, flat, sides convex, not at all angulate. Eye large, EL 1.4–1.7 (1.5) × first flagellomere; OMD 0.75–1.04 (1.00) × EL; upper margin nearly coincident with occipital corner. Mandible with seven or eight teeth.

Thorax: Moderately robust to robust, PW 0.43–0.72 (0.70) × WL. Basal face of propodeum, in profile, flat or slightly rounded, broadly rounded into longer posterior face.

Petiole: Elongate-cuneate in profile, summit narrowly rounded; crest, from behind, weakly notched; from above about twice wider than long.

Vestiture: Clypeus with a few erect hairs; two pair of very short erect hairs on margins of frontal lobes and a pair on vertex. Thorax without erect hairs. Crest of petiole without erect hairs. First two gastric terga without erect hairs on disc; remaining terga with scattered suberect discal hairs. Scape and outer tibial faces without visible hairs of any declination.

Pubescence fine, sparse and short on head and mesosomal dorsum; longer and a little denser on mesosomal side and on gastric terga; everywhere appressed, but with some suberect pubescence on basal area of first tergum.

Integument: Moderately shiny over most areas, clypeus polished, with scattered fine punctures; malar area somewhat shagreened, with sparse, elongate punctures; frontal lobes closely, sharply and finely punctate; frons and vertex similar but punctures a little finer.

Color: Light brownish yellow; occiput sometimes brownish; appendages paler.

Female.—Measurements: HL 1.67–1.73; HW 1.67–1.77; SL 1.57–1.67; EL 0.53–0.57; WL 3.5–3.7; PW 2.0–2.2 mm.

Head: As broad as, or a little broader than long, CI 100–104; longer than, or as long as, scape, SI 92–100. In frontal view, broadest below eyes, sides weakly convex. Occiput, in frontal view, flat, corners broadly rounded. Eye large, EL 1.3–1.5 × first flagellomere; OMD 1.0–1.6 × EL; IOD 2.2–2.9 × OD; OOD 1.8–

2.5 × OD. Mandible variable, usually with five conspicuous, widely spaced teeth (in addition to apical tooth) and with two to four smaller denticles between these. Fifth segment of maxillary palp broad over much of its length, narrowed at base and apex.

Thorax: Robust, PW 0.54–0.63 × WL. In profile, posterior two-thirds of mesoscutum flattened. Scutellum slightly convex, strongly sloping and forming continuous plane with metanotum and base of propodeum.

Petiole: Compressed in profile, crest narrowly rounded; distinctly notched in frontal view; from above, about three times wider than long.

Vestiture: Head with sparse, short, suberect hairs across occiput and with scattered longer hairs (about 0.5 × MOD); frontal lobes with sparse short, suberect to erect hairs; clypeus with numerous short and long suberect to erect hairs on disc; malar area with 3–6 short, decumbent to suberect hairs. Mesoscutum with scattered short and long, suberect to erect hairs; scutellum with 4–6 long, erect hairs and a few short, erect hairs; side of thorax with widely scattered, short, erect hairs; propodeum without erect hairs over base, disc and sides; terga with scattered, short, suberect to erect hairs on discs which are progressively longer on succeeding segments. Inner face of profemur without erect hairs, though 15+ present along lower margin; meso- and metatibia with numerous fine, decumbent hairs.

Forewing with fringe hairs along apical margin; hindwing with fringe hairs along apical and posterior margins.

Pubescence appressed, general, abundant only on malar area, sides of thorax, propodeum, scape and first four terga.

Integument: Clypeus and supraclypeal area smooth or lightly shagreened between sparse, coarse punctures; frontal lobes moderately shiny between close micropunctures and sparse coarse punctures; occiput dull and shagreened between close micropunctures and sparse coarse punctures; malar area dull and shagreened between close, coarse, elongate punctures.

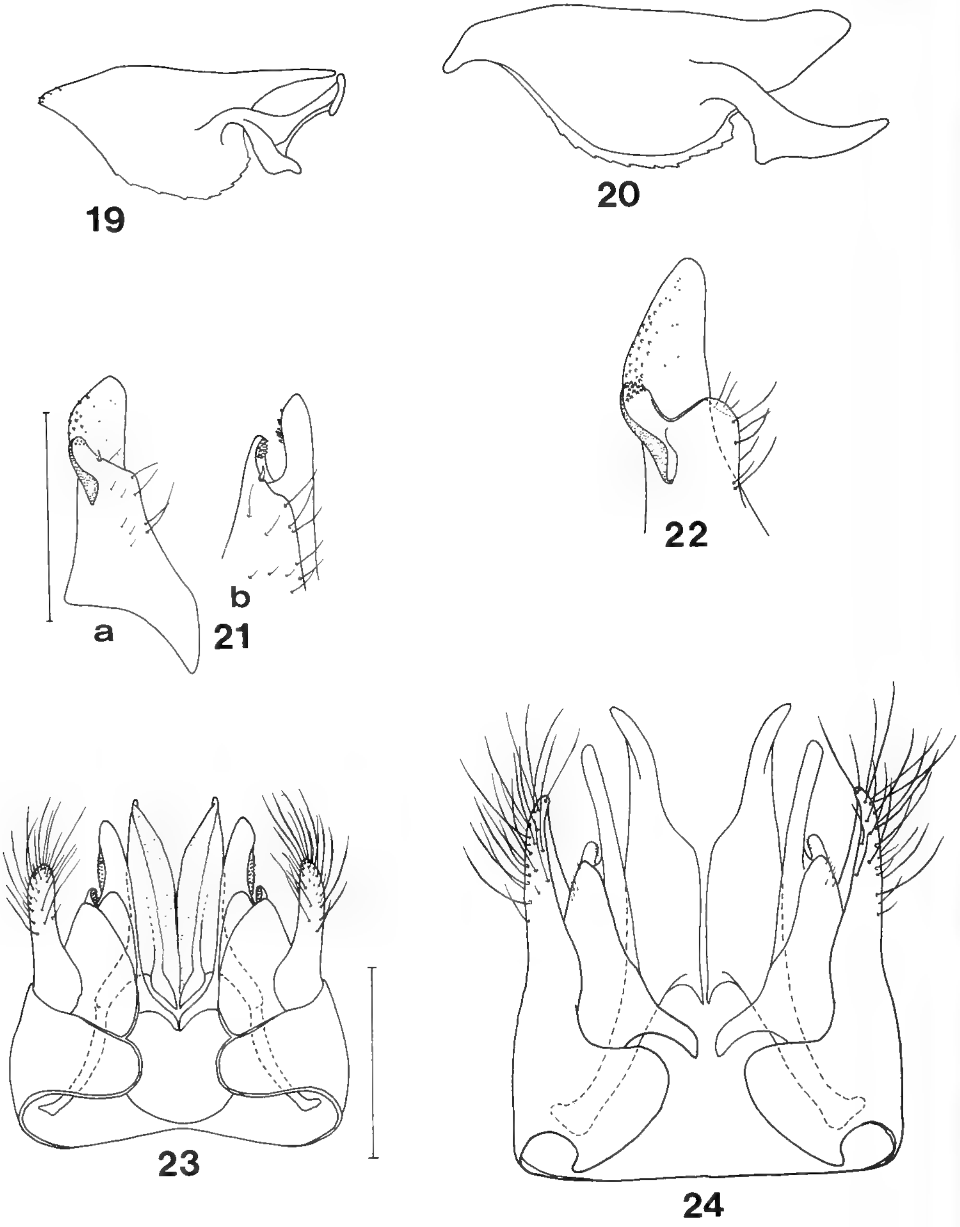
Pronotum moderately shiny, sides and dorsal margin closely micropunctate, neck with punctures very obscure. Parapsis shiny, with close micropunctures and sparse coarse punctures; mesoscutal disc shiny, with sparse micropunctures, nearly impunctate in middle. Scutellum shiny, with scattered micropunctures and a few coarse punctures (from which the long hairs arise). Anepisternum and katepisternum moderately shiny between close micropunctures and sparse coarse, piliferous punctures. Propodeum dull, densely shagreened and closely micropunctate.

First three terga shiny between close micropunctures and scattered coarse punctures, punctures a little more separated and less distinct on second segment.

Color: Yellow, frontal area of head light brown; appendages paler yellow. Wings clear, veins and stigma light to medium brown.

Male.—Measurements: HL 0.62–0.70 (0.66); HW 0.53–0.60 (0.57); SL 0.66–0.73 (0.66); EL 0.28–0.30 (0.30); OMD 0.10–0.15 (0.13); WL 1.23–1.40 (1.30); PW 0.70–0.80 (0.77) mm.

Head: Margins slightly convergent toward mandibular insertions; distinctly longer than broad, CI 79–88 (85); a little shorter than, to a little longer than, scape, SI 95–114 (100); OMD 0.33–0.50 (0.44) × EL; anterior ocellus little smaller than lateral ocelli; IOD 2.50–3.50 (3.00) × OD; OOD 1.00 × OD. Mandible without preapical teeth, preapical notch weak or absent. Clypeus usually with transverse preapical depression.



Figs. 19–24. *Myrmecocystus* spp., male terminalia, 19–20, aedeagus in profile: 19, *M. arenarius* and 20, *M. christineae*; same scale as 23–24. 21–22, inner view of volsella (and ventral view, 21): 21, *M. arenarius* and 22, *M. christineae*; scale = 0.125 mm. 23, 24, genital capsule, ventral view: 23, *M. arenarius* and 24, *M. christineae*; scale = 0.25 mm.

Thorax: Stout, PW 0.52–0.59 (0.59) × WL. Propodeum, in profile, without defined basal face.

Petiole: Sharply cuneate in profile; in frontal view, crest weakly notched; in dorsal view about twice wider than long.

Vestiture: Erect hairs short and sparse on clypeus, absent from frontal lobes; a single pair, short and suberect, in ocellar area; absent from mesoscutum; four to six short, suberect hairs on scutellum; first three terga without erect hairs, but with sparse, decumbent hairs; remaining terga and the sterna with moderately long, suberect to erect sparse hairs. Hairs of tibiae short, fine and decumbent to appressed. Scape with appressed pubescence only. Wings as in female.

Integument: Moderately shiny on most areas, shiny between notaulices, with sparse piligerous micropunctures: scattered coarse punctures on mesokatepisternum.

Color: Uniformly brownish; appendages pale yellowish. Wings clear, veins and stigma light brown.

Terminalia: Figures 20, 22, 24.

Type Material

Holotype worker, Morningstar Mine Rd., elev. 4200′–4260′, 9.5 mi NNE Cima, San Bernardino Co., CALIF., 14 Apr. 1977 (C. D. George and R. R. Snelling; RRS No. 77-9); allotype male, same data but RRS No. 77-10; holotype and allotype in LACM. Paratypes: 16 females, 724 workers, 68 males, same data, RRS No. 77-9, 10, 16. Paratypes in AMNH, GCW, LACM, MCZ, USNM.

Etymology

This species is dedicated to Christine D. George who materially assisted in collecting and studying this new species and who is currently investigating *Myrmecocystus* ecology in the Mojave Desert.

Distribution

At present known only from the Ivanpah Mountains of the Mojave Desert. The species probably occurs in suitable habitats of adjacent ranges in California and Nevada.

Discussion

In my revision of *Myrmecocystus* the nominate subgenus was divided into the *mexicanus, pyramicus* and *testaceus* species groups. The present species appears to be annectant between the *mexicanus* group and the *pyramicus* group. The mesosomal profile of the worker is very similar to that of *mexicanus* group species, as is the number of mandibular teeth of the female and worker. The displacement of the eyes of the worker toward the occipital margin is about as in the *pyramicus* group, although this is shared with *navajo* in the *mexicanus* group. The great reduction in erect body hairs in both female and worker accords with the *pyramicus* group.

Following is a revised key to the species of *Myrmecocystus* s. str. to include *M. christineae.*

Key to Species of *Myrmecocystus* S. Str.

Workers

1. Dorsal surface of propodeum strongly, angularly projected upward over posterior two-thirds; erect hairs very sparse, with few or none on outer face of hind tibia; upper eye margin little below upper margin of head . . . 2

– Dorsal surface of propodeum either flat or evenly convex; body often abundantly hairy; upper eye margin usually well below upper margin of head 3

2. With at least two erect pronotal hairs as long as apical breadth of scape; first tergum with a few erect hairs on disc; hind tibia with a few erect hairs on outer face beyond basal third . . . . *ewarti* Snelling

– Erect pronotal hairs, when present, shorter than apical breadth of scape; first tergum without erect discal hairs; hind tibia without erect hairs on outer face beyond basal third . . . . *pyramicus* M. Smith

3. Fully erect hairs conspicuous on thoracic dorsum, discs of first and second terga and on scape and tibiae 4

– No erect hairs on thoracic dorsum, discs of first and second terga, scape or tibiae . . . . *christineae* n. sp.

4. Head, pronotum and gaster with abundant appressed pubescence; mid and hind tibiae usually with numerous erect hairs along apical half of outer face; upper eye margin often distinctly below occipital corner; if metanotal suture impressed, HL exceeds 1.3 mm 5

– Head, pronotum and gaster shiny, with little or no appressed pubescence; mid and hind tibiae with not more than 3 or 4 erect hairs beyond basal third of outer face, usually none; upper eye margin coincident with occipital corner; metanotal suture deeply impressed and dorsal face of propodeum convex . . . . *navajo* Wheeler

5. Large, highly polymorphic species, HL 1.0–2.0 mm or more, usually in excess of 1.3 mm; metanotal suture usually impressed and propodeum as long as high or longer, juncture of dorsal and posterior faces broadly rounded 6

– Smaller, moderately polymorphic species, HL 0.8–1.4 mm; metanotal suture not impressed; propodeum higher than long, juncture of dorsal and posterior faces abruptly rounded, often subangulate . . . . . . *testaceus* Emery

6. Eye with numerous erect hairs which are longer than diameter of ocular facets; mandible with 8 or 9 teeth; color uniformly brownish, gaster a little darker . . . . *melanoticus* Wheeler

– Eye with erect hairs, when present, very diffuse, length less than diameter of ocular facets; mandible with 9 or 10 teeth; color usually distinctly yellow, but may be extensively brownish in southern populations . . . . *mexicanus* Wesmael

Females

1. Fifth segment of maxillary palp broadest in middle, narrowed basally and apically; hind femur without erect hairs on dorsal surface; hind tibia with hairs decumbent, never fully erect 2

– Fifth segment of maxillary palp broadest well basad of middle, gradually narrowed toward apex or parallel sided; hind femur with erect hairs on dorsal surface; hind tibia with abundant fully erect and suberect hairs 5

2. Antennal scape with decumbent or appressed hairs only except a few erect hairs at tip; ocelli normal, OD less than 0.12 mm 3

– Antennal scape with conspicuous coarse erect and suberect hairs; ocelli large, OD greater than 0.15 mm .... *navajo* Wheeler

3\. Fourth segment of maxillary palp gradually widened from base to apex; fine punctures of parapsis abundant and uniformly spaced (Figs. 17, 18); side of frontal lobe shiny between close, fine punctures 4

– Fourth segment of maxillary palp distinctly clavate (Fig. 9); fine punctures of parapsis very irregularly spaced (Fig. 16); side of frontal lobe dull and roughened between fine punctures which are at least partially obscured .... *christineae* n. sp.

4\. Fine punctures of parapsis conspicuously coarser than those of disc of mesoscutum (Fig. 17); first tergum with fewer than 6 erect hairs on disc, often none; interocellar distance about equal to ocellocular distance .... *pyramicus* M. Smith

– Fine punctures of parapsis not obviously coarser than those of disc of mesoscutum (Fig. 18); first tergum with at least 12 erect to suberect hairs on disc; interocellar distance less than ocellocular distance .. *ewarti* Snelling

5\. Thorax and gaster brown, legs usually yellowish; HW usually less than 1.85 mm; penultimate segment of maxillary palp slender, parallel-sided .... *testaceus* Emery

– Thorax and gaster light brownish yellow to yellow, legs concolorous with thorax; HW 1.90 mm or more; usually more than 2.0 mm; penultimate segment of maxillary palp distinctly broadest basad ... *mexicanus* Wesmael

Males

1\. Scape and tibia without conspicuous standing hairs; hind wing with fringe hairs on posterior margin 2

– Scape always and tibia usually with conspicuous standing hairs; posterior margin of hind wing variable 4

2\. Forewing with conspicuous fringe hairs along apical margin; HL less than 0.80 mm 3

– Forewing without fringe hairs along apical margin; HL in excess of 0.90 mm .... *pyramicus* M. Smith

3\. Mesopleuron shiny, indistinctly, or not at all, shagreened; forewing usually with discoidal cell .... *ewarti* Snelling

– Mesopleuron slightly shiny, distinctly shagreened; forewing without discoidal cell .... *christineae* n. sp.

4\. Occipital hairs shorter than maximum diameter of lateral ocellus; posterior and/or apical margins of hind wing with at least a few long fringe hairs .. 5

– Many occipital hairs longer than maximum diameter of lateral ocellus; hind wing without fringe hairs .... *testaceus* Emery

5\. Small species, HW less than 0.8 mm; scape with scattered erect hairs, tibia with numerous decumbent hairs; apical margin of forewing without fringe hairs .... *navajo* Wheeler

– Large species, HW greater than 0.9 mm; scape and tibia usually with abundant erect or suberect hairs; if erect hairs reduced or absent, apical margin of forewing with at least vestiges of fringe .... *mexicanus* Wesmael and *melanoticus* Wheeler

Literature Cited

Snelling, Roy R. 1976. A revision of the honey ants, genus *Myrmecocystus* (Hymenoptera: Formicidae). Nat. Hist. Mus. Los Angeles Co. Bull., 24:1–163.

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Natural History Museum of Los Angeles County, 900 Exposition Blvd., Los Angeles, California 90007.

Bull. Southern California Acad. Sci.
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A Multivariate Study of Morphological Variation of the Limpet *Notoacmea depicta* (Hinds) and its Synonyms *Notoacmea gabatella* (Berry) and *Notoacmea lepisma* (Berry) (Gastropoda: Acmaeidae)

David R. Lindberg

Abstract.—A multivariate study of morphological variation of the limpet *Notoacmea depicta* (Hinds) and its synonyms *Notoacmea gabatella* (Berry) and *Notoacmea lepisma* (Berry) (Gastropoda: Acmaeidae) by David R. Lindberg, *Bull. Southern California Acad. Sci.*, 81(2):87–96, 1982. Three nominal species of marine plant limpets from southern California are examined using discriminant function analysis. Two of the species, *Notoacmea depicta* and *N. gabatella* had been synonymized earlier based on radular morphology. The results of the discriminant analysis allow for the synonymization of *N. lepisma* with *N. depicta*. The apertural variation seen in the 3 forms of *N. depicta* appears to be related to the intraspecific variation in the host plant *Zostera marina*. The oval form of *N. depicta* is reported and illustrated from Mugu Lagoon, Ventura County. This is a new northern locality record for this form and the first report of its occurrence on *Z. marina*.

Introduction

Acmaeid limpets are one of the groups of mollusks in which interspecific shell variation can be less than intraspecific shell variation. This situation results because many acmaid species are polytypic with several ecotypes. When an ecotype of a polytypic species occurs in the same habitat as a monotypic species, the variation between the 2 species can be less than the variation between the ecotypes of the polytypic species. Convergent shell morphologies can occur in almost all habitats but are most common in species that are epiphytic or epizoic. Therefore, care must be exercised when making taxonomic decisions based strictly on shell characters especially when the limpets are from specialized habitats. Moreover, the question as to whether the variation of the specimens in hand results from interspecific differences or simply intraspecific variation becomes very important.

The human eye is a poor tool to resolve this question. As so cogently stated by Bookstein (1978:172) "The human eye is wired for *Gestalt*, for recognition rather than quantification. It is notoriously bad at apprehending population variance." Thus, the question is best answered by statistical analysis, particularly multivariant morphometrics. Limpet shells are well suited for this type of analysis because their simple shapes are easily described by linear measurements.

Whether intraspecific or interspecific, much of the variation seen in limpets can usually be correlated with some aspect of the habitat. For example, correlations exist between shell shape and host plant/animal shape and between shell color and substrate color. What is usually not considered is the pattern of variation that results when a limpet, whose morphology is determined in part by its substrate, occurs on a host that has several ecotypes that differ morphologically. In this case the intraspecific variation of the host is reflected in the intraspecific variation of the limpet.

In an earlier paper (Lindberg 1980) I synonymized *Notoacmea gabatella* (Berry 1960) with *Notoacmea depicta* (Hinds 1842) on the basis of radular morphology. Unlike shell morphology, radulae in members of the family Acmaeidae are considered to be species-specific (Dall 1871; Grant 1937; McLean 1966; Christiaens 1975a, b). The shells of both taxa have similar color patterns and sculpturing. The only marked difference between them is apertural shape. In *N. gabatella* the aperture is oval; in *N. depicta* the aperture is compressed laterally. Thus, I considered the 2 taxa to be extreme forms of a single species; the oval form occurring on brown algae or rocks and the compressed form on the marine angiosperm *Zostera marina.*

A third nominal species, *Notoacmea lepisma* (Berry 1940), appears to be intermediate between the 2 forms of *N. depicta.* Because *N. lepisma* is known only from early Pleistocene deposits at San Pedro, California the radula is not available for comparison. Rather than synonymize *N. lepisma* with *N. depicta* solely because it has a similar shell sculpture and coloration, I decided to compare statistically *N. lepisma* with the 2 forms of *N. depicta.* Discriminant function analysis was used to determine (1) the morphological characters that distinguish the 3 taxa, (2) whether *N. lepisma* occupies, statistically, an intermediate position between the 2 forms of *N. depicta,* and (3) whether *N. lepisma* intergrades with either form. This latter question was particularly important because neither McLean (1966) nor I (Lindberg 1980) had discerned, by eye, any overlap betwen *N. lepisma* and either form of *N. depicta.* This paper reports the results of the discriminant function analysis. A new northern record for the oval form of *N. depicta* is also reported.

Abbreviations are as follows: CAS, Department of Invertebrate Zoology, California Academy of Sciences, San Francisco; LACM, Section of Malacology, Natural History Museum of Los Angeles County, Los Angeles; LACMIP, Section of Invertebrate Paleontology, Natural History Museum of Los Angeles County; SDMNH, San Diego Museum of Natural History, San Diego; UCB, Department of Paleontology, University of California, Berkeley.

Materials and Methods

The analysis used 105 specimens of *N. depicta* (65 compressed forms and 40 oval forms) and 28 specimens of *N. lepisma.* The *N. depicta* specimens were from 8 localities in southern California and Baja California; *N. lepisma* material was from 4 Pleistocene localities at San Pedro, California (Table 1).

Each specimen was assigned to 1 of 3 groups (compressed form, oval form, or *N. lepisma*), and measured to the nearest 0.1 mm with vernier calipers. Six measurements (variables) of each shell were recorded (Fig. 1a): (1) total length, (2) the distance of the apex from the anterior edge of the aperture (apexpos), (3) height, (4) width at ¼ of the length from the anterior edge of the shell (widfron), (5) width at ½ the distance from the anterior edge (width), and (6) width at ¾ of the total length from the anterior edge (widend).

The data were analyzed with the Statistical Package for the Social Sciences (SPSS) (Nie, Hull, Jenkins, Steinbrenner, and Bent 1975). Means and standard deviations of the variables and Pearson correlation coefficients—to evaluate linear

Table 1. Material examined.

Taxon	Depository—No.	Locality	Remarks
N. depicta			
Oval	SDMNH—48479	Laguna Beach, CA	
	CAS—24622	San Pedro, CA	
	LACMIP—332	San Pedro, CA (Miraflores Ave.)	Middle Pleistocene
Compressed	CAS—17663A	Cabo San Lucas, Baja CA	
	CAS—40002	San Diego, CA	
	CAS—19292	San Diego, CA	
	CAS—24623	San Diego, CA	
	CAS—24624	San Diego, CA	
N. lepisma	LACMIP—4151	San Pedro, CA (Hill Top Quarry)	Early Pleistocene
	LACMIP—64	San Pedro, CA (Hill Top Quarry)	Early Pleistocene
	LACMIP—228	San Pedro, CA (Nob Hill)	Middle Pleistocene
	LACMIP—142	San Pedro, CA (2nd & Orizaba St.)	Late Pleistocene

relationships between pairs of variables—were calculated. The discriminant analysis program of the SPSS was used to determine the variables that are most important in distinguishing between the 3 groups. Two computations are performed by the program. The first calculates discriminant function(s) for the groups being analyzed and individual discriminant scores for each member of a group. The second part of the program compares the original group assignment of a member with its predicted assignment based on its discriminant score.

Two combinations of groups were analyzed. First all 3 groups were compared and the original group assignments of the specimens evaluated. A second analysis compared the oval and compressed forms of *N. depicta*. The *N. lepisma* data were not included in the analysis but were entered for the classification phase of the program. See Blackith and Reyment (1971) for a discussion of the use of discriminant function analysis in morphometrics.

Results

Figure 1, which shows the relative sizes and proportions of the 3 taxa, was prepared from the means of the 6 variables. Pearson correlation coefficients indicated that the variables in all 3 groups are significantly correlated with one another ($P < 0.01$) with the exception of apexpos and height in *N. lepisma* ($P > 0.10$).

During the stepwise addition of variables, widend was removed from the discriminant analysis because of its low discriminating power (Wilks' lambda). Two canonical discriminant functions were calculated for the 3 group analysis (Table 2). The first function accounts for 94.7% of the variance. Width and length coefficients are 2 to 3 times more important than the other characters for discriminating among the 3 groups. Height and widfron are approximately equal

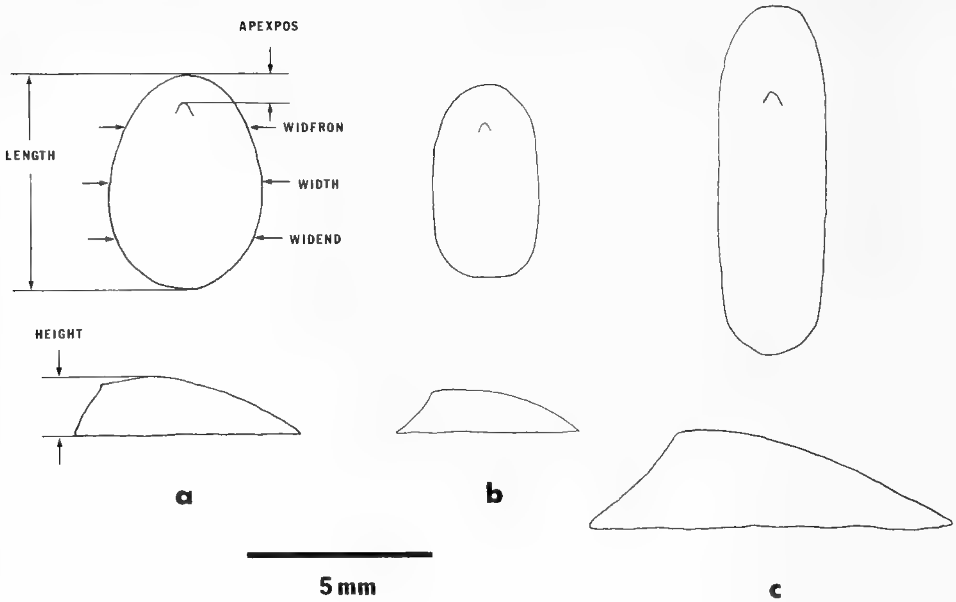

Fig. 1. Dorsal and lateral views of (a) the oval form of *Notoacmea depicta,* (b) *N. lepisma,* and (c) the compressed form of *N. depicta.*

and their importance almost twice that of apexpos. The second function accounts for 5.3% of the variance. Widfron and width are approximately 2 to 3 times more important than any other character. Length and apexpos make the smallest contributions to function 2. The combination of positive and negative coefficients indicates that the differences between the 3 groups are not due to size but represent changes in shape. A scatter diagram of the individual discriminant scores for function 1 and function 2 (Fig. 2) shows the intermediate position of the *N. lepisma* specimens.

The classification computations identify 4 compressed forms of *N. depicta* and 7 oval forms as specimens of *N. lepisma.* Conversely, 4 specimens identified as *N. lepisma* were classified as oval forms of *N. depicta.* Based on the characters measured 88.7% of the specimens had been correctly classified.

The second analysis discriminated between the forms of *N. depicta* and then classified the *N. lepisma* specimens relative to these 2 forms. The single discrim-

Table 2. Canonical discriminant functions.

		Characters				
Groups	Function	Length	Width	Height	Widfron	Apexpos
1, 2, 3	1	−1.613	1.898	0.550	−0.586	−0.292
	2	−0.561	−1.617	−0.810	1.697	0.576
1, 2	1	−1.571	2.448	0.781	−1.283	−0.346

Groups: 1 = *N. depicta* oval form, 2 = *N. depicta* compressed form, 3 = *N. lepisma.*

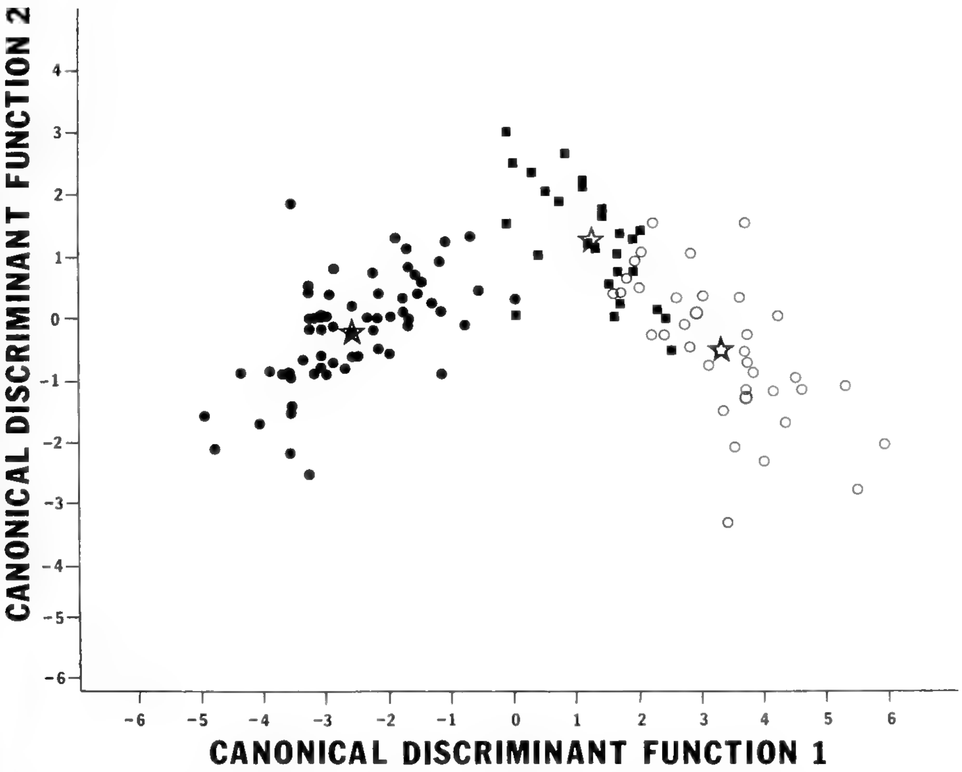

Fig. 2. Scatter diagram of individual discriminant function scores for 3 group analysis. ● = compressed form, ■ = *Notoacmea lepisma*, ○ = oval form, ☆ = group centroids.

inant function was similar to discriminant function 1 of the first analysis. The relative importance of the coefficients and their signs were the same (Table 2). A frequency histogram of the individual discriminant scores for the oval, compressed, and *N. lepisma* specimens again shows the intermediate position of *N. lepisma*. Moreover, overlap of *N. lepisma* with both forms of *N. depicta* is readily apparent (Fig. 3). Overlap is present also in Figure 2, but is not as obvious. During the classification phase of the program, 9 specimens of *N. lepisma* were classified as compressed forms of *N. depicta* while the remaining 19 specimens were classified as oval forms. Two specimens of *N. lepisma* have discriminant scores that indicate they are intermediate between the 2 forms of *N. depicta*. In one case the probability that the specimen is an oval form of *N. depicta* is only 0.53. In the other case the probability that the specimen is a compressed form is only 0.57. The other specimens have probability scores between 0.72 and 1.00 ($\bar{x} = 0.96$; s.d. = 0.07).

Discussion

Width and length differences distinguish the 2 forms of *N. depicta*. Canonical function 1 contrasts width with length (Fig. 2). Thus, the compressed form of *N. depicta* is relatively longer and narrower than the oval form. Discrimination

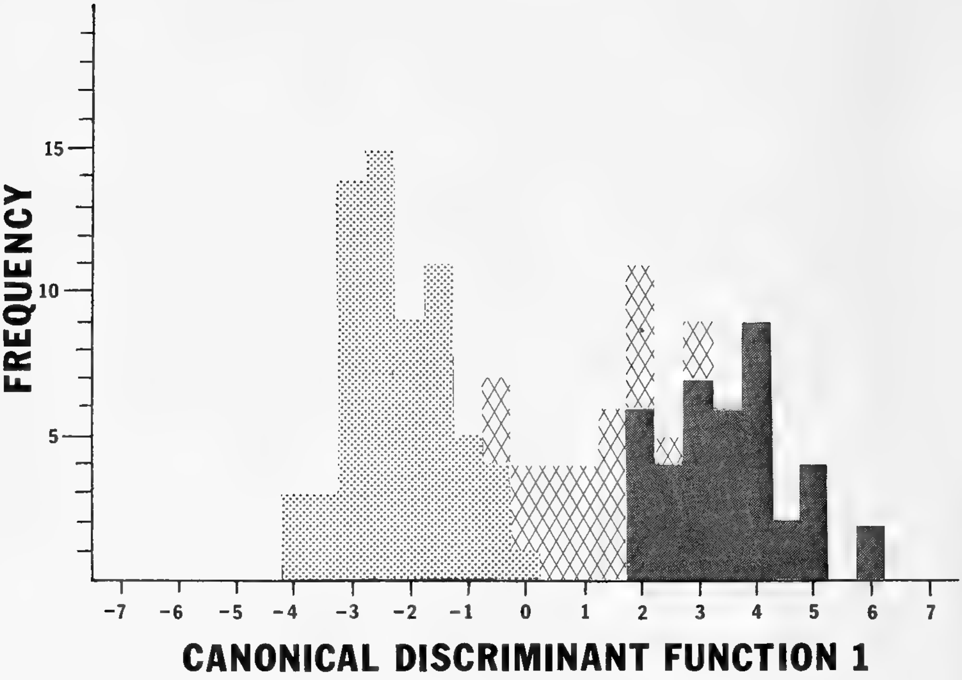

Fig. 3. Frequency histogram of individual discriminant scores for 2 group analysis (*Notoacmea lepisma* ungrouped). Stipled = compressed form, hatched = *N. lepisma,* solid = oval form.

between *N. lepisma* and the 2 forms of *N. depicta* occurs along canonical function 2 (Fig. 2). Here widfron is contrasted with width and height, and in *N. lepisma* widfron is relatively greater than both width and height. In the 2 forms of *N. depicta* the reverse is indicated.

The scatter diagram (Fig. 2) and the histogram (Fig. 3) of discriminant scores clearly show the intermediate position of *N. lepisma.* In addition, *Notoacmea lepisma* shares characters with both forms of *N. depicta.* It is similar to the oval form in length and to the compressed form in width. The ratio of apexpos to height in *N. lepisma* is almost identical to that of the compressed form of *N. depicta,* while its height to width ratio is almost identical to the oval form. When width on length for the 3 groups is plotted (Fig. 4a), the resulting scatter diagram is suggestive of 3 distinct taxa. However, plotting height on length (Fig. 4b) suggests a single taxon. The overall morphology of *N. lepisma* most resembles a dwarf, compressed form of *N. depicta.* This relationship is apparent in Fig. 4a where *N. lepisma* attains the same width as the compressed form at one half of the length.

Contrary to the earlier observations of McLean (1966) and myself (Lindberg 1980), *N. lepisma* does intergrade with both the compressed and oval forms of *N. depicta.* Instead of 3 distinct taxa there appear to be 3 forms of a single species.

Based on the above morphological analysis I consider *N. lepisma* (Berry 1940) to be a third form of *N. depicta* (Hinds 1842), and I therefore place *N. lepisma* in synonymy with *N. depicta.* This action is based on the intergradation of *N. lepisma* with both the oval and compressed forms of *N. depicta,* its similar shell

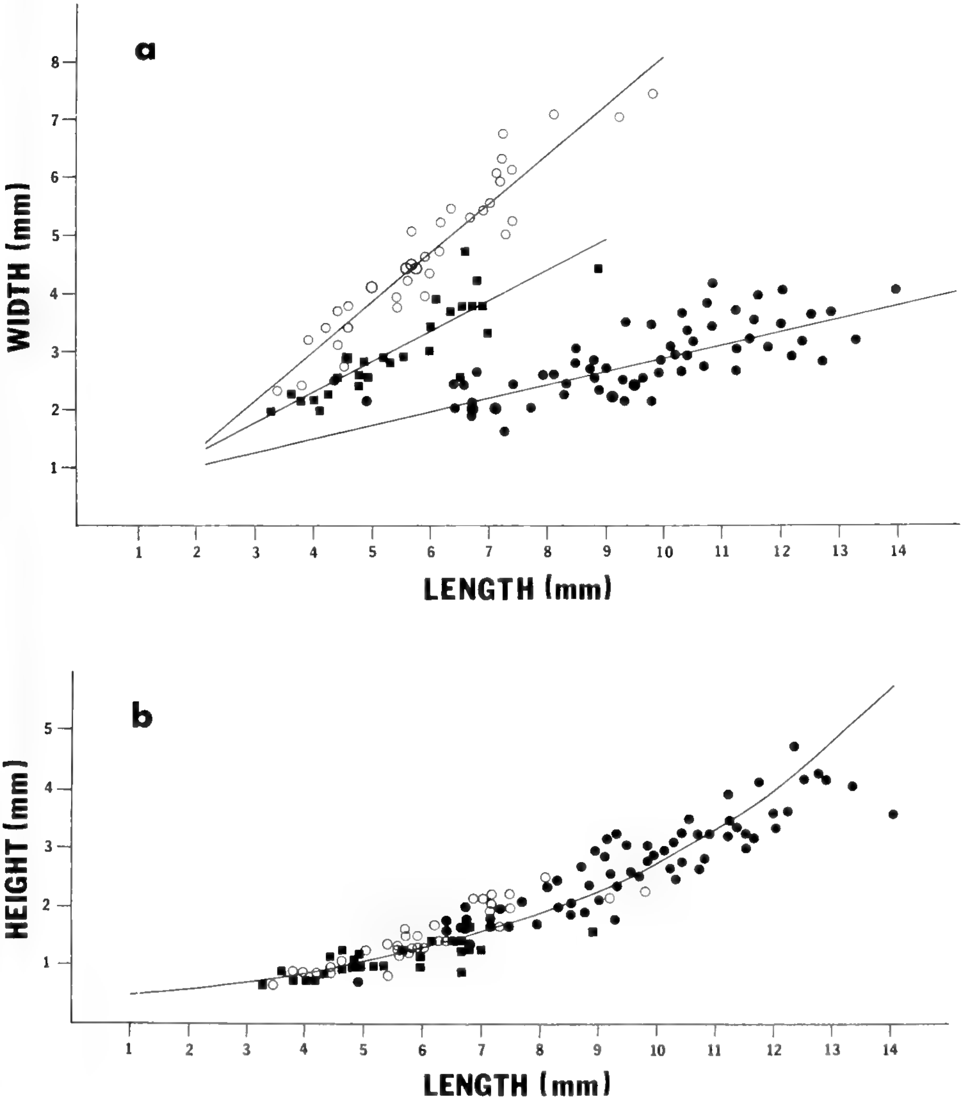

Fig. 4. Scatter diagram and fitted regression lines of length on (a) width and (b) height. ● = compressed form, ■ = *Notoacmea lepisma*, ○ = oval form. Correlation coefficients (a) ● = .7717, ■ = .9007, ○ = .9266; (b) .9307.

proportions, coloration, and sculpturing, and the presence of this supposed fossil species among Recent specimens of *N. depicta*. The form is herein referred to as the dwarf form of *N. depicta*.

In my earlier paper (Lindberg 1980), I suggested that the oval form of *N. depicta* occurred on rocks and brown algae along the open coast of southern California. This was based on data with museum specimens and the paleoecological setting of a fossil assemblage that contained large numbers of the oval form. The paleo-

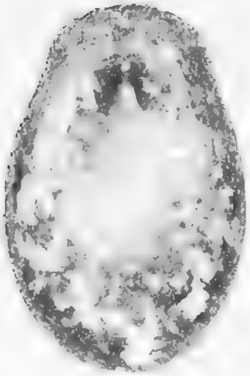

Fig. 5. *Notoacmea depicta,* LACM 17231. Shell length = 8.7 mm.

ecological setting of fossil assemblages that contain *N. lepisma* and a study of marine angiosperm literature has provided additional information regarding the habitats of the 3 forms.

The paleoecology of the oval and compressed forms has been given earlier (Lindberg 1980). Oval forms are associated with open coast, subtidal biofacies, while the compressed form is associated with protected, estuarine biofacies. Occasionally both forms are present in the same assemblage (e.g. LACMIP Loc. 332). At these localities the oval forms are extremely abundant and the compressed forms rare. The compressed forms were probably transported from shallower, estuarine habitats to the offshore depositional environment.

The dwarf form is found in the same type of biofacies as the oval form and it is not uncommon for them to co-occur (e.g. LACMIP Loc. 64, LACMIP Loc. 228). Only the dwarf and oval forms are known from the early Pleistocene (LACMIP Loc. 64; Lomita Marl). The earliest record of the compressed form is middle Pleistocene (LACMIP Lob. 332). Burch's (1946) report of *N. depicta* in the Lomita Marl is based on specimens of the dwarf form.

Recent specimens of the dwarf form have been collected from *Zostera marina* in estuarine habitats (Draper 1973; this study). However, dwarf forms are rare in this habitat and account for fewer than 6% of the population.

The difference in shell width between the compressed and oval forms is thought to be related to the width of the substrate. On narrow *Zostera* blades *N. depicta* quickly reaches a limited shell width, but on substrates such as rocks or larger plants shell growth is unrestricted and the oval form results. The same type of narrow versus wide dichotomy is also present in *Z. marina.* The blades of *Z. marina* vary between 2 and 12 mm in width. Moreover, the 2 forms (narrow vs. wide) occupy different habitats. The wide form occurs subtidally and has been collected at depths between 5 and 30 m off southern California and Baja California (den Hartog 1970). The narrow form occurs intertidally. According to den Hartog (1970), when both forms occur at a single locality they do not intergrade and intermediate specimens cannot be found. However, when wide and narrow forms from different localities are compared it may not be possible to distinguish the 2 phenotypes. Based on this information I hypothesize that the predominant habitat of all 3 forms of *N. depicta* is *Z. marina.* The oval forms occurs on subtidal, wide-blade *Z. marina,* the compressed form on intertidal, narrow-blade *Z. marina,* and the dwarf form in both habitats but predominately subtidal at least in the Pleistocene.

More information on the 3 forms of *N. depicta* is required to test this hypothesis. Recent specimens in museum collections are almost always compressed forms. Whether the oval and dwarf forms are actually rare or simply have been overlooked is not known. Examination of subtidal *Zostera* beds in southern California may be productive.

Subsequent to the analyses another specimen lot of oval forms was located at LACM. The 9 specimens (LACM 17231) were collected after 1960 at Mugu Lagoon in Ventura County, California (34°06′N, 119°06′W) from *Z. marina.* The 7 smaller specimens are typical oval forms but the larger specimens are quite different. The anterior portion of the aperture is compressed while the middle and posterior portions are typical of the oval form (Fig. 5). It appears that these specimens were able to conform only the anterior portion of the shell to the narrow-blade *Zostera* and ultimately overgrew the substrate. The opposite situation (compressed forms on nonlimiting substrates) has been observed by Horgan (1976) for *Notoacmea paleacea* (Gould 1853), a limpet that occurs on *Phyllospadix* spp. He found that specimens of *N. paleacea* that settled on the green alga *Ulva* sp. had shells that were compressed laterally although the substrate was not limiting.

A segment of the radula was present in one of the specimens from Mugu Lagoon. The radular morphology is similar to that of the compressed form. This is the second radula recovered from an oval form of *N. depicta.* The radula preparation is deposited in the LACM.

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Literature Cited

Berry, S. S. 1940. New Mollusca from the Pleistocene of San Pedro, California. I. Bulls. Amer. Paleont., 25:1–18.

———. 1960. Notices of new eastern Pacific Mollusca. IV. Leaflets in Malac., 1:115–122.

Blackith, R. E., and R. A. Reyment. 1971. Multivariate morphometrics. Academic Press, ix + 412 pp.

Bookstein, F. L. 1978. The measurement of biological shape and shape change. Lect. Notes Biomath., 24:191 pp.

Burch, J. Q. 1944–1946. Distributional list of west American marine mollusks from San Diego, California to the Polar Sea. Minutes Conch. Club So. Calif. nos. 33–63 (pagination by issue).

Christiaens, J. 1975a. Revision provisoire des mollusques marins recents du la famille des Acmaeidae et description de deux nouveaux sous-generes: *Simplacmaea* nov. subgen. et *Collisellacmaea* nov. subgen. Inform. Soc. Belge Malac., 4:3–18.

———. 1975b. Revision provisoire des mollusques marins recents du la famille des Acmaeidae (seconde partie). Inform. Soc. Belge Malac., 4:91–116.

Dall, W. H. 1871. On the limpets: with special reference to the species of the west coast of America, and to a more natural classification of the group. Amer. Jour. Conch., 6:227–282.

den Hartog, C. 1970. The sea-grasses of the world. Verh. K. Ned. Akad. Wet. Afd. Natuurk. D. Tweede Reeks, 59:1–275.

Draper, B. 1973. Minute shells. Part 3. The Tabulata, 6:8–12.

Gould, A. A. 1853. Descriptions of shells from the Gulf of California and the Pacific coasts of Mexico and California. Boston Jour. Nat. Hist., 6:374–408.

Grant, A. R. 1937. A systematic revision of the genus *Acmaea* Eschscholtz, including consideration of ecology and speciation. Ph.D. Thesis, Univ. Calif., Berkeley, Calif., 432 pp.

Hinds, R. B. 1842. Descriptions of new shells. Ann. Mag. Nat. Hist., 10:81–84.

Horgan, D. A. 1976. Population studies of the stenotopic limpet *Notoacmea paleacea* on its sea grass host, *Phyllospadix torreyi.* West. Soc. Malac. Ann. Rept., 9:17–18.

Lindberg, D. R. 1980. *Notoacmea gabatella* (Berry), an outer coast form of *Notoacmea depicta* (Hinds) (Mollusca: Acmaeidae). The Veliger, 22:265–272.

McLean, J. H. 1966. West American prosobranch Gastropoda: superfamilies Patellacea, Pleurotomariacea, and Fissurellacea. Ph.D. Thesis, Stanford Univ., Stanford, Calif., x + 262 pp.

Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent. 1975. SPSS statistical package for the social sciences 2nd Ed. McGraw-Hill, xxiv + 675 pp.

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Research Notes

A New Species of *Scolelepis* (Polychaeta: Spionidae) from California Sandy Beaches

Studies by Kolpack and Straughan (1971), Trask (1971), Patterson (1974), Straughan and Patterson (1975), Straughan (1973, 1974a, b, c, 1975, 1978, 1979) and Straughan and Hadley (1980) report *Scolelepis squamata* (Müller) (recorded as *Nerinides acuta* (Treadwell) or *Scolelepis acuta* (Treadwell)) as the most common spionid of central and southern California sandy beaches. A review of the *S. squamata* from these studies has revealed two other forms of *Scolelepis* Blainville. One of the forms is described herein as a new species; a description of the other is omitted for lack of complete material. The holotype and paratypes of the new species are deposited in the collections of the Allan Hancock Foundation (AHF), University of Southern California, Los Angeles. The re-examination of material and subsequent species description were funded by Southern California Edison, Rosemead, California.

Scolelepis bullibranchia, n. sp.

Material examined.—Huntington Beach, 23 April 1971, (Holotype, AHF 1375; 4 paratypes, AHF 1376); Zuma Beach, 4 Dec. 1971, (1); Scripps Beach, 20 April 1976, (19); Santa Cruz Island, 20 Jan. 1978, (1); Estero Bay, Site 0, Feb. 1974, (3).

Diagnosis.—Prostomium pointed, extending posteriorly as a caruncle to setiger 2; caruncle attached to dorsum. Occipital cirrus absent. Peristomium well developed, without lateral wings. Branchiae beginning on setiger 2, continuing to far posterior segments; branchiae distally free from dorsal lamellae. Anterior setigers with capillary setae only; median and posterior neuropodia with tridentate hooded hooks and capillary setae, notopodia with capillary setae only.

Description.—Holotype complete, 128 segments, 73 mm long and 1.8 mm wide. Body widest anteriorly, rectangular in cross section, tapering posteriorly becoming sub-quadrate in cross section.

Prostomium inflated, anteriorly acuminate; slightly tapering posteriorly to the level of a transverse row of 4 eyespots, then constricting to a narrow caruncle extending to setiger 2 (Fig. 1a). Occipital cirrus absent. Palps extending posteriorly to about setiger 21; small basal sheaths smooth. Peristomium well developed without lateral wings.

Setiger 1 much reduced, with petaloid dorsal and ventral lamellae; notosetae absent (Fig. 1b). Dorsal lamellae from setiger 2 with lateral margins somewhat thickened, terminating in pointed tips free from branchiae (Fig. 1c). Ventral lamellae broadly rounded, increasing in size posteriorly (Fig. 1c–d); at setigers 21–29 lamellae dividing to ventral and interramal lamellae (Fig. 1e). Interramal lamellae becoming distally bluntly pointed in posterior segments (Fig. 1f). Branchiae distally pointed, basally fused to dorsal lamellae, distally free (Fig. 1c–d); lateral margins at first thickened, then becoming swollen with darkened glandular inclu-

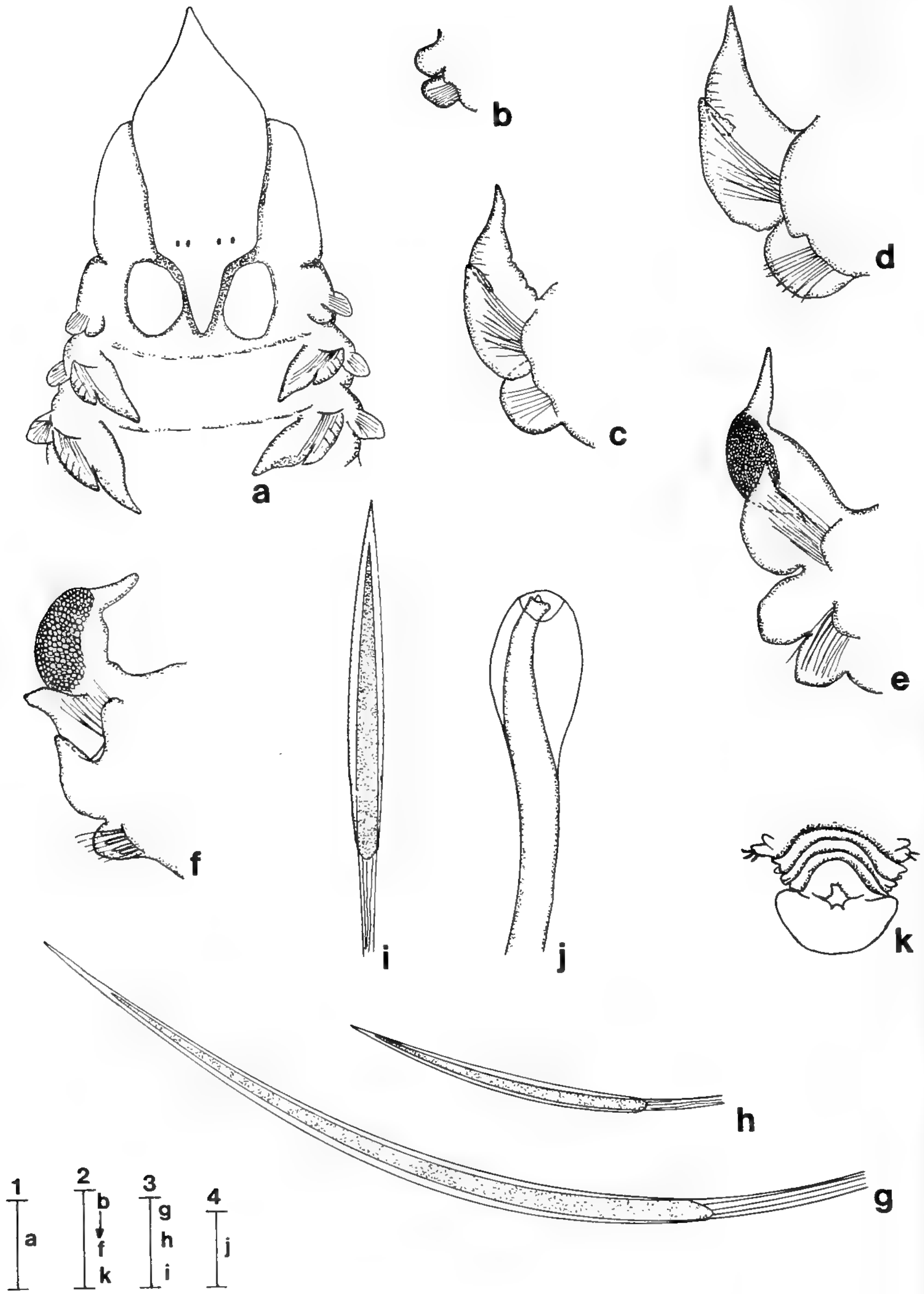

Fig. 1. *Scolelepis bullibranchia* n. sp. a, anterior end, dorsal view; b, left setiger 1, anterior view; c, left setiger 6, anterior view; d, left setiger 10, anterior view; e, left setiger 29, anterior view; f, left setiger 40, anterior view; g, superior capillary notoseta; h, sabre seta; i, anterior capillary notoseta; j, neuropodial tridentate hooded hook; k, pygidium, dorsal view. (Scale 1 = 500 μm; 3 = 50 μm; 4 = 20 μm).

sions at setigers 16–22 (Fig. 1e–f). Branchiae continuing posteriorly except for last 3–5 segments.

Capillary noto- and neurosetae of anterior setigers arranged in anterior and posterior tiers. Anterior setigers with 5–6 longer superior setae (Fig. 1g); neurosetae include 3–4 inferiormost saber setae (Fig. 1h). All capillary setae with smooth sheaths; shafts striated and granulated (Fig. 1i); granulations becoming obscure in posterior setigers. Tridentate hooded hooks beginning in neuropodia 32–47 (Fig. 1j).

Pygidium with large mushroom shaped ventral pad; anus dorsal with crenulate anterior and lobed posterior margins (Fig. 1k).

Distribution.—*S. bullibranchia* is known from California open coast sandy beaches from Estero Bay south to San Diego.

Etymology.—The specific name *bullibranchia* (feminine; *bulla,* Latin = blister) refers to the structure of the branchiae.

Discussion

Presently four species of *Scolelepis* are known from California: *S. squamata, S. tridentata* (Southern) (see Light 1977), *S. yamaguchii* (Imajima) (see Light 1978) and *S. foliosa* (Auduoin and Milne-Edwards) (=*Nerine foliosa occidentalis* Hartman *fide* Pettibone 1963) (see Hartman 1969). *S. bullibranchia* is separable from these species by the absence of notosetae on setiger 1. *S. bullibranchia* most closely resembles *S. aitutakii* Gibbs from the central Pacific Cook Islands (Gibbs 1972). Both species possess glandular branchial structures, lack an occipital cirrus and lack notosetae on setiger 1. *S. bullibranchia* differs from *S. aitutakii* as follows: (1) glandular branchial structures are lateral, swollen and elongate oval in the former and terminal, flattened and triangular in the latter, (2) anterior branchiae are free distally from the dorsal lamellae, instead of fused and (3) hooded hooks are tridentate versus bidentate.

Literature Cited

Gibbs, P. E. 1972. Polychaete annelids from the Cook Islands. J. Zool., Lond., 168:199–220.

Hartman, O. 1969. Atlas of the Sedentariate Polychaetous Annelids from California. Allan Hancock Found., Univ. of So. Calif., Los Angeles, 812 pp.

Kolpack, R., and D. Straughan. 1971. Biological survey for the environmental impact statement of construction of a two mile offshore pipeline between Ormond Beach and Port Hueneme to Southern California Edison. 40 pp.

Light, W. J. 1977. Spionidae (Annelida: Polychaeta) from San Francisco Bay, California: a revised list of nomenclatural changes, new records, and comments on related species from the northeastern Pacific Ocean. Proc. Biol. Soc. Wash., 90:66–88.

———. 1978. Invertebrates of the San Francisco Bay Estuary System. Spionidae (Polychaeta, Annelida). The Boxwood Press, Pacific Grove, Calif. 211 pp.

Patterson, M. M. 1974. Intertidal Macrobiology of Selected Sandy Beaches in Southern California. Univ. of So. Calif. Sea Grant Program. USC-SG-9-74. Los Angeles, Calif., 41 pp.

Pettibone, M. H. 1963. Revision of some genera of polychaete worms of the family Spionidae, including the description of a new species of *Scolelepis.* Proc. Biol. Soc. Wash., 76:89–104.

Straughan, D. 1973. The influence of the Santa Barbara Oil spill (January–February, 1969) on the intertidal distribution of marine organisms. Report presented to the Western Oil and Gas Association June 1973. 67 pp.

———. 1974a. Intertidal survey at Estero Bay. Pp. K60–K106 *in* Applicants Draft Environmental Impact Report. Estero Bay Deepwater Terminal and Estero Bay to Richmond Pipeline Project by Standard Oil Company of California "Corporate Engineering Department." 4 Appendix K.-1: Marine Biological Baseline—Estero Bay and Morro Bay.

———. 1974b. Survey of intertidal areas in the northern side of the entrance of Morro Bay. Pp. K214–K240 *in* Applicants Draft Environmental Impact Report. Estero Bay Deepwater Terminal and Estero Bay to Richmond Pipeline Project by Standard Oil Company of California "Corporate Engineering Department." 4 Appendix K.-6: Marine Biological Baseline—Estero Bay and Morro Bay.

———. 1974c. Survey of distribution and abundance of intertidal invertebrates in areas adjacent to the Santa Maria Refinery Ocean Discharge, August, 1974. Report presented to Union Oil Company of California. 33 pp.

———. 1975. Intertidal sandy beach macrofauna at Los Angeles-Long Beach Harbor Part II. Marine Studies of San Pedro Bay, California. Part 8. Pub. Univ. of So. Calif.: 89-107.

———. 1978. Sandy beach and slough community analysis. Southern California Baseline Study. Intertidal, Year Three. II, Report 8.0; III, Report 3.0; IV, Report 3.0. Submitted to Bureau of Land Management, Washington, D.C. 20240. 152+39+123 pp.

———. 1979. Influence of power generating facilities on southern California coastal waters. Phase 4. Study of Environmental Conditions in King Harbor. April 1, 1977–March 31, 1978. Final Report on Field Biology of Sandy Beaches (1974–1975). Submitted to Southern California Edison, Los Angeles. 79-RD-19: 81 pp.

———, and D. Hadley. 1980. Ecology of southern California island sandy beaches. Pp. 369–394 *in* The California Islands: Proceedings from a multidisciplinary Symposium. February, 1978. (D.M. Power, ed.). Santa Barbara Museum of Natural History. vii + 787 pp.

———. and M. Patterson. 1975. Intertidal sandy beach macrofauna at Los Angeles-Long Beach Harbor Part I. Marine Studies of San Pedro, Bay, California. Part 8. Pub. Univ. of So. Calif.: 75-88.

Trask, T. 1971. A study of three sandy beaches in the Santa Barbara, California area. Pp. 159–178 *in* Biological and Oceanographical Survey of the Santa Barbara Channel Oil Spill 1969–1970, Vol. I. Allan Hancock Found., Univ. of So. Calif., Los Angeles. vi + 426 pp.

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McWilliams, K. L. 1970. Insect mimicry. Academic Press, vii + 326 pp.

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

Brattstrom, B. H. 1969. The Condor in California. Pp. 369–382 *in* Vertebrates of California. (S. E. Payne, ed.), Univ. California Press, xii + 635 pp.

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Research Notes

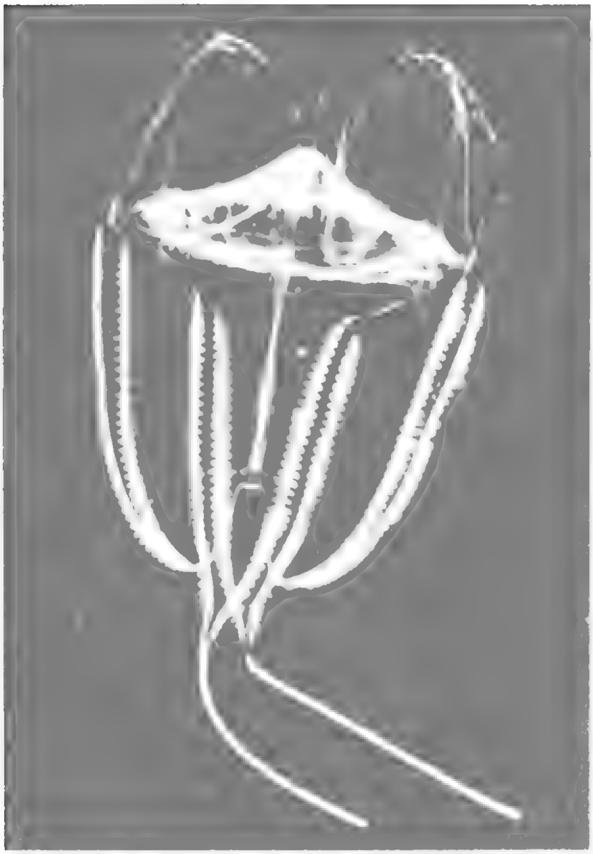
COVER: A colony of salps, *Cyclosalpa pinnata*. Each member of the colony is a clone off the same parent; the young are produced during the asexual stage of the life cycle.

This is the third picture of our series on UFOS (Unfamiliar Fauna of the Open Seas), photographed by Jonathan Trent, graduate student at Scripps Institute of Oceanography.

SOUTHERN CALIFORNIA ACADEMY OF SCIENCES

BULLETIN

Volume 81 Number 3



BCAS-A81(3) 101–152 (1982) DECEMBER 1982

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Date of this issue 24 November 1982

Bull. Southern California Acad. Sci.
81(3), 1982, pp. 101–105

The Identity of "*Helminthoglypta*" *tularica* (Bartsch) (Gastropoda: Pulmonata)

Barry Roth

Abstract.—The identity of "*Helminthoglypta*" *tularica* (Bartsch) (Gastropoda: Pulmonata) by Barry Roth, *Bull. Southern California Acad. Sci.,* 81(3):101–105, 1982. The land snail *Epiphragmophora traskii tularica* Bartsch 1916, said to come from Tulare County, California, but not collected since its original description, is a junior synonym of *Plesarionta orcutti* (Dall 1900) from northwestern Baja California, Mexico. *P. orcutti* is assigned to genus *Plesarionta* on protoconch and anatomical characters.

The identity of the land snail currently known as *Helminthoglypta tularica* (Bartsch 1916) has been a problem to malacologists studying the west American fauna. According to Pilsbry (1939), the holotype and paratype of this species were collected by the Californian conchologist Henry Hemphill and sent to W. G. Binney, who passed them on to Pilsbry as an unknown species. Pilsbry (1895, 1897, 1898) cited these specimens three times in faunal lists, under the Hemphill manuscript name *Epiphragmophora traskii* var. *tularensis* (*non Arionta tudiculata* var. *tularensis* Hemphill in Binney 1892). All three of Pilsbry's usages are *nomina nuda.* Bartsch (1916) validly described the species as *Epiphragmophora traskii tularica,* based on the same specimens. The types were labeled as coming from Frasers Mills, Tulare County, California, which was formerly located near the present site of Mountain Home (NW ¼ sec. 35, T. 19 S, R. 30 E, Mt. Diablo Base and Meridian; USGS Camp Nelson, Calif., Quadrangle, 15-minute Series [Topographic]) (Hanna 1938).

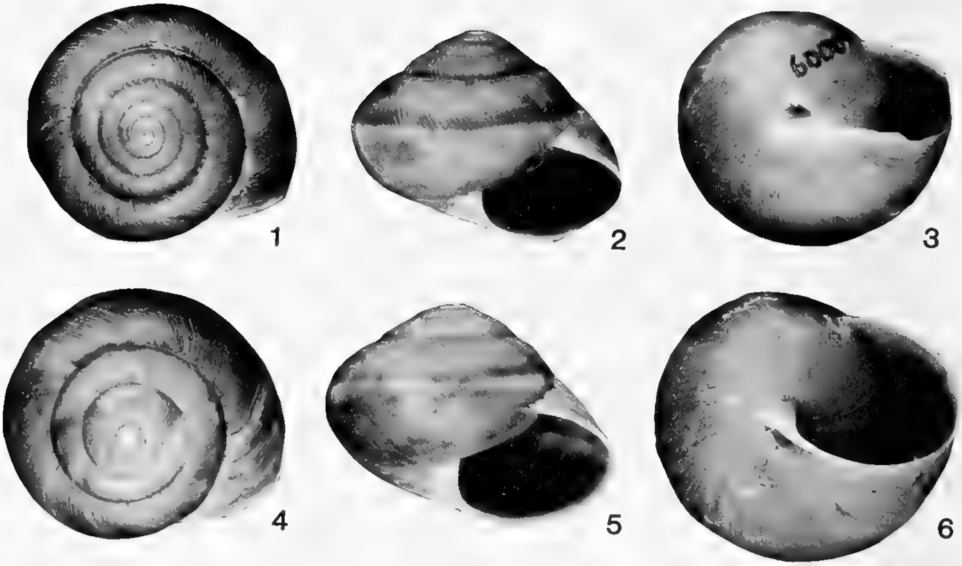
Pilsbry (1939:200–201) assigned the species to the genus *Helminthoglypta* while remarking, "it is a peculiar shell which does not seem closely comparable to any known to me." Its locality, in the southern Sierra Nevada, is remote from other members of the *H. traskii* group, which are largely restricted to the Los Angeles Basin and Peninsular Ranges physiographic provinces of California (Roth 1973). Hanna did not collect the species near Mountain Home; he seems to have confused it with *Helminthoglypta* (née *Arionta*) *tularensis* (Hemphill in Binney 1892). Since then, no other investigator has located "*H.*" *tularica* in the southern Sierras, although many competent field workers have searched for it. Smith (1970) cited it as a "lost" species.

Through the courtesy of G. M. Davis, Curator, Department of Malacology, Academy of Natural Sciences of Philadelphia (ANSP), I have been able to examine the holotype and paratype of "*H.*" *tularica.* They prove to be identical to the Baja California helminthoglyptid *Plesarionta orcutti* (Dall 1900), itself a rather poorly known taxon. The synonymy is therefore as follows:

Plesarionta orcutti (Dall 1900)
Figures 1–6

(?) "unmottled depressed species (number 1321)," Orcutt 1886:62.

Epiphragmophora traskii var. *tularensis* Hemphill, Pilsbry 1895:199 (*nomen nudum*). *Non Arionta tudiculata* var. *tularensis* Hemphill in Binney 1892:187.



Figs. 1–6. *Plesarionta orcutti* (Dall 1900). 1–3, holotype, *Epiphragmophora traskii tularica* Bartsch 1916, ANSP 60009; top, apertural, and basal views; diameter 20.6 mm. 4, 5, specimen from original lot of *Epiphragmophora orcutti* Dall, CAS 030112; top and apertural views; diameter 21.9 mm. 6, CAS 030116, "San Rosario, Lower California," *ex* H. Hemphill collection; basal view; diameter 22.6 mm.

Epiphragmophora (Helminthoglypta) traski tularensis Pilsbry 1897:59 (*nomen nudum*).—1898:5 (*nomen nudum*).

Epiphragmophora orcutti Dall 1900:104, pl. 8, Fig. 19. *Non Sonorella baileyi orcutti* Bartsch 1904:196 (=*Micrarionta harperi orcuttiana* Bartsch 1937:33).

Epiphragmophora traskii tularica Bartsch 1916:615, pl. 116, Figs. 1–3.

Helminthoglypta tularica (Bartsch), Pilsbry 1939:200, Fig. 101.—Ingram 1946: 82.—Smith 1970:42.

Micrarionta (Xerarionta) orcutti (Dall), Pilsbry 1939:255.

Type material.—*E. orcutti,* no reference to type specimens in original. One syntype, 6608/7103 Department of Geological Sciences, University of California, Riverside (Mount 1973). Type locality, "Rosario mesas, in northern Lower California" [El Rosario, Baja California Norte, Mexico], C. R. Orcutt coll., May 1886 (Dall 1900). Three additional specimens from the original lot, California Academy of Sciences Department of Invertebrate Zoology CAS 030112. *E. t. tularica,* holotype ANSP 60009, paratype ANSP 325151. Type locality, "Frasers Mills, Tulare County, California" (Bartsch 1916), in error; probably from El Rosario, Baja California Norte, Mexico.

Two earlier citations of holotype numbers from *E. t. tularica* by Pilsbry (1939; "ANSP 70703") and Baker (1962: "ANSP 60009a") are erroneous.

Discussion.—Several characters demonstrate that the holotype and paratype of *Epiphragmophora traskii tularica* are specimens of *Plesarionta orcutti.* The initial one-quarter whorl is smooth and somewhat depressed. Thereafter, the sculpture of the embryonic shell consists of irregular, wavy, anastomosing radial riblets, partly broken into granules, especially just below the suture. The same type of embryonic sculpture occurs in *P. orcutti* and in *Plesarionta stearnsiana* (Gabb 1868) from southwestern San Diego County, California, and northwestern Baja California Norte. In contrast, embryonic sculpture in *Helminthoglypta* consists of fine, overall wrinkle-granulation, varying in strength from species to species, but rarely forming distinct radial riblets. In the *H. traskii* group, to which Bartsch (1916) assigned his *tularica,* distinct, dot-like papillae in forwardly-descending series are superimposed upon the wrinkle-granulation. The type specimens of *E. t. tularica* have no such papillae. Bartsch claimed that they required search to be seen; I deem them absent.

The post-embryonic sculpture consists of raised wrinkles paralleling the lines of growth, incised by numerous fine spiral grooves, "cutting merely the tops of the wrinkles and not the furrows between them" (Dall 1900:105, for *E. orcutti*). The spiral grooves are stronger and farther apart on the shoulder of the whorl than on the base.

Most species of *Helminthoglypta* have a narrow, dark, spiral band just above the periphery, either plain or with light borders above and below. The ground color of the shell is approximately the same on both sides of the band. The type specimens of *E. t. tularica* have a poorly defined pale border below the peripheral band, but none above, and the shoulder is darker than the base of the shell. There are merely the faintest traces of a light zone above the band in the paratype, and none in the holotype. This same pattern—a dark shoulder and no light zone above the peripheral band—occurs in several *Plesarionta* species including *P. orcutti* and *P. stearnsiana.* The *E. t. tularica* types are a purplish-brown color not found in *Helminthoglypta.*

The holotype of *E. t. tularica* is 20.6 mm in diameter and has 5.5 whorls (counting by the method of Pilsbry 1939:Fig. B); the paratype is 20.8 mm in diameter and has 5.4 whorls. Both are subadult, without reflected peristome. Adult *P. orcutti* in the California Academy of Sciences and the private collection of Walter B. Miller, Tucson, Arizona, range from 20.5 to 25.5 mm in diameter and have 5.3 to 5.7 whorls. *P. orcutti* differs from *P. stearnsiana* in lacking the latter's copious, opaque, whitish dappling. Most populations of *P. stearnsiana* have less distinct spiral grooves than *P. orcutti. Xerarionta redimita* (Binney 1858) from San Clemente Island, California, the only other species similar enough to require comparison, has a stronger, more uniform granulation of the shell surface; the fine spiral grooves are often weak or lacking, and the axial wrinkles are rendered granular by minute, close, incised striae oblique to the lines of growth. The peripheral band is plain, rarely with a faint pale border below, and the ground color is uniform reddish brown, sometimes slightly darker on the shoulder. Its reproductive anatomy, of course, is that of *Xerarionta* Pilsbry 1913, lacking a verge (Pilsbry 1939:Fig. 102c').

Epiphragmophora orcutti is here assigned to the genus *Plesarionta* Pilsbry 1939, because its protoconch is similar to that of the type species, *P. stearnsiana.* The embryonic shell is smaller and more tightly coiled than in *Xerarionta* (cf. Clapp's [1906] comparison of *P. stearnsiana* and *X. kellettii,* refigured by Pilsbry, 1939: 216, Fig. 108), and the radial riblets are wavy, not straight. Walter B. Miller (pers. comm. 1979) reports that the genitalia of *P. orcutti* are like those of *P. stearnsiana*; that is, with a small verge separating the penis from the epiphallus (see Pilsbry

1939:Fig. 102a). Both *Xerarionta* and *Plesarionta,* formerly subgenera of *Micrarionta* Ancey 1880, were raised to generic rank by Miller (1981).

As Carl C. Christensen has pointed out to me (pers. comm. 1979), Orcutt's (1886:62) "unmottled depressed species (number 1321)" from Baja California, which Binney in the same paper (Orcutt 1886:61) found to have genitalia like *P. stearnsiana,* may refer to *P. orcutti.* The relationship between *P. orcutti* and *P. stearnsiana* is a subject for future investigation.

Plesarionta orcutti is known only from a limited area in the vicinity of El Rosario, Baja California Norte (30°02′N, 115°46′W). The CAS collection contains material collected there by a number of workers. The allocation of the types of *E. t. tularica* to Frasers Mills, Tulare County, is surely erroneous. Evidence that Henry Hemphill himself owned material of *P. orcutti* exists in the CAS collection in the form of one specimen, *ex* Hemphill collection no. 14124, cataloged as from "San Rosario, Lower California," and formerly identified as a variety of *P. stearnsiana* (Fig. 6). It does not appear that Hemphill himself collected at El Rosario. He probably received his material from C. R. Orcutt. Orcutt's own account of his visit to El Rosario in 1886, when he collected the types of *E. orcutti* and possibly of *E. t. tularica,* was published by DuShane (1971).

I am grateful to G. M. Davis and staff of the Academy of Natural Sciences of Philadelphia for the loan of types of *Epiphragmophora traskii tularica.* I thank Walter B. Miller and Carl C. Christensen for their thoughtful criticisms and contributions to the manuscript, and Fred G. Hochberg for his timely assistance.

Literature Cited

Bartsch, P. 1904. Notes on the genus *Sonorella,* with descriptions of new species. Smithson. Miscel. Coll., 47:187–200.

———. 1916. The Californian land shells of the *Epiphragmophora traskii* group. Proc. U.S. Nat. Mus., 51:606–619.

———. 1937. *Micrarionta harperi orcuttiana,* new name. Nautilus, 51:33.

Binney, W. G. 1892. A fourth supplement to the fifth volume of The Terrestrial Air-breathing Mollusks of the United States and Adjacent Territories. Bull. Mus. Compar. Zool., 22:164–204.

Clapp, G H. 1906. *Epiphragmophora kellettii* (Fbs.) and *E. stearnsiana* (Gabb). Nautilus, 20: 13–16.

Dall, W. H. 1900. Additions to the insular land-shell faunas of the Pacific Coast, especially of the Galapagos and Cocos Islands. Proc. Acad. Nat. Sci. Philadelphia, 52:88–106.

DuShane, H. 1971. The Baja California travels of Charles Russell Orcutt. Dawson's Book Shop, 75 pp.

Hanna, G. D. 1938. The type locality of "*Helix tudiculata* var. *tularensis* Hemphill." Nautilus, 52: 7–9.

Ingram, W. M. 1946. A check list of the helicoid snails of California. Bull. So. California Acad. Sci., 45:61–93.

Miller, W. B. 1981. *Helminthoglypta reederi* spec. nov. (Gastropoda: Pulmonata: Helminthoglyptidae) from Baja California, Mexico. Veliger, 24:46–48.

Mount, J. D. 1973. Type specimens of Mollusca from the Charles R. Orcutt collection now at the University of California, Riverside. Veliger, 16:200–202.

Orcutt, C. R. 1886. On Lower California land shells. West American Scientist, 2:61–62.

Pilsbry, H. A. 1895. Guide to the study of helices (Helicidae, vol. 7). Manual of Conchology, ser. 2, 9:161–336.

———. 1897–1898. A classified catalogue of American land shells, with localities. Nautilus, 11: 45–48, 59–60, 71–72, 83–84, 93–96, 105–108, 117–120, 127–132, 138–144.

———. 1898. A classified catalogue with localities of the land shells of America north of Mexico [Reprint of above], 35 pp.

———. 1939. Land Mollusca of North America (north of Mexico). Acad. Nat. Sci. Philadelphia, Monog. 3, 1(1):1–573.

Roth, B. 1973. The systematic position of *Helminthoglypta traskii fieldi* Pilsbry, 1930 (Gastropoda: Stylommatophora). Bull. So. California Acad. Sci., 72:148–155.

Smith, A. G. 1970. American Malacological Union Symposium, rare and endangered mollusks. 6. Western land snails. Malacologia, 10:39–46.

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California Academy of Sciences, Golden Gate Park, San Francisco, California 94118.

Bull. Southern California Acad. Sci.
81(3), 1982, pp. 106–120

New Records and New Species of the Genus *Lebbeus* (Caridea: Hippolytidae) in the Eastern Pacific Ocean

Mary K. Wicksten[1] and Matilde Méndez G.[2]

Abstract.—New records and new species of the genus *Lebbeus* (Caridea: Hippolytidae) in the eastern Pacific Ocean by Mary K. Wicksten and Matilde Méndez G., *Bull. Southern California Acad. Sci.*, 81(3):106–120, 1982. *Lebbeus scrippsi* n. sp. and *L. splendidus* n. sp. are described from off the coasts of Peru and Chile. *Lebbeus vicinus montereyensis* n. subsp. is described from Monterey Bay, California and off western Mexico. Southern range extensions are given for *L. grandimanus, L. lagunae, L. possjeticus,* and *L. zebra. Lebbeus brandti* is reported for the first time in the eastern Pacific. We suggest that *L. curvirostris* Zarenkov may belong to the genus *Nauticaris,* and that *L. bidentatus* Zarenkov may be a southern race of *L. washingtonianus* (Rathbun). A key is presented for all the species of *Lebbeus* in the eastern Pacific.

Shrimps of the genus *Lebbeus* inhabit cool temperate to Arctic waters. The majority of species are recorded from the northern Pacific Ocean. Keys to the species, illustrations, and distributional data have been given previously by Rathbun (1904), Wicksten (1979), and Butler (1980). Recent examination of specimens from the Allan Hancock Foundation (AHF), the Instituto del Mar del Perú (IMARPE), Scripps Institution of Oceanography (SIO), and the U.S. National Museum of Natural History (USNM) has resulted in the finding of two undescribed species, a new subspecies, and additional distributional data.

Lebbeus scrippsi n. sp.
Plates 1–2

Description.—Rostrum short, not reaching end of second segment of antennular peduncle. One spine on dorsal surface of carapace posterior to orbit. One to 4 spines on dorsal surface of rostrum proper, 2 or 3 on ventral surface posterior to apex.

Carapace smooth. Supraorbital, antennal, and pterygostomial spines present.

Abdomen smooth. Pleura of segments 1 to 4 rounded. Pleura of segment 5 with sharp distolateral points. Sixth segment 1.25× as long as fifth, with sharp lateral points. Telson with 3 pairs dorsal spines placed at half length of telson and posteriorly. Tip of telson rounded, with 2 pair spines and setae. Telson 1.25× length of sixth abdominal segment.

Eyes small. Cornea of eye darkly pigmented, reaching base of posterior ventral rostral spine.

First segment of antennular peduncle with sharp spine on ventral margin of median border. Three sharp spines along distal margin of first segment. Second segment 0.5× as long as first, with sharp distal spine. Third segment about 0.5× as long as second, with sharp distal spine. Antennular peduncle shorter than scaphocerite. Upper antennular flagellum thickened, consisting of single ramus.

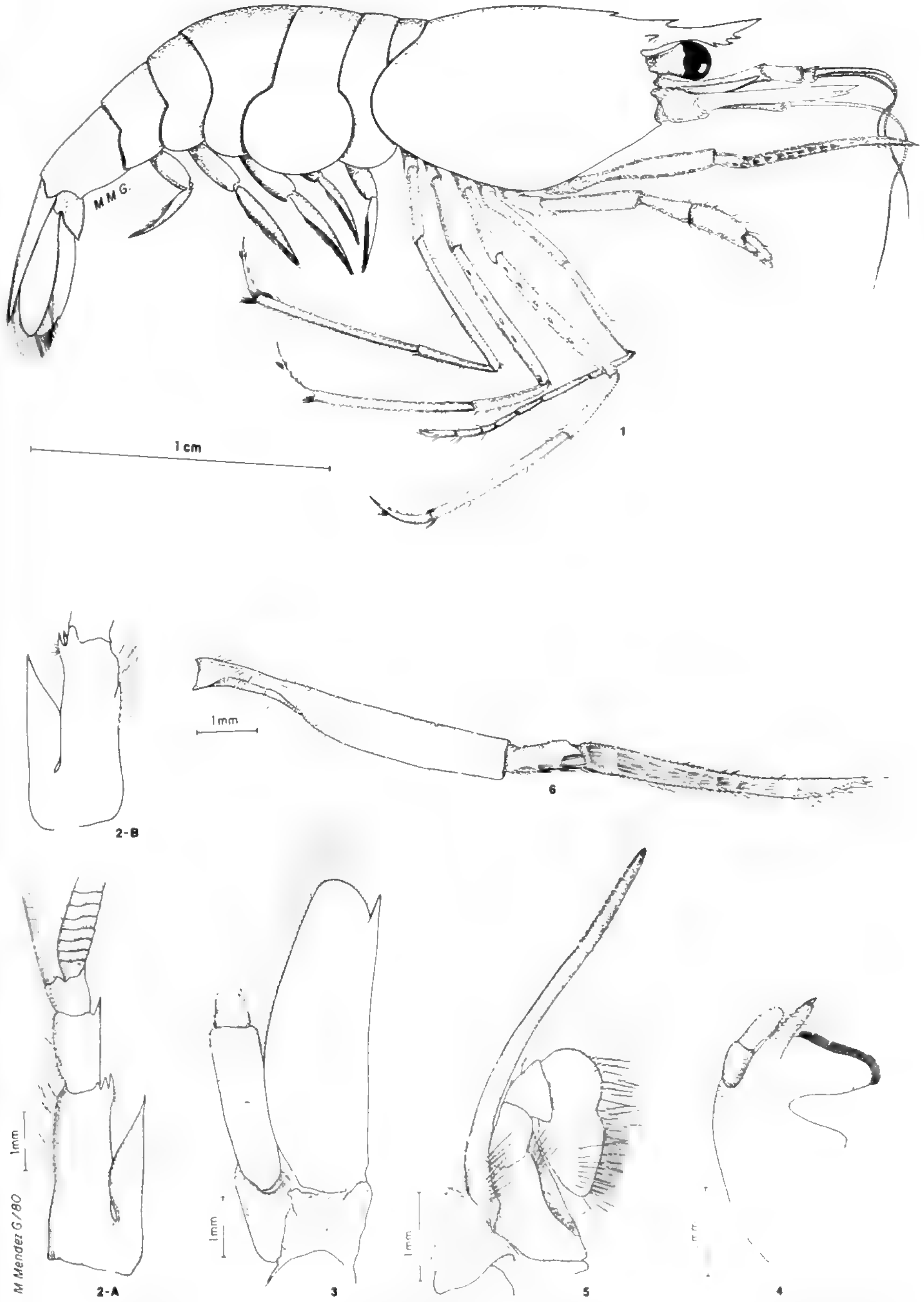

Plate 1. *Lebbeus scrippsi,* n. sp. Female paratype, 32.0 mm total length. Off Altura de Pucusana, Peru. Fig. 1. Body in lateral view; 2A, right first antenna; 2B, left first antenna; 3, right second antenna and scaphocerite; 4, right mandible; 5, right second maxilliped; 6, right third maxilliped in median view.

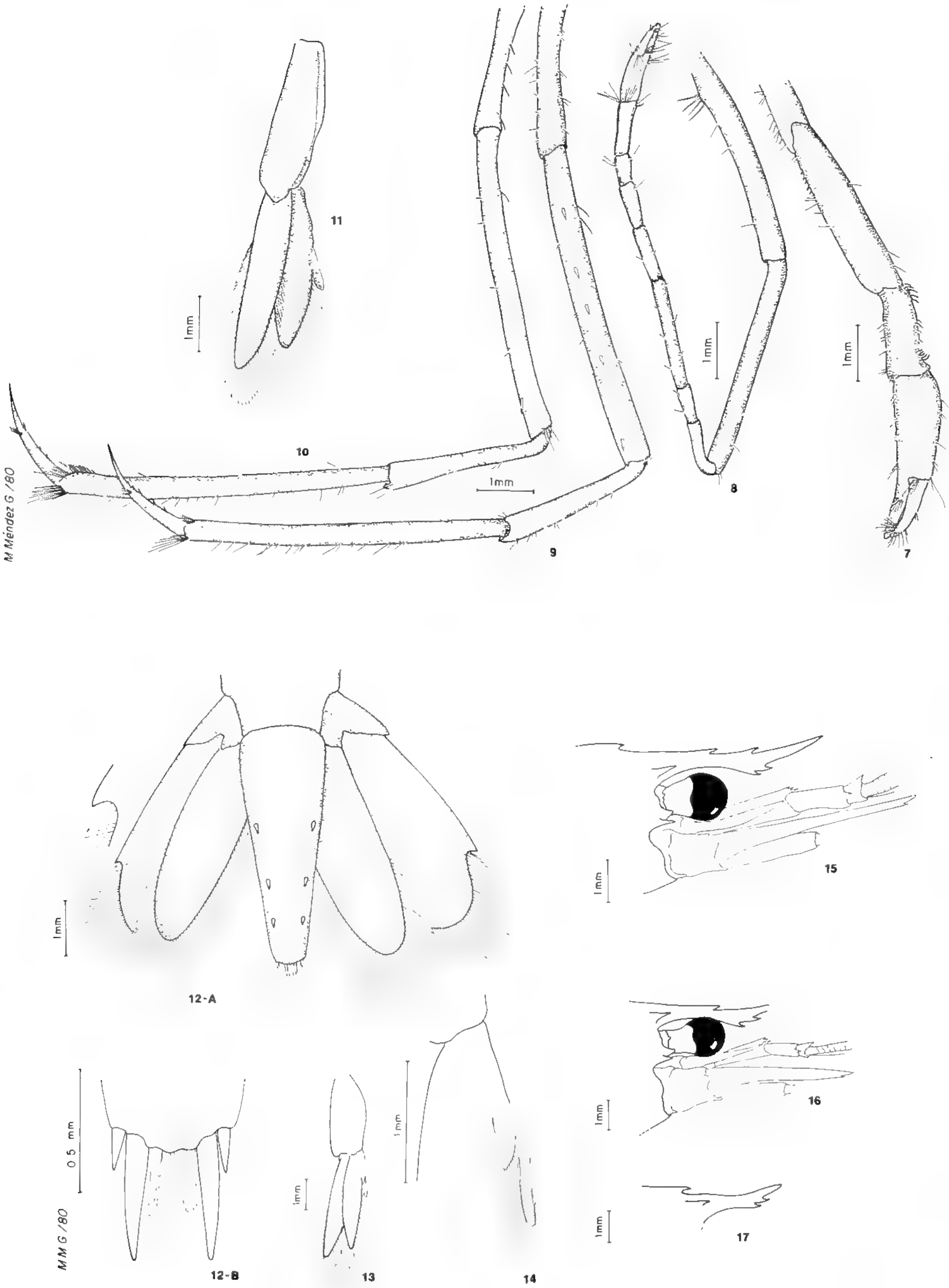

Plate 2. *Lebbeus scrippsi,* n. sp. 7, right first pereiopod; 8, right second pereiopod; 9, right fourth pereiopod; 10, right fifth pereiopod; 11, right second pleopod in frontal view; 12A and B, telson and uropod. 13–14, male, from south of Mollendo, Peru. 13, right second pleopod in frontal view; 14, appendices masculina and interna. 15–17, individuals from south of Mollendo, Peru, showing variations in shape. 15–16, anterior part of body; 17, unusual rostrum.

Scaphocerite 2.8× as long as wide. Outer margin straight, with strong final tooth, blade exceeding tooth. Antennular peduncle reaching distal three-quarters of scaphocerite. Two sharp spines at base of scaphocerite.

Mandible with slender incisor process, ending in 2 teeth. Molar process bearing numerous spinules. Palp two-jointed. First maxilla with slender lower endite, broad upper endite, and stout palp. Second maxilla with lower endite reduced, consisting of 2 lobes. Upper endite larger and bilobed. Scaphognathite and palp well developed. First maxilliped with bilobed epipod. Endites of coxa and basis separated by notch. Palp two-jointed. Caridean lobe large. Second maxilliped with epipod, podobranch, and exopod. Third maxilliped reaching beyond scaphocerite. Ultimate segment about 3× longer than penultimate, slightly shorter than antepenultimate. Sharp, dark spines at end of ultimate segment. Epipod present, but no exopod. Branchial formula:

	Maxillipeds			Pereiopods				
	1	2	3	1	2	3	4	5
Pleurobranchs	–	–	–	+	+	+	+	+
Arthrobranchs	–	–	–	–	–	–	–	–
Podobranchs	–	+	–	–	–	–	–	–
Epipods	+	+	+	+	+	–	–	–
Exopods	+	+	–	–	–	–	–	–

First pereiopods shorter than scaphocerite, chelate. Dactyl 0.4× propodus. Propodus stout. Carpus 0.84× length of propodus. Merus twice length of carpus. Ischium 0.4× length of merus.

Second pereiopods longer than scaphocerite, chelate. Dactyl 0.5× length of propodus. Carpus with 7 segments, the third of these the longest. Entire carpus 5× length of propodus. Merus 0.5× length of carpus. Ischium same length as merus.

Third pereiopods longer than scaphocerite. Dactyl simple, slender, 0.4× length of propodus. Carpus 0.5× length of propodus. Merus twice length of carpus, with 5–6 spines. Ischium 0.5× length of merus. Fourth pereiopod similar to third, but with 4–5 meral spines. Fifth pereiopod similar to fourth, but without meral spines.

Second pleopods with appendix interna in both sexes. In male, appendix masculina much longer than appendix interna.

Uropods equal to telson, broadly ovate. Exopod with straight outer margin ending in small tooth. A larger tooth internal to this tooth.

Material.—HOLOTYPE: AHF 724; female, ovigerous. Off Arica, Chile (18°40.5′S, 70°36.0′W to 18°32.2′S, 70°29.8′W), 768–968 m. 25-foot otter trawl, 7 May 1972, R.V. *Thomas Washington,* R. Wisner and S. Luke, collectors. SIO station MV72-II-27. Male, paratype, AHF; female, paratype, SIO, female, paratype, USNM. Twenty-two additional specimens in this lot, all returned to SIO.—Paratypes, male and female. Off Altura de Pucusana, Peru (12°33′S, 77°22.5′W), 800 m, 4 February 1972, *SNP-1* station 31, cruise 7201, L. A. Flores and L. Curotto, collectors, IMARPE.—Additional material: 7 specimens, one with sacculinid. Off Arica, Chile (18°44.7′S, 70°40.7′W to 18°40.2′S, 70°35.1′W), 1108–1164 m, 25-foot otter trawl, 7 May 1972, R.V. *Thomas Washington,* R. Wisner and S. Luke, collectors, SIO station MV72-II-26, SIO.—2 specimens. South of

Mollendo, Peru (17°05′S, 72°16.9′W), 800 m, dredged, 27 January 1972, *SNP-1* station 7, cruise 7201, L. A. Flores and L. Curotto, collectors, IMARPE.

Measurements in millimeters.—Holotype: total length 31.5, rostrum 3.0, carapace 8.4, abdomen 14.6, telson 3.5, (broken at tip), scaphocerite 5.2, third maxilliped 10.3, first pereiopod 10.5, second pereiopod 15.6, third pereiopod 16.8. Total lengths (tip of rostrum to end of uropods) of paratypes: 37.5, 41.2, 36.5, 27.6, 32.0.

Remarks.—*Lebbeus scrippsi* is related to *L. polaris* (Sabine), *L. grandimanus* (Brazhnikov), and *L. brandtii* (Brazhnikov). Both *L. brandtii* and *L. grandimanus* have short rostra, not exceeding the scaphocerite. *Lebbeus brandtii* has no ventral teeth on the rostrum posterior to the apex. It has a pronounced hump on the dorsal surface of the third abdominal segment (Balss 1914). *Lebbeus grandimanus* has 4 large teeth on the carapace posterior to the orbit. *Lebbeus polaris* has a rostrum longer than the scaphocerite, with 0–2 dorsal spines and 3–4 ventral spines. None of these related species is known to occur on the western coast of South America.

Taken with *Lebbeus scrippsi* at stations 7 and 31 were the penedi shrimp *Benthesicymus tanneri* Faxon, the caridean shrimps *Acanthephyra approxima* Bate, *Pasiphaea magna* Faxon, *Glyphocrangon alata* Faxon, and *Sclerocrangon atrox* Faxon; the polychelid lobster *Stereomastis sculpta pacifica* (Faxon), the deep-sea lobster *Nephropsis occidentalis* Faxon, the axiid lobster *Iconaxius cristagalli* (Faxon), the galatheid crabs *Munidopsis hamata* Faxon, *Munidopsis quadrata* Faxon, and *Munida propinqua* Faxon; the lithodid crab *Lithodes panamensis* Faxon, and the brachyuran crabs *Trachycarcinus hystricolsus* Garth and *Trachycarcinus corallinus* Faxon. The bottom at station 31, cruise 7201 was soft mud with detritus (del Solar and Flores 1972; Méndez 1979).

Lebbeus scrippsi is named in honor of Scripps Institution of Oceanography.

Lebbeus splendidus n. sp.

Plates 3–5

Description.—Rostrum long, upcurved, exceeding scaphocerite. Two spines on dorsal surface of carapace posterior to orbit, 2–3 spines on rostrum proper. Distal half of upper margin bare of spines. Five to 9 lower spines, the proximal 4 closer together than the other spines. Apex acute.

Carapace smooth. Supraorbital spine tiny. Antennal and pterygostomial spines present. Groove along distal branchial region.

Abdomen smooth. Pleura of segments 1–4 rounded. Third segment broadly overreaching fourth on dorsal margin. Pleura of segment 5 with sharp points. Sixth segment 1.5× length of fifth, with sharp lateral points. Telson with 3 pairs dorsal spines placed just before half its length and posteriorly. Tip of telson rounded, with 2 pair long spines and 4 setose spines. Telson 1.3× as long as sixth abdominal segment.

Eyes large, rounded. Cornea darkly pigmented, reaching base of second dorsal spine of rostrum.

First segment of antennular peduncle with 2 sharp spines on dorsal distal margin. Stylocerite sharp, as long as first segment. Second segment 0.75× length of first, with sharp distal spines. Third segment very short, 0.33× length of second seg-

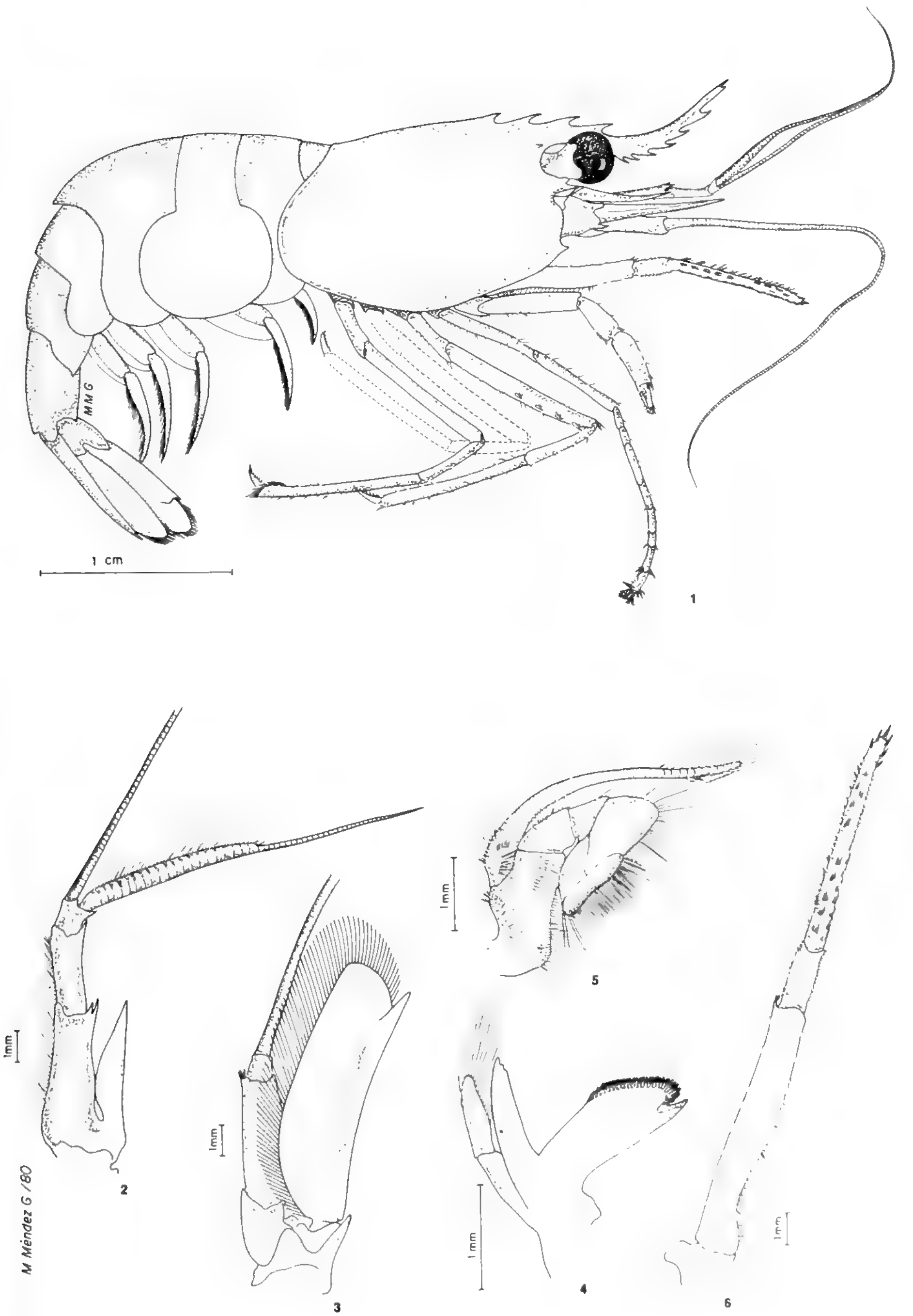

Plate 3. *Lebbeus splendidus*, n. sp. Female, 51.2 mm, southwest of Lobos de Tierra, Peru. Fig. 1, lateral view; 2, right first antenna; 3, right second antenna; 4, right mandible; 5, right second maxilliped; 6, right third maxilliped in media view.

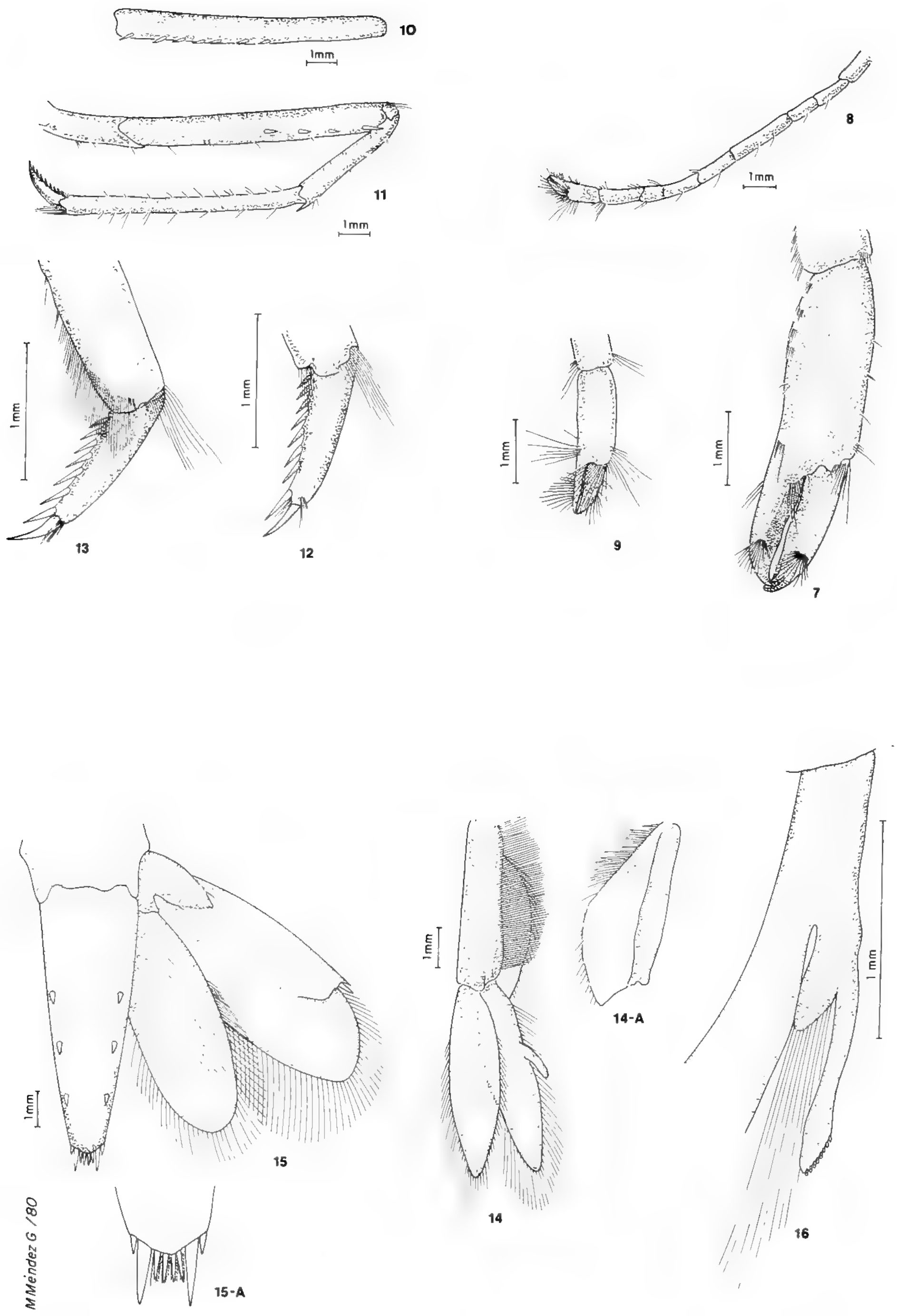

Plate 4. *Lebbeus splendidus,* n. sp. 7, chela of right first pereiopod; 8, carpus and chela of right second pereiopod; 9, chela of right second pereiopod; 10, merus of left third pereiopod; 11, right third pereiopod; 12, dactyl of right third pereiopod; 13, dactyl of right fifth pereiopod; 14, right second pleopod in frontal view; 14A, basipodite of right second pleopod; 15, telson and uropods; 15A, apex of telson; 16, right second pleopod from male 37.9 mm total length, southwest of Lobos de Tierra, Peru, showing appendices masculina and interna.

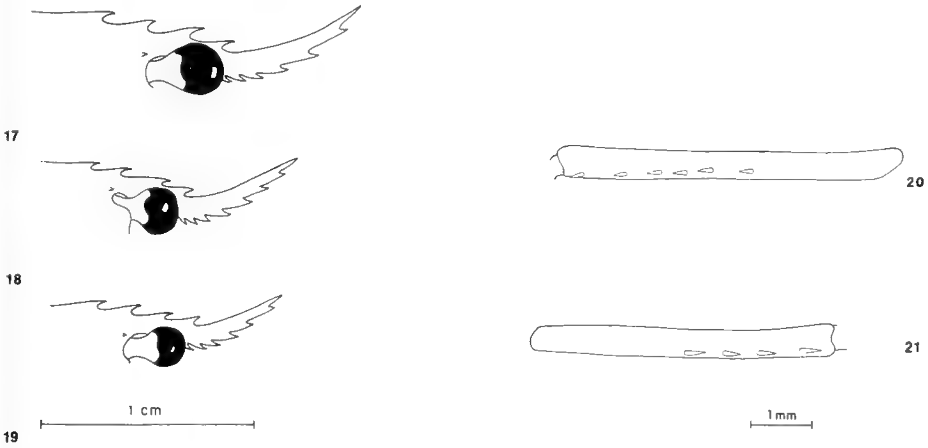

Plate 5. *Lebbeus splendidus,* n. sp. 17–19, eyes and rostra, showing variation. 17, from female 50.0 mm total length; 18, from male, 37.9 mm total length; 19, from female, 34.2 mm total length. 20, merus of left third pereiopod from male, 37.9 mm total length; 21, merus of right third pereiopod from female, 34.2 mm total length.

ment, with sharp distal spine. Antennular peduncle shorter than scaphocerite. Upper antennular flagellum thickened, consisting of single ramus.

Scaphocerite 2.66× as long as wide. Outer margin slightly concave, with strong final tooth; blade exceeding tooth. Antennular peduncle reaching nearly to tooth. Two spines present at base of scaphocerite.

Mandible, maxillae, and maxillipeds resembling those of *L. scrippsi.*

Branchial formula:

	Maxillipeds			Pereiopods				
	1	2	3	1	2	3	4	5
Pleurobranchs	–	–	–	+	+	+	+	+
Arthrobranchs	–	–	–	–	–	–	–	–
Podobranchs	–	+	–	–	–	–	–	–
Epipods	+	+	+	+	+	–	–	–
Exopods	+	+	–	–	–	–	–	–

First pereiopods shorter than scaphocerite, chelate. Dactyl 0.25–0.3× length of propodus. Carpus 0.75× length of propodus. Merus twice length of carpus. Ischium 0.17× length of merus.

Second pereiopods longer than scaphocerite, chelate. Dactyl 0.4× length of propodus. Carpus with 7 segments, the third of these the longest. Entire carpus 5× length of propodus. Merus 0.6× length of carpus. Ischium same length as merus.

Third pereiopods longer than scaphocerite. Dactyl slender, about 0.2× length of propodus. Merus 2× length of carpus, with 4–7 sharp distal ventral spines. Ischium 0.4× length of merus. Fourth pereiopod similar. Fifth pereiopod without meral spines.

Second pleopods with narrow, ovate endopods and exopods in both sexes. Appendix interna present. In male, appendix masculina longer than appendix interna.

Uropods longer than telson, broadly ovate. Exopod with straight outer margin ending in small tooth. A larger tooth internal to this tooth.

Material.—HOLOTYPE, AHF 7116; female, ovigerous. Southwest of Lobos de Tierra, Peru (6°31′S, 81°01′W), 712–744 m, 17 May 1971, *SNP-1* station 12, cruise 7105, E. M. del Solar, M. Viacava, and J. Velez, collectors.—Six females and two males, paratypes, same station, IMARPE.—Paratype, female. Between Lobos de Tierra and Lobos de Afuera, Peru (6°42′S, 80°47′05″W), 1090–1100 m, 22 January 1974, beam trawl, *SNP-1* station 23, USNM.—One additional female, same station, AHF.

Measurements in millimeters.—Holotype: total length (tip of rostrum to tip of telson) 50.1, rostrum 11.9, carapace 11.2, abdomen 20.7, telson 8.3, third maxilliped 17.1, scaphocerite 6.6, first pereiopod 13.2, second pereiopod 19.4, third pereiopod 26.6. Total lengths of other specimens: 44.2, 40.7, 36.3, 53.5, 29.8, 51.2, 50.0, 37.9, 34.2.

Remarks.—*Lebbeus splendidus* resembles *L. polaris* from Arctic waters. Both species have epipods on the first two pereiopods. The rostrum of *L. polaris,* with only 3–4 ventral spines, does not curve as prominently as that of *L. splendidus. Lebbeus polaris* has one spine at the distal end of the first segment of the antennular peduncle, *L. splendidus* has two spines. The dactyls of the third pereiopods in *L. polaris* end in two stout spines, those of *L. splendidus* are slender. In *L. splendidus* there is a tuft of setae at the distal end of the propodus of the third pereiopod.

Taken with *L. splendidus* at station 12, cruise 7105 was the peneid shrimp *Benthesicymus* sp., the carideans *Heterocarpus hostilis* Faxon, *Heterocarpus affinis* Faxon, *Pantomus affinis* Chace, *Acanthephyra approxima, Nematocarcinus agassizii* Faxon, and *Bathypalaemonella* sp; the hermit crab *Pagurus* sp., and the lithodid crabs *Lithodes ? panamensis* and *Glyptolithodes cristatipes* Faxon.

Lebbeus vicinus montereyensis n. subsp.
Plate 6

Lebbeus polaris: Wicksten, 1978:6, fig. 6.
Not *Alpheus polaris* Sabine 1821:238, pl. II, figs. 5, 8.

Description.—Rostrum of female long and slender, usually longer than scaphocerite, slightly upcurved in anterior part. Rostrum of male shorter than scaphocerite. Upper margin with 3–4 teeth, 2–3 of them on carapace. Lower margin with 4 teeth.

Carapace smooth, arched dorsally, with median dorsal carina running nearly 0.75 of its length, with supraorbital, antennal, and pterygostomial spines.

Abdominal segments rounded dorsally, the third with posterior margin triangularly produced in the median. Pleura of first 4 segments rounded, that of fifth shaped like broad, blunt triangle. Sixth segment 1.75× length of fifth, ending in sharp point. Telson reaching at least to end of uropods, but broken in all specimens; bearing 2 pair small spines along posterolateral margin.

Eyes large, darkly pigmented, reaching about 0.75× length of first segment of antennular peduncle.

Antennular peduncle shorter than antennal scale. First segment longest, with prominent sharp spine at upper distal margin and lateral blunt process which overreaches articulation with second segment. Stylocerite strong, sharp, reaching

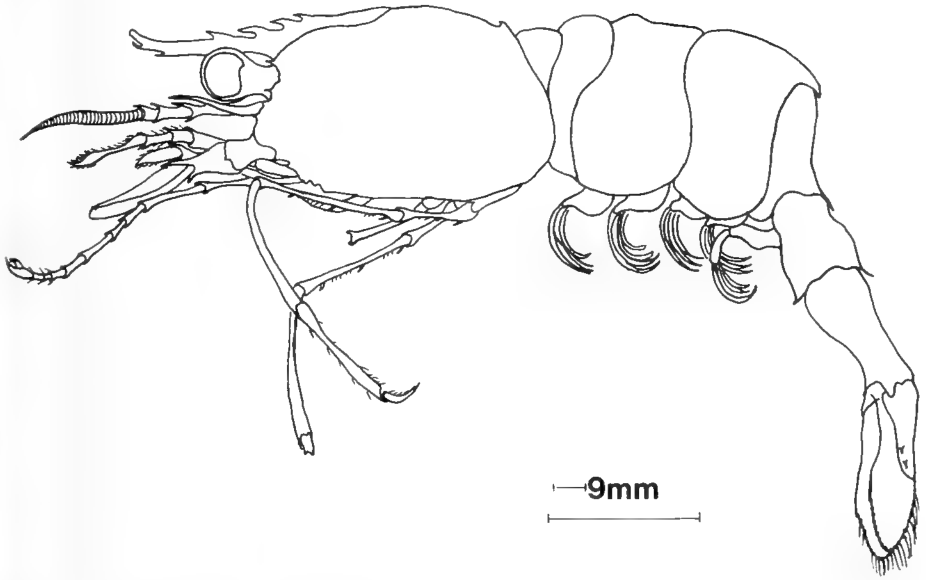

Plate 6. *Lebbeus vicinus montereyensis*, n. subsp. Female, 58.3 mm total length. Off Punta Banda, Baja California, Mexico. Frontal margin of carapace, rostrum, telson, and pereiopods broken in this specimen.

end of first segment. Second segment about 0.5× length of first, with spine on dorsal anterior margin. Third segment small, about 0.5× length of second, with sharp dorsal tooth. Inner flagellum slender, outer flagellum short and broad.

Antennal peduncle reaching beyond middle of scaphocerite. Scaphocerite shorter than female rostrum, with broad lamella greatly overreaching lateral tooth.

Mandible with distinct incisor process and two-jointed palp. First maxilla with bilobed palp, broad upper endite and narrow lower endite. Second maxilla with lower endite reduced to 2 short lobes. Upper endite large, bilobed. Palp and scaphognathite well developed. First maxilliped with exopod, two-jointed palp, epipod, and prominent caridean lobe. Second maxilliped with epipod and podobranch. Third maxilliped without exopod but with epipod; overreaching scaphocerite. Ultimate segment 3.5× length of penultimate, shorter than antepenultimate. Ultimate segment with prominent distal spines and setae. Antepenultimate segment with distinct outer anterolateral tooth. Branchial formula:

	Maxillipeds			Pereiopods				
	1	2	3	1	2	3	4	5
Pleurobranchs	–	–	–	+	+	+	+	+
Arthrobranchs	–	–	–	–	–	–	–	–
Podobranchs	–	+	–	–	–	–	–	–
Epipods	+	+	+	+	–	–	–	–
Exopods	+	+	–	–	–	–	–	–

First pereiopods strong and short, chelate. Dactyl less than 0.5× propodus. Carpus equal to palm, merus 1.5× propodus. Second pereiopod long and slender, exceeding scaphocerite by entire chela and last 3 carpal segments. Chela small, about 0.2× carpus. Carpus with 7 segments, the third by far the longest. Merus about 0.6× carpus. Ischium slightly shorter than merus. Third pereiopod with dactyl about 0.2× propodus, provided with 6 spines. Carpus about 0.6× propodus. Merus about as long as propodus, with 1 prominent distolateral spine and 4–6 smaller lateral spines. Fourth pereiopod similar to third, but with only 4 smaller lateral meral spines as well as prominent spine. Fifth pereiopod with 3 small lateral meral spines, but no prominent distolateral spine.

Second pleopod of female with appendix interna; that of male with appendix interna and appendix masculina.

Uropods broad, ovate.

Material.—HOLOTYPE: AHF 606; female. West of Punta Banda, Baja California, Mexico (31°18′N, 117°36′W), 2068–2086 m, 30-foot otter trawl, 13 February 1960, Parker and Yonge, collectors; SIO catalogue number C2572. Also two ovigerous females, paratypes, same station, to SIO and male, smashed, AHF.—Female, "Gulf of California," 2824 m, 8 March 1959, R. Wisner, collector, AHF.—Female, paratype. Monterey Submarine Canyon, California (36°45.3′N, 122°04.7′W to 36°45.7′N, 122°04.8′W), 954–1044 m, U.S.N.S. *De Steiguer* cruise, 19 November 1975, California Academy of Sciences.

Measurements in millimeters.—Holotype: total length 65.7, rostrum 10.0, carapace 15.0, abdomen and telson 37.7, telson 6.9 (broken), third maxilliped 21.6, first pereiopod 17.2, second pereiopod 25.1, third pereiopod 31.6. Total lengths of other specimens: 58.3, 50.5, 31.6, 58.8.

Remarks.—We have compared our material of the new subspecies with the types and two other specimens of *L. vicinus vicinus* (Rathbun) from Alaskan waters. Our specimens differ from the northern subspecies primarily in having fewer dorsal spines on the rostrum and carapace. The northern shrimp have 6–8 dorsal spines; the southern ones have only 3–4. In northern females, the pterygostomial spine is more prominent than in southern females. The pleura of the fifth abdominal segment often end in sharp points in northern specimens rather than in a triangle. The last 2 spines of the dactyl of the third pereiopod in northern specimens often are stout, giving the dactyl the appearance of being biunguiculate. The stylocerite of the northern subspecies does not reach the end of the first segment of the antennular peduncle. In the southern subspecies, the stylocerite reaches to the end of this segment.

The description and illustration given by Rathbun (1902, 1904, as *Spirontocaris vicina*) are brief. Our material from California and Mexico, however, generally is similar to the northern specimens. It is difficult to state the degree of variation in a species known from so few individuals, especially when they are separated by a great distance. We suspect, however, that our southern specimens show adaptations to life at greater depths. Our material was collected at 954–2824 m; the northern subspecies, off Alaska at 570–750 m. Perhaps *L. vicinus* inhabits waters of a given cold temperature, living deeper in southern waters.

At the time of a previous study, only one specimen of the new subspecies was available. This animal, like all our specimens so far, was damaged. The lack of epipods on the second pereiopods was assumed to be due to breakage. The specimen therefore was identified as *L. polaris* (Wicksten 1978). However, all specimens of the new subspecies lack epipods on the second pereiopods. The distal margin of the pleura of the fifth abdominal segment in *L. polaris* forms a sharp point, not a rounded triangle. No specimens of *L. vicinus* have the lamellate rostral form illustrated for *L. polaris* by Kobyakova (1955). *Lebbeus polaris* has not been reported south of Alaskan waters on the American Pacific coast (Butler 1980).

Lebbeus vicinus montereyensis is named after Monterey Bay, California, where one of the specimens was collected.

Comments on *Lebbeus curvirostris* and *Lebbeus bidentatus*

Zarenkov (1976) described three species of *Lebbeus* taken off Peru and Chile: *L. curvirostris, L. bidentatus,* and *L. carinatus.* We have been unable to examine material of any of these species. Of the three, *L. curvirostris* probably belongs to the genus *Nauticaris.* Members of this latter genus have arthrobranchs on all the pereiopods, as described. *Lebbeus bidentatus* is similar to *L. washingtonianus* (Rathbun). It has epipods on the first three pereiopods. The illustration of the broken holotype shows two spines on the anterodorsal part of the carapace and two on the dorsal part of the rostrum proper, with four ventral rostral spines. *Lebbeus washingtonianus* also has epipods on the first three pereiopods. It has 1–2 anterodorsal spines on the carapace, three dorsal rostral spines, and 2–3 ventral rostral spines. In *L. bidentatus,* there are six spines on the merus of the third pereiopod, in *L. washingtonianus,* there are five. Both have four meral spines on the fourth pereiopod. The proportions of the segments of the antennular peduncle are similar. Both occupy the same depth range. *Lebbeus bidentatus* may represent a southern race of *L. washingtonianus. Lebbeus carinatus* differs from other species of *Lebbeus* in the eastern Pacific in having epipods on all of the first four pereiopods.

Extensions of Range

Lebbeus brandti (Brazhnikov)

Recorded range.—Sagami Bay, Japan, 120 m (Balss 1914); Sea of Okhotsk, 12 m, 10–55 m (Brazhnikov 1907; Kobyakova 1937).

Material.—Three specimens. Smeaton Arm, Wilson Bay, Alaska (55°20′N, 130°50′W), 172 m, 17 Sept. 1981, trawl 903, VTN, Inc. collectors. One specimen with bopyroid isopod as parasite.

Remarks.—This is the first record of this species in the eastern Pacific Ocean.

Lebbeus grandimanus (Brazhnikov)

Recorded range.—Bering Sea, Commander Islands, Pribilof Islands to San Juan Island, Washington; Race Rocks, Okhotsk Sea, Sea of Japan, to Peter the Great Bay, 6–180 m (Butler 1980).

Material.—Three specimens. Northwest Island, Pond, Puget Sound, Washington, U.S.A., 1974, L. R. McCloskey, USNM.

Lebbeus lagunae (Schmitt)

Recorded range.—Pacific Grove to Tanner Bank, California (Wicksten 1978).

Material.—One specimen. Between Coronado Islands, Mexico and Pt. Loma, California (32°32.8′N, 117°15.5′W), 55 m, 26 Nov. 1949, Carl L. Hubbs station H49-116, AHF.—One specimen. Reef on south side of Punta Banda, Baja California, Mexico (31°45′N, 116°50′W), depth not recorded, 3 Feb. 1951, Carl L. Hubbs station H51-21, AHF.

Lebbeus possjeticus Kobyakova

Recorded range.—Type locality, Possjet Bay, Pacific coast of U.S.S.R. (Kobyakova 1967).

Material.—One specimen. Bering Island, 3 m, donated by Zoological Institute of Leningrad, #957, USNM.—One specimen. Off San Nicolas Island, California (33°15′30″N, 119°24′40″W–33°16′10″N, 119°24′30″W), 52–57 m, rocks. 12 April 1940, R.V. *Velero III* station 1123–40, AHF.

Remarks.—This small shrimp may follow zones of cold water, occurring in deeper water toward the south. The specimens examined have prominent folds on the dorsal surface of the second abdominal segment, as mentioned by Butler (1980).

Lebbeus zebra (Leim)

Recorded range.—New Brunswick, Nova Scotia, and Chaleurs Bay, Newfoundland (Couture and Trudel 1968); Bering Sea and Kamchatka (Makarov 1935, as *Hetairus zebra*); British Columbia (Butler 1964).

Material.—Two specimens. 13 miles SSE of East Point, Santa Rosa Island, California (33°40′55″N, 119°52′30″W–33°42′32″N, 119°50′10″W), 113–140 m, with rocks, crinoids, sponges, and ophiuroids; 25 August 1941, *Velero III* station 1385-41, AHF.

Remarks.—We have compared our specimens with the shrimp taken off British Columbia by Butler (1964) and specimens taken at St. Mary Bay, Nova Scotia. The identity of the specimen from British Columbia "remains in doubt" (Butler 1980). It more closely resembles *L. schrencki* (Brazhnikov) than the animals from California, which conform closely to the animals from the east coast of Canada. The specimens from California lack a transverse furrow on the dorsal surface of the second abdominal segment.

Key to the Species and Subspecies of *Lebbeus* in the Eastern Pacific Ocean

1\. Epipods on only the first pereiopods 2
– Epipods on at least the first and second pereiopods 3
2\. Rostrum with 6–8 dorsal spines, stylocerite not reaching end of first segment of antennular peduncle . . . . *Lebbeus vicinus vicinus* (Rathbun)
– Rostrum with 3–4 dorsal spines, stylocerite reaching end of first segment of antennular peduncle . . . . *Lebbeus vicinus montereyensis* n. subsp.
3\. Epipods on first and second pereiopods 4
– Epipods on at least first to third pereiopods 7
4\. Carapace with 4 large dorsal spines posterior to orbit. (Often associated with sea anemone, *Cribrinopsis fernaldi*) . . . . *Lebbeus grandimanus* (Brazhnikov)
– Carapace with 1–2 dorsal spines posterior to orbit. (Associations not known) 5
5\. Dactyl of third pereiopod simple, without spines . . *Lebbeus scrippsi* n. sp.
– Dactyl of third pereiopod with spines 6

6. First segment of antennular peduncle with 2 anteroexternal spines. Rostrum with 5–9 ventral spines .... *Lebbeus splendidus* n. sp.
– First segment of antennular peduncle with 1 anteroexternal spine. Rostrum with 4 or less ventral spines 7
7. Rostrum longer than antennular peduncle, with 3–4 ventral spines ... . *Lebbeus polaris* (Sabine)
– Rostrum barely reaching end of first segment of antennular peduncle, with 1 or no ventral spines .... *Lebbeus brandti* (Brazhnikov)
8. Epipods on first to fourth pereiopods .... *Lebbeus carinatus* Zarenkov
– Epipods on first to third pereiopods 9
9. Pleura of first to fifth abdominal segments ending in 1–3 spines .... *Lebbeus groenlandicus* (Fabricius)
– Pleura of at least first to third abdominal segments pointed to rounded, but not ending in 1–3 spines 10
10. Rostrum reduced to spine on frontal margin of carapace. Three spines on anterior dorsal midline of carapace .... *Lebbeus lagunae* (Schmitt)
– Rostrum prominent, not reduced to spine. 1–2 spines on anterior dorsal midline of carapace 11
11. Antennular peduncle extending to near middle of scaphocerite. Small subtidal species 12
– Antennular peduncle extending nearly to end of scaphocerite. Large species of continental slopes 14
12. Dorsal surface of second abdominal segment without transverse furrow and fold. Rostrum shorter than eye .... *Lebbeus zebra* (Leim)
– Dorsal surface of second abdominal segment with transverse furrow and fold. Rostrum longer than eye 13
13. Rostrum short, not reaching end of first segment of antennular peduncle, with 2–5 dorsal spines and 1 ventral spine .... *Lebbeus schrencki* (Brazhnikov)
– Rostrum reaching to end of scaphocerite, with 5–7 dorsal spines and 3–4 ventral spines .... *Lebbeus possjeticus* Kobyakova
14. First segment of antennular peduncle with 1 spine, bi- or trifurcated. Northern hemisphere .... *Lebbeus washingtonianus* (Rathbun)
– First segment of antennular peduncle with 3 spines. Southern hemisphere .... *Lebbeus bidentatus* Zarenkov

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Literature Cited

Balss, H. 1914. Ostasiatische Decapoden II. Die Natantia und Reptantia. Pp. 1–101 *in* Doflein, F. Beiträge zur Naturgeschichte Ostasiens. Abhandlungen der Bayerischen Akademie der Wissenschaften, suppl. vol. 2, part 10.

Butler, T. H. 1964. Records of shrimps (Order Decapoda) from British Columbia. J. Fish. Res. Bd. Canada, 21:419–421.

———. 1980. Shrimps of the Pacific coast of Canada. Canad. Bull. Fish. Aquatic Sci. 202. 280 pp.

Couture, R., and P. Trudel. 1968. Les crevettes des eaux cotieres du Quebec. Naturaliste Canadien, 95:857–885.

Kobyakova, Z. I. 1937. Desjatinogie Raki (Decapoda) Okhotskogo i Japonskogo Morei. Leningrad Universitet Uchenye Zapiski, Annals. Seriia Biologisches, 15:93–154.

———. 1955. Order Decapoda. Pp. 200–207 *in* Pavlovskii, E. N., ed. Atlas of the invertebrates of the far eastern seas of the U.S.S.R. Akad. Nauk USSR, Zool. Inst. (English translation, Israel Program for Scientific Translations, Jerusalem, 1966.)

———. 1967. Desjatinogie Raki (Crustacea, Decapoda) Zaliva Posjet (Japonskoe More). Pp. 230–246 *in* Issledovanija Fauny Morei 5(13). Biotsenozy Posjet Japonskogo Morja. Akad. Nauk SSSR, Zool. Inst.

Makarov, V. V. 1935. Bescheibung neuer Dekopoden-Formen aus den Meeren des Fernen Ostens. Zool. Anz., 109:319–325.

Méndez, M. 1979. Un estudio sobre los Decapoda Natantia (Crustacea) del Mar Peruano. Tesis Doctoral. Prog. Acad., Ciencias Biológicas. Univ. N. M. de San Marcos, Peru. 219 pp.

Rathbun, M. J. 1902. Descriptions of new decapod crustaceans from the west coast of North America. Proc. U.S. Nat. Mus., 24(1272):885–905.

———. 1904. Decapod crustaceans of the northwest coast of North America. Harriman Alaska Exped., 10:1–219.

Sabine, J. 1821. Invertebrate animals. Pp. 219–239 *in* Parry, W. E. Journal of a voyage for the discovery of a north-west passage from the Atlantic to the Pacific. London: J. Murray. Appendix X, Natural History.

Solar, E. del, and L. A. Flores. 1972. Exploración de Crustaceos (Zona Sur) Crucero 7201 *SNP-1.* Callao: Instituto del Mar del Peru, Serie de Informes Especiales IM-107.

Wicksten, M. K. 1978. The species of *Lebbeus* in California (Crustacea: Caridea: Hippolytidae). Occ. Papers Allan Hancock Found., N.S. No. 1. 8 pp.

———. 1979. Zoogeographical affinities of the broken back shrimp (Caridea: Hippolytidae) of western South America. Pp. 627–634 *in* Proc. Internat. Symp. Mar. Biogeogr. and Evol. in So. Hemisphere (Auckland, July 1978). Vol. 2. N.Z. DSIR Info. Series 137.

Zarenkov, N. A. 1976. K faune desjatinogikh rakoobraznykh priamerikanskikh juzhnugo polusharija. Biologija Morja, 5:8–18.

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Late Pleistocene Vertebrates from a Mormon Mountain Cave in Southern Nevada

George T. Jefferson

Abstract.—Late Pleistocene Vertebrates from a Morman Mountain Cave in Southern Nevada by George T. Jefferson, *Bull. Southern California Acad. Sci.*, 81(3):121–127, 1982. A mammalian assemblage of latest Pleistocene Early Recent age containing animals no longer living in southern Nevada has been recovered from a limestone cave on the north side of the Mormon Mountains, Lincoln County, Nevada, approximately 112 kilometers northeast of Las Vegas. The cave is developed in late Paleozoic limestones and lies at an elevation of approximately 1372 meters above sea level in an area which supports a pinyon-juniper, sagebrush floristic community. Some of the fossil species from the cave have modern representatives that presently live in this habitat. Other species, such as *Ochotona princeps* (pika), *Marmota flaviventris* (marmot), and *Citellus lateralis* (golden mantled ground squirrel) either do not now range into southern Nevada or are present only at the highest elevations in this region, in pine or fir forest at elevations about 2135 meters. The fossil occurrence of *Ochotona, Marmota,* and *Citellus lateralis* in southern Nevada is anomalous relative to their present distribution and suggests that pine and fir floras were at least 610 to 915 meters lower in elevation when these taxa were living in the area. Upward shifts of floristic communities in the Southwest have been attributed to the warming trend of post-Wisconsin climates over the past 8000 to 11,000 years. Changes in the distribution of small mammals in the Southwest have occurred in response to geographic shifts of floristic communities.

The difference in elevation between the cave assemblage and Recent small mammal faunas of similar composition is compared to the difference in elevation between radiocarbon-dated fossil floras and Recent floras. These correlations provide an approximate minimum age of 8000 years before present for the assemblage.

An assemblage of fossil rodents and other small mammals (Table 1) has been recovered from a limestone cave on the north side of the Mormon Mountains, Lincoln County, Nevada (Fig. 1). The age of the assemblage is at least as old as latest Pleistocene (late Wisconsin) and no younger than sub-Recent. Some of the fossil species from the cave are extralocal in their southern occurrence at this site.

The material was collected in the spring of 1966 by W. Daily, G. Lewis and the author, affiliated with the Department of Earth Sciences, University of California, Riverside, California. Fossil bearing matrix was dry screened through one tenth inch mesh at the site. Identifications were made by direct comparison with the Recent mammalogy collections of the Natural History Museum of Los Angeles County. The small mammals were identified on the basis of dentitions only.

The cave is developed in late Paleozoic limestones and lies at approximately 1372 m (meters) above sea level in an area which presently receives 20 cm

Table 1. Recent mammal fauna and cave assemblage.

	Recent fauna Mormon Mountains	Cave assemblage	
		Identified specimens	Relative percentage
Phrynosoma platyrhinos		2	.5
Notiosorex crawfordi		2	.5
Myotis yumanensis	X		
M. californicus	X		
M. sublatus	X		
M. sp.		3	.7
Lasionycteris noctivagans	X		
Pipistrellus hesperus	X		
Eptesicus fuscus	X	2	.5
Lasiurus borealis			
Corynorhinus townsendi		14	3.5
Antrozous pallidus	X	1	.2
Tadarida brasiliensis	X		
Procyon lotor	X		
Bassariscus astutus	X		
Mustela frenata	X		
Spilogale gracilis	X		
Mephitis mephitis	X		
Taxidea taxus	X		
Vulpes macrotis	X		
Urocyon cinereoargenteus	X		
Canis latrans	X		
Felis concolor	X	1	.2
Lynx rufus	X		
Ochotona princeps		18	4.5
Lepus californicus	X		
Sylvilagus auduboni	X		
Sylvilagus nuttalli		31	7.8
Eutamias dorsalis (?)		26	6.5
E. amoenus		1	.2
Marmota flaviventris		17	4.3
Citellus variegatus	X	3	.7
C. townsendi	X		
C. tereticaudus	X		
C. lateralis		10	2.5
Perognathus longimembris	X		
P. penicillatus	X		
P. formosus	X		
Perognathus parvus		2	.5
Dipodomys merriami	X		
D. deserti	X		
Thomomys bottae	X		
Onychomys torridus	X		
Reithrodontomys megalotus	X	6	1.5
Peromyscus crinitus	X		
P. eremicus	X		
P. boyllii	X		
Peromyscus maniculatus	X	34	8.5
P. truei	X	9	2.3
Neotoma lepida	X		

Table 1. Continued.

	Recent fauna Mormon Mountains	Cave assemblage Identified specimens	Cave assemblage Relative percentage
Neotoma cinerea			
Microtus sp. (*longicaudus*?)		28	7.1
Erethizon dorsatum	X		
Ovis canadensis	X	5	1.2
Odocoileus hemionus	X		

(Recent fauna courtesy of P. J. Herlan of the Nevada State Museum.)

(centimeters) of annual precipitation and supports a pinyon-juniper community. This places the site within the Upper Sonoran Life Zone of Hall (Hall 1946). Some species from the cave still live in this habitat (Table 1). Other species such as *Ochotona princeps* (pika), *Marmota flaviventris* (marmot), and *Citellus lateralis* (golden mantled ground squirrel) presently do not range into southern Nevada or occur only at the highest elevations within the region, in pine or fir forests at elevations above 2135 m within Transitional and Boreal Life Zones (Hall 1946).

Changes in the geographic ranges of small mammals inhabiting Boreal and Transitional Zones is attributed to shifts in vegetation and climatic conditions (Wells and Jorgensen 1964; Wells and Berger 1967; Van Devender and King 1971; Phillips and Van Devender 1974; Van Devender and Spaulding 1979; Grayson 1981; Mead 1981).

Mode of Occurrence of Fossils

Accumulations of numerous mandibles and limb elements chiefly of small mammals were discovered at two sites near the back of the cave, about 45 m from the entrance. The fossils appear to have been eroded from an older fissure filling which now forms the back wall of the cave (Fig. 2, site A), and in the case of site B (Fig. 2), subsequently washed into a small cave pond.

The material from site A was recovered from a powdery brick-red silty clay which has slumped from the wall of the cave. The wall consists of angular boulder to cobble-sized blocks of limestone set in a matrix of clay. The clay occurs only at site A and, with the limestone blocks, appears to be the remnant of an older fissure filling that probably extended to the surface. The specimens from site A are permeated with the clay and some are stained red.

The material from site B was recovered from a friable clay rich, light tan to light pink, vuggy, calcareous tufa-like deposit which fills a shallow depression about 30 cm deep. Evidently the depression once held a small pond and the fossils may have been concentrated there by running water. Most material is coated with a layer of calcareous tufa. A few specimens are stained red which suggests that they were redeposited from pre-existing fissure fill material.

None of the deposits at sites A or B were stratified. The specimens are scattered randomly throughout the deposit, and none are articulated. Some of the large mammals are represented by single limb bones. No evidence of wood rat activity was discovered within the cave.

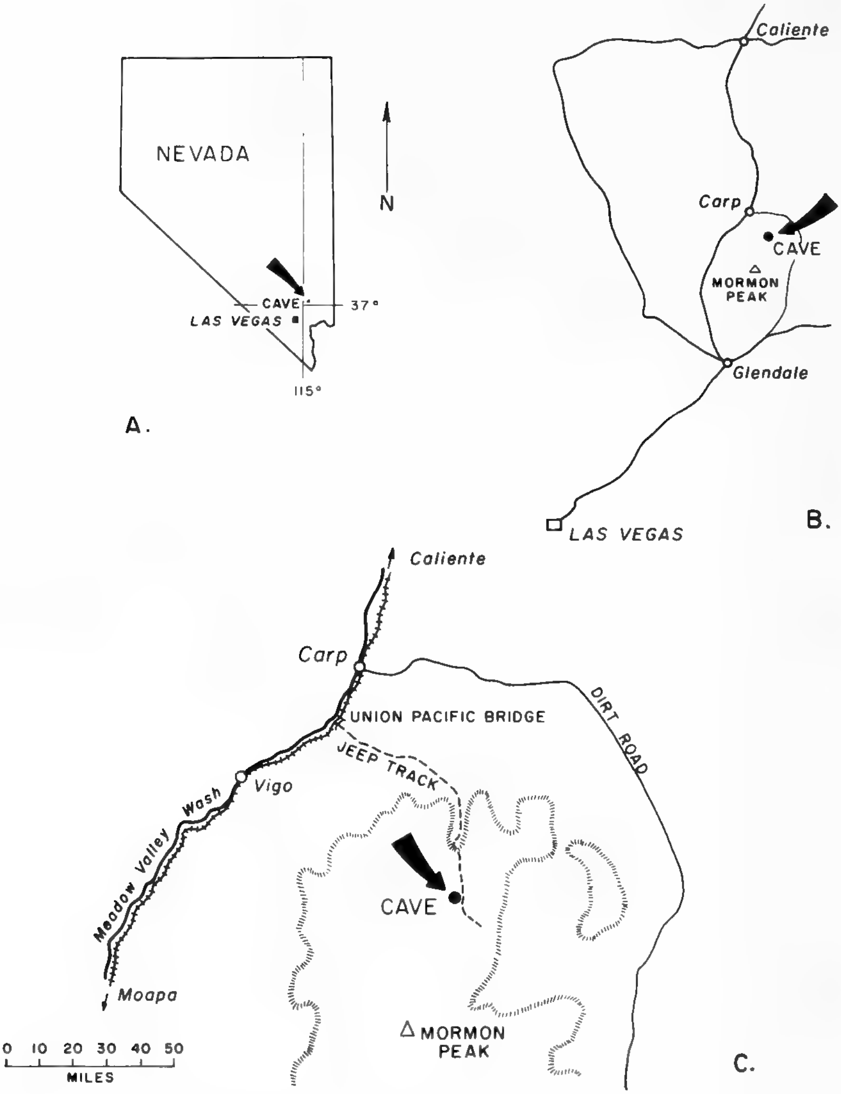

Fig. 1. Map showing the location of Mormon Mountain Cave relative to southern Nevada (A), Las Vegas (B), and an enlargement of the Mormon Mountain area (C). The hachured line in map C incidates the approximate extent of mountainous terrain.

Paleobiogeography

Localities in southern Nevada and the eastern Mojave Desert, California, which have yielded similar small mammal faunas of late Pleistocene age include Mescal Cave, Mercury Ridge, Kokoweef Cave, and Rampart Cave (Wilson 1942; Martin, et al. 1961; Mehringer 1966, 1977; Grayson 1981). The late Pleistocene (Wisconsin) distribution of small mammals in this area seems to have been controlled by biogeography of floristic communities (Mehringer 1966, 1977; Grayson 1981; Thompson and Mead 1982) and relative to their extant representatives, most

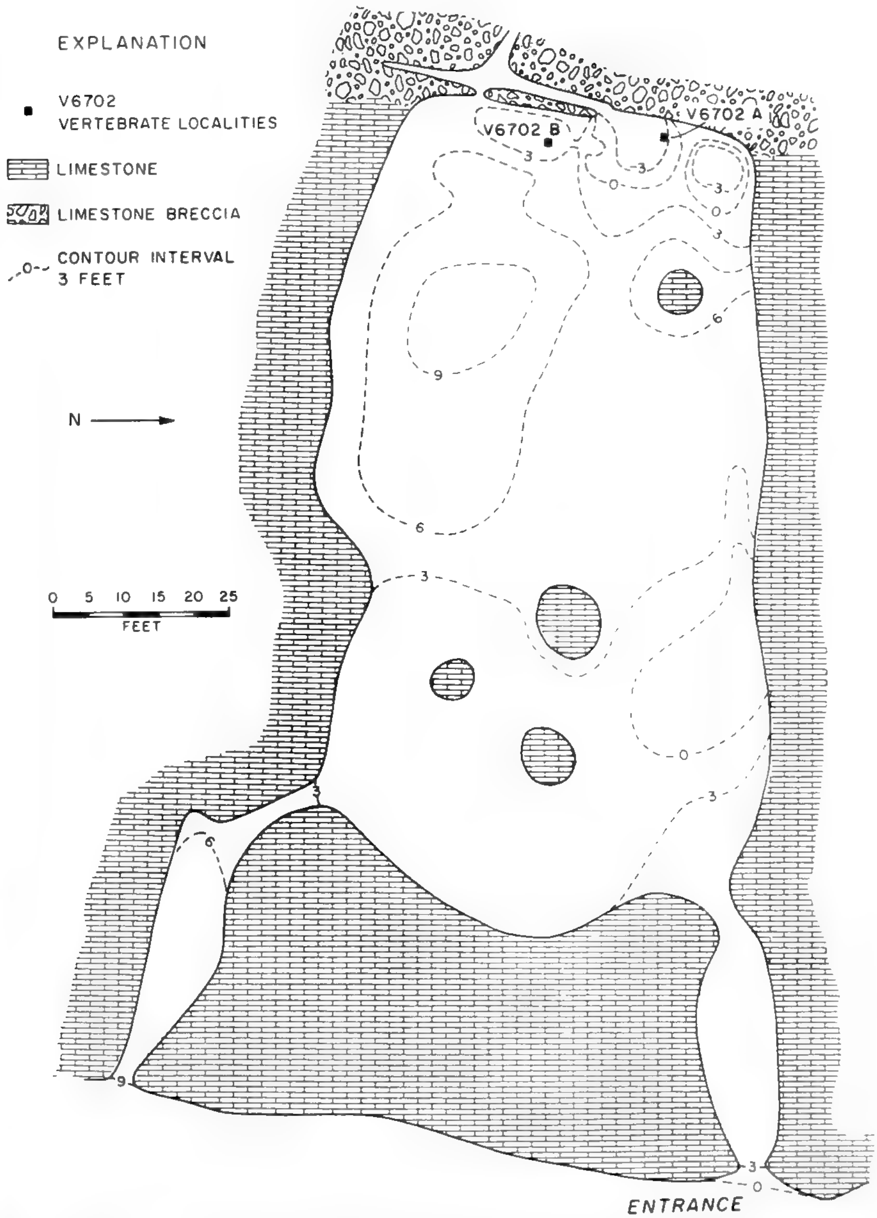

Fig. 2. Sketch map of the floor of Mormon Mountain Cave. Three foot topographic contours are approximately located. University of California, Riverside vertebrate fossil locality V6702A, slumped fissure fill; and B, dry cave pond are shown.

fossil species found at these localities exhibit a southern, extralocal extension of their geographic range at anomalously low elevations. The geographic range of fossil Boreal and Transitional species extended to the south at elevations which are now well within a drier warmer Sonoran Zone. Upward shifts in the elevations of floristic community elements in the Southwest are attributed to the warming trend of climates over the past 8000 to 11,000 years (Phillips and Van Devender 1974; Van Devender and Mead 1976; Van Devender and Spaulding 1979; Mead 1981). Seven of the taxa recovered from Mormon Mountain Cave about 72.4 percent of the total assemblage, are restricted to high elevations or occur only in northern Nevada today (Hall 1946; Hall and Kelson 1959). They are *Ochotona princeps, Sylvilagus nuttalli, Eutamias amoenus, Marmota flaviventris, Citellus lateralis, Neotoma cinerea* and *Microtus* sp. (Table 1). These taxa presently prefer habitats in Transitional or Boreal Zones, yellow pine to spruce-fir forests as high as timber line. Apparently at least the higher portions of the Mormon Mountains supported the Pleistocene equivalent of a Boreal Life Zone. As spruce-fir forests and yellow pine forests became restricted and finally disappeared in the Mormon Mountains, so did mammalian species adapted to these habitats.

A number of other taxa including most of the bats, *Citellus variegatus, Reithrodontomys megalotis, Peromyscus maniculatus, P. truei,* and *Ovis canadensis* presently inhabit the Mormon Mountains (Table 1). Some elements range from the Lower to Upper Sonoran Zones, occasionally invading habitats in the Transitional Zone. The Upper Sonoran to Transitional species may have co-existed with some of the Boreal to Transitional species no longer present in the Mormon Mountains.

Antiquity of the Assemblage

The difference in elevation between radiocarbon dated late Pleistocene floras and Recent floras indicates the amount of change in the elevation of life zones with respect to time. The magnitude of elevational shifts of the life zones of fossil small mammals compared to their extant representatives can be correlated with the dated shifts of floras.

In southern Nevada, Boreal mammalian species associated with a spruce-fir floristic community presently occur at elevations above 2745 m, about 1375 m higher than the cave. Transitional species associated with a yellow pine community occur approximately 915 m higher than the cave.

Studies of fossil pollen and plant remains from the Mojave Desert and southern Nevada indicate that late Wisconsin floras were a maximum of about 1000 m lower in elevation and extended farther to the south than their modern counterparts. Floral displacements of this magnitude have occurred over the past 11,000 years (Wells and Berger 1967; Phillips and Van Devender 1974; Mehringer 1977; Van Devender and Mead 1976; Mead 1981; Thompson and Mead 1982). A 1375 m elevational shift in the Boreal cave species suggests that they are at least 11,000 years or older.

However, if fossil Boreal elements lived at the top of the Mormon Mountains, an elevation of 2363 m, and were introduced into the cave, then their present occurrence above 2745 m indicates an elevational displacement of at least 382 m. Displacements of this magnitude have been recorded in the Grand Canyon (Van Devender and King 1971) and in Sonora (Phillips and Van Devender 1974) south of the Mormon Mountains since late Wisconsin times.

The unusual occurrence of Boreal, Transitional and Sonoran elements may reflect an extended period during which the cave remained a site of fossil accumulation until early Recent time. Modern floras were apparently established 8000 to 8500 years ago (Wells and Jorgensen 1964; Mead 1981). Unfortunately knowledge of the magnitude and timing of late Wisconsin and sub-Recent shifts in the elevations of floras is not precise. Plants apparently responded to climatic changes in an individual manner rather than as communities (Van Devender and Mead 1976). Furthermore, the extrapolation of the timing of these events from the life zone affinities of extant species of small mammals is a tenuous approximation. Further work may show that this procedure is a valid means of estimating the age of fossil assemblages in parts of the southwestern United States.

Literature Cited

Grayson, D. K. 1981. A Mid-Holocene Record for the Heather Vole, *Phenacomys* cf. *intermedius*, in the Central Great Basin and its Biogeographic Significance. J. Mamm., 62(1):115–121.

Hall, E. R. 1946. Mammals of Nevada. Univ. California Press, xi + 710 pp.

Hall, E. R., and K. R. Kelson. 1959. Mammals of North America. Roland Press, New York, 2 vols., 1083 pp.

Martin, P. S., B. E. Sables, and D. Shutler, Jr. 1961. Rampart Cave Coprolite and Ecology of the Shasta Ground Sloth. Amer. J. Sci., 295:102–127.

Mead, J. I. 1981. The Last 30,000 Years of Faunal History within the Grand Canyon, Arizona. Quaternary Research, 15:311–326.

Mehringer, P. J. 1966. Some Notes on the Late Quaternary Biogeography of the Mojave Desert. Dept. of Geochronology, Univ. Ariz., Interim Research Rept., 11:1–17.

———. 1977. Great Basin Late Quaternary Environments and Chronology. Pp. 113–167 *in* Models and Great Basin Prehistory. (D. D. Fowler, ed.), Desert Res. Inst. Pubs. in the Soc. Sci. No. 12, 213 pp.

Phillips, A. M., and T. R. Van Devender. 1974. Pleistocene Middens from the Lower Grand Canyon of Arizona. J. Arizona Acad. Sci., 9(3):117–119.

Thompson, R. S., and J. I. Mead. 1982. Late Quaternary Environments and Biogeography in the Great Basin. Quaternary Research, 17:39–55.

Van Devender, T. R., and J. E. King. 1971. Late Pleistocene Vegetational Records in Western Arizona. J. Arizona Acad. Sci., 6(4):240–244.

Van Devender, T. R., and J. I. Mead. 1976. Late Pleistocene and Modern Plant Communities of Shinumo Creek and Peach Springs Wash, Lower Grand Canyon, Arizona. J. Arizona Acad. Sci., 11:16–22.

Van Devender, T. R., and W. G. Spaulding. 1979. Development of Vegetation and Climate in the Southwestern United States. Sci., 204:701–710.

Wells, P. V., and R. Berger. 1967. Late Pleistocene History of Coniferous Woodland in the Mojave Desert. Sci., 155:1640–1647.

Wells, P. V., and C. G. Jorgensen. 1964. Pleistocene Wood Rat Middens and Climatic Change in the Mojave Desert: A Record of Juniper Woodlands. Sci., 143:1171–1173.

Wilson, R. W. 1942. Preliminary Study of the Fauna of Rampart Cave, Arizona. Carnegie Inst. Washington Publ., 530:169–185.

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Bull. Southern California Acad. Sci.
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Reproduction of Feral Goats on Santa Catalina Island, California

Bruce E. Coblentz

Abstract.—Reproduction of Feral Goats on Santa Catalina Island, California by Bruce E. Coblentz. *Bull. Southern California Acad. Sci.*, 81(3):128–137, 1982. Natality of feral goats on Santa Catalina Island appeared to be a density-dependent response to forage quality and quantity. Conception rates ranged from 1.11 corpora lutea/pregnancy in a poor forage area to 1.80 corpora lutea/pregnancy in a good forage area. Body weight, dressed weight, hind foot length, horn length, and kidney fat index of goats from the good forage area were significantly greater ($P < 0.05$) than those from the poor forage area. Partial control of goats on the island increased natality; total removal of feral goats was recommended.

Introduction

Where they occur on islands, feral goats (*Capra hircus*) have been condemned (Yocom 1967; Baker and Reeser 1972; Coblentz 1978) due to their adverse effects upon native insular biota (Greenway 1958; Atkinson 1964; Thorne 1967; Yocom 1967; Sykes 1969; Baker and Reeser 1972; Spatz and Mueller-Dumbois 1973; Coblentz 1977). Little research effort has been directed at feral goats (Bates 1956; Coblentz 1978), and consequently little is known about factors which influence population size, reproduction, and recruitment, and the manner in which goat populations respond to cropping. Studies of reproduction in feral goats were conducted in New Zealand and some of its offshore islands. Most of the available data resulted from goat control operations of the New Zealand Wildlife Service in which a number of individual goats were examined during a single large-scale eradication (Williams and Rudge 1969; Rudge and Clark 1978); such information represents only a single point in time. Only Rudge (1969) has studied feral goat reproduction over an extended period.

The objective of this study was to assess reproduction in feral goats on Santa Catalina Island, California, during several seasons, and relate reproduction to physical condition of the animals and habitat quality.

Study Area and Methods

Santa Catalina Island (Catalina) is located approximately 35 km off the coast of southern California at the Palos Verdes Peninsula. The island is about 35 km long and ranges in width from less than 0.85 km at the isthmus to about 12.9 km at its center (Fig. 1). Catalina is approximately 196 km^2 in area. Much of the island is rugged and precipitous; the two highest points abruptly rise to approximately 610 m.

The island has an oceanic, Mediterranean climate consisting of hot, dry summers and mild damp winters. Rainfall, averaging 31.5 cm, usually occurs between October and late April.

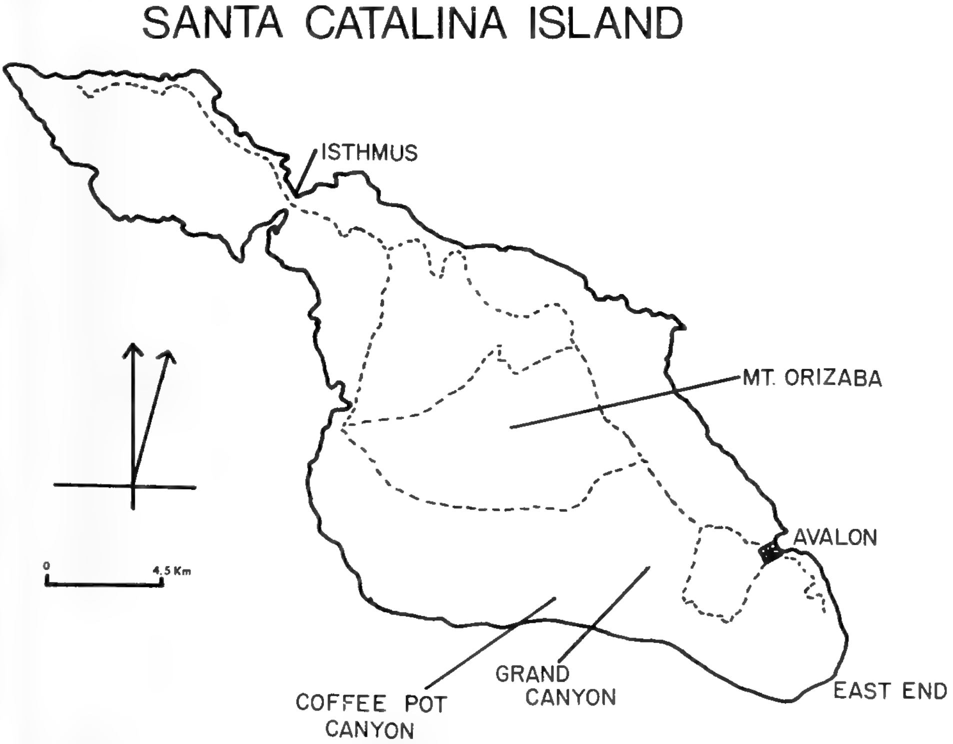

Fig. 1. Map of Santa Catalina Island, California, showing approximate locations of the Grand Canyon study herd, Mt. Orizaba, and Coffee Pot Canyon.

Goats were first introduced to the island in the early 1800's (Dunkle 1950), but the date that they first became feral is uncertain. Accurate estimates of goat numbers in the past were unavailable; there were between 5000 and 8000 individuals during the period of this study.

Goats were collected during the periods of July 1971 to April 1973, December 1974, and May 1975. In the first two collection periods, adult female goats were collected in an opportunistic manner from several herds by shooting. During the May 1975 collection period, adult female goats were specifically collected from only two herds; one living in what was judged to be a good forage area (Mt. Orizaba, Fig. 2) and the other in what was judged to be a poor forage area (Coffee Pot Canyon, Fig. 3).

On Catalina, goats occurred in herds between which there was limited interchange of individuals, and which utilized exclusively traditional home ranges (Coblentz 1974). Goats of the Coffee Pot herd had no access to areas of good forage within their herd home range. I did not have the resources or time to precisely calculate and manipulate the density of a specific population of goats, and then monitor the functional responses of both the goats and their habitat to those changes (a handicap also expressed by Errington (1946)). Instead, two discrete populations were chosen to represent different levels of saturation of the habitat, and were sampled to obtain data indicative of a long term study.

Fig. 2. Habitat typical of the quality occupied by Mt. Orizaba goats on Santa Catalina Island, California.

Carcasses of goats were weighed and measured in the field. Samples were collected, placed in plastic bags, labelled and frozen. Whole weights and field dressed weights were obtained with a spring scale accurate to the nearest lb (0.45 kg), other weights were taken with a similar scale accurate to the nearest ½ lb (0.27 kg). Linear measurements were taken to the nearest ⅛ inch (3.2 mm). Kidney fat index (Riney 1955) was calculated with weights obtained with a triple beam balance accurate to 0.1 g. Femur marrow fats were obtained by extracting the fat by ether extraction and weighing the samples on an electronic balance accurate to the nearest 0.001 g. Goat densities, herd condition, and juvenile : adult ratios were based on field observations. Forage quantity and quality were subjectively evaluated by field observation of species composition, percent cover, and average height of the herbaceous layer (Coblentz 1977).

Results

Rate of Pregnancy

Of 102 adult females collected during the study, 64 (62.7 percent) were either pregnant or had at least one corpus luteum. In contrast, Rudge (1969) found a pregnancy rate of 37.7 percent in New Zealand where goats were pregnant during all months. Thirty-eight (37.3 percent) of the females collected in this study were lactating, and 20 (19.6 percent) were both pregnant and lactating. Only 8 of 64 (12.5 percent) pregnant females were as young as 2 years; one of these was 1 year old. Most female goats on the island apparently did not breed until they were 1.5 to 2.5 years old. Only 5 females younger than about 2 years old were observed

Fig. 3. Typical goat habitat in Coffee Pot Canyon, Santa Catalina Island, California.

in estrous. Under better conditions than were found on Catalina, feral goats can conceive at only 6 months of age (Yocom 1967; Rudge 1969), while ibex (*Capra ibex*) may not conceive until 5 to 6 years of age in stable populations (Grzimek and Nievergelt 1968).

Pregnancy rate varied with season of collection and the locality where goats were collected. Of 56 female goats collected from July 1971 to April 1973, 30 (53.6 percent) were pregnant. The pregnancy rates in December 1974 (n = 22) and May 1975 (n = 24) were both somewhat higher (77.3 and 70.8 percent respectively, Table 1), most likely due to the better forage conditions available during that Winter-Spring growing season. In the May 1975 sample, the rate of pregnancy of the Orizaba goats (90.9 percent) was nearly double that of the goats from Coffee Pot Canyon (53.8 percent, Table 2).

Rate of Twinning

The twinning rate of Catalina goats varied by habitat quality, season, and by herd (Tables 1 and 2). Of 29 kids born in the Grand Canyon herd in April 1972, there were 6 sets of twins and 17 singles (26.1 percent twinning rate) or 1.26 kids per pregnancy. This rate was the highest observed in that herd and was comparable to goats on Macauley Island where Williams and Rudge (1969) reported a 25 percent twinning rate. In contrast 26 1-month old kids were observed in north shore herds on Catalina in March 1972 (excellent forage area), and of these there were 9 sets of twins and 8 singles for a 55.6 percent twinning rate and 1.53 kids per pregnancy.

In May 1975, female reproductive tracts from Mt. Orizaba goats and from

Table 1. Reproductive status of adult female feral goats collected from Santa Catalina Island, California.

Status	July 1971– April 1973 n = 56	Dec. 1974 n = 22	May 1975 n = 24
Pregnant	30 (53.6%)	17 (77.3%)	17 (70.8%)
Recent parturition	—	3 (15.6%)	2 (8.3%)
Pregnant and lactating	8 (14.3%)	8 (36.4%)	4 (16.7%)
Non-pregnant and lactating	13 (23.2%)	1 (4.5%)	4 (16.7%)
Percent reproducing	76.8	95.4	95.8
Twinning rate[a]	13.3%	15.0%	47.4%
Single conception rate	86.7%	85.0%	52.6%
Corpora lutea/pregnancy	1.13	1.20	1.47

[a] Based on embryo counts when possible, otherwise on counts of corpora lutea. Expressed as a percentage of pregnant and recent parturition.

Coffee Pot Canyon were examined (Table 2). The twinning rate for Orizaba females was 80 percent, more than 7 times the twinning rate of females from Coffee Pot Canyon (11.1 percent). These results provided evidence that the rate of twinning was dependent, at least in part, upon the quality and quantity of forage available to females.

Indices of Condition

Selected measurements and condition indices of adult females were used to test the hypothesis that goats of the Mt. Orizaba and Coffee Pot Canyon herds were of measurably different condition. Goats taken from the Orizaba herd had significantly greater whole weight, field dressed weight, horn length, hind foot length, and kidney fat index (t-test, $P < 0.05$, Table 3), all of which were indicative of animals in better condition.

Discussion

Reproductive Potential

Domestic goats have a high reproductive potential. Colby et al. (1969) reported that 115 female domestic goats from New Mexico produced 242 kids from 115 pregnancies. In that study, 77.4 percent of the females had multiple births for a natality rate of 2.1 kids per pregnancy. Feral goats, especially those in hunted populations, also can have a high reproductive rate. Rudge and Smit (1970) determined that a hunted population of goats in New Zealand had a recruitment rate (survival to reproductive age) of 0.475. They derived a minimum estimate of r of 0.375, and made the observation that a population reduced by 80 percent would increase to 90 percent of the former level in 4 years.

Williams and Rudge (1969) reported an adult female to kid ratio of 1:0.66, and presented a figure of recruitment of 1.7 kids per female per year, based on the assumption that the females that were simultaneously pregnant and lactating were giving birth twice within a 12 month period. They did not substantiate this assumption, but Rudge (1969) demonstrated that exceptional female goats living

Table 2. Comparison of pregnancy and fecundity in adult female feral goats collected from two herds on Santa Catalina Island, California during May 1975.

	Orizaba n = 11	Coffee Pot Canyon n = 13
Pregnant	10 (90.9%)	7 (53.8%)
Recent parturition	—	2 (15.4%)
Pregnant and lactating	4 (36.4%)	—
Non-pregnant and lactating	1 (9.1%)	2 (15.4%)
Percent reproducing	100	84.7
Twinning rate[a]	80.0%	11.1%
Single conception rate[a]	20.0%	88.9%
Corpora lutea/pregnancy	1.80	1.11

[a] Based on embryo counts when possible, otherwise on counts of corpora lutea. Expressed as a percentage of pregnant and recent parturition.

in areas with good forage conditions do have a birth frequency greater than 1 per year.

Catalina goats apparently averaged less than one birth per year. Four individually recognized females of the Grand Canyon herd, having available forage intermediate in quality and quantity between that of Coffee Pot Canyon and Orizaba goats, gave birth twice during the initial 22 month portion of the study; these births were spaced an average of 16 months apart (0.75 births/female/year). Some old females did not give birth at all during the study. In contrast, during December 1974, 36.4 percent of all female goats collected were simultaneously pregnant and lactating (Table 1), suggesting the possibility of some females giving birth twice within a single year. The excellent forage conditions during the winter of 1974–75, resulting from high effective rainfall, could have allowed that possibility.

Factors Affecting Recruitment

Documentation of density-dependent natality or survivorship in mammals is relatively infrequent. Density-dependent natality or survivorship has been supported by several researchers (Errington 1946; Calhoun 1948; Emlen et al. 1948; O'Roke and Hamerstrom 1948; Cheatum and Severinghaus 1950; Taber and Dasmann 1958; Caughley 1970; Hines 1975), and most authors accept the concept (for example Keith 1974:43, Caughley 1977:175). McCullough (1979) demonstrated elaborately that white-tailed deer (*Odocoileus virginianus*) populations do respond to changes in numbers.

Recruitment in Catalina goats apparently was a density-dependent response of the population to a widely and rapidly changing carrying capacity, as measured by forage availability (Coblentz 1977). Females bred during any of 4 distinct breeding peaks each year (Coblentz 1980a), and consequently were subjected to widely varying environmental conditions within years. As a result, survivorship of goats born in different birth peaks was widely variable, with a low of zero for juveniles born in some late summer peaks. In addition, recent observations (Coblentz, 1979, 1980b, pers. obs.) indicated that herds which were subjected to more intensive sport hunting or population control measures had a noticeably greater proportion of juveniles, as well as an apparently higher birth rate.

Table 3. Means and associated 95 percent confidence limits of physical measurements of adult female Catalina Island goats from two discrete herds, May 1975. Numbers in parentheses indicate sample size.

Measurement	Mt. Orizaba	Coffee Pot Canyon
Whole wt. (lbs)[1]	66.0 ± 10.2	49.8 ± 5.1
(kg)	30.0 ± 4.6	22.6 ± 2.3
	(11)	(13)
Field dressed wt. (lbs)[1]	40.3 ± 4.9	29.1 ± 2.6
(kg)	18.3 ± 2.2	13.2 ± 1.2
	(11)	(13)
Percent field dressed weight	61.7 ± 4.7	58.7 ± 1.8
	(11)	(13)
Percent viscera	38.3 ± 4.7	41.3 ± 1.8
	(11)	(13)
Hind foot (cm)[1]	24.4 ± 0.3	23.5 ± 0.5
	(11)	(13)
Horn length (cm)[1]	18.6 ± 2.6	12.5 ± 1.8
	(11)	(13)
Rumen wt. full (lbs)	9.2 ± 1.7	9.2 ± 1.7
(kg)	4.2 ± 0.8	4.2 ± 0.8
	(11)	(12)
Rumen fill (lbs)	7.4 ± 1.6	7.6 ± 1.5
(kg)	3.4 ± 0.7	3.5 ± 0.7
	(11)	(12)
Percent rumen	14.0 ± 2.2	17.9 ± 1.7
	(11)	(12)
Kidney fat index (%)[1]	50.3 ± 16.4	26.3 ± 5.9
	(11)	(13)
Femur marrow fat (%)	74.7 ± 12.8	67.6 ± 7.2
	(9)	(11)

[1] Significantly different ($P < 0.05$) between herds.

Early juvenile mortality was probably the most important factor limiting the growth of goat populations on Catalina Island. Kids that died during the first weeks of life were never located, although their absence was taken to be conclusive evidence of their death. During the initial 22 month study period, juveniles up to 1 year had a ratio of 0.475 per adult female. In the collections of the same period, there were 0.867 corpora lutea per adult female. If each corpus luteum is assumed to have represented at least 0.9 embryos, as in white-tailed deer (*Odocoileus virginianus*) (Haugen 1975), then prenatal plus juvenile mortality was at least 39 percent.

There was a tendency toward greater successful production of kids in months during or immediately following peak production of annual vegetation (Coblentz 1974) due to the higher condition level of the female during pregnancy which occurred during the growing season. The availability of high quality forage for at least the first month or two following parturition presumably contributed to juvenile survival by enhancing the ability of the females to produce milk. Although herds across the island showed little synchrony of breeding and birth peaks, the quadrimodal breeding system (Coblentz 1980a) allowed for at least one crop of kids to be born in each herd at a favorable time.

As is most often, data collected from Catalina goats offered only subjective evidence for a density-dependent response to habitat quality. Density-dependent changes in natality, mortality, recruitment, and individual condition are all most readily determined by comparison. As inferred in this study, density-dependent responses were not related to absolute density, but to the subjectively evaluated ratio of population density to carrying capacity. The narrower the ratio, the greater the envrionmental resistance to population increase, and the more graphic the differences in herd condition. The Orizaba and Coffee Pot herds appeared to have similar densities, yet Orizaba goats had higher natality and were larger and in better condition because of the better forage conditions.

Differences between the Orizaba and Coffee Pot herds can be related to density-dependent responses. Reproduction was the most graphic difference found (Table 2). However, other significant differences were also enlightening (Table 3). In interpreting Table 3, it was not surprising that there was virtually no difference in femur marrow fat between goats of the 2 herds. Femur marrow fat is one of the last fat depots to be mobilized, at least in white-tailed deer (Cheatum 1949), when the animal undergoes a negative energy balance. Conversely, it is one of the first areas where fat is deposited. Fat is removed from the perirenal capsule before femur marrow fat is withdrawn.

Complete removal of goats from most of Santa Catalina Island has been recommended (Center for Natural Areas 1980; Coblentz 1980b) due to their destructive effects on the island's habitats. Numerous unofficial goat control programs have been conducted on Catalina in the last 20 years (D. Propst, pers. comm.), however, without exception the only result of these programs has been the rapid recovery of the affected herds (pers. obs.). The potentially high recruitment rate of feral goats (Rudge and Smit 1970), and the density-dependent nature of natality and recruitment indicated by this study, suggest that total removal of goats is an absolute prerequisite to habitat recovery.

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Literature Cited

Atkinson, I. A. E. 1964. Relations between feral goats and vegetation in New Zealand. Proc. New Zea. Ecol. Soc., 11:39–44.

Baker, J. K., and D. W. Reeser. 1972. Goat management problems—Hawaii Volcanoes National Park. U.S. Dept. Int. National Park Serv. Res. Rept. No. 2. 63 pp.

Bates, M. 1956. Man as an agent in the spread of organisms. Pp. 788–804 *in* Man's role in changing the face of the Earth. William L. Thomas, Jr., Ed. Univ. of Chicago Press, Chicago. 1193 pp.

Calhoun, J. B. 1948. Mortality and movement of brown rats (*Rattus norvegicus*) in artificially supersaturated populations. J. Wildl. Manage., 12:167–172.

Caughley, G. 1970. Eruption of ungulate populations, with emphasis on Himalyan Thar in New Zealand. Ecology, 51:53–72.

———. 1977. Analysis of vertebrate populations. John Wiley and Sons, New York. 234 pp.

Center for Natural Areas. 1980. Santa Catalina Island Natural Resources Management Plan. Open file report. Los Angeles County Dept. of Parks and Recreation, Los Angeles, Calif.

Cheatum, E. L. 1949. Bone marrow as an index of malnutrition in deer. New York State Cons., 3: 19–22.

———, and C. W. Severinghaus. 1950. Variations in fertility of white-tailed deer related to range conditions. Trans. 15th N. Amer. Wildl. Conf., 15:170–189.

Coblentz, B. E. 1974. Ecology, behavior, and range relationships of the feral goat. Unpubl. Ph.D. Thesis. Univ. of Michigan, Ann Arbor. 259 pp.

———. 1977. Some range relationships of feral goats on Santa Catalina Island, California. J. Range Manage., 30:415–419.

———. 1978. The effects of feral goats (*Capra hircus*) on island ecosystems. Biol. Conserv., 13: 279–286.

———. 1980a. A unique ungulate breeding pattern. J. Wildl. Manage., 44:929–933.

———. 1980b. Feral herbivores—Work element 3 of Santa Catalina Island Resource Management Plan. Open file report. Los Angeles County Dept. of Parks and Recreation, Los Angeles, Calif. 23 pp.

Colby, B. E., D. A. Evans, S. J. Lyford, W. B. Nutting, and D. N. Stein. 1969. Dairy goat's breeding, feeding, management. Amer. Dairy Goat Assoc. Leaflet No. 439. 77 pp.

Dunkle, M. B. 1950. Plant ecology of the Channel Islands of California. Allen Hancock, Pacif. Exped., 13:247–386.

Emlen, J. T., A. W. Stokes, and C. P. Winsor. 1948. The rate of recovery of decimated populations of brown rats in nature. Ecology, 29(2):133–145.

Errington, P. L. 1946. Predation and vertebrate populations. Qaurt. Rev. Biol., 21:144–177, 221–245.

Greenway, J. C. 1958. Extinct and vanishing birds of the world. Spec. Publ. No. 13. Amer. Committee Internatl. Wildl. Protect., New York. 518 pp.

Grzimek, B., and B. Nievergelt. 1968. Alpine ibex. Pp. 475–480 *in* Grzimek's animal life encyclopedia. Vol. 13. Van Nostrand Reinhold Co., New York. 565 pp.

Haugen, A. O. 1975. Reproductive performance of white-tailed deer in Iowa. J. Mammal., 56:151–159.

Hines, W. W. 1975. Black-tailed deer behavior and population dynamics in the Tillamook Burn, Oregon. Oregon Wildl. Comm., Wildl. Res. Rept. No. 5. 31 pp.

Keith, L. B. 1974. Some features of population dynamics in mammals. XI Internatl. Cong. Game Biol., Stockholm, 11:2–58.

McCullough, D. R. 1979. The George Reserve deer herd. The University of Mich. Press, Ann Arbor, Mich. 271 pp.

O'Roke, E. C., and F. N. Hamerstrom, Jr. 1948. Productivity and yield of the George Reserve deer herd. J. Wildl. Manage., 12:78–86.

Riney, T. 1955. Evaluating condition of free-ranging red deer (*Cervus elaphus*), with special reference to New Zealand. N.Z. J. Sci. Tech., B36:429–463.

Rudge, M. R. 1969. Reproduction of feral goats (*Capra hircus* L.) near Wellington, New Zealand. N.Z. J. Sci., 12:817–827.

———, and T. J. Smit. 1970. Expected rate of increase of hunted populations of feral goats (*Capra hircus* L.) in New Zealand. N.Z. J. Sci., 13:256–259.

———, and J. M. Clark. 1978. The feral goats of Raoul Island, and some effects of hunting on their body size and population density. N.Z. J. Zool., 5:581–589.

Spatz, G., and D. Mueller-Dumbois. 1973. The influence of feral goats on koa tree production in Hawaii Volcanoes National Park. Ecology, 54:870–876.

Sykes, W. R. 1969. The effects of goats on vegetation of the Kermedec Islands. Proc. N.Z. Ecol. Soc., 11:13–16.

Taber, R. D., and R. F. Dasmann. 1958. The black-tailed deer of the chaparral. Calif. Dept. Fish and Game, Game Bull. No. 8. 163 pp.

Thorne, R. F. 1967. A flora of Santa Catalina Island, California. Aliso, 6:1–77.

Williams, G. R., and M. R. Rudge. 1969. A population study of feral goats (*Capra hircus* L.), from Macauley Island, New Zealand. Proc. N.Z. Ecol. Soc., 16:17–28.

Yocom, C. F. 1967. Ecology of feral goats in Haleakala National Park, Mauii, Hawaii. Amer. Midl. Natur., 77:418–451.

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Preliminary List of the Insects and Related Terrestrial Arthropoda of Socorro Island, Islas Revillagigedo, Mexico

José G. Palacios-Vargas,[1] Judith Llampallas[1] and Charles L. Hogue[2]

Abstract.—A preliminary list of insects and related terrestrial arthropoda from Socorro Island, Islas Revillagigedo, Mexico. By José G. Palacios-Vargas, Judith Llampallas and Charles L. Hogue, *Bull. Southern California Acad. Sci.,* 81(3):138–147, 1982. Over half of the 128 species listed are newly recorded. Soil microarthropods (mites and springtails) are cited for the first time from the island.

Socorro Island is the largest of four islands comprising the Archipelago Revillagigedo. It is oceanic and volcanic in origin, major extrusive activity having occurred during the Miocene and Pliocene (Blásquez 1960a; Bryan 1949). It is located some 480 km SSW of Cabo San Lucas, Baja California and 592 km W of Cabo Corrientes, Jalisco. Politically, the archipelago, belongs to the state of Colima, Mexico.

Socorro is perhaps the most interesting of the group because of its relatively large size and extensive relief (Mt. Evermann rises to an elevation of 1050 m) and consequent varied habitats for insects, arachnids and related terrestrial arthropods. Clarion Island and San Benedicto are both much smaller and less elevated than Socorro and the latter suffered virtual annihilation of its fauna during recent explosive vulcanism (1952); Roca Partida is little more than a rock jutting from the sea.

Socorro generally has a warm, xeric climate, with a mean annual rainfall of 761 mm. Its soils are derived from basaltic rock and are mostly fine, particulate argylaceous silts (Blásquez 1960b). At higher elevations (500–900 m) the climate is subhumid and still higher (above 900 m), temperate subhumid (Miranda 1960).

Mainly because of its geographic isolation and the volcanic history of the island, its floral diversity is very poor, comprised of only a few more than 100 species of vascular plants (Rzedowski 1978). The vegetation of the subhumid zone is a tropical forest, with major associations of *Dodonaea viscosa* thickets, *Ficus cotinifolia* forests, and *Bumelia socorrensis-Psidium galapageium* forest. High on the central mountain, there is even a meadow. More detailed information on the vegetation is found in Medina (1957).

A bibliography to 1957 and other basic data about the Revillagigedo Islands were compiled and published by Richards and Brattstrom (1959). Few papers deal with the insects and related arthropods, the fauna of which remains largely unknown on Socorro and the other three islands as well. The soil microfauna is particularly poorly known and recent discoveries by the senior authors have inspired the compilation of this list. The new records given here are the partial result of two recent expeditions to the island: the Steele Expedition (5–10 June 1977; C. L. Hogue collector) and the Gerardo Guerra Expedition (16–18 October 1977; J. G. Palacios-Vargas collector). The material collected by William A.

McDonald and Claude Blodget on the 1955 "Crest" expedition by Scripps Institution of Oceanography and formerly housed at the University of California, Los Angeles, has been deposited in the Natural History Museum of Los Angeles County. These and other collections known to us (e.g. California Academy of Sciences) contain many additional undetermined species. A total of 128 determined and unidentified species are definitely known from Socorro. The total insect, arachnid and related terrestrial arthropod fauna may number as high as several hundred species.

The microarthropods were collected by the senior author and determined with the aid of the second; most of the pyerygota were collected and identified by Hogue with the aid of the various specialists named as determiners in the list. Authority for each record in the following list is indicated after the name cited: "OD" if contained in the original description, "Orig." if a new record in the authors' collections and identified by the authors.

ARACHNIDA

SCORPIONIDA
  Vaejovidae
    Vaejovis janssi Williams, 1980.—OD (As *Vejovis mexicanus decipiens* Hoffmann, 1931 by Vázquez 1960.)
ARANEAE
  Theridiidae
    Latrodectus mactans (Fabricius, 1775).—Orig. C. L. Hogue det.
    Steatoda quadrimaculata (O. P. Cambridge, 1896).—Levi 1957.
  Anyphaenidae
    Anyphaena judicata Cambridge, 1896.—Platnick and Lau 1975.
  Dysderidae
    Ariadna weaveri Beatty, 1970.—OD.

ACARIDA

MESOSTIGMATA
  Ascidae
    Cheiroseius sp.—Orig.
  Macrochelidae
    Genus sp.—Orig.
  Uropodidae
    Genus sp.—Orig.
  Parasitidae
    1 undetermined genus and species.—Orig.
PROSTIGMATA
  Rhagidiidae
    Rhagidia weyerensis (Packard, 1888).—Orig.
  Bdellidae
    Bdellodes sp.—Orig.
  Cunaxidae
    Cunaxa taurus (Kramer, 1881).—Orig.
    Cunaxa sp.—Orig.

Smaridiidae
  1 undetermined genus and species.—Orig.
Trombiculidae
  Trombicula alfredugesi Oudemans, 1910.—Vázquez 1960 (Confirmed as probable by Loomis, pers. comm.)
CRYPTOSTIGMATA
  Hypochthoniidae
    Hypochthonius rufulus Kock, 1836.—Orig.
  Nothridae
    Nothrus sp.—Orig.
  Hermanniellidae
    Hermanniella sp.—Orig.
  Plasmobatidae
    Plasmobates sp.—Orig.
  Gymnodamaeidae
    Allodamaeus sp.—Orig.
  Damaeidae
    1 undetermined genus and species.—Orig.
  Carabodidae
    Austrocarabodes sp.—Orig.
  Oribatulidae
    Scheloribates sp.—Orig.

HEXAPODA

PROTURA
  Protentomidae
    1 undetermined genus and species.—Orig.
DIPLURA
  Japygidae
    1 undetermined genus and species.—Orig.
COLLEMBOLA
  Hypogastruridae
    Xenylla cf. *humicola* (Fabricius, 1780).—Orig.
  Neanuridae
    Friesea haldanei Rapoport and Mano, 1969.—Orig.
    Friesea sp.—Orig.
    Pseudachorutes sp. ca. *lunatus* Folsom, 1916.—Orig.
    Pseudachorutes sp.—Orig.
  Onychiuridae
    Mesaphorura cf. *yossii* Rusek, 1977.—Orig.
    Onychiurus encarpatus Denis, 1931.—Orig.
  Isotomidae
    Folsomides americanus Denis, 1931.—Orig.
    Folsomides cf. *angularis* (Axelson, 1905).—Orig.
    Isotomiella minor (Schaeffer, 1896).—Orig.
  Entomobryidae
    Lepidocyrtus cf. *helenae* Snider, 1967.—Orig.
    Lepidocyrtus sp. ca. *pallidus* Reuter, 1890.—Orig.
    Pseudosinella violenta (Folsom, 1924).—Orig.

Seira sp.—Orig.
Janetschekbrya cf. *arida* Christiansen and Bellinger, 1980.—Orig.
Neelidae
Megalothorax incertus Börner, 1903.—Orig.
Dicyrtomidae
Dicyrtoma atra (Linnaeus, 1758).—Orig.
Sminthuridae
Sphaeridia pumilis Krausbauer, 1898.—Orig.
Sphaeridia n. sp.—Orig.
THYSANURA
Lepismatidae
1 undetermined genus and species.—Orig.
ODONATA
Libellulidae
Pantala flavescens (Fabricius, 1798).—Vázquez 1960.
ISOPTERA
Termitidae
Kalotermes hubbardi Banks, 1901.—Light 1930, 1935.
Kalotermes jouteli Banks, 1901.—Light 1930, 1935.
Kalotermes marginipennis (Latreille, 1817).—Light 1935.
DERMAPTERA
Labiduridae
Labidura riparia (Pallas, 1773).—Orig. C. L. Hogue det.
ORTHOPTERA
Blattidae
Latiblatella picturata Hebard, 1922.—Orig. F. W. Fisk det.
Acrididae
Trimerotropis pallidipennis pallidipennis (Burmeister, 1838).—Vázquez 1960.
Schistocerca americana socorro Dirsh, 1974.—OD (As *Schistocerca vaga vaga* by Vázquez 1960.)
Tettigoniidae
Neoconocephalus maxillosus (Fabricius, 1831).—Vázquez 1960.
Gryllidae
Gryllus sp.—[As *Gryllus assimilis* (Fabricius, 1775).—Vázquez 1960.]
Oecanthus varicornis (F. Walker, 1869).—Vázquez 1960.
Cycloptilum erraticum Scudder, 1893.—Hebard 1932 and Vázquez 1960.
HEMIPTERA (See Heidemann 1901)
Nabidae
Nabis sp.—Orig. C. L. Hogue det.
Pentatomidae
Acrosternum hilare (Say, 1832).—Orig. C. L. Hogue det.
Nezara sp.—Orig. C. L. Hogue det.
Lygaeidae
Lygus keiferi Van Duzee, 1933.—OD.
HOMOPTERA
Acanaloniidae
Acanalonia clarionensis Van Duzee, 1933.—OD.
Cicadellidae
Omanolidia keiferi Nielson, 1982.—OD.

Paralebra keiferi Young, 1957.—OD.
Diceratolebra sola Young, 1957.—OD.

MALLOPHAGA

Philopteridae

Penenirmus quadripustulatus (Kellogg and Mann, 1912).—(As *Docophorus californiensis* var. *quadripustulatus* Kellogg and Mann, 1912.)

Saemundssonia breviantenna (Piaget, 1880).—Kellogg and Mann 1912:58 (As *Docophorus breviantennatus* Piaget, 1880.)

Quadraceps birostris (Giebel, 1874).—Kellogg and Mann 1912:58 (As *Nirmus gloriosus* Kellogg and Kuwana, 1902.)

Bruelia melanococa (Carriker, 1903).—Kellogg and Mann 1912:59–60 (As *Nirmus melanococcus* Carriker, 1903.)

Columbicola columbae (Linnaeus, 1758).—Kellogg and Mann 1912:62 (As *Lipeurus baculus* Nitzsch, 1818.)

Menoponidae

Actornithophilus milleri (Kellogg and Kuwana, 1902).—Kellogg and Mann 1912:63 (As *Colpocephalum milleri* Kellogg and Kuwana, 1902.)

Eidmanniella aurifasciata (Kellogg, 1899).—Kellogg and Mann 1912:65 (As *Menopon singularis* Kellogg and Kuwana, 1902.)

Austromenopon becki (Kellogg, 1906).—Kellogg and Mann 1912:65 (As *Menopon becki* Kellogg, 1906.)

COLEOPTERA

Cicindelidae

Cicindela trifasciata sigmoidea LeConte, 1851.—Horn 1936 and Orig., C. Nagano det. (As *Cicindela tortuosa* LeConte, 1851 by Vázquez 1960; *Cicindela trifasciata ascendens* LeConte, 1851 by Cazier 1954.)

Carabidae

Selenophorus pyritosus Dejean, 1829.—Orig. D. Shpeley det.

Dytiscidae

Rhantus calidus (Fabricius, 1792).—Orig.

Scarabaeidae

Ataenius hoguei Cartwright and Spangler 1981.—OD.

Elateridae

Nematodes cuneatus (Guerín, 1843.).—Orig. E. C. Becker det.

Dicrepidius sp. cf. *D. corvinus* Candèze, 1859.—Orig. E. C. Becker det.

Bostrichidae

Amphicerus cornutus (Pallas, 1772).—Orig. C. L. Hogue det. (As *Apate punctipennis* Leconte, 1858 and *Sinoxylon* sp. by Vázquez 1960.)

Trogidae

1 undetermined genus and species.—Vázquez 1960.

Tenebrionidae

Phaleria debilis LeConte, 1866.—Vázquez 1960; Triplehorn and Watrous 1979:289 (As *Phaleria insularis* Champion, 1886 by Vázquez 1960.)

Hypogena tricornis Dalman, 1823.—Blaisdell 1943 (As *Ulosonia tricornis.* See Spilman 1973:42 for nomenclatural problems associated with this species.)

Cerambycidae (See Linsley 1935)

Stenodontes dasytomus socorroensis Linsley and Chemsak, 1966.—OD. [As *Stendodontes (Mallodon) molarius* Linsley (not Bates), 1942.]
Acanthoderes socorrensis Linsley, 1942.—OD (As *Acanthoderes peninsularis* Linsley (not Horn), 1935.)
Neoclytus steelei Chemsak and Linsley, 1978.—OD.
Neoptychodes trilineatus Linnaeus, 1781.—Chemsak and Linsley 1978.
Oreodera glauca pacifica Chemsak and Linsley, 1978.—OD.
Trichastylopsis hoguei Chemsak and Linsley, 1978.—OD.

NEUROPTERA
Chrysopidae
Chrysopa collaris Schneider, 1851.—Orig. P. Adams det.
Coniopterigidae
Coniopteryx simplicior Meinander, 1981.—OD.

LEPIDOPTERA
Sphingidae
Manduca sexta (Linnaeus, 1763).—Orig. C. L. Hogue det.
Perigonia lusca continua Vázquez, 1958b.—OD.
Erinnyis obscura socorroensis Clark, 1926.—OD.
Lycaenidae
Strymon columella socorroica (Vázquez, 1958a).—OD.
Noctuidae
Callopistria floridensis (Guenée, 1852).—Orig.
Anomis editrix (Guenée, 1852).—Orig.
Agrotis subterranea n. ssp.—Orig.
Agrotis malefida Guenée, 1852.—Orig.
Cobubatha limbata (H. Edwards, 1881).—Orig.
Catabena vitrina (Walker, 1851).—Orig.
Forsebia perlaeta (H. Edwards, 1882).—Orig.
Melipotis perpendicularis (Guenée, 1852).—Orig.
Melipotis famelica (Guenée, 1852).—Orig.
Melipotis acontioides Guenée, 1852.—Orig.
Melipotis n. sp.—Orig.
Mythimna possibly *imperfecta* (Smith, 1894).—Orig.
Ophiuche minualis minualis (Guenée, 1854).—Orig.
Peridroma saucia (Hübner, 1808).—Orig.
Platysenta sutor (Guenée, 1852).—Orig.
Pseudaletia sequax Franclemont, 1951.—Orig.
Platysenta selenosa (Guenée, 1852).—Orig.
Physula migralis (Guenée, 1852).—Orig.
Ponometia exigua (Fabricius, 1803).—Orig.
Spodoptera sunia (Guenée, 1852).—Orig.
Pieridae
Phoebis sennae (Linnaeus, 1758).—Orig. C. L. Hogue det. (Sight record.)
Choreutidae
Tortyra n. sp.—Orig.
Hesperiidae
Erynnis zarucco funeralis (Scudder and Burgess, 1870).—Vázquez 1960.

DIPTERA
  Culicidae
    Aedes taeniorhynchus (Wiedmann, 1821).—Aitken 1942; Vázquez 1960.
  Ceratopogonidae
    Dasyhelea calvescens Macfie, 1938.—Wirth 1978.
  Chironomidae
    Telmatogeton latipennis Wirth, 1949.—OD.
    Thalassomya pilipes Edwards, 1926.—Wirth 1969.
  Mycetophilidae
    1 undetermined genus and species
  Calliphoridae
    Cochliomyia macellaria (Fabricius, 1775).—Vázquez 1960.
  Sciaridae
    1 undetermined genus and species.—Orig.
  Asilidae
    Adrenosoma n. sp.—Orig. E. M. Fisher det.
  Syrphidae
    Procecidochares flavipes Aldrich, 1929.—OD.
    Volucella ca. *V. anna* Williston, 1887.—Cole 1969.
  Muscidae
    Fannia scalaris (Fabricius, 1794).—Orig. C. L. Hogue det.
  Sarcophagidae
    Peckia craigi Dodge, 1964.—OD.
    Helicobia morionella (Aldrich, 1930).—Dodge 1964.
    Socorromyia blodgeti Dodge, 1964.—OD.
HYMENOPTERA
  Megachilidae
    Lithurge socorroensis Mitchell, 1938.—OD.
  Halictidae
    Lasioglossum sp.—Orig. R. R. Snelling det.
  Sphecidae
    Bembix sp.—Orig. C. L. Hogue det. (See Williams 1926:349.)
  Formicidae
    Camponotus socorroensis Wheeler, 1934.—OD.
    Pheidole hyatti Emery, 1895.—Wheeler 1934.
    Solenopsis geminata (Fabricius, 1804).—Wheeler 1934.
    Forelius foetidus keiferi Wheeler, 1934.—OD.
    Camponotus picipes Wheeler, 1933.—OD.
    Hypoponera sp.—Orig. R. R. Snelling det.

CHILOPODA

SCOLOPENDROMORPHA
  Scolopendridae
    Scolopendra tenuitarsis Pocock, 1895.—Vázquez 1960.

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Literature Cited

Aitken, T. H. G. 1942. Contributions toward a knowledge of the insect fauna of Lower California. No. 6 Diptera: Culicidae. Proc. California Acad. Sci., Ser. 4, 24:161–170.

Aldrich, J. M. 1929. A revision of the two-winged flies of the genus *Procecidochares* in North America, with an allied new genus. Proc. U.S. Nat. Mus., 76(2):1–13.

Banks, N. 1901. Papers from the Hopkins Stanford Galapagos Expedition 1898–1899, V. Entomological Results (5): Thysanura and Termitidae. Proc. Washington Acad. Sci., 3:541–546.

Beatty, J. A. 1970. The spider genus *Ariadna* in the Americas (Araneae, Dysderidae). Bull. Mus. Comp. Zool., 139(8):433–517.

Blaisdell, F. E. 1943. Contributions toward a knowledge of the insect fauna of Lower California. No. 7. Coleoptera: Tenebrionidae. Proc. California Acad. Sci., Ser. 4, 24:171–288.

Blásquez, L. 1960a. IV. Hidrogeología. Pp. 67–100 *in* Adem, J. et al. 1960. La Isla Socorro, Archipielago de Las Revillagigedo. Monogr. Inst. Geofisica, Univ. Nac. Autónoma México, 2:1–234.

———. 1960b. V. Edafología. Pp. 101–126 *in* Adem, J. et al. 1960. La Isla Socorro, Archipielago de Las Revillagigedo. Monogr. Inst. Geofisica, Univ. Nac. Autónoma México, 2:1–234.

Bryan, W. B. 1949. High-silica alkaline lavas of Clarion and Socorro Islands, Mexico—their genesis and regional significance. PhD thesis, Univ. Wisconsin, (Dissertation Abstracts, 20:989. 1959)

Cartwright, O. L., and Spangler, P. J. 1981. A new *Ataenius* from Socorro Island, Mexico (Coleoptera: Scarabaeidae: Aphodiinae). Proc. Entomol. Soc. Washington, 83(4)785–789.

Cazier, M. A. 1954. A review of the Mexican tiger beetles of the genus *Cicindela* (Coleoptera, Cicindelidae). Bull. Amer. Mus. Nat. Hist., 103:227–310.

Chemsak, J. A., and E. G. Linsley. 1978. Additions to the Cerambycidae of the Revilla Gigedo Islands (Coleoptera). Bull. Southern California Acad. Sci., 77:138–142.

Clark, B. P. 1926. Description of twelve new Sphingidae and remarks upon some other species. Proc. New England Zool. Club, 9:45–59.

Cole, F. R. 1969. The flies of western North America. Univ. California Press, Berkeley xi, 693 pp.

Dirsh, V. M. 1974. Genus *Schistocerca* (Acridomorpha, Insecta). Junk, The Hague vii, 238 pp.

Dodge, H. R. 1964. Sarcophagid flies from the Revillagigedo Islands (Diptera:Sarcophagidae). Proc. Entomol. Soc. Washington, 66:47–54.

Hebard, M. 1932. New species and records of Mexican Orthoptera. Trans. Amer. Entomol. Soc., 58:201–371.

Heidemann, O. 1901. Papers from the Hopkins Stanford Galapagos Expedition, 1898–1899. I. Entomological results (I) Hemiptera. Proc. Washington Acad. Sci., 3:336–370.

Kellogg, V. L. and W. M. Mann. 1912. Mallophaga from islands of Lower California. Entomol. News, 23:56–65.

Horn, W. 1936. Check list of the Cicindelidae of Oceania. Occ. Pap. B.P. Bishop Mus., 12:3–11.

Levi, H. W. 1957. The spider genera *Crustulina* and *Steatoda* in North America, Central America and the West Indies (Araneae, Theridiidae). Bull. Mus. Comp. Zool., 117(3):365–424.

Light, S. F. 1930. Termites collected by T. T. Craig on Socorro Island. Pan-Pacific Entomol., 6:178–180.

———. 1935. The Templeton Crocker Expedition of the California Academy of Sciences, 1932. No. 20. Termites. Proc. California Acad. Sci., Ser. 4, 21:233–258.

Linsley, E. G. 1935. Cerambycidae from the Revillagegedo Islands, Mexico. Pan-Pacific Entomol., 11(2):72–74.

———. 1942. Contributions toward a knowledge of the insect fauna of Lower California. No. 2. Coleoptera: Cerambycidae. Proc. California Acad. Sci., Ser. 4, 24(2):21–96, pl. 4–5.

———, and J. A. Chemsak. 1966. Cerambycidae of the Revilla Gigedo Islands. Proc. California Acad. Sci., Ser. 4, 33:249–254, 1 tab.

Medina, G. M. 1957. Memoria de la expedición científica a las Islas Revillagigedo. Imprenta Universitaria, Guadalajara 244 pp.

Meinander, M. 1981. A review of the genus *Coniopteryx* (Neuroptera, Coniopterygidae). Ann. Entomol. Fenn., 47(4):97–110.

Miranda, F. 1960. VI. Vegetación. Pp. 127–152 *in* Adem, et al. 1960. La Isla Socorro, Archipielago de Las Revillagigedo. Monogr. Inst. Geofísica, Univ. Nac. Autónoma México, 2:1–234.

Mitchell, T. B. 1938. The genus *Lithurgus* (Hymenoptera: Megachilidae). Psyche, 45:146–155.

Nielson, M. W. 1982. A revision of the subfamily Coelidiinae (Homoptera: Cicadellidae). IV. Tribe Coelidiini. Pacific Insects Monogr. 38:1–318.

Platnick, N. I., and A. Lau. 1975. A revision of the *celer* group of the spider genus *Anyphaena* (Araneae, Anyphaenidae) in Mexico and Central America. Amer. Mus. Novitates, 2575:1–36.

Richards, A. F., and B. H. Brattstrom. 1959. Bibliography, cartography, discovery and exploration of the Islas Revillagigedo. Proc. California Acad. Sci., Ser. 4, 29:315–360.

Rzedowski, J. 1978. Vegetación de México. Ed. Limusa, Mexico. 432 pp.

Spilman, T. J. 1973. Nomenclatural problems in six genera of Tenebrionidae. Proc. Entomol. Soc. Washington, 75:39–44.

Triplehorn, C. A., and L. E. Watrous. 1979. A synopsis of the genus *Phaleria* in the United States and Baja California (Coleoptera:Tenebrionidae). Coleopterists Bull., 33:275–295.

Van Duzee, E. P. 1933. The Templeton Crocker Expedition of the California Academy of Sciences, 1932. No. 4. Characters of twenty four species of Hemiptera from the Galapagos Islands and the coast and islands of Central America and Mexico. Proc. California Acad. Sci., Ser. 4, 21: 25–46.

Vázquez G., L. 1958a. Notas sobre Lepidópteros de las Islas Revillagigedo. I. Ann. Inst. Biol. México, 28:301–307.

———. 1958b. Notas sobre Lepidópteros de las Islas Revillagigedo. II. Ann. Inst. Biol. México, 29:349–353.

———. 1960. X. Observaciones sobre los artropodos. Pp. 217–234 *in* Adem, J. et al. 1960. La Isla Socorro, Archipielago de Las Revillagigedo. Monogr. Inst. Geofísica, Univ. Nac. Autónoma México, 2:1–234.

Wheeler, W. M. 1933. The Templeton Crocker Expedition of the California Academy of Sciences, 1932. No. 6. Formicidae of the Templeton Crocker Expedition. Proc. California Acad. Sci., Ser. 4, 21:57–64.

———. 1934. Ants from the islands of the west coast of Lower California and Mexico. Pan-Pacific Entomol., 10:132–144.

Williams, F. X. 1926. Expedition of the California Academy of Sciences to the Galapagos Islands, 1905–1906. XVIII. The bees and aculeate wasps of the Galapagos Islands. Proc. California Acad. Sci., Ser. 4, 2:347–357.

Williams, S. C. 1980. Scorpions of Baja California, Mexico, and adjacent islands. Occ. Pap. California Acad. Sci., 135:1–127.

Wirth, W. W. 1949. A revision of the clunionine midges with descriptions of a new genus and four new species (Diptera: Tendipedidae). Univ. California Publ. Entomol., 8:151–182.

———. 1969. New species and records of Galapagos Diptera. Proc. California Acad. Sci., Ser. 4, 36:571–594.

———. 1978. New species and records of intertidal biting midges of the genus *Dasyhelea* Kieffer from the Gulf of California (Diptera:Ceratopogonidae). Pacific Insects, 18:191–198.

Young, D. A. 1957. The leafhopper tribe Alebrini (Homoptera: Cicadellidae). Proc. U.S. Nat. Mus., 107:127–277.

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81(3), 1982, pp. 148–151

Research Note

Effects of Feral Sheep on the Spatial Distribution of Artifacts on Santa Cruz Island

Spatial distribution of artifacts is of fundamental importance in archeology. Increasing sophistication in spatial analysis (Whallon 1973) has been accompanied by concern over the effects of disruptive processes on artifact distribution and subsequent interpretation (Gifford 1978). Published studies have identified floods (Isaac 1967; Gifford 1978), burrowing mammals (Jewell and Dimbleby 1966), treefalls (Gifford 1978), and gravity (Rick 1976) as agents that can cause substantial modification of preexisting artifact distribution. Quantitative evaluation has been limited to floods (Isaac 1967; Gifford 1978) and gravity (Rick 1976).

Trampling by hoofed animals such as cattle (*Bos taurus*), sheep (*Ovis aries*), and goats (*Capra hircus*) also may alter artifact distribution; effects of trampling on vegetation and soils are well documented (Knoll and Hopkins 1959; Tanner and Mamaril 1959; Edmond 1964; Webb and Stielstra 1979). The disruptive influence of trampling may be particularly important in areas where management practices permit livestock, either domestic or feral, to achieve high concentrations. I report here an experiment designed to evaluate the effects of feral sheep on distribution of flakes in simulated archeological sites on Santa Cruz Island, California.

Santa Cruz Island, about 25,000 ha in area, lies 40 km south of Santa Barbara. The island has a history of human occupation dating back at least 8000 years, represented by an estimated 2700 archeological sites that are remarkably well preserved (Glassow 1980). Domestic sheep were introduced to Santa Cruz Island during the 1800's (Towne and Wentworth 1945) and eventually became feral.

My study was conducted in a 100-ha area of rolling hills 3 km west of Picacho Diablo, the highest peak on the island. A fence divided the area; feral sheep were abundant on one side, averaging two/ha, but were seen infrequently on the other side. The side with low sheep density supported a dense layer of herbaceous vegetation, chiefly annual grasses, whereas the side with high sheep density was mostly exposed soil that had been stripped bare of herbaceous vegetation.

Archeological sites were simulated with chert flakes obtained from a natural deposit at the east end of the island; chert had been used to manufacture chipped stone tools by the Indian inhabitants of the island (Glassow 1977). I fractured pieces of chert to form 40 thin, irregularly shaped flakes, each 2–4 cm long and 1–9 g in weight. Flakes were painted red and numbered to facilitate subsequent location and identification. At each of five simulated sites, I marked a 1-m square on the ground and placed eight flakes at 0.5-m intervals on the perimeter, one flake at each corner and one at the midpoint of each side. I drove two wooden stakes into the center of each square to identify the site.

Three experimental sites were established on the side of the fence with high sheep density: two on sheep bedgrounds (8° and 24° slope), and one at an intersection of sheep trails (0° slope). Two control sites were established on the side with low sheep density (0° and 27° slope). All sites were located on actual archeological sites, as evidenced by accumulations of crushed mollusk shells, pieces of

Table 1. Comparison of simulated archeological sites exposed to either high or low density of feral sheep for six months.

	High Sheep Density	Low Sheep Density
Total number of flakes	48	16
Flakes lost (%)	67	6
Flakes moved (%)	33	25
Flakes untouched (%)	0	69
Average net displacement of flakes (cm)	564	11
Average monthly frequency of flake movement (%)	86	4
Average movement of flakes since preceding location (cm)	295	11

projectile points, and fragments of stone bowls. The sites were established 6 November 1979. At monthly intervals thereafter for six months, the area around each site was searched for flakes, and the positions of all flakes located were plotted in reference to their original positions. At the final search in May 1980, I raked the soil to a depth of 5 cm within 2 m of each site to expose buried flakes.

During the first monthly search, I was unable to locate many flakes in the experimental sites. The absence of herbaceous cover may have left the red flakes visible to animals, which may have removed them. Consequently, on 6 December I assembled three new groups of eight flakes each, marked them only with a small numeral, and placed one group over each of the experimental sites.

Color did not seem to affect disappearance of flakes; there was no statistical difference ($P > 0.05$, chi-square test) between numbers of red and naturally colored flakes that remained missing at the conclusion of the experiment. Flake color was ignored in subsequent analyses.

After six months, sites exposed to high sheep density had been destroyed; two-thirds of the flakes could not be relocated, and the remainder had been moved from their original positions (Table 1). Conversely, sites exposed to low sheep density were largely undisturbed; only 6% of flakes were lost, and more than two-thirds had been left untouched. The few disturbed flakes were found within 39 cm of their original positions, whereas flakes exposed to high sheep density were displaced as much as 2614 cm.

Monthly examination of flake locations indicated that disturbance of sites exposed to high sheep density was a frequent, ongoing process. Of flakes relocated in a given month, 86% in experimental sites had moved since last located, compared with 4% of flakes in control sites. Moreover, experimental flakes disturbed in a given month had been displaced an average of 295 cm since last located, whereas control flakes had been displaced an average of only 11 cm.

Displacement and loss of flakes could have been caused by several factors, all ultimately linked to feral sheep. Destruction of vegetation by sheep left flakes exposed, and animals may have discovered and removed them. Foxes (*Urocyon littoralis*) in particular have a reputation on the island for carrying off objects. A combination of vegetation removal and direct disturbance to soil by sheep probably promoted erosion, resulting in displacement of flakes with soil movement. The most important factor in flake movement probably was direct trampling and kicking by sheep. The greatest movement by any flake, over 26 m, was across level ground and occurred along a well-used sheep trail. Flakes disturbed from the site established at the sheep trail intersection were all dispersed in the direction of sheep travel. I found one flake that had been shattered, presumably trampled by sheep.

Although chert flakes used in this study were not artifacts, disturbance of an actual artifact was documented. In January I found a dull-red projectile point near an experimental site exposed by recent rain. Subsequent monthly searches of the area failed to relocate the point, indicating it had disappeared along with most of the flakes in the adjacent experimental site.

Results of this study provide documentation that hoofed animals can alter preexisting distributions of artifacts substantially and rapidly. For this reason, detailed interpretation of spatial relationships should be avoided at sites that have supported concentrations of hoofed animals. In particular, many oceanic islands are or have been inhabited by high densities of feral livestock and may be affected. Other areas of concern include water sources in arid lands, sites which attract concentrations of hoofed animals, both wild and domestic, and often are associated with valuable archeological deposits.

Acknowledgments

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Literature Cited

Edmond, D. B. 1964. Some effects of sheep treading on the growth of 10 pasture species. N.Z. J. Agric. Res., 7:1–16.

Gifford, D. P. 1978. Ethnoarchaeological observations of natural processes affecting cultural materials. Pp. 77–101 *in* Explorations in ethnoarchaeology. (R. A. Gould, ed.), Univ. New Mexico Press, Albuquerque, 329 pp.

Glassow, M. A. 1977. Archaeological overview of the northern Channel Islands including Santa Barbara Island. National Park Service, Western Archaeological Center, Tucson, Arizona, 249 pp.

Glassow, M. A. 1980. Recent developments in the archeology of the Channel Islands. Pp. 79–99 *in* The California Islands: proceedings of a multidisciplinary symposium. (D. M. Power, ed.), Santa Barbara Museum of Natural History, Santa Barbara, Calif., 787 pp.

Isaac, G. 1967. Towards the interpretation of occupation debris: some experiments and observations. Kroeber Anthropol. Soc. Papers, 37:31–57.

Jewell, P. A., and G. W. Dimbleby. 1966. The experimental earthwork on Overton Down, Wiltshire, England: the first four years. Proc. Prehist. Soc., 32:313–342.

Knoll, G., and H. H. Hopkins. 1959. The effects of grazing and trampling upon certain soil properties. Trans. Kansas Acad. Sci., 62:221–231.

Rick, J. W. 1976. Downslope movement and archaeological intrasite spatial analysis. Am. Antiquity, 41:133–144.

Tanner, C. B., and C. P. Mamaril. 1959. Pasture soil compaction by animal traffic. Agron. J., 51: 329–331.

Towne, C. W., and E. N. Wentworth. 1945. Shephard's empire. Univ. Oklahoma Press, Norman, 364 pp.

Webb, R. H., and S. S. Stielstra. 1979. Sheep grazing effects on Mojave Desert vegetation and soils. Environ. Manage., 3:517–529.

Whallon, R. 1973. Spatial analysis of occupation floors I: application of dimensional analysis of variance. Am. Antiquity, 38:266–278.

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INSTRUCTIONS FOR AUTHORS

The BULLETIN is published three times each year (April, August, and November) and includes articles in English n any field of science with an emphasis on the southern California area. Manuscripts submitted for publication hould contain results of original research, embrace sound principles of scientific investigation, and present data n a clear and concise manner. The current AIBS *Style Manual for Biological Journals* is recommended as a guide or contributors. Consult also recent issues of the BULLETIN. Authors should strive for directness and lucidity, chieved by use of the active voice. Special attention should be given to consistency in tense, unambiguous eference of pronouns, and logically placed modifiers.

MANUSCRIPT PREPARATION

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An abstract summarizing in concise terms the methods, findings, and implications discussed in the paper *must* ccompany a *feature article. Abstract should not exceed 100 words.*

A feature article comprises approximately five to thirty typewritten pages. Papers should usually be divided into he following sections: abstract, introduction, methods, results, discussion and conclusions, acknowledgments, and iterature cited. Avoid using more than two levels of subheadings.

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McWilliams, K. L. 1970. Insect mimicry. Academic Press, vii + 326 pp.

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

Brattstrom, B. H. 1969. The Condor in California. Pp. 369–382 *in* Vertebrates of California. (S. E. Payne, ed.). Univ. California Press, xii + 635 pp.

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COVER: Comb Jelly or *Beroe cumis* is shaped like a watermelon, ranging in size from about three to twenty four inches in length. Eight rows of bristles waver rhythmically to provide mobility. Reproductive salps form chains extending fifty feet.

This is the fourth picture of our series on UFOS (Unfamiliar Fauna of the Open Seas) photographed by Jonathan Trent, a graduate student at Scripps Institute of Oceanography.

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SOUTHERN CALIFORNIA ACADEMY OF SCIENCES

BULLETIN

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Date of this issue 21 April 1983

Bull. Southern California Acad. Sci.
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A List of The Extinct Fossil Birds of California

Hildegarde Howard

Abstract.—A list of the extinct fossil birds of California by Hildegarde Howard. *Bull. Southern California Acad. Sci.,* 82(1):1–11. 1983. Ninety-six extinct species of birds are now known from fossil deposits in California, all within the Cenozoic Era. These are listed in taxonomic order together with the geologic age, formation and locality from which they were first recorded.

Forty years ago Loye Miller and Ida DeMay (1942) published a list and discussion of the paleo-avifauna of California. This covered the first forty years of discovery and recording of fossil birds in the state, an era that began with the description of *Mancalla californiensis* Lucas 1901 from the Third Street tunnel excavation in Los Angeles.

Except for the Los Angeles County Museum Science Series booklet, "Fossil Birds" (Howard 1962), which included the fossil record for California, there has been no further review of the subject. That publication, however, was designed for the lay reader and provided no comprehensive listing of species. It seems appropriate, therefore, to mark another forty year period of progress in paleontological research by presenting an updated list of the extinct birds now known from California, together with the geologic and North American Mammal Ages, formation and locality from which each was first recorded.

The 1942 list of over 180 birds found as fossils in California included 44 extinct species. One of these, however, was later synonymized with a previously described species (*Meleagris richmondi* Shufeldt 1915 = *Meleagris californica* (Miller 1909)). As of 1982, with more than 250 fossil birds known from California, the number of extinct species totals 96. All occur within deposits of Cenozoic age.

In terms of years before the present, the time spans of the geologic epochs within the Cenozoic Era are now estimated as follows (Berggren and Van Couvering 1974): Pleistocene 10,000 to 1,800,000 years; Pliocene 1,800,000 to 5,000,000 years; Miocene 5,000,000 to 22,500,000 years; Oligocene 22,500,000 to 38,000,000 years; Eocene 38,000,000 to 54,000,000 years; Paleocene 54,000,000 to 65,000,000 years.

The earliest known California bird is an owl, *Protostrix californiensis*, from the late Eocene of San Diego County. There are no avian records from the Paleocene or Oligocene. Forty extinct species are known from the Miocene, 15 from the Pliocene, and 40 from the Pleistocene. An additional species, *Lechusa stirtoni* Miller 1956, cited from the Pliocene, has recently been synonymized with the living Barn Owl, *Tyto alba*, tests on the bone having shown that the specimen is not a fossil (Chandler 1982b). Included in the Pleistocene record is the recently extinct Passenger Pigeon (*Ectopistes migratorius*), which, although abundant into the twentieth century elsewhere in the United States, has no historic record in California. There are now two Pleistocene records of *E. migratorius* in California, one from Rancho La Brea, Los Angeles County (Howard 1937) and one from a stream terrace deposit in Bonita, San Diego County (Chandler 1982a).

In addition to the extinct birds known to have existed in the state, approximately 160 extant species have been identified from California's Pleistocene deposits, although some of the identifications are tentative. The distinction of the bones of living species from those of closely related Pleistocene forms has been a matter of question for many years (Howard 1947a and 1947b). Studies of the large collection of bones of raptorial birds from the Rancho La Brea asphalt seeps raised the question of possible ancestral relationship of *Gymnogyps amplus* to the California Condor of today (*G. californianus*), and the owl, *Bubo sinclairi* (described from Potter Creek Cave, Shasta County) to the living Horned Owl (*B. virginianus*), recorded from Rancho La Brea. The use of the trinomial, as a temporal, rather than a geographic subspecies, has been suggested as a means of expressing this relationship. More recently, Olson (1976), in a review of the caracaras, placed the Pleistocene *Polyborus prelutosus* as a temporal subspecies of *Polyborus plancus.* Olson (1974) also questioned the validity of the species *Fulica hesterna,* believing the bones from the Pleistocene Palm Springs Formation in the Anza Borrego Desert to be assignable to *Fulica americana.* Among the living species recognized from the Pleistocene, the Golden Eagle (*Aquila chrysaetos*), represented by hundreds of bones in the Rancho La Brea collection, is also a candidate for temporal subspecific recognition. As in the case of the condor, the Rancho La Brea *A. chrysaetos* specimens show skull variations from the living form, as well as proportional distinction in the limbs (Howard 1947b). Unfortunately, lack of such large series of fossils for most of the Pleistocene species cited makes it impossible to analyze them so thoroughly.

Methods of Procedure

The following list of California's extinct avian species is arranged by order and family following, for the most part, the 5th edition (1957) of the American Ornithologists' Union Checklist of North American Birds. However, the placing of the flamingos, Family Phoenicopteridae, in the Order Charadriiformes follows recent studies by Olson and Feduccia (1980). The recognition of the grouse and turkeys as subfamilies within the Family Phasianidae follows Brodkorb (1964), but the genera *Agriocharis* Chapman 1896 and *Parapavo* Miller 1916 are synonymized with *Meleagris* Linnaeus 1758 as recently recommended by Steadman (1980). As proposed by Campbell (1979:85), the eagle, *Morphnus woodwardi* Miller 1911, is assigned to the extinct genus *Amplibuteo* Campbell 1979.

The evaluation of the extinct families follows the Catalogue of Fossil Birds (Brodkorb 1963, 1964, 1967, 1971, 1978) in part. Continuing studies, however, justify the recognition of the Plotopteridae and Teratornithidae at the family rather than the subfamily level. In fact, Campbell and Tonni (1980:67) have indicated that a reassessment of the taxonomic position of the Family Teratornithidae is under study. As a matter of record the Family Palaeoscinidae is listed here, although Brodkorb (1978) synonymizes the family with the Subfamily Myadestinae under the Family Muscicapidae.

In the few instances in which species now recorded from California were first described from another state, the original state is placed in brackets preceding the first recorded California locality. Otherwise all California references apply to the type locality. In some cases modified data are given for the locality and formation name. For example, some earlier papers referred the Sharktooth Hill Bonebed to the Temblor Formation, whereas the currently recognized name for this rock unit is the Round Mountain Silt. Also, epoch designations have, in many instances, been changed owing to the establishment of an internationally recognized Miocene-Pliocene boundary at about five million years (see Repenning and Tedford 1977:2–6 for an analysis of this boundary revision as it affects Pacific coast terminology). The North American Land Mammal Ages, which divide, and in some instances overlap the geologic epochs (see Berggren and Van Couvering 1974, fig. 1, and Repenning and Tedford 1977, Table 1), further clarify the age of the rock units involved. As these Land Mammal Ages have now been correlated with marine rock units, they are included here in parentheses following the geologic epochs.

Bibliographic references through 1970 for the species listed herein, as well as additional locality records, may be obtained from the Catalogue of Fossil Birds, Parts 1–5 (Brodkorb 1963, 1964, 1967, 1971, 1978). References for species described since Brodkorb's work, and additional locality records (Add. loc.) cited subsequent to the Catalogue's treatment of the order and family involved are listed here in Literature Cited.

Extinct Species of Fossil Birds of California
With Age, Formation and Locality from which first recorded[1]

Order Gaviiformes

  Family Gaviidae—Loons

    Gavia brodkorbi Howard 1978—Late Miocene (Clarendonian), Monterey Formation, Laguna Niguel, Orange County.

    Gavia concinna Wetmore 1940—Latest Miocene or Early Pliocene (Hemphillian), Etchegoin Formation, Sweetwater Canyon, Monterey County.

    Gavia howardae Brodkorb 1953—Late Pliocene (Blancan), San Diego Formation, San Diego, San Diego County.

Order Podicipediformes

  Family Podicipedidae—Grebes

    Podiceps parvus (Shufeldt 1913)—[Pleistocene, Oregon] Late Pliocene? (Blancan?), Tulare Formation, oil well, Kern County (Wetmore 1937).

    Podiceps subparvus (L. Miller and Bowman 1958)—Late Pliocene (Blancan), San Diego Formation, San Diego, San Diego County.

Order Procellariiformes

  Family Diomedeidae—Albatrosses

    Diomedea californica Miller 1962—Middle Miocene (Barstovian), Round Mountain Silt, Sharktooth Hill Bonebed, Kern County. (Add. loc., Howard 1978).

    Diomedea milleri Howard 1966—Middle Miocene (Barstovian), Round Mountain Silt, Sharktooth Hill Bonebed, Kern County.

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[1] Extinct Suborders, Families and Genera are marked with an asterisk.*

Family Procellariidae—Fulmars and Shearwaters

Fulmarus hammeri Howard 1968—Late Miocene (Clarendonian), Monterey Formation, Laguna Hills, Orange County.

Puffinus inceptor Wetmore 1930—Middle Miocene (Barstovian), Round Mountain Silt, Sharktooth Hill Bonebed, Kern County.

Puffinus mitchelli L. Miller 1961—Middle Miocene (Barstovian), Round Mountain Silt, Sharktooth Hill Bonebed, Kern County.

Puffinus priscus L. Miller 1961—Middle Miocene (Barstovian), Round Mountain Silt, Sharktooth Hill Bonebed, Kern County. (Add. loc., Howard 1968a).

Puffinus calhouni Howard 1968—Late Miocene (Clarendonian), Monterey Formation, Laguna Hills, Orange County.

Puffinus barnesi Howard 1978—Late Miocene (Clarendonian), Monterey Formation, Laguna Niguel, Orange County.

Puffinus diatomicus L. Miller 1925—Late Miocene (Clarendonian), Sisquoc Formation, Lompoc, Santa Barbara County.

Puffinus felthami Howard 1949—Early Pliocene (Hemphillian), Repetto Fauna, Capistrano? Formation, Corona del Mar, Orange County.

Puffinus kanakoffi Howard 1949—Late Pliocene (Blancan), San Diego Formation, San Diego, San Diego County.

Family Hydrobatidae—Storm Petrels

Oceanodroma hubbsi L. Miller 1951—Late Miocene to Early Pliocene (Hemphillian), Capistrano Formation, Capistrano Beach, Orange County.

Order Pelecaniformes

*Suborder Odontopterygia Spulski 1910

*Family Pseudontornithidae Lambrecht 1933—Bony-toothed Birds

**Osteodontornis orri* Howard 1957—Late Miocene (Clarendonian), Monterey Formation, Tepusquet Canyon, Santa Barbara County. (Add. locs., Howard 1968a, 1978).

Suborder Sulae Sharpe

Family Sulidae—Boobies and Gannets

Sula pohli Howard 1958—Late Miocene (Clarendonian), Modelo Formation, Studio City, Los Angeles County.

Sula willetti L. Miller 1925—Late Miocene (Clarendonian), Sisquoc Formation, Lompoc, Santa Barbara County.

Sula humeralis L. Miller and Bowman 1958—Late Pliocene (Blancan), San Diego Formation, San Diego, San Diego County.

**Paleosula stocktoni* (L. Miller 1935)—Late Miocene (Clarendonian) Valmonte Diatomite Member of Monterey Formation, Lomita, Los Angeles County.

**Miosula media* Miller 1925—Late Miocene (Clarendonian) Sisquoc Formation, Lompoc, Santa Barbara County. (Add. loc.? Howard 1978).

**Miosula recentior* Howard 1949—Late Pliocene (Blancan), San Diego Formation, San Diego, San Diego County.

Morus vagabundus Wetmore 1930—Middle Miocene (Barstovian), Round Mountain Silt, Sharktooth Hill Bonebed, Kern County.

Morus lompocanus (L. Miller 1925)—Late Miocene (Clarendonian) Sisquoc Formation, Lompoc, Santa Barbara County. (Add. locs., Howard 1968a and 1978).

Morus magnus Howard 1978—Late Miocene (Clarendonian), Monterey Formation, Laguna Niguel, Orange County.

Morus revanus Howard 1936—Late Pleistocene (Rancholabrean), Palos Verdes Sand, Playa del Rey, Los Angeles County. (Add. loc., Howard 1968b).

Family Phalacrocoracidae—Cormorants

Phalacrocorax femoralis L. Miller 1929—Late Miocene (Clarendonian), Modelo Formation, Calabasas, Los Angeles County.

Phalacrocorax kennelli Howard 1949—Late Pliocene (Blancan), San Diego Formation, San Diego, San Diego County.

Phalacrocorax rogersi Howard 1932—Early Pleistocene? (Irvingtonian?), Santa Barbara Formation, Veronica Springs Stone Quarry, Santa Barbara County.

*Family Plotopteridae Howard 1969—Oar-winged Swimmers

**Plotopterum joaquinensis* Howard 1969—Early Miocene (Arikareean), Pyramid Hill Local Fauna, Pyramid Hill Sand member of Jewett Sands, Pyramid Hill, Kern County.

Order Ciconiiformes

Family Ciconiidae—Storks

Ciconia maltha L. Miller 1910—Late Pleistocene (Rancholabrean), Rancho La Brea asphalt seeps, Los Angeles, Los Angeles County. (Add. loc., Jefferson et al. 1982).

Mycteria wetmorei Howard 1935—Late Pleistocene (Rancholabrean), Rancho La Brea asphalt seeps, Los Angeles, Los Angeles County.

Order Anseriformes

Family Anatidae

Subfamily Anserinae—Geese

**Presbychen abavus* Wetmore 1930—Middle Miocene (Barstovian), Round Mountain Silt, Sharktooth Hill Bonebed, Kern County. (Add. loc., Howard 1968a).

Branta howardae L. Miller 1930—Late Miocene (Clarendonian), Ricardo Formation, Ricardo, Kern County.

Branta dickeyi L. Miller 1924—Late Pleistocene (Rancholabrean), McKittrick asphalt seeps, Kern County.

Subfamily Tadorninae—Sheld-ducks

**Anabernicula gracilenta* Ross 1935—Late Pleistocene (Rancholabrean) McKittrick asphalt seeps, Kern County.

**Brantadorna downsi* Howard 1963—Middle Pleistocene (Irvingtonian), Vallecito Creek Local Fauna, Palm Springs Formation, Anza Borrego Desert, San Diego County.

Subfamily Aythyinae—Diving Ducks

Bucephala fossilis Howard 1963—Middle Pleistocene (Irvingtonian), Vallecito Creek Local Fauna, Palm Springs Formation, Anza Borrego Desert, San Diego County.

**Chendytes milleri* Howard 1955—Early Pleistocene? (Irvingtonian), Equivalent of San Pedro Formation, San Nicolas Island.

**Chendytes lawi* L. Miller 1925—Late Pleistocene (Rancholabrean), Palos Verdes Sand, Santa Monica, Los Angeles County. (Add. locs., Howard 1968b and Morejohn 1976).

Subfamily Oxyurinae—Stiff-tailed Ducks

Oxyura bessomi Howard 1963—Middle Pleistocene (Irvingtonian), Vallecito Creek Local Fauna, Palm Springs Formation, Anza Borrego Desert, San Diego County.

Order Falconiformes

Family Cathartidae—American Vultures

Sarcoramphus kernensis (L. Miller 1931)—Latest Miocene (Hemphillian), Kern River Formation, Poso Creek, Kern County.

Coragyps occidentalis L. Miller 1909—Late Pleistocene (Rancholabrean) Rancho La Brea asphalt seeps, Los Angeles, Los Angeles County.

Gymnogyps amplus L. Miller 1911—Late Pleistocene (Rancholabrean), Samwell Cave, Shasta County. (*G. californianus* in Rancho La Brea asphalt seeps reassigned to *G. amplus* (Fisher 1944)). (Add. locs.? Downs et al. 1959, and Howard 1968b).

**Breagyps clarki* (L. Miller 1910)—Late Pleistocene (Rancholabrean), Rancho La Brea asphalt seeps, Los Angeles, Los Angeles County.

*Family Teratornithidae L. Miller 1909—Teratorns

**Teratornis incredibilis* Howard 1952—[Late Pleistocene, Nevada] Middle Pleistocene (Irvingtonian), Vallecito Creek Local Fauna of Palm Springs Formation, Anza Borrego Desert, San Diego County (Howard 1963).

**Teratornis merriami* Miller 1909—Late Pleistocene (Rancholabrean), Rancho La Brea asphalt seeps, Los Angeles, Los Angeles County. (Add. loc., Jefferson et al. 1982).

**Cathartornis gracilis* L. Miller 1910—Late Pleistocene (Rancholabrean), Rancho La Brea asphalt seeps, Los Angeles, Los Angeles County.

Family Accipitridae—Hawks, Eagles, Old World Vultures

**Miohierax stocki* Howard 1944—Early Miocene (Arikareean), Tick Canyon Formation, Vasquez Canyon, Los Angeles County.

Buteogallus fragilis (L. Miller 1911)—Late Pleistocene (Rancholabrean), Rancho La Brea asphalt seeps, Los Angeles, Los Angeles County (Add. loc.? W. E. Miller 1971, p.8).

Buteogallus milleri (Howard 1932)—Late Pleistocene (Rancholabrean) Hawver Cave, Eldorado County.

**Amplibuteo woodwardi* (L. Miller 1911)—Late Pleistocene (Rancholabrean), Rancho La Brea asphalt seeps, Los Angeles, Los Angeles County.

**Wetmoregyps daggetti* (L. Miller 1915)—Late Pleistocene (Rancholabrean), Rancho La Brea asphalt seeps, Los Angeles, Los Angeles County.

Spizaetus grinnelli (L. Miller 1911)—Late Pleistocene (Rancholabrean), Rancho La Brea asphalt seeps, Los Angeles, Los Angeles County.

**Neogyps errans* L. Miller 1916—Late Pleistocene (Rancholabrean) Rancho La Brea asphalt seeps, Los Angeles, Los Angeles County.

**Neophrontops vallecitoensis* Howard 1963—Middle Pleistocene (Irvingtonian), Vallecito Creek Local Fauna of Palm Springs Formation, Anza Borrego Desert, San Diego County.

**Neophrontops americanus* L. Miller 1916—Late Pleistocene (Rancholabrean), Rancho La Brea asphalt seeps, Los Angeles, Los Angeles County.

Family Pandionidae—Ospreys

Pandion homalopteron Warter 1976—Middle Miocene (Barstovian), Round Mountain Silt, Sharktooth Hill Bonebed, Kern County.

Family Falconidae—Falcons and Caracaras

Falco swarthi L. Miller 1927—Late Pleistocene (Rancholabrean), McKittrick asphalt seeps, Kern County.

Polyborus prelutosus Howard 1938—Late Pleistocene (Rancholabrean), Rancho La Brea asphalt seeps, Los Angeles, Los Angeles County.

Order Galliformes

Family Cracidae—Chachalacas

**Boreortalis tedfordi* (L. Miller 1952)—Middle Miocene (Barstovian), Barstow Formation, Barstow, San Bernardino County.

Family Phasianidae

Subfamily Tetraoninae—Grouse

Dendragapus gilli milleri Jehl 1969—Late Pleistocene (Rancholabrean) Samwel Cave, Shasta County [species originally named *Palaeotetrix gilli* Shufeldt 1891, from Pleistocene of Oregon].

Subfamily Meleagridinae—Turkeys

Meleagris anza (Howard 1963)—Middle Pleistocene (Irvingtonian), Vallecito Creek Local Fauna of Palm Springs Formation, Anza Borrego Desert, San Diego County.

Meleagris californica (L. Miller 1909)—Late Pleistocene (Rancholabrean), Rancho La Brea tar seeps, Los Angeles, Los Angeles County. (Add. loc., W. E. Miller 1971 p.48).

Order Gruiformes

Family Gruidae—Cranes

Grus conferta A. Miller and Sibley 1942—Late Miocene (Hemphillian), Siesta Formation, Black Hawk Ranch, Contra Costa County.

Family Rallidae—Rails and Coots

Fulica hesterna Howard 1963—Middle Pleistocene (Irvingtonian), Vallecito Creek Local Fauna of Palm Springs Formation, Anza Borrego Desert, San Diego County.

Order Charadriiformes

Family Scolopacidae—Godwits, etc.

Limosa vanrossemi L. Miller 1925—Late Miocene (Clarendonian), Sisquoc Formation, Lompoc, Santa Barbara County.

Family Phoenicopteridae—Flamingos

**Megapaloelodus connectens* A. Miller 1944—[Miocene, South Dakota] Middle Miocene (Barstovian), Barstow Formation, Barstow, San Bernardino County (L. Miller 1950).

Phoenicopterus copei Shufeldt 1891—[Late Pleistocene, Oregon] Late Pleistocene (Rancholabrean), Manix Lake Beds, San Bernardino County (Jefferson et al. 1982).

Phoenicopterus minutus Howard 1955—Late Pleistocene (Rancholabrean) Manix Lake Beds, San Bernardino County.

Family Alcidae—Auk-like Birds

Subfamily Alcinae

Uria brodkorbi Howard 1981—Late Miocene (Clarendonian), Sisquoc Formation, Lompoc, Santa Barbara County.

Uria paleohesperis Howard 1982—Latest Miocene (Hemphillian), San Luis Rey River Local Fauna of San Mateo Formation, Oceanside, San Diego County.

Cepphus olsoni Howard 1982—Latest Miocene (Hemphillian), San Luis Rey River Local Fauna of San Mateo Formation, Oceanside, San Diego County.

Brachyramphus pliocenus Howard 1949—Late Pliocene (Blancan), San Diego Formation, San Diego, San Diego County.

Ptychoramphus tenuis L. Miller and Bowman 1958—Late Pliocene (Blancan), San Diego Formation, San Diego, San Diego County.

Aethia rossmoori Howard 1968—Late Miocene (Clarendonian), Monterey Formation, Laguna Hills, Orange County.

Cerorhinca dubia L. Miller 1925—Late Miocene (Clarendonian), Sisquoc Formation, Lompoc, Santa Barbara County.

*Subfamily Mancallinae—Flightless Auks

**Praemancalla lagunensis* Howard 1966—Late Miocene (Clarendonian), Monterey Formation, Laguna Hills, Orange County.

**Praemancalla wetmorei* Howard 1976—Late Miocene (Clarendonian), Monterey Formation, Laguna Niguel, Orange County.

**Alcodes ulnulus* Howard 1968—Late Miocene (Clarendonian), Monterey Formation, Laguna Hills, Orange County.

**Mancalla cedrosensis* Howard 1971—[Latest Miocene-Early Pliocene, Cedros Island, Baja California]. Early Pliocene (Hemphillian), Lawrence Canyon Local Fauna of San Mateo Formation, Oceanside, San Diego County (Howard 1982).

**Mancalla californiensis* Lucas 1901—Early Pliocene (Hemphillian), Repetto Formation, Los Angeles, Los Angeles County. (Add. loc., Howard 1970).

**Mancalla diegensis* (L. Miller 1937)—Late Pliocene (Blancan), San Diego Formation, San Diego, San Diego County. (Add. locs., Howard 1970 and 1982)

**Mancalla milleri* Howard 1970—Late Pliocene (Blancan), San Diego Formation, San Diego, San Diego County. (Add. loc., Howard 1982).

**Mancalla emlongi* Olson 1981—Late Pliocene (Blancan), San Diego Formation, Pacific Beach, San Diego County.

Order Columbiformes

Family Columbidae—Pigeons and Doves

Ectopistes migratorius (Linnaeus 1766)—[Recent, eastern North America]. Late Pleistocene, Rancho La Brea asphalt seeps, Los Angeles, Los Angeles County (Howard 1937). (Add. Loc., Chandler 1982A)

Order Strigiformes

*Family Protostrigidae Wetmore 1933—Ancient Owls

***Protostrix californiensis* Howard 1965—Late Eocene (Uintan), Poway Formation, San Diego, San Diego County.

Family Strigidae—Typical Owls

Bubo sinclairi L. Miller 1911—Late Pleistocene (Rancholabrean), Potter Creek Cave, Shasta County.

Strix brea Howard 1933—Late Pleistocene, (Rancholabrean), Rancho La Brea asphalt seeps, Los Angeles, Los Angeles County.

Asio priscus Howard 1964—Late Pleistocene (Rancholabrean), Tecolote Member of Santa Rosa Island Formation, Arlington Canyon, Santa Rosa Island.

Order Passeriformes

*Family Palaeoscinidae Howard 1957—Early Passerines

***Palaeoscinis turdirostris* Howard 1957—Late Miocene (Clarendonian), Monterey Formation, Tepusquet Canyon, Santa Barbara County.

Family Icteridae—Blackbirds

***Pandanaris convexa* A. Miller 1947—Late Pleistocene (Rancholabrean), Rancho La Brea asphalt seeps, Los Angeles, Los Angeles County.

Euphagus magnirostris A. Miller 1929—Late Pleistocene (Rancholabrean), Rancho La Brea asphalt seeps, Los Angeles, Los Angeles County.

Family Emberizidae—Towhees, etc.

Pipilo angelensis Dawson 1948—Late Pleistocene (Rancholabrean), Rancho La Brea asphalt seeps, Los Angeles, Los Angeles County.

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Literature Cited

Note: Bibliographic references through 1970 for the species listed herein, as well as additional locality records, may be obtained from the Catalogue of Fossil Birds, Parts 1–5 (Brodkorb 1963–1978).

Berggren, W. A., and J. A. Van Couvering. 1974. The late Neogene: Biostratigraphy, geochronology and paleoclimatology of the last 15 million years in marine and continental sequences. Palaeogeogr., Palaeoclimatol., Palaeoecol., 16:1–216.

Brodkorb, P. 1963. Catalogue of Fossil Birds, Part 1 (Archaeopterygiformes through Ardeiformes). Bull. Florida State Mus. Biol. Sci., 7(4):179–293.

———. 1964. Catalogue of Fossil Birds, Part 2 (Anseriformes through Galliformes). Bull. Florida State Mus. Biol. Sci., 8(3):195–335.

———. 1967. Catalogue of Fossil Birds, Part 3 (Ralliformes, Ichthyornithiformes, Charadriiformes). Bull. Florida State Mus. Biol. Sci., 11(3):99–220.

———. 1971. Catalogue of Fossil Birds, Part 4 (Columbiformes through Piciformes). Bull. Florida State Mus. Biol. Sci., 15(4):163–266.

———. 1978. Catalogue of Fossil Birds, Part 5 (Passeriformes). Bull. Florida State Mus. Biol. Sci., 23(3):139–228.

Campbell, K. E., Jr. 1979. The non-passerine Pleistocene avifauna of the Talara Tar Seeps, northwestern Peru. Life Sci. Contrib. Royal Ontario Mus., 118:1–203.

Campbell, K. E., Jr., and E. P. Tonni. 1980. A new genus of teratorn from the Huayquerian of Argentina (Aves: Teratornithidae). *In* Papers in avian paleontology honoring Hildegarde Howard (K. E. Campbell, Jr., ed.). Nat. Hist. Mus. of Los Angeles County Contrib. Sci. No. 330: 59–68.

Chandler, R. M. 1982a. A second record of Pleistocene Passenger Pigeon from California. Condor, 84:242.

———. 1982b. A reevaluation of the Pliocene owl *Lechusa stirtoni* Miller. Auk, 99:580–581.

Downs, T., H. Howard, T. Clements, and G. A. Smith. 1959. Quaternary animals from Schuiling Cave in the Mojave Desert, California. Los Angeles Co. Mus. Contrib. Sci. No. 29, 21 pp.

Fisher, H. 1944. The skulls of the cathartid vultures. Condor, 46:272–296.

Howard, H. 1947a. A preliminary survey of trends in avian evolution from Pleistocene to Recent time. Condor, 49:10–13.

———. 1947b. An ancestral golden eagle raises a question in taxonomy. Auk, 64:287–291.

———. 1962. Fossil Birds, with especial reference to the birds of Rancho La Brea. Los Angeles Co. Mus. Sci. Ser. No. 17, Paleon. No. 10, 44 pp.

———. 1966. Additional avian records from the Miocene of Sharktooth Hill, California. Los Angeles Co. Mus. Contrib. Sci. No. 114, 11 pp.

———. 1968a. Tertiary birds from Laguna Hills, Orange County, California. Los Angeles Co. Mus. Contrib. Sci. No. 142, 21 pp.

———. 1968b. Fossil Birds. Pp. 42–45 *in* Prehistory of Santa Rosa Island, by Phil C. Orr. Santa Barbara Mus. Natural History, 253 pp.

———. 1969. A new avian fossil from Kern County, California. Condor, 71:68–69.

———. 1970. A review of the extinct avian genus, *Mancalla.* Los Angeles Co. Mus. Contrib. Sci. No. 203, 12 pp.

———. 1971. Pliocene avian remains from Baja California. Los Angeles Co. Mus. Contrib. Sci. No. 217, 17 pp.

———. 1976. A new species of flightless auk from the Miocene of California (Alcidae:Mancallinae). *In* Collected papers in avian palentology honoring the 90th birthday of Alexander Wetmore (S. L. Olson, ed.). Smithsonian Contrib. Paleobiology, 27:141–146.

———. 1978. Late Miocene marine birds from Orange County, California. Nat. Hist. Mus. Los Angeles County Contrib. Sci. No. 290, 26 pp.

———. 1981. A new species of murre, genus *Uria,* from the late Miocene of California (Aves: Alcidae). Bull. So. Calif. Acad. Sci., 80:1–12.

———. 1982. Fossil birds from Tertiary marine beds at Oceanside, San Diego County, California, with descriptions of two new species of the genera *Uria* and *Cepphus* (Aves:Alcidae). Nat. Hist. Mus. Los Angeles County Contrib. Sci. No. 341, 15 pp.

Jefferson, G. T., J. R. Keaton, and P. Hamilton. 1982. Manix Lake and the Manix Fault. Field Trip Guide. San Bernardino Co. Mus. Assoc. Quarterly, 29(3–4):1–47.

Jehl, J. R., Jr. 1969. Fossil grouse of the genus *Dendragapus.* Trans. San Diego Soc. Nat. Hist., 15(12):165–174.

Miller, L., and I. DeMay. 1942. The fossil birds of California. An avifauna and bibliography with annotations. Univ. Calif. Publ. Zool., 47(4):47–142.

Miller, W. E. 1971. Pleistocene vertebrates of the Los Angeles Basin and vicinity (exclusive of Rancho La Brea). Bull. Los Angeles Co. Mus. Nat. Hist., Science: No. 10, 124 pp.

Morejohn, G. V. 1976. Evidence of the survival to Recent times of the extinct flightless duck *Chendytes lawi* Miller. *In* Collected papers in avian paleontology honoring the 90th birthday of Alexander Wetmore (S. L. Olson, ed.). Smithsonian Contrib. Paleobiol. No. 27:207–211.

Olson, S. L. 1974. The Pleistocene rails of North America. Condor, 76:169–175.

———. 1976. A new species of *Milvago* from Hispaniola, with notes on other fossil caracaras from the West Indies (Aves: Falconidae). Proc. Biol. Soc. Washington, 88(33):355–366.

———. 1981. A third species of *Mancalla* from the Late Pliocene San Diego Formation of California (Aves:Alcidae). Journal of Vertebrate Paleontology. 1(1):97–99.

Olson, S. L., and A. Feduccia. 1980. Relationships and evolution of flamingos (Aves:Phoenicopteridae). Smithsonian Contrib. Zool. No. 316, 73 pp.

Repenning, C. A., and R. H. Tedford. 1977. Otarioid seals of the Neogene. Geol. Surv. Prof. Paper 992, 93 pp.

Steadman, D. W. 1980. A review of the osteology and paleontology of turkeys (Aves:Meleagridinae). *In* Papers in avian paleontology honoring Hildegarde Howard (K. E. Campbell, Jr., ed.). Nat. Hist. Mus. Los Angeles County Contrib. Sci. No. 330:131–207.

Warter, S. L. 1976. A new osprey from the Miocene of California (Falconiformes:Pandionidae). *In* Collected papers in avian paleontology honoring the 90th birthday of Alexander Wetmore (S. L. Olson, ed.). Smithsonian Contrib. Paleobiol. No. 27:133–139.

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Studies on North American Bees of the Genus *Hylaeus*. 6. An Adventive Palaearctic Species in Southern California (Hymenoptera: Colletidae)

Roy R. Snelling

Abstract.—Studies on North American bees of the genus *Hylaeus*. 6. An adventive Palaearctic species in Southern California (Hymenoptera: Colletidae). Roy R. Snelling. *Bull. Southern California Acad. Sci.*, 82(1):12–16, 1983. *Hylaeus* (*Spatulariella*) *punctatus* (Brullé) is a common, widespread bee in the western Palaearctic Region, occurring in the countries bordering the Mediterranean Sea. This paper records *H. punctatus* from Playa del Rey, Los Angeles County, California; this is the first record for both the subgenus and species in the Western Hemisphere. Figures and descriptive notes are provided to aid in the separation of this bee from other North American species of *Hylaeus.*

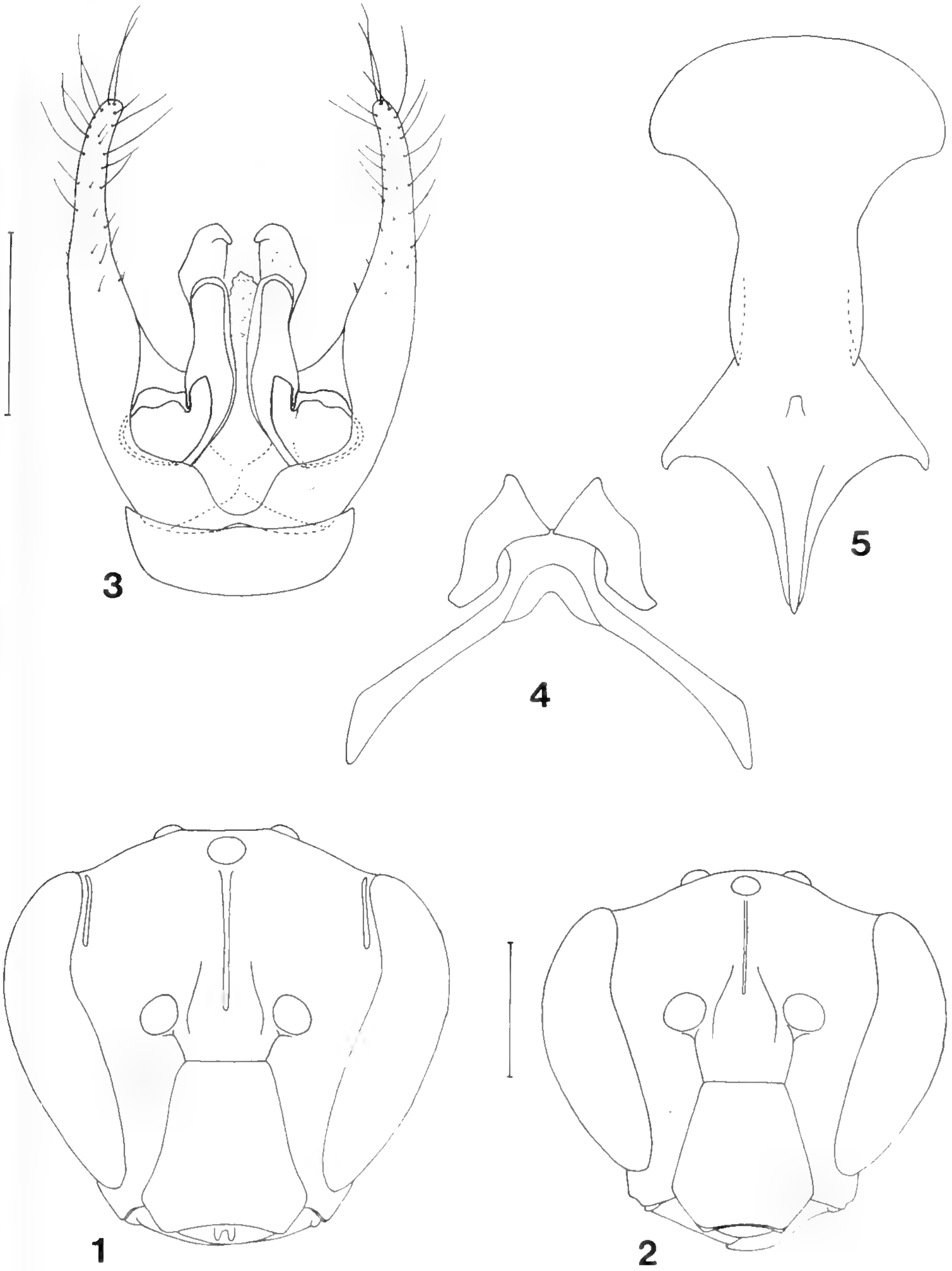
While collecting bees and other Hymenoptera in conjunction with a general survey of the biota of the Ballona Creek area of Playa del Rey, Los Angeles County, California, I found an unusual hylaeine bee to be abundant. These specimens proved to be *Hylaeus* (*Spatulariella*) *punctatus* (Brullé, 1832), a common species in the Mediterranean area of the Palaearctic Region. Dathe (1980) gave the distribution as "Mediterranean, also sporadic in Central Europe." Warncke (1972) recorded the species from France, Corsica, Sicily, Italy, Dalmatia, Serbia, Monte Negro, Greece, Macedonia and Bulgaria, and its presence in Spain was noted by Ceballos (1956). In addition, the subspecies, *H. p. longimacula* (Alfken, 1936) has been described from Lebanon and is known from Greece and Turkey as well. The collections of the Natural History Museum of Los Angeles County include specimens of *H. punctatus* from Cyprus, Czechoslovakia, Austria and Greece.

The first specimen taken at Playa del Rey, a male, was collected on 9 June 1981, on flowers of *Brassica geniculata* (Cruciferae). Three additional males were taken on flowers of *Apium graveolens* (Umbelliferae) on 11 June 1981. By late July 1981, specimens of both sexes were abundant, mostly on *Foeniculum vulgare* (Umbelliferae). All of these plants are adventive from the western Palaearctic Region.

Systematics

No representative of the subgenus *Spatulariella* Popov, 1939, has been previously reported from the New World. In my key to the Nearctic subgenera of *Hylaeus* (Snelling 1966), male *Spatulariella* will run to couplet 6 where it fails to agree with either lug. The following modification may be made to that key to include male *Spatulariella*:

5. Apical process of sternite 8 with numerous branched hairs along lateral margins; distal lobes of sternite 7 rounded apically .... *Hylaeana* Michener
– Apical process of sternite 8 bare, or with several branched hairs on apical



Figs. 1–5. *Hylaeus* (*Spatulariella*) *punctatus*. 1, Female head, frontal view; 2, Male head, frontal view; scale line = 0.50 mm; maculate areas stippled. 3, Male genital capsule, ventral view; 4, male seventh sternite; 5, male eight sternite; scale line (Figs. 3–5) = 0.25 mm.

margin; distal lobes of sternite 7 acute (Fig. 4) or narrowly rounded apically .... 5′

5′. Distal process of sternite 8 flat, broadly spatulate (Fig. 5) and visibly protruding from genital opening; gonostyli slender, extending much beyond apices of penis valves (Fig. 3) .... *Spatulariella* Popov

– Distal process of sternite 8 narrow, not at all distally flattened and spatulate; gonostyli stout and hardly surpassing apices of penis valves 6

In that portion of the key treating females, the subgenus *Spatulariella* will run to couplet 13 where it does not agree well with either alternative. To accommodate *Spatulariella* the key may be modified thus:

12. Punctures of horizontal area of tergite 1, and usually of tergite 2 as well, dense and distinct; facial fovea usually ending midway between eye and ocellus; posterior declivity of basal triangle of propodeum separated from horizontal face by distinct transverse carina .... *Paraprosopis* Popov

– Punctures of tergites 1 and 2 fine, usually separated by two or more times a puncture diameter; if denser, *then* apical margin of tergite 2 reflexed upward; facial fovea usually ending nearer eye than ocellus, rarely attaining midpoint; posterior declivity of basal triangle of propodeum separated from horizontal face by a carina or not .... 12′

12′. Anterior face of mesepisternum separated from lateral face by distinct lamelliform carina .... *Spatulariella* Popov

– Anterior face of mesepisternum abruptly rounded into lateral face, no carina present 13

Both sexes of *Spatulariella* possess a distinct lamelliform carina between the anterior and lateral faces of the mesepisternum, perhaps the best recognition characteristic by which to differentiate *Spatulariella* from the native Nearctic groups. Some species of the Neotropical subgenus *Hylaeopsis* Michener, 1954, also have a carinate mesepisternum. In that subgenus, however, the pronotal collar is transversely carinate or crested and the oblique propodeal carina is present and sharply defined. Neither condition is true of *Spatulariella.*

The male face marks are somewhat variable in the specimens from Playa del Rey. In most, the clypeus is mostly pale yellowish, with black along the apical margin and very narrowly black along the lateral margin below the tentorial pit (Fig. 2). Lateral face marks terminate truncately a little above the level of the base of the clypeus and rarely extend laterad to the inner eye margin. In a few males the clypeus has only a broad, longitudinal, median bar and there are no lateral marks. The mandible, labrum and scape are consistently without pale marks.

Most of the Playa del Rey females have well developed lateral face marks which fill most of the area between the clypeus and the eye, extending along the inner eye margin to about the level of the middle of the antennal socket (Fig. 1). A preapical, median clypeal spot is present in many specimens. A few individuals have the lateral face mark much reduced and the clypeus always wholly black.

In general, these specimens match most closely the color variant found in southern Europe (Italy and Greece), rather than the darker form present in Austria and Czechoslovakia. The lateral face marks of the female do not extend far up the inner eye margins as they do in the subspecies *H. p. longimacula.*

Since *Hylaeus* females have a propensity for nesting in a wide variety of preformed cavities in wood and other materials, it is hardly surprising that the species has been introduced into the New World. Indeed, the surprise is that more species of *Hylaeus* have not been similarly introduced. Apparently, only one other Palaearctic species, H. (*H.*) *bisinuatus* Foerster, 1871, has been successful; this species occurs over much of the United States (Snelling 1970, 1975) and is the only other hylaeine collected at Playa del Rey.

Various other wood- or twig-nesting bees have from time to time been introduced into the United States and become established. *Megachile* (*Eutricharaea*) *pacifica* (Panzer) and *Lithurge* (*L.*) *chrysurus* (Fonscolombe) are two megachilids so introduced. Presumably, the former species was introduced sometime during, or shortly after, World War II (Hurd 1979); once established, the species spread rapidly and is now a important pollinator of alfalfa. *Lithurge chrysurus* was reported from New Jersey by Roberts (1978) where it appears to be a recently adventive species. The anthophorid species, *Ceratina dallatorreana* Friese, 1896, was first collected in central California in 1949. This Mediterranean species is now firmly established in California and is extending its range (Daly 1966).

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Literature Cited

Alfken, J. D. 1936. Neue *Prosopis*-Arten vom Libanon. Konowia, 15:51–53.

Brullé, A. 1832. Expédition scientifique de Morée. Section des Sciences physiques, Zoologie III. Part 2, Insectes, pp. 1–29, 64–395. Paris.

Ceballos, G. 1956. Catalogo de los Himenopteros de España. Trab. Inst. Español Entomol. 554 pp.

Daly, H. V. 1966. Biological studies on *Ceratina dallatorreana*, an alien bee in California which reproduces by parthenogenesis (Hymenoptera:Apoidea). Ann. Entomol. Soc. Amer., 59:1138–1154.

Dathe, H. H. 1980. Die Arten der Gattung *Hylaeus* F. in Europa (Hymenoptera: Apoidea, Colletidae). Mitt. zool. Mus. Berlin, 56:207–294.

Foerster, A. 1871. Monographie der Gattung *Hylaeus* F. (Latr). Verh. zool.-bot. Ges. Wien, 21:873–1084.

Hurd, P. D., Jr. 1979. *In* K. V. Krombien et al., Catalog of Hymenoptera of America north of Mexico. Smithsonian Inst., Washington, D.C., 2:2057.

Michener, C. D. 1954. Bees of Panamá. Bull. Amer. Mus. Nat. Hist., 104:1–176.

Popov, V. B. 1939. Subgeneric groups of genus *Prosopis* F. Comptes Rendus (Dokl.) Acad. Sci. U.R.S.S., 25:167–170.

Roberts, R. B. 1978. The nesting biology, behavior and immature stages of *Lithurge chrysurus*, an adventitious wood-boring bee in New Jersey (Hymenoptera: Megachilidae). Jour. Kans. Entomol. Soc., 51:735–745.

Snelling, R. R. 1966. Studies on North American bees of the genus *Hylaeus*. 3. The Nearctic subgenera (Hymenoptera: Colletidae). Bull. So. Calif. Acad. Sci., 65:164–175.

———. 1970. Studies on North American bees of the genus *Hylaeus*. 5. The subgenera *Hylaeus* s. str. and *Paraprosopis* (Hymenoptera: Colletidae). Contr. Sci. L.A. Co. Mus. Nat. Hist. 180, 59 pp.

———. 1975. Taxonomic notes on some colletid bees of western North America with descriptions of new species (Hymenoptera: Colletidae). *Ibid.* 267, 9 pp.

Warncke, K. 1972. (1970). Beitrag zur Systematik and Verbreitung der Bienengattung *Prosopis* F. in der Westpaläarktis. Bull. Rech. agron. Gembloux, N.S., 5:745–768.

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Calcanea of Members of the Viverridae

Howard J. Stains

Abstract.—Calcanea of members of the Viverridae. Howard J. Stains. *Bull. Southern California Acad. Sci.* 82(1):17–38, 1983. Calcanea of 20 genera (30 species) of Viverrids are described. Members of various subfamilies, except those of the Hemigalinae, form distinct groups, with those of the Herpestinae being most obvious by having a pronounced medio-laterally sloped cuboid surface on the calcaneal distal end.

Calcanea of representatives of 4 of 6 subfamilies of Viverridae were available for study. Members of the subfamilies Galidiinae and Cryptoproctinae were not included.

Members of the family Viverridae are extremely variable in calcaneal characteristics. In some cases, calcanea are found that resemble in some feature those of many other carnivore families. Sometimes it is easier to characterize calcanea at a relatively low taxonomic level rather than by higher category; subfamilies of Viverridae, for example, are easier to characterize than the family, and each species can be placed in the proper subfamily with ease on the basis of the calcaneum. This bone perhaps could be useful in determining the taxonomic placement of miscellaneous calcanea found in the fossil record as well as living taxa.

Viverridae are least well represented of all Families of carnivores I have studied. In all, there are 18 genera and approximately 40 species that were unavailable to me: Viverridae (*Prionodon* (*linsang, pardicolor*), *Macrogalidia musschenbroeki, Genetta* (*lehmanni, rubiginosa*), *Poiana richardsoni, Pseudogenetta villiersi, Civettictis civetta*); Paradoxurinae (*Paradoxurus* (*jerboni, zeylonensis*)); Hemigalinae (*Chrotogale owstoni, Eupleres* (*goudotii, major*), *Fossa fossa, Hemigalus* (*Diplogale*) *hosei*); Galidiinae (*Galidia concolor, Galidictis* (*fasciata, striata*), *Mungotictis* (*lineatus, substriatus*), *Solanoia unicolor*); Herpestinae (*Herpestes* (*fuscus, javanicus, puntatissimus, semitorquatus, smithi, urva, vitticollis*), *Liberiictis kuhni, Paracynictis selousi, Rhynchogale melleri, Bdeogale crassicauda, Mungos ansorgei, Helogale* (*Hirtula, parvula*), *Crossarchus* (*alexandri, gambianus*), *Dologale dybowskii*); Cryptoproctinae (*Cryptoprocta ferox*).

Twenty genera (30 species) were examined and are described in this work; thus, approximately half of the genera and slightly more than half of the species of viverrids still need to be studied. Calcaneal terminology has been described by Stains (1959, 1962, 1973, 1976) and by Robinette and Stains (1970). Ewer (1973: 4, 51–56, 190–202, 275–278, 304, 322–325, 400–405) discussed classification, skeleton, food habits, social organization, reproduction, and courtship in the viverrids. Walker (1964 II:1224–1262) reviewed the family taxonically and biologically.

Calcanea of Viverrids

Subfamily Viverrinae

Four of seven genera and nine of 14 species within Viverrinae were examined. Viverrinae members have calcanea with a small distinct sustentaculum lacking an expanded shelf or much development of a shelf, a small medial articular surface which does not extend to near the cuboid surface, the distal edge of the medial articular surface is proximal to the trochlear process' greatest expansion, a cuboid surface more or less at right angles to the calcaneal long axis, the distal end of the body usually extends distally beyond the cuboid, and a well-developed trochlear process which is variable but often small and near the distal end of the bone with the proximal edge being distal to the distal edge of the medial articular surface (Figs. 1f, g, h, i, m, n, dd, cc).

Genetta genetta—Small-spotted Genet

Probably within the size range of *Genetta genetta* are calcanea of: *Genetta* (*tigrina, victoriae*), *Osbornictis piscivora, Viverra tangulunga* and *Viverricula indica* in Viverrinae; *Arctogalidia trivirgata, Nandinia binotata, Paguma larvata,* and *Paradoxurus hermaphroditis* in Paradoxurinae; *Cynogale bennetti* and *Hemigalus derbyanus* in Hemigalinae; and *Atilax paludinosus, Herpestes ichneumon* and *Mungos mungo* in Herpestinae (Table 1).

The genera shape of calcanea of *Genetta genetta* (Fig. 1m) is close to those of *Viverra tangalunga* (Fig. 1i). There is no indication of a shelf leading from the medial articular surface in *G. genetta* and this condition also is absent in specimens of *V. tangalunga.* Calcanea of *G. genetta* lack the prominent extension of the body beyond the cuboid surface and a resulting notch is not as evident as in *V. tangalunga.* The trochlear process forms a shelf without an evident distinct knob in *G. genetta* as in *V. tangalunga.*

Viverricula indica (Fig. 1j) has a dorsal extension of the body beyone the cuboid but in other respects is quite similar to calcanea of *Genetta genetta,* although, as in *Viverra tangalunga,* there is more expression of a trochlear knob in *Viverricula.*

Calcanea of *Genetta tigrina* (Fig. 1n) have a better developed trochlear knob than that of *Genetta genetta* although only one specimen of *G. genetta* was available for study. The proximal edge of the trochlear process is more distal in one specimen of *G. genetta* than it is in any of 18 specimens of *G. tigrina* (Fig. 1n). There is less development of the sustentacular shelf in *G. genetta* than in *G. tigrina.*

In terms of a distinct trochlear knob, *Genetta victoriae* (Fig. 1dd) is more similar to *G. tigrina* than to *G. genetta.*

Genetta genetta is more similar to *Osbornictis piscovora* than other species of *Genetta* examined. Both *Osbornictis* (Fig. 1cc) and *G. genetta* have a trochlear shelf with little or no development of a trochlear knob. Single specimens of both species are similar in measurements and indices. *Osbornictis* seems to have a more slender (2.5 mm) and longer (7.9 mm) posterior articular surface than does the calcaneum of *G. genetta* (width 2.9 mm, length 7.1 mm) (width measured at point of change of slope of posterior articular surface, midway up surface in area of least width). Calcanea of these two forms probably are difficult to distinguish and may cause some questions as to the validity of *Osbornictis* as a separate genus.

Species	#	TL		W		D-VH		LWB	
		Range	Avg.	Range	Avg.	Range	Avg.	Range	Avg.
VIVERRINAE									
Genetta genetta	1		19.6		9.0		7.4		2.5
Genetta tigrina	18	18.8–21.1	19.9	8.9–11.1	9.7	6.7–7.6	7.2	2.5–3.6	3.0
Genetta victoriae	1		22.6		11.8		9.5		2.6
Osbornictis piscivora	1		21.0		9.0		7.4		2.8
Viverra civetta	4	30.4–37.7	32.6	16.2–18.5	17.6	11.9–15.8	14.4	5.4–6.5	6.0
Viverra megaspila	2	28.8–33.9	31.4	14.2–17.6	15.9	11.2–14.7	13.0	4.2–5.5	4.9
Viverra tangalunga	3	24.6–25.9	25.3	11.8–13.2	12.6	8.8–10.2	9.5	3.4–3.9	3.7
Viverra zibetha	11	27.7–33.9	30.5	14.3–18.4	15.4	10.7–13.8	11.9	4.2–6.5	4.8
Viverricula indica	13	18.2–24.2	22.0	9.6–12.2	10.9	7.2–10.0	8.6	3.0–4.3	3.6
PARADOXURINAE									
Arctitis binturong	7	34.7–40.2	37.3	17.1–21.3	19.5	11.8–14.5	13.2	5.0–6.1	5.3
Arctogalidia trivirgata	1		20.2		10.0		7.4		2.8
Nandinia binotata	5	21.5–24.1	22.6	10.5–12.5	11.7	7.8–8.7	8.3	2.9–3.5	3.3
Paguma larvata	7	23.4–29.9	25.6	11.3–15.7	13.2	8.3–12.1	9.9	3.1–5.1	3.8
Paradoxurus hermaphroditis	14	19.9–24.8	22.3	9.6–12.2	11.0	6.7–8.9	8.0	2.8–3.7	3.1
HEMIGALINAE									
Cynogale bennetti	2	25.3–25.6	25.5	11.8–12.1	12.0	10.1–10.4	10.3	3.5–3.7	3.6
Hemigalus derbyanus	2	20.3–21.8	20.8	11.5–11.8	11.2	7.7–7.8	7.8	2.7–3.8	3.3
HERPESTINAE									
Atilax paludinosus	11	22.6–26.0	24.8	9.8–11.5	10.7	8.7–10.7	9.7	2.5–4.0	3.3
Cynictis penicillata	4	15.7–17.2	16.3	7.8–8.4	8.1	6.2–7.0	6.5	2.4–2.8	2.6
Herpestes auropunctatus	1		12.4		5.5		4.7		1.6
Herpestes brachyurus	2	17.2–20.6	18.9	8.0–10.0	9.0	7.0–7.9	7.5	2.1–2.8	2.5
Herpestes edwardsi	4	15.0–17.2	16.2	7.5–9.0	8.4	6.1–7.2	6.6	2.0–2.8	2.5
Herpestes ichneumon	9	22.0–26.1	23.8	10.2–13.0	11.2	8.8–10.2	9.5	2.6–3.7	3.2
Herpestes pulverulentus	1		15.1		7.1		6.1		2.4
Herpestes sanquineus	6	13.7–15.1	14.4	6.6–8.2	7.2	5.1–6.1	5.6	1.8–2.0	1.9
Ichneumia albicauda	4	29.3–30.6	29.8	12.4–13.8	12.9	10.9–11.8	11.4	3.8–4.5	4.2
Suricata suricatta	3	13.7–14.4	14.0	7.0–7.4	7.1	5.6–5.9	5.8	2.5–2.7	2.6
Xenogale microdon	1		24.8		10.3		10.0		3.2
Bdeogale nigripes	1		27.0		13.9		10.7		4.4
Mungos mungo	2	19.3–20.9	20.1	8.6–9.0	8.8	8.0–8.9	8.5	2.8–3.1	3.0
Crossarchus obscurus	2	14.7–16.4	15.6	6.1–7.5	6.8	5.6–6.6	6.1	1.7–2.3	2.0

Although *Genetta genetta* is about the size of *Arctogalidia trivirgata,* calcanea of *Genetta tigrina* overlap in size those of *Arctogalidia* (Table 1). Calcanea of both species of *Genetta* can be easily distinguished based on a smaller medial articular and more distal trochlear process so that the proximal edge of the trochlear process is level with the distal edge of the medial articular surface; the distal edge of the medial articular surface in *A. trivirgata* is level with or distal to the distal edge of the trochlear process (Fig. 1c).

Nandinia binotata (Fig. 1e) has a large, more proximally located trochlear process and a large medial articular surface so that the proximal edge of the trochlear process is proximal to the distal edge of the medial articular surface not about even as in both species of *Genetta* (Fig. 1n and m). The calcanea of *Paguma larvata* (Fig. 1b) and *Paradoxurus hemaphroditus* (Fig. 1d) are similar to *Nandinia* and can be distinguished from *Genetta genetta* on the same basis.

The medial articular surface tends to be much larger in *Cynogale* (Fig. 1k) than in *Genetta* (Fig. 1m). There probably is no overlap in size of medial articular surfaces of *Cynogale* and *G. genetta. Hemigalus derbyanus* (Fig. 1-l) has a more prominent trochlear knob and a greater width/length index.

An exaggerated cuboid medio-lateral slope will separate all genera and species of Herpestinae from all members of Viverrinae which lack this slope. Specimen examined and illustrated: AM 80740, Fig. 1m.

Genetta tigrina—Large-spotted Genet

Genera and species with calcanea within the size range of *Genetta tigrina* are *G. genetta,* already discussed, perhaps *G. victoriae, Osbornictis piscivora, Viverricula indica, Nandinia binotata, Arctogalidia trivirgata, Paradoxurus hermaphroditus, Hemigalus derbyanus* and a number of distinctly different members of Herpestinae (Table 1).

Genetta tigrina (Fig. 1n) differs from *Osbornictis piscivora* (Fig. 1cc) as it does from *G. genetta*; there is a distinct trochlear knob on the calcaneum of *G. tigrina.*

Genetta victoriae (Fig. 1dd), like *G. tigrina,* has a distinct trochlear knob. There probably is no, or very little, overlap in size of these two species, *G. victoriae* being larger (Table 1). These calcanea would be difficult to tell apart if there is an overlap in size.

Genetta tigrina (Fig. 1n) differs from *Viverricula indica* (Fig. 1j) in having a more proximal trochlear knob; from *Arctogalidia trivirgata* (Fig. 1c) and *Nandinia binotata* (Fig. 1e) in having a more distal trochlear knob and a smaller medial articular surface; from *Paradoxurus hermaphroditus* (Fig. 1d), as well as the other paradoxurines, in having a much smaller medial articular surface.

Hemigalus derbyanus has a greater width/total length index (55–57, avg 56) than *G. tigrina* (45–53, avg 49). The greatest expansion of the distal end of the body is at the ventro-medial edge of the cuboid in *Hemigalus* (Fig. 1-l), and at the dorso-medial edge in *G. tigrina.*

Specimens examined: AM 51543, 83327, 83336 (yg), 83338, 83340, 83342, 83344 (yg), 83345, 83349, 83351–2, 83356–7, 83360, 150447; NM 25307, 35400, 164583, 164751 (yg), 270284 (AM 150447 illustrated, Fig. 1n).

Genetta victoriae—Lake Victoria Genet

A single calcaneum of *Genetta victoriae* (Fig. 1dd) resembles that of *G. tigrina*, previously discussed, but is larger. Comparisons of *G. victoriae* with species perhaps having the same size calcanea can be made using the discussions under *Genetta tigrina.*

Specimen examined and illustrated: AM 51406, Fig. 1dd.

Osbornictis piscivora—Congo Water Civet

A single specimen of *Osbornictis piscivora* has a sustentaculum and medial articular surface characteristic of Viverrinae. There is a slight development of a sustentacular shelf. The trochlear process forms a massive shelf (Fig. 1cc) similar in some respects to *Genetta genetta* (Fig. 1m), *Viverra civetta* (Fig. 1g) and *V. megaspila* (Fig. 1f). There is no distinct trochlear knob in *Osbornictis* as in *Genetta tigrina* (Fig. 1n). Comparisons of *G. genetta* with *Osbornictis* have been made under *G. genetta.*

Viverra civetta and *V. megaspila* are species with larger calcanea. Discussions of species within the same size range under *Genetta genetta* also can be used for *Osbornictis.*

Specimen examined and illustrated: AM 51514, Fig. 1cc (holotype).

Viverra civetta—African Civet

The calcanea of *Viverra civetta* are larger than eight other species of this subfamily examined (Table 1). There is an overlap in total length of this calcaneum with two of the other three species of *Viverra.*

Viverra civetta (Fig. 1g) have calcanea with a shelf-like trochlear process located more distally. *Viverra civetta, V. tangalunga* and *V. megaspila* have poorly defined anterior articular surfaces. Calcanea of *V. zibetha* have a better-developed anterior articular surface and an extension of this anterior articular surface onto the edge of the body which extends prominently distal to the cuboid surface; *V. tangalunga* is closest to *V. zibetha* in this respect. There may be no overlap in size of the calcanea of *V. tangalunga* and *V. civetta.*

The calcanea of *V. civetta* are difficult to distinguish from those of *V. megaspila.* Least width of body averages slightly smaller in *V. megaspila* and least width of body divided by dorso-ventral height ranges from 40 to 45 (avg 42) in *V. civetta* while the two specimens of *V. megaspila* are 37 and 38.

In general, calcanea of *Genetta* and *Osbornictis* are smaller and lack the distal-internal extension of the body towards the anterior articular surface which is present in *Viverra.* The trochlear process of *Genetta* is obviously grooved and often knob-like, continuing as a broad trochlear shelf as in *Viverra.*

Members of Paradoxurinae within or near the same size range of *Viverra civetta* are *Arctictis binturong* and *Paguma larvata.* Both *Arctictis* (Fig. 1a) and *Paguma* (Fig. 1b) differ from *Viverra civetta* (Fig. 1g) in having large medial articular surfaces on a sustentacular shelf that extends almost to the cuboid, and a proximal edge of the trochlear process which is never distal to the distal edge of the medial articular surface.

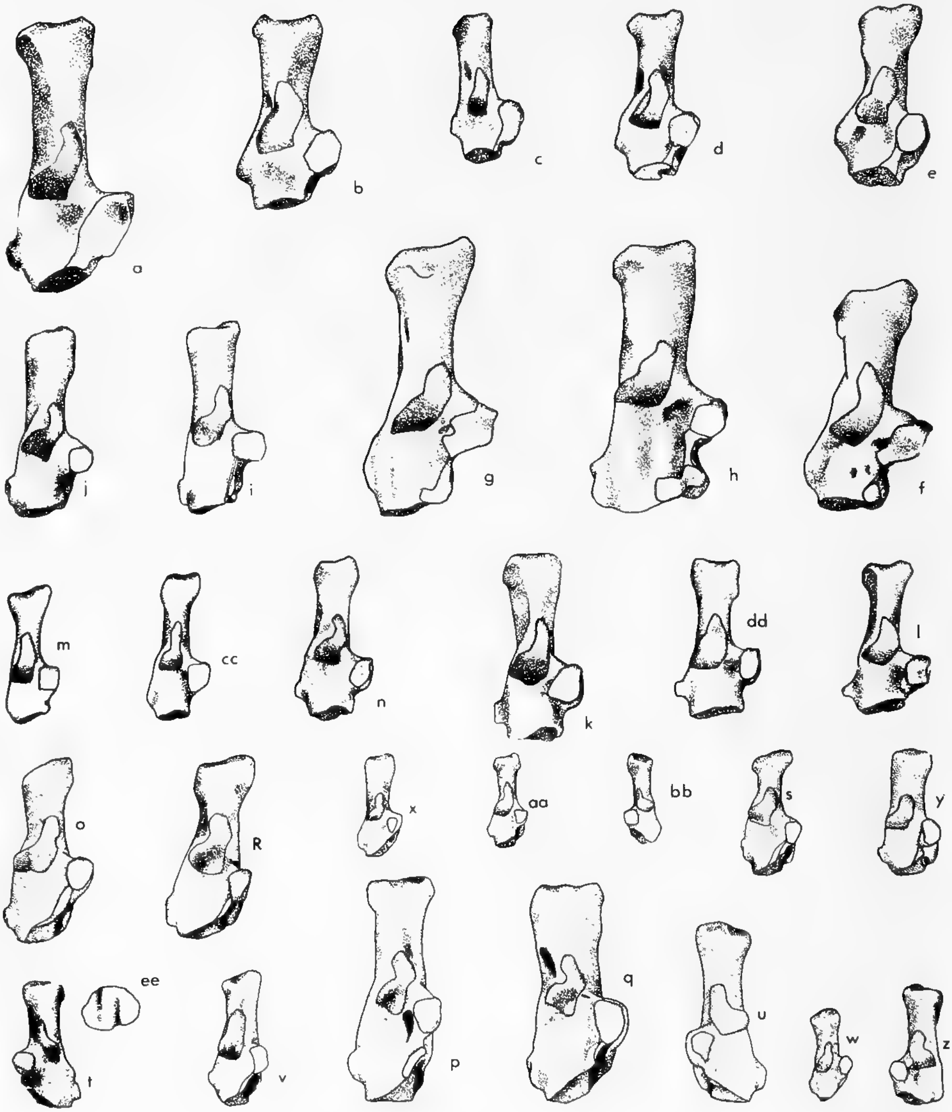

Fig. 1. Calcanea of members of the Viverridae. a. *Arctictis binturong*; b. *Paguma larvata*; c. *Arctogalidia trivirgata*; d. *Paradoxurus hemaphroditus*; e. *Nandinia binotata*; f. *Viverra megaspila*; g. *Viverra civetta*; h. *Viverra zibetha*; i. *Viverra tangalunga*; j. *Viverra indica*; k. *Cynogale benetti*; l. *Hemigalus derbyanus*; m. *Genetta genetta*; n. *Genetta tigrina*; o. *Atilax paludinosus*; p. *Ichneumia albicauda*; q. *Bdeogale nigripes*; r. *Herpestes ichneumon*; s. *Herpestes brachyurus*; t. *Mungos mungo*; u. *Xenogale microdon*; v. *Cynictis penicillata*; w. *Suricata suricatta*; x. *Herpestes pulverulentus*; y. *Herpestes edwardsi*; z. *Crossarchus obscurus*; aa. *Herpestes sanquineus*; bb. *Herpestes auropunctatus*; cc. *Osbornictis piscivora*; dd. *Genetta victoriae*.

Members of Hemigalinae could be confused with some members of Viverrinae. Members of Hemigalinae (Fig. 1k and l) have a broader sustentaculum extending farther towards the cuboid than members of the Viverrinae as well as having a smaller trochlear process.

The exaggerated cuboid slope will separate all genera and species of the Herpestinae from *V. civetta.*

Specimens examined: AM 51797, 51805, 86716; NM 270236 (AM 51797 illustrated, Fig. 1g).

Viverra megaspila—Large-spotted Civet

Comparisons of the calcanea of *V. megaspila* with other viverrids are discussed under *V. civetta* as these two species are similar; *V. megaspila* having a lower least width of body/dorso-ventral height index and a more obvious continuation of the trochlear shelf proximally (Fig. 1f).

Specimens examined: NM 267187, 270480 (NM 270480 illustrated, Fig. 1f).

Viverra tangalunga—Malay Civet

Viverra tangalunga has the smallest calcaneum examined (Table 1). The trochlear process is distinct, grooved, and located at the distal end of a slightly developed trochlear shelf (Fig. 1i). There is indication of a small anterior articular surface joined to the medial articular surface by a small waist in two of the three specimens available. The distal edge of the medial articular surface is slightly distal to the distal edge of the posterior articular surface with no expansion of a sustentacular shelf distally.

In size, calcanea of *V. tangalunga* overlap those of *Viverricula indica,* three genera in the Paradoxurinae (*Nandinia, Paguma,* and *Paradoxurus*), *Cynogale* in the Hemigalinae and three genera in the Herpestinae (*Atilax, Herpestes ichneumon,* and perhaps *Bdeogale*).

Viverricula indica has a smaller trochlear process (Fig. 1j) and, in all specimens examined (13), is slightly smaller in total length than three specimens of *Viverra tangalunga.*

Members of Paradoxurinae (Fig. 1b, d, and e) have expanded medial articular surfaces and a trochlear process with a distal edge usually proximal to or equal with the distal edge of the medial articular surface; this process in *V. tangalunga* is entirely distal to the medial articular surface (Fig. 1i).

Cynogale (Fig. 1k) has a sustentaculum that differs from that of *V. tangalunga* in having a sustentacular shelf extending almost to the cuboid.

Herpestines all have extremes in slope of the cuboid surface. There is only a slight slope of this surface in calcanea of *V. tangalunga.*

Specimens examined: AM 20790; NM 49931, 49975 (NM 49975 illustrated, Fig. 1i).

Viverra zibetha—Asiatic Civet

Calcanea of *Viverra zibetha* (Fig. 1h) are similar in size to those of *V. civetta* and *V. megaspila* (Table 1) previously discussed and are more similar in shape of the trochlear process to *V. tangalunga* (Fig. 1i) which has a smaller calcaneum.

Also, with calcanea of the same size are *Paguma larvata, Ichneumia albicauda,* and *Bdeogale nigripes.* Calcanea of *Paguma larvata* (Fig. 1b) have a more massive trochlear shelf and a trochlear process located more proximally than that of *V. zibetha* (Fig. 1h). The distal edge of the trochlear process in *P. larvata* is even with the distal edge of the medial articular surface. In *V. zibetha,* the proximal edge of the trochlear process is distal to the distal edge of the medial articular surface.

The calcanea of both *I. albicauda* (Fig. 1p) and *B. nigripes* (Fig. 1q) have a strongly slanted cuboid. This surface is almost at right angles to the long axis of the bone in *V. zibetha* (Fig. 1h).

Specimens examined: AM 43099, 43100, 113769; NM 22464, 240208, 256673, 258004, 258227 (yg), 258336–7 (yg), 258339, 258340 (yg), 258341 (NM 22464 illustrated, Fig. 1h).

Viverricula indica—Lesser Oriental Civet

Calcanea of *Viverricula indica* are smaller than those of the genus *Viverra* although approached by *Viverra tangalunga* (Table 1). In this subfamily, the calcanea of *Viverricula* resemble those of *Viverra tangalunga* (Fig. 1i) and *V. zibetha* (Fig. 1h) most closely. There could conceivably be an overlap in size with *V. tangalunga* discussed previously. *Genetta* (*genetta, tigrina* and *victoriae*), discussed under each species, lack the dorsal extension of the body beyond the cuboid surface but in other respects are quite similar to calcanea of *Viverricula.*

Other viverrids within the size range are: *Arctogalidia trivirgata, Nandinia binotata, Paguma larvata, Paradoxurus hemaphroditus,* perhaps *Cynogale bennetti, Hemigalus derbyanus, Atilax paludinosus,* perhaps *Cynictis penicillata, Herpestes* (*brachyurus,* perhaps *edwardsi,* and *ichneumon*), *Xenogale microdon,* and *Mungos mungo.*

Paradoxurines (*Arctogalidia, Nandinia, Paguma,* and *Paradoxurus*) have enlarged medial articular surfaces with sustentacular processes extending to or almost to the cuboid (Fig. 1c, e, b, and d). Calcanea of *Viverricula* (Fig. 1j) have a small medial articular surface and no sustentaculum extension towards the cuboid.

Herpestines (*Atilax, Cynictis, Xenogale, Mongos,* and *Herpestes*) have calcanea with an extreme medio-lateral sloping of the cuboid surface (Fig. 1o, v, u, t, r, s, and y).

Cynogale bennetti (Fig. 1k) and *Hemigalus derbyanus* (Fig. 1-l) have a slight sustentacular shelf which the calcanea of *Viverricula* lack (Fig. 1j). *Viverricula* usually have a dorsal extension of the body beyond the cuboid surface which calcanea of *Cynogale* and *Hemigalus* lack.

Specimens examined: AM 35351, 43127–8, 54831–2, 58377, 113770, 113775; NM 83663, 240007, 258005–6, 258333–5 (AM 54832 illustrated, Fig. 1j).

Subfamily Paradoxurinae

Most paradoxurines have an immense sustentaculum and a medial articular surface extending almost to the cuboid surface, a cuboid surface more or less at right angles to the long axis, a distal end of the body approximately equal with the cuboid surface, and the distal end of a knob-like trochlear process which, in most cases, is level with the distal edge of the medial articular surface or distal to the greatest expansion of the trochlear process.

Arctitis binturong—Binturong

Arctitis binturong, sometimes called the bear-cat, is the largest viverrid and has the largest calcanea (more than 30 mm in length and 15 mm in width) (Table 1).

A massive medial articular surface is broadly connected to the anterior articular surface (Fig. 1a) in six of the seven specimens examined. The trochlear process is small, grooved in three of the seven specimens and blends in with the trochlear shelf. The distal edge of the trochlear process is about level with the distal edge of the medial articular surface. In most specimens, the posterior articular surface tends to be to the most dorsal part of the calcaneum. All have the typical carnivore type of "hooked" tuberosity.

Some calcanea of *Viverra* (*civetta, magaspila* and *zibetha*) are as long or as wide as those of *A. binturong* (Table 1). These three species have been discussed.

Specimens examined: AM 22906, 35469, 80162–3, 90279, 119600; NM 49642 (AM 90279 illustrated, Fig. 1a).

Arctogalidia trivirgata—Small-toothed Palm Civet

The one specimen of *Arctogalidia trivirgata* has a massive shelfless sustentaculum, a large medial articular surface, a slightly grooved and small trochlear process which has a distal edge proximal to the distal edge of the medial articular surface, a smooth elongate posterior articular surface, a distinct pit at the inner edge of the cuboid surface as in *Paradoxurus,* and a dish-shaped dorsal table (Fig. 1c). In some respect, the calcaneum, especially the elongate posterior articular surface of *Arctogalidia,* is similar to that of the procyonid *Potos flavus* (Stains 1973: Fig. 4c). The broader sustentaculum and poorly grooved trochlear process of *Arctogalidia* easily separates these two, however.

Other viverrids in the size range of *Arctogalidia* are *Viverricula indica, Genetta tigrina,* and perhaps *Genetta genetta, G. victoriae* and *Osbornictis piscivora* (all five discussed previously), *Nandinia bonotata, Paguma larvata* (young only), *Paradoxurus hermaphroditus, Hemigalus derbyanus, Herpestes brachyurus,* and *Mungos mungo.*

Nandinia binotata is slightly larger than *Arctogalidia* in calcaneal measurements but as only one specimen of *Arctogalidia* was available for study there is probably an overlap in measurements (Table 1). In genera shape, the two species are similar (Fig. 1c and e). The posterior articular surface of *Arctogalidia* (Fig. 1c) is almost parallel with the long axis, that of *Nandinia* (Fig. 1e) is at more of an angle. The greater tuberosity is strongly hooked when viewed from a lateral aspect in *Arctogalidia*; has a slight hook in *Nandinia.* A minute anterior articular surface is present in *Arctogalidia*; an obvious anterior articular surface is present and is joined to the medial articular surface by a thin waist in *Nandinia.* The trochlear process of *Arctogalidia* is small; that of *Nandinia* is proportionately more massive. *Arctogalidia* has a distinct pit near the inner edge of the cuboid surface which *Nandinia* lacks.

Paguma larvata (Fig. 1b), like *Arctogalidia,* has a large medial articular surface and a small trochlear process. The trochlear process is slender and in most cases has an open grooved knob which is not distinctive dorsally. Although 19 specimens were available for study, 12 of these were subadults or young, thus only seven specimens are indicated in Table 1. There is an overlap in size when young specimens of *Paguma* are compared to adult specimens of *Arctogalidia.* However, there probably is no overlap in size when only adult specimens are compared. Dorso-ventral height of the calcanea of *Arctogalidia* is especially smaller (Table

1), even smaller than in young *Paguma.* The posterior articular surface, like in *Nandinia,* is at more of an angle to the long axis of the bone in *Paguma* (Fig. 1b). *Paguma* also lacks the distinct pit near the inner edge of the cuboid.

Paradoxurus hermaphroditus (Fig. 1d) has a large medial articular surface and an extension of the sustentacular shelf to the cuboid. The medial articular surface is proportionately longer and extends farther towards the cuboid in *Arctogalidia* (Fig. 1c). Medial articular surface and anterior articular surface are joined by an thin waist in *Paradoxurus*; the anterior articular surface and waist are minute in the one specimen of *Arctogalidia.* In shape of the posterior articular surface, some specimens of *Paradoxurus* are similar to the long narrow surface exhibited by *Arctogalidia.* The greater tuberosity of *Paradoxurus* tends to be hooked like *Arctogalidia.* A small, ungrooved trochlear process; no distinct sustentacular shelf ventral to the dorsal table; and an abrupt dorsal turning of the cuboid edge of the dorsal table as characteristics of *Arctogalidia* which should distinguish the calcanea of this genus from those of *Paradoxurus.* Calcanea of these two species are extremely similar, however.

Hemigalus derbyanus (Fig. 1-l) has a smaller medial articular surface and a small trochlear process in which the proximal edge is distal to the distal edge of the medial articular surface. In *Arctogalidia,* the enlarged medial articular surface is such that the distal edge of this surface is distal to the distal edge of the trochlear process (Fig. 1c). *Hemigalus* also lacks the greater tuberosity, has a shorter and stouter posterior articular surface, and lacks the abrupt upturning of the dorsal table found in *Arctogalidia.*

The calcanea of both *Herpestes brachyurus* (Fig. 1s) and *Mungos Mungo* (Fig. 1t) have sharply medio-lateral sloping cuboid surfaces; that of *Arctogalidia* (Fig. 1c) is more perpendicular to the long axis of the bone.

Specimen examined and illustrated: NM 267594, Fig. 1c

Nandinia binotata—Two-spotted Palm Civet

Specimens of *Nandinia binotata* examined have calcanea that probably fall within the size range of: *Genetta* (*genetta, victoriae,* and *tigrina*), *Osbornictis piscivora, Viverra tangalunga, Viverricula indica* and *Arctogalidia trivirgata,* which have been discussed previously; as well as *Paguma larvata, Paradoxurus hermaphroditus, Cynogale bennetti, Hemigalus derbyanus, Atilax paludinosus, Herpestes* (*brachyurus* and *ichneumon*), *Xenogale microdon,* and *Mungos mungo* (Table 1).

Nandinia (Fig. 1e) has a calcaneum typical of paradoxurines in having an enlarged medial articular surface, and expansion of the sustentacular shelf to the cuboid surface, a trochlear process which has the distal edge of this process located even with or slightly proximal to the distal edge of the medial articular surface, and an oval cuboid surface (Taylor 1976:241).

Paradoxurus hermaphroditus (Fig. 1d) and *Paguma larvata* (Fig. 1b) have trochlear processes located slightly more distal than those of *Nandinia* (Fig. 1e) so that the distal edge of this process is slightly distal to the distal edge of the medial articular surface; except for *Arctitis* (Fig. 1a), *Paradoxurus* and *Paguma* have the most distally located trochlear processes of members of the subfamily examined. *Paradoxurus* has a norrower posterior articular surface than *Nandinia.* Measurements and proportions of these two genera are similar, the greatest difference being that *Nandinia* has, on the average, a wider calcaneum (Table 1). The flexibility of the ankle and foot (Taylor 1970:48–49) perhaps results from this wider calcaneum.

Cynogale bennetti (Fig. 1k) and *Hemigalus derbyanus* (Fig. 1-l) have smaller, more distally located trochlear processes and smaller medial articular surfaces so that the proximal edge of the trochlear process is about even with the distal edge of the medial articular surface.

The members of the Herpestinae, *Atilax paludinosus* (Fig. 1o), *Herpestes brachyrus* (Fig. 1s), *H. icheumon* (Fig. 1r), *Xenogale microdon* (Fig. 1u), and *Mungos mungo* (Fig. 1t) have the medio-lateral sloping cuboid.

Specimens examined: AM 35440, 51461, 51469, 86712, 134969, (AM 134969 illustrated, Fig. 1e).

Paguma larvata—Masked Palm Civet

Previously discussed species with calcanea within or near the same size range as those of *Paguma larvata* are: *Genetta victoriae, Viverra* (*civetta, tangalunga,* and *zibetha*), *Viverricula indica, Arctogalidia trivirgata,* and *Nandinia binotata.* Other species within the calcaneal size of *Paguma* are: *Paradoxurus hermaphroditus, Cynogale bennetti, Atilax paludinosus, Herpestes ichneum,* and *Bdeogale nigripes.* Discussion of comparisons of these species (except *Paradoxurus*) with *Nandinia binotata* also will serve to distinguish them from *Paguma.*

Calcanea of *Paguma* (Fig. 1b) have the broadest posterior articular surface of the paradoxurines examined. The trochlear process is small and in some cases greatly reduced almost to the point of being absent. However, inspection of the ventral side of the bone reveals an obvious, almost flat, grooved trochlear knob. The distal edge of the trochlear process is slightly distal to the distal edge of the medial articular surface.

Some specimens of *Paradoxurus* (Fig. 1d) have even a greater reduction of the trochlear process than found in *Paguma. Paguma,* on the average, possess a larger calcaneum in all measurements than *Paradoxurus* but the indices are the same (Table 1). Other than size, the two species would be difficult to separate on the basis of calcanea.

Specimens examined: AM 43123 (yg), 60099 (yg), 60159 (yg), 85041 (yg), 174297 (yg); NM 240209, 253511–12, (both yg), 254640, 254689 (yg), 254916, 254924 (yg), 255003, 255458 (yg), 255562 (yg), 260613 (yg) (NM 255003 illustrated, Fig. 1b).

Paradoxurus hermaphroditus—Common Palm Civet

Comparisons of calcanea of *Paradoxurus* with members of similar size in the Viverrinae (*Genetta genetta, G. tigrina, G. victoriae, Osbornictis piscivora, Viverra tangalunga,* and *Viverricula indica*) and Paradoxurinae (*Arctogalidia trivirgata, Nandinia binotata,* and *Paguma larvata*) have been discussed. The similarity of the calcanea of *Paguma* to those of *Paradoxurus* has been discussed. Other species with calcanea within the size range are found in the Hemigalinae (*Hemigalus* *derbyanus*), and Herpestinae (*Atilax paludinosus, Herpestes brachyurus, H. ichneumon, Xenogale microdon,* and *Mungos mungo*).

Members of the Hemigalinae all have a trochlear process located distal to the distal edge of the medial articular surface. Herpestines have a cuboid surface at approximately a 45 degree medio-lateral angle to the long axis of the bone; that of *Paradoxurus* is almost at a right angle.

Specimens examined: AM 35090, 35780, 55799, 113032, 113771; NM 49702, 49868, 196623, 197243, 198064, 252598 (yg), 256912 (yg), 258001, 258003 (yg), 258007 (yg), 258224, 258226 (yg), 267595, 277230 (AM 113032 illustrated, Fig. 1d).

Subfamily Hemigalinae

Hemigalids have calcanea intermediate in characteritics between members of the Viverrinae and Paradoxurinae in terms of the sustentaculum and the medial articular surface. The cuboid surface of hemigalines is similar to that of paradoxurines, and the small, knob-like trochlear process is located distally so that the proximal edge of this process is equal in position with the distal edge of the medial articular surface. There is some development of a sustentacular shelf. The distal edge of the medial articular surface is proximal to the greatest expansion of the trochlear process as is also true of members of the Viverrinae.

Cynogale bennetti—Otter Civet

Calcanea of *Cynogale bennetti* have a medial articular surface almost as massive as those of paradoxurines but the small knob of the trochlear process is located distally such that the proximal edge is even with the distal edge of the medial articular surface (Fig. 1k) as in *Lutra canadensis* (Stains 1976: Fig. 1n). In addition, there is less expansion of the sustentaculum distally and ventrally in *Cynogale* than in paradoxurines, resulting in a more obvious and raised portion of the body ventral to the sustentaculum in *Cynogale.*

The greatest difference between *Cynogale* and viverrines is in the larger medial articular surface of *Cynogale.* There is a development of a slight sustentacular shelf in *Cynogale* which usually is absent in viverrines.

Cynogale has a calcaneum with a cuboid surface almost at right angles to the long axis of the bone, those of herpestines (*Atilax,* Fig. 1o; *Herpestes ichneumon,* Fig. 1r; and *Bdeogale,* Fig. 1q) have a medio-lateral slanted cuboid surface.

The single specimen of the other genus examined in the Hemigalinae, *Hemigalus derbyanus* (Fig. 1-l), is smaller than *Cynogale,* and has a less massive medial articular surface. There is also less obvious development of the sustentacular shelf in *Hemigalus* than *Cynogale.* Viewing the calcanea from the cuboid end of the bone, the two genera are easily distinguished. The cuboid surface in *Cynogale* tends to be elongated in a more dorso-ventral direction; that of *Hemigalus* in a medio-lateral direction. Thus, the trochlear process in *Cynogale* comes off at a sharp angle from the outline of the cuboid surface and in *Hemigalus* comes off almost straight from the ventral edge of the cuboid.

Specimens examined: NM 49869, 49975, (NM 49975 illustrated, Fig. 1k).

Hemigalus derbyanus—Banded Palm Civet

Comparative discussions under *Cynogale bennetti* can be used to distinguish *Hemigalus* from members of the various subfamilies. Discussion of the similarity of the calcanea of *Genetta, Cynogale,* and *Hemigalus* is found under *Genetta genetta.*

Specimens examined: NM 49927, 197239 (NM 49927 illustrated, Fig. 1-l).

Subfamily Herpestinae

Distally, calcanea of the herpestines slope from the outer edge of the cuboid to the base of the medial articular surface; the cuboid is slanted, not perpendicular to the main axis of the calcaneum. This characteristic will separate all members of the Herpestinae from individuals of all other subfamilies examined. Such a medio-lateral slope provides a more rigid locking system than that of a flat, dorso-ventral slope, resulting in an ankle which is less flexible and perhaps of more value in a terrestrial species.

Discussions under all other subfamilies have mentioned the characteristic cuboid slope of the herpestines, thus genera in the Herpestinae will be discussed only in terms of their similarities and differences with other genera and species in this group.

Atilax paludinosus—Water Mongoose

Calcanea of *Atilax paludinosus* are intermediate in size to other herpestines (Table 1). Within the same size range are: *Herpestes ichneumon, Bdeogale nigripes, Xenogale microdon* and perhaps *Herpestes brachyurus, Ichneumia albicauda,* and *Mungos mungo.*

The trochlear process in this genus is extremely variable from present and slightly grooved (six specimens) to entirely absent (five specimens). When present, the process is near the distal end (Fig. 1o). The center of the medial articular surface is near the distal edge of the posterior articular surface. A sustentacular shelf is absent or minute. An elongated anterior articular surface is located on the dorsal table at the inner edge of the cuboid surface and usually is joined to the medial articular surface. The posterior articular surface is smooth, with the distal half dropping abruptly. The greater tuberosity is reminiscent of that found in the Hyaenidae; that is, it is knob-like, tends to be shifted inwardly, and lacks a grooved appearance.

The one specimen of *Bdeogale nigripes* has a proportionately wider calcaneum than that of *Atilax.* The greatest width of the 11 specimens examined is 11.5 mm (avg 10.7) and that of *Bdeogale* is 13.9 mm. Width divided by total length produces an index ranging from 41 to 47 (avg 44) in *Atilax* and 52 in *Bdeogale.* The least width of body of *Bdeogale* also is larger (4.4 mm) than that of *Atilax* (2.5–4.0, avg 3.3 mm) producing a slightly higher least width of body/dorso-ventral height index (*Atilax,* 27 to 42, avg 34; *Bdeogale* 41). *Bdeogale* calcaneum has a well-developed groove on the body, ventro-lateral to the outer proximal edge of the posterior articular surface. The sustentaculum and medial articular surface of *Bdeogale* are larger and extend almost to the inner edge of the cuboid (Fig. 1q). The distance between the inner edge of the cuboid surface and the distal edge of the medial articular surface of *Atilax* is approximately the same as the longitudinal width of the medial articular surface. The dorsal table of *Atilax* forms a smooth curved surface, that of *Bdeogale* has a distinct valley between the trochlear process and the remainder of the dorsal table (Fig. 1q). Another specimen of *Bdeogale,* an immature specimen, has characteristics of the one adult specimen mentioned above.

The more rounded, slightly sloping, greater tuberosity of *Xenogale microdon* (Fig. 1u) will separate the calcanea of this species from *Atilax* (Fig. 1o). The dorsal table of *Xenogale* is level, not rounded as in *Atilax.*

Calcanea of *Atilax* and *Herpestes ichneumon* are difficult to distinguish. The sustentaculum of *H. ichneumon* (Fig. 1r) extends closer to the cuboid than that of *Atilax* (Fig. 1o) so that the deep pit at the dorso-medial edge of the cuboid surface is bordered by the sustentaculum. In *Atilax,* there is a slight distance between this pit and the sustentaculum proper. In general, the calcanea of *Atilax* are proportionately narrower than *H. ichneumon*; width/total length index of *Atilax* ranging from 41 to 47 (avg 44) and that of *H. ichneumon* from 43 to 50 (avg 47). Other proportions of these two species are similar.

Calcanea of two specimens of *Herpestes brachyurus* are much smaller than those of *Atilax* and there probably is no overlap in size. *Herpestes brachyurus* (Fig. 1s) lacks the deep pit near the dorso-medial edge of the cuboid surface but is similar to *Atilax* in position of sustentaculum. There is no overlap in dorso-ventral heights (*H. brachyurus,* 7.0–7.9, avg 7.5 mm; *Atilax,* 8.7–10.7, avg 9.7 mm). Calcanea of *H. brachyurus* do not overlap those of *Atilax* in length but do in width which is reflected in the width/total length index (*H. brachyurus,* 47–49, avg 48; *Atilax,* 41–47, avg 44).

Ichneumia albicauda (Fig. 1p) have larger calcanea than *Atilax* in all measurements except least width of body where there is some overlap. The sustentaculum and medial articular surface, in relation to the cuboid surface, are proximal in both species (Fig. 1p and o). The distance between these 2 surfaces in both species is approximately equal to the longitudinal width of the medial articular surface. The tuberosity of *Ichneumia* tends to be flatter with a slight dorsal groove (Fig. 1p). The tuberosity of *Atilax* is a broad basin-like pit. The medial articular surface of *Atilax* is oriented at a slight slant dorsally from the more dorsal-proximal edge to the more ventral-distal edge. In *Ichneumia* this surface is at a more pronounced slant.

Only two specimens of *Mungos mungo* were available for study. Both are at least 6 mm shorter than the smallest of the 11 specimens of *Atilax* and there probably is no overlap in size. The dorso-ventral height of *Mungos* is proportionately larger in relationship to length of the calcaneum with an index from 42 to 43; *Atilax* ranges from 37 to 42, avg 39. The other indices are similar for the two species (Table 1). The dorsal table of calcanea of *Mungos* (Fig. 1t) is similar to *Atilax* as is the sustentacular position. A pit at the dorso-medial edge of the cuboid surface is broad and shallow in *Mungos,* deep in *Atilax.* A second pit, present in *Mungos* at the base of the sustentaculum, is absent in *Atilax.* The greater tuberosity of *Mungos* (Fig. 1ee) has two deep grooves running from the inner to the outer edge of the tuberosity about 1/3 and 2/3 the distance from the dorsal to the ventral edge; *Atilax* lacks such grooves (Fig. 1o). Perhaps the digging habit of *Mungos* is reflected in the grooved greater tuberosity.

Specimens examined: AM 35743, 35771, 83331, 83337, 83339, 83341 (yg), 83347, 83350, 83353–4, 83359; NM 26708 (AM 83347 illustrated, Fig. 1o).

Cynictis penicillata—Yellow Mongoose

Four specimens of *Cynictis penicillata* have a well-defined trochlear process, the proximal edge of which is level with the distal edge of the medial articular surface (Fig. 1v). The distal edge of the trochlear process is about level with a point half way between the proximal edge of the trochlear process and the distal (cuboid) end of the bone. The sustentaculum is separated from the cuboid by a well-developed pit and groove. This groove is obvious when the calcaneum is viewed from the lateral side and the medio-lateral slope of the cuboid is obvious from a dorsal view. A slender anterior articular surface is present and joined to the medial articular surface by a thin waist. The posterior articular surface is slightly sigmoid in three of four specimens. The greater tuberosity is knob-like with a small flattened area on the dorso-medial side.

Within the size range of *Cynictis* are the calcanea of: *Herpestes* (*brachyurus, edwardsi, pulverulentus,* and *saquineus*), *Suricata suricatta,* and *Crossarchus obscurus.*

A prominent shortening of the body distally by the deep groove and pit between the cuboid and the sustentaculum will distinguish *Cynictis* from all genera of the same size. *Herpestes brachyurus, H. edwardsi, H. saquineus,* and *Crossarchus obscurus* also have this prominent resulting notch but the notch is more distal due to being a narrow groove without the pit. *H. pulverulentus* lacks the notch as do two of three specimens of *Suricata suricatta.*

Cynictis has a more massive body producing a greater least width of body/dorso-ventral height index (38–40, avg 39) than most species of *Herpestes* (30–41, avg 33–39), and *Crossarchus* (30–35, avg 33). *Suricata* (44–47, avg 45) has a much greater index than *Cynictis.*

Of the species listed above, *Suricata* (Fig. 1w) is most similar to *Cynictis* especially in the presence of the deep groove and pit, although these do not form the more proximal notch as in *Cynictis.* There probably is no overlap in size of these two species and the index listed above will separate them.

Specimens examined: AM 22739, 54095, 81755, 90282 (AM 54095 illustrated, Fig. 1v).

Herpestes auropunctatus—Small Indian Mongoose

Only one specimen of *Herpestes auropunctatus* was available for study. This specimen is smaller than any other viverrid examined, approximately 12.4 mm long and 5.5 mm wide (Table 1). *Herpestes sanquineus* and *Suricata suricatta* might approach *H. auropunctatus* in smallness of size. The sustentaculum does not extend distally to the edge of the cuboid in *H. auropunctatus* (Fig. 1bb) as in *H. sanquineus* (Fig. 1aa). *Suricata* has an enlarged pit area between the cuboid and sustentaculum. The anterior articular surface of *Suricata* borders this enlarged pit (Fig. 1w). Specimen examined and illustrated AM 60068, Fig. 1bb.

Herpestes brachyurus—Short-tailed Mongoose

The calcaneum of *Herpestes brachyurus* has a deep groove between cuboid and body, producing a distal notch when viewed from the later aspect. The cuboid surface tends to be dish-shaped. Other herpestines the size of *H. brachyurus* are *Cynictis penicillata* (discussed previously), *H. edwardsi, Mungos mungo* and perhaps *Crossarchus obscurus.*

Calcanea of *H. brachyurus* (Fig. 1s) and *H. edwardsi* (Fig. 1y) are similar. In the few specimens available, there is a difference in the width/total length index; *H. brachyurus* ranging from 47 to 49 (avg 48), and *H. edwardsi* from 50 to 55 (avg 52). The sustentaculum does not extend as far distally in *H. brachyurus* (Fig. 1s) as in *H. edwardsi* (Fig. 1y) and an additional articular surface is present between the anterior articular surface and the cuboid in *H. brachyurus.* The greater tuberosity of *H. brachyurus* (Fig. 1s) is slanted so that the inner side is more proximal than the external-lateral side. The greater tuberosity of *H. edwardsi* lacks this slant and the proximal end is more at right angles to the long axis (Fig. 1y).

The distal end of the posterior articular surface is at a greater angle (more abrupt) in *Mungos mungo* (Fig. 1t) than *H. brachyurus* (Fig. 1s). The trochlear process tends to be distal to the sustentaculum in *Mungos*; in *H. brachyurus* this process and the sustentaculum are at approximately the same level. The slightly narrower calcanea produces a smaller width/total length index in *Mungos* (43–45, avg 44) than in *H. brachyurus* (47–49, avg 48), and a greater dorso-ventral height/total length index of 42–43 (avg 42) for *M. mungo* and 38–41 (avg 39) for *H. brachyurus.* If the latter index is subtracted from the former, a more obvious difference is obtained: *H. brachyurus,* 5.8 to 10.1; *M. mungos,* 0.5 to 3.1.

Crossarchus obscurus has a distinctly grooved trochlear process on the distal end of a well-developed trochlear shelf (Fig. 1z). The groove on the trochlear process of *H. brachyurus* is not as distinct or deep, even though the calcaneum is larger. The trochlear shelf is more massive, not as thin and distinct as that of *Crossarchus.* The tuberosity of *Crossarchus* has a distinct rounded area anteriorly, then a slight groove, followed by an abrupt raised area on the internal half.

Specimens examined: NM 49925, 198071 (NM 198071 illustrated, Fig. 1s).

Herpestes edwardsi—Indian Grey Mongoose

Members of the Herpestinae examined within the size range of *Herpestes edwardsi* and already discussed are *Cynictis penicillata* and *Herpestes brachyurus.* In addition, *Herpestes pulverulentus, H. sanquineus, Crossarchus obscurus,* and perhaps *Suricata suricatta* are within this size range.

H. pulverulentus has a more rounded trochlear shelf (Fig. 1x) without the obvious trochlear process possessed by *H. edwardsi* (Fig. 1y). The width thus tends to be proportionately less in *H. pulverulentus* than *H. edwardsi* resulting in a small width/total length index in *H. pulverulentus.* The medial articular surface of *H. pulverulentus* is minute and the cuboid edge of the dorsal table slopes abruptly from the sustentaculum to the distal end of the bone.

H. sanquineus (Fig. 1aa) has a sustentaculum that extends almost to the cuboid so that the distal cuboid end of the bone slopes from the sustentaculum to the trochlear side at a steep angle, as in *H. pulverulentus. H. edwardsi* contains a swelling from the sustentaculum to the inner cuboid edge, resulting in a less pronounced slope (Fig. 1y). The greater tuberosity of *H. sanquineus* possesses a dorsal flattened area that tends to slope towards the posterior articular surface, thus, if observed from the lateral aspect, this tuberosity appears more peaked than either rounded or more or less flat as in *H. edwardsi.* From the dorsal aspect, the greater tuberosity of *H. sanquineus* is more proximal on the inner side (Fig. 1aa); that of *H. edwardsi* tends to be flat (Fig. 1y).

Crossarchus, like *H. sanquineus,* has a sloping greater tuberosity (Fig. 1z). The trochlear process is at the calcaneal distal edge in *Crossarchus* and slightly proximal from the distal edge in *H. edwardsi* (Fig. 1y). *Crossarchus* also has a thin, well-developed trochlear shelf which in *H. edwardsi* is massive with a knob-like trochlear process. The width/total index in *H. edwardsi* is greater (50–55, avg 52) than that of *Crossarchus* (42–46, avg 44).

Calcanea of *Suricata suricatta* have a deep pit between the cuboid and sustentaculum with an elongate obvious anterior articular surface (or continuation of the medial articular surface) lying on the dorsal edge of this pit (Fig. 1w). Like *H. edwardsi,* the greater tuberosity tends to be flat. The proportionately larger least width of body measurements results in a greater least width of body/dorsoventral height index for *Suricata* (44–47, avg 45) compared to *H. edwardsi* (32–41, avg 38).

Specimens examined: AM 35441, 70006, 70048; NM 241124 (AM 35441 illustrated, Fig. 1y).

Herpestes ichneumon—Greater Grey Mongoose

Herpestes ichneumon has the largest calcaneum of any *Herpestes* examined (Table 1). Within the calcaneal size range of *H. ichneumon* are *Atilax paludinosus,* previously discussed, *Xenogale microdon* and perhaps *Ichneumia albicauda, Bdeogale nigripes,* and *Mungos mungo.*

Herpestes ichneumon (Fig. 1r) has a slanting tuberosity, a well-developed trochlear process (grooved in three of 10 specimens) with shelf, and a well-developed longitudinal pit at the distal edge of the sustentaculum. There is also a groove at the distal edge of the body, between the body and the concave cuboid, that is continuous with the longitudinal pit. There is a poorly developed anterior articular surface and an additional articular surface between the anterior articular surface and the cuboid in eight of 10 specimens which probably articulates with the novicular.

The calcanea of *Xenogale microdon* (Fig. 1u) tend to have a curved rather than a strongly slanting greater tuberosity. The pit or groove at the distal edge of the body is not as well-developed as in *H. ichneumon.* In many respects the shapes and proportions of the calcanea of these two species are similar and thus may be difficult to distinguish.

There is probably no overlap in size of calcanea of *Herpestes ichneumon* and *Ichneumia, I. albicauda* being larger. *I. albicauda* lacks the deep pit between the cuboid and sustentaculum, and has a well developed, elongate anterior articular surface (Fig. 1p). One of four specimens of *I. albicauda* has a slightly grooved trochlear process, the rest are ungrooved.

The sustentaculum and medial articular surface of *Bdeogale nigripes* are expanded and extend almost to the cuboid (Fig. 1q), trochlear process large and grooved, greater tuberosity flat across the proximal end, and dorsal table raised with a distinct valley separating the trochlear process from the dorsal table. These characteristics should easily distinguish *Bdeogale* from *Herpestes ichneumon* (Fig. 1r).

Mungos mungo has a calcaneum that lacks the single deep basin-like pit between the sustentaculum and cuboid; instead, two pits are present, one distal to the sustentaculum and the other proximal to the cuboid. Because of the grooved area across the greater tuberosity, the tuberosity of *M. mungo* (Fig. 1t) looks flatter than strongly slanted as in *H. ichneumon* (Fig. 1r).

Specimens examined: AM 35182, 82278–9, 83330, 83334, 83343, 83346, 83358; NM 258111 (AM 83358 illustrated, Fig. 1r).

Herpestes pulverulentus—Cape Grey Mongoose

One specimen of *Herpestes pulverulentus* was available for study. Probably within the size range of *H. pulverulentus* are *Cynictis penicillata* and *H. edwardsi,* previously discussed, and *Herpestes sanquineus, Suricata suricatta* and *Crossarchus obscurus.*

The least width of body in *H. pulverulentus* is greater than any of six specimens of *H. sanquineus,* producing a greater least width of body/dorso-ventral height index (Table 1). Whether such proportions would be maintained if other specimens were available is questionable. The tuberosity of *H. pulverulentus* (Fig. 1x) is more massive than *H. sanquineus* (Fig. 1aa). The proximal edge of the medial articular surface of *H. pulverulentus* is approximately equal with the distal edge of the posterior articular surface (Fig. 1x), slightly proximal to the distal edge of the posterior articular surface in *H. sanquineus* (Fig. 1aa).

Calcanea of *Suricata suricatta* are rounded to flat on the proximal end of the greater tuberosity (Fig. 1w); that of *H. pulverulentus* is more proximal toward the inner side and thus slightly slanting (Fig. 1x). *Suricata* has a more massive dorsal table thus does not slant as abruptly at the dorsal end of the bone, a well-developed pit between the cuboid and sustentaculum, and a better developed anterior articular surface.

The calcaneum of *Crossarchus obscurus* has a thin, well-developed sustentacular shelf with the trochlear process more distal in relation to the medial articular surface (Fig. 1z). The trochlear process is at approximately the same level in *H. pulverulentus* (Fig. 1x). The trochlear process of *Crossarchus* also is located farther distally than that of *H. pulverulentus.*

Specimen examined and illustrated: NM 238036, Fig. 1x.

Herpestes sanquineus—Slender Mongoose

Herpestes sanquineus have calcanea within the size range of *H. edwardsi* and *H. pulverulentus,* previously discussed, and *Suricata suricatta* and *Crossarchus obscurus.*

Calcanea of *H. sanquineus* lack a deep pit between the cuboid and sustentaculum which is present in *Suricata.* The greater tuberosity is slanting in *H. sanquineus* (Fig. 1aa) rather than rounded from the dorsal aspect as in *Suricata* (Fig. 1w).

The enlarged, thin trochlear shelf with the resulting more dorsal trochlear process in *Crossarchus* will distinguish *Crossarchus* (Fig. 1z) from *H. sanquineus* (Fig. 1aa).

Specimens examined: AM 82766, 83332, 83337, 83362; NM 251749, 251796 (yg), 251961 (NM 251961 illustrated, Fig. 1aa).

Ichneumia albicauda—White-tailed Mongoose

Of herpestine Calcanea examined, those of *Ichneumia* (Table 1) are the largest. Within the size range of *I. albicauda* are calcanea of perhaps *Atilax paludinosus* and *Herpestes ichneumon,* already compared, and *Bdeogale nigripes.*

Calcanea of *Bdeogale* (Fig. 1q) have a more massive medial articular surface than *I. albicauda,* which extends almost to the level of the inner edge of the cuboid. Thus, there is a continual slope from the distal edge of the sustentaculum to the external distal edge of the cuboid. In *I. albicauda* (Fig. 1p) this slope extends distally from the sustentaculum to the inner distal edge of the cuboid then changes angles to the external distal edge of the cuboid. The cuboid articulation limits rotation of the foot. The resulting elongated dorsal table of *I. albicauda* is lined on the internal edge of a narrow, elongate anterior articular surface.

Specimens examined: AM 83328, 83355; NM 163294, 306263 (NM 306263 illustrated, Fig. 1p).

Suricata suricatta—Grey Meerkat

Calcanea of *Suricata suricatta* have an enlarged dish-like pit between the cuboid and the base of the sustentaculum which is edged by an elongate anterior articular surface joining the medial articular surface (Fig. 1w). The similarity of *Cynictis penicillata* (Fig. 1v) has been discussed. The smaller size and more distal trochlear process of the calcanea of *Suricata* will separate these species. The tuberosity of *Suricata* tends to be flat or slightly rounded; that of *Cynictis* is sloping, more proximal on the medial side. Species of *Herpestes* within or near the size range of *Suricata* are *H. edwardsi, H. pulverulentus,* and *H. sanquineus.* These three species have been discussed previously.

Also within the size range of *Suricata* is *Crossarchus obscurus.* The expanded, thin trochlear shelf and absence of a dish-like pit between the cuboid and sustentaculum of *Crossarchus* will distinguish *Crossarchus* from *Suricata. Crossarchus* also tends to have a more distally located sustentaculum (Fig. 1z).

Specimens examined: AM 35637, 35646, 90441 (AM 35646 illustrated, Fig. 1w).

Xenogale macrodon

Xenogale macrodon has a flat to slightly rounded greater tuberosity (Fig. 1u). Of the species of *Herpestes,* only *H. edwardsi* (Fig. 1y) has this feature but *H. edwardsi* is below the size range of *Xenogale.*

The single specimen of *Xenogale* falls within the size range of *Atilax paludinosus, Herpestes ichneumon* and perhaps *Bdeogale nigripes.* The flat to rounded greater tuberosity of *Xenogale* (Fig. 1u) separates this specimen from the strongly sloped tuberosity of *Atilax* (Fig. 1o). *Xenogale* is approached more closely in this respect by *Herpestes ichneumon* (Fig. 1r). *H. echneumon* has an obvious pit between the cuboid and sustentaculum which is not as obvious in *Xenogale.*

Bdeogale nigripes (Fig. 1q) has an expanded medial articular surface and an extension of the sustentaculum to the inner edge of the cuboid surface.

Xenogale is considered synonymous with *Herpestes* by some authors (Walker 1964:1250; Ewer 1973:405) and the similar calcanea of *H. edwardsi* supports this view.

Specimen examined and illustrated: AM 51610, Fig. 1u.

Table 2. Indices for calcanea of members of the Viverridae.

	W/TL		D-VH/TL		LWB/D-VH	
Species	Range	Avg.	Range	Avg.	Range	Avg.
VIVERRINAE						
Genetta genetta		46		38		34
Genetta tigrina	45–53	49	34–38	36	34–52	42
Genetta victoriae		52		42		27
Osbornictis piscivora		43		35		38
Viverra civetta	48–53	50	39–42	40	40–45	42
Viverra megaspila	49–52	51	39–43	41	37–38	38
Viverra tangalunga	48–52	50	36–40	38	33–42	39
Viverra zibetha	48–54	51	38–41	39	37–47	40
Viverricula indica	46–53	50	35–42	39	36–47	42
PARADOXURINAE						
Arctitis binturong	46–56	52	33–38	35	35–43	41
Arctogalidia trivirgata		50		37		38
Nandinia binotata	48–55	52	35–40	37	33–44	40
Paguma larvata	42–55	50	33–42	37	32–43	38
Paradoxurus hermaphroditus	47–52	49	33–39	36	34–45	39
HEMIGALINAE						
Cynogale bennetti		47	40–41	40	35–36	35
Hemigalus derbyanus	55–57	56	37–38	37	35–49	42
HERPESTINAE						
Atilax paludinosus	41–47	44	37–42	39	27–42	34
Cynictis penicillata	49–52	50	40–41	40	38–40	39
Herpestes auropunctatus		44		38		34
Herpestes brachyurus	47–49	48	38–41	39	30–35	33
Herpestes edwardsi	50–55	52	38–42	41	32–41	38
Herpestes ichneumon	43–50	47	38–43	40	29–37	34
Herpestes pulverulentus		47		40		39
Herpestes sanquineus	46–56	50	36–41	39	33–37	35
Ichneumia albicauda	42–47	43	37–40	38	34–39	37
Suricata suricatta	50–51	51	40–42	41	44–47	45
Xenogale microdon		42		40		32
Bdeogale nigripes		52		40		41
Mungos mungo	43–45	44	42–43	42		35
Crossarchus obscurus	42–46	44	38–40	39	30–35	33

Bdeogale nigripes—Black-footed Mongoose

Of the Herpestinae, *Bdeogale nigripes* has the greatest expansion of the medial articular surface similar to the condition found in members as the Paradoxurinae. The greater tuberosity tends to be flat rather than sloping (Fig. 1q). There is a well-developed groove ventro-lateral to the posterior articular surface. A distinct valley is present between the trochlear process and the dorsal table. The large trochlear process is distinctly grooved.

Within the size range of *Bdeogale* are calcanea of *Atilax paludinosus, Herpestes ichneumon* and *Ichneumia*—all three of which have been discussed previously.

Specimens examined: AM 51580 (yg), 51581 (AM 51581 illustrated, Fig. 1q).

Mungos mungo—Banded Mongoose

A broad, shallow pit is present on the calcanea of *Mungos mungo* between the inner edge of the cuboid and the sustentaculum. A second pit is present at the base of the sustentaculum. The greater tuberosity of *Mungos* has a deep groove (Fig. 1t). The dorsal side of the trochlear process is slightly dorsal in position in relationship to the dorsal side of the sustentaculum.

Species with calcanea of similar size (*Atilax paludinosus, Herpestes brachyurus* and *Herpestes ichneumon*) have been discussed.

Specimens examined: NM 251762, 252296 (NM 251762 illustrated, Fig. 1t).

Crossarchus obscurus—Cusimanse

The trochlear process of this small viverrid, *Crossarchus obscurus,* is distinctly grooved and located on the distal end of a thin, well-developed trochlear shelf (Fig. 1z). The greater tuberosity is grooved vertically about one-third dorsally from the ventral edge and has a knob dorsal to this groove on the medial side. Dorsal to this knob is a slight groove followed by a gently rounded area. From a dorsal aspect, the tuberosity is sloping from the inner toward the outer edge (Fig. 1z).

Other herpestines within the size range of *Crossarchus* have been discussed (*Herpestes auropunctatus, H. brachyurus, H. edwardsi, H. pulverulentus, H. sanquineus, Suricata suricatta*).

Specimens examined: NM 269834, 300798 (NM 300798 illustrated, Fig. 1z).

Conclusions

Calcanea of members of the family Viverridae can be placed easily into subfamilies, except perhaps those of the Hemigalinae. Species within each subfamily have calcanea that are quite similar.

Members of the Viverrinae, Paradoxurinae and Hemigalinae have calcanea with cuboid surfaces more or less at right angles to the longitudinal axis of the bone. The cuboid surface of the Herpestinae tends to be less than at a right angle.

Members of the Viverrinae have a small medial articular surface and little or no development of a sustentacular shelf. *Viverra* and *Viverricula* lack any extension of the sustentacular shelf. Within these two genera, two groups are recognized; *Viverra civetta* and *V. megaspila* form one group, and *V. tangalunga, V. zibetha* and *Viverricula indica* form the other. *Genetta* and *Osbornictis* have a slight development of the sustentacular shelf. *Osbornictis* and *Genetta genetta* have more development of a trochlear shelf, whereas *Genetta tigrina* and *G. victoriae* have a distinct knob like process similar to that in *Viverricula.*

Paradoxurines have an immense medial articular surface and a sustentacular shelf that extends almost to the cuboid. The distal edge of the medial articular surface is even with, or distal to, the greatest expansion of the trochlear process. Calcanea of all paradoxurines are quite similar, those most difficult to distinguish from each other being *Arctogalidia, Paguma* and *Paradoxurus.* In many respects, other than size, *Arctitis* and *Nandinia* are similar.

Calcanea of the two genera in the Hemigalinae are intermediate between calcanea of the Viverrinae and Paradoxurinae in size of the medial articular surface and expression of the sustentacular shelf. The Hemigalinae resembles the Viverrinae in that the distal edge of the medial articular surface is proximal to the greatest expansion of the trochlear process.

All herpestines have an extreme medio-lateral slanting of the cuboid surface. Some members of this subfamily have a greater tuberosity reminiscent of the type found in the Hyaenidae (Stains 1962); this is especially true of *Atilax paludinosus*. Calcanea of *Bdeogale* and *Suricata* appear to be quite similar and tend to form the nucleus of one group; *Crossarchus* and *Mungos* tend to form the nucleus of a second group. In the *Suricata-Bdeogale* group are *Cynictis, Xenogale,* and *Herpestes* (*edwardsi, ichneumon,* and *pulverulentus*). In the *Crossarchus-Mungos* group are *Atilax, Ichneumia,* and *Herpestes sanquineus*. *Herpestes brachyurus* has characteristics of both groups.

Literature Cited

Ewer, R. F. 1973. The Carnivores. Cornell University Press. 494 pp.

Robinette, H. R., and H. J. Stains. 1970. Comparative study of the calcanea of the pinnipedia. J. Mammal., 51(3):527–541.

Stains, H. J. 1959. Use of the calcaneum in studies of taxonomy and food habits. J. Mamm., 40(3): 392–401.

———. 1962. Osteological data used in mammal classification. Syst. Zool., 11(3):127–130.

———. 1973. Comparative study of the calcanea of members of the Ursidae and Procyonidae. Bull. So. California Acad. Sci., 72(3):137–148.

———. 1976. Calcanea of members of the Mustelidae. Part II. The Mellivorniae, Melinae, Mephitinae, and Lutrinae. Bull. So. California Acad. Sci., 75(3):249–257.

Taylor, M. E. 1970. Locomotion in some East African viverrids. J. Mamm., 51(1):42–51.

———. 1976. The functional anatomy of the hindlimb of some African Viverridae (Carnivora). J. Morph., 148(2):227–254.

Walker, E. P. 1964. Mammals of the World. Volume II. Pp. 647–1500. The Johns Hopkins Press, Baltimore.

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Bull. Southern California Acad. Sci.
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Research Notes

Light/Dark Control of Diurnal Acid Metabolism in the Submerged Aquatic *Isoetes howellii*

It has been demonstrated recently that the leaves of the submerged aquatic *Isoetes howellii* Engelmann (Isoetaceae) possess a diurnal acidification-deacidification cycle strongly resembling that observed in terrestrial CAM (Crassulacean Acid Metabolism) plants (Keeley 1981a). In *I. howellii* leaves there is an overnight increase of 100–200 μequivalents titratable acidity per gram fresh weight, the bulk of which is due to malic acid. It was also demonstrated that these leaves are capable of substantial CO_2-fixation in the dark, the primary product being malic acid. More recent studies show that these plants have a net uptake of CO_2 at night and, depending upon conditions, this can exceed daytime CO_2 uptake (Keeley and Bowes 1982). It was suggested (Keeley 1981a) that diurnal acid metabolism may have been selected for in this aquatic plant because of low availability of CO_2 for photosynthesis during the day and there is some evidence for this (Keeley 1981b). Studies of other *Isoetes* species, representing a range of habitats, indicates that diurnal acid metabolism is common in the genus (Keeley 1982).

The purpose of this study was to determine the extent of light/dark control on malic acid accumulation in submerged leaves of *Isoetes howellii.*

I. howellii is an aquatic or amphibious lower vascular plant with quill-like leaves (15–30 cm) arising from an underground corm. It is distributed throughout California and other western states in temporary pools (Munz 1959). The individuals utilized in this study were obtained in the spring of 1979 from "vernal pools" on Miramar Naval Air Station, San Diego County, California, USA.

Mature *I. howellii* were transplanted, along with substrate, to an aquarium where the water level was maintained above the tips of the leaves. The aquarium was kept in an environmental chamber with a 12 hr photoperiod and 30°C light/20°C dark air temperature. Photon flux density of 400 $\mu E\ m^{-2}\ sec^{-1}$ (PAR) was provided with a combination of incandescent and fluorescent bulbs. IRGA studies show CO^2-uptake in the light by *I. howellii* is light saturated at $<400\ \mu E\ m^{-2}\ sec^{-1}$ (Keeley and Bowes 1982). All experiments were initiated with the photo period running from 0600 hr (Pacific Standard Time) to 1800 hr or 1800 hr to 0600 hr.

Every 12 hours, at 0600 hr (AM) and 1800 hr (PM), two samples of several leaves each were washed with distilled water, blotted dry, weighed, and ground in a mortar with cold distilled water. This extract was filtered through cheesecloth, deproteinized with 1 N perchloric acid and centrifuged at low speed. The supernatant was assayed spectrophotometrically using an enzymatic end-product assay of Gutmann and Wahlefeld (1974).

The normal nighttime acidification and daytime deacidification cycle in *I. howellii* involved a diurnal fluctuation of >100 μeq/g FW. This pattern changed abruptly when the light/dark cycle was disturbed. Figure 1 shows that, under continuous light (beginning at the end of the normal light period), the malic acid concentration rose to a level intermediate to control AM and PM levels. Over

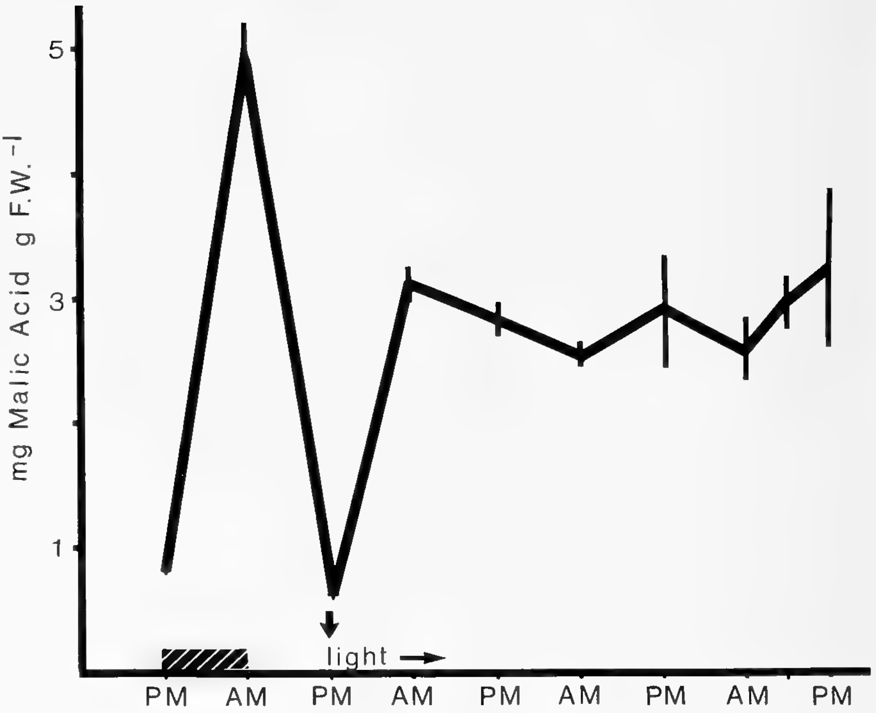

Fig. 1. Effect of continuous light on malic acid concentration (mg per gm fresh weight) in leaves of *I. howellii* at 0600 hr (AM) and 1800 hr (PM). Striped lines indicate darkness. Controlled conditions were disrupted at the arrow by continuous light. Points are the mean of 2 replicates, vertical lines indicate ±1 S.E. of the mean.

the 72 hr period of continuous light, malic acid concentration fluctuated very little around this intermediate level with no diurnal rhythm.

When lights were left off at the end of the dark period, malic acid concentrations dropped in the first 12 hrs (Fig. 2). Over the 12 hr dark period malic acid levels continued to drop to a level approximating PM levels under controlled conditions.

Figure 3 shows the effect of shifting the light/dark cycle 12 hr. This was accomplished by interjecting a 24 hr dark period followed by a return to the 12 hr light/12 hr dark cycle but offset such that the end of the light period occurred at 0600 hr and the dark period ended at 1800 hr. Malic acid concentration immediately started "tracking" the photo period; acidification during the dark (0600 hr to 1800 hr) and deacidification during the light (1800 hr to 0600 hr). During the first 72 hr after the photo period was shifted, the malic acid fluctuations were 40% lower than controls. This experiment was continued for another 72 hrs during which measurements were not made. When measurements were resumed it was observed that within 144 hrs after the original shift in the light/dark cycle the malic acid fluctuations approached control levels.

Conclusions

It is apparent that the acidification/deacidification cycle in *Isoetes howellii* leaves is not an endogenous rhythm. Continuous light or dark immediately disrupts the

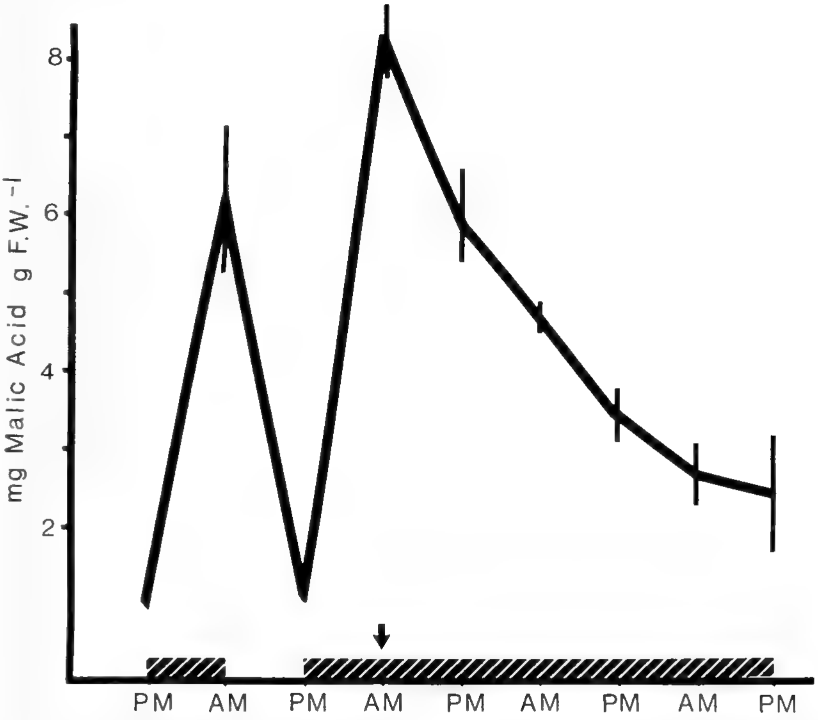

Fig. 2. Effect of continuous dark on malic acid concentration in leaves of *I. howellii* at 0600 hr (AM) and 1800 hr (PM). Striped lines indicate darkness. Controlled conditions were distrupted at the arrow by continuous dark. Points are the mean of 2 replicates, vertical lines indicate ±1 S.E. of the mean.

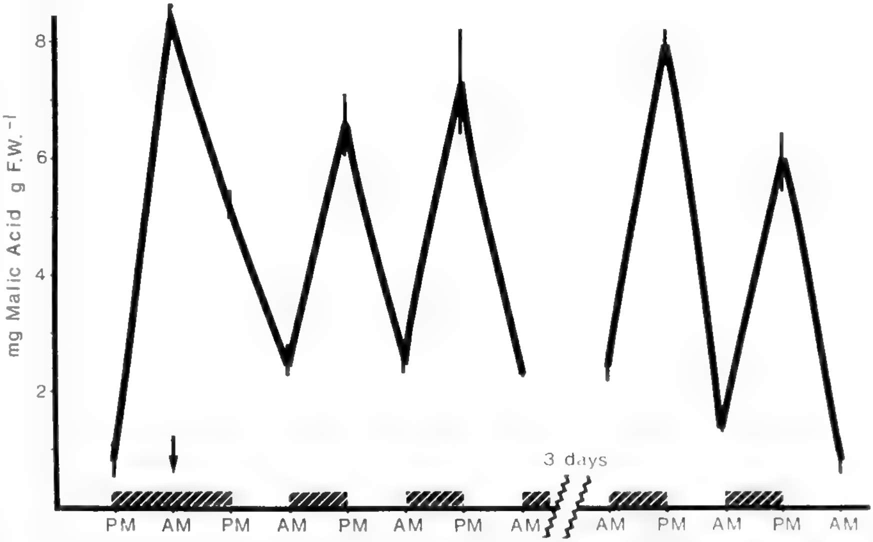

Fig. 3. Effect of reversed light/dark cycle on malic acid concentration in *I. howellii* leaves. Striped lines indicate darkness. Light/dark cycle was reversed at the arrow so that dark began at 0600 hr (AM) and light began at 1800 hr (PM). Points are the mean of 2 replicates, vertical lines indicate ±1 S.E. of the mean.

normal pattern of malic acid build-up and breakdown. The strong control exerted by the light/dark cycle is evidenced by the abrupt reversal of acidification/deacidification after a 12 hr shift in the photo period.

Literature Cited

Gutmann, I., and W. A. Wahlefeld. 1974. L-Malate: Determination with malate dehydrogenase and NAD. *In* Bergmeyer, H. U. (ed.), Methods of enzymatic analysis, Vol. 4:1585–1589 Academic Press, New York.

Keeley, J. E. 1981a. *Isoetes howelli*: A submerged aquatic CAM plant? American Journal of Botany, 68:420–424.

———. 1981b. Diurnal acid metabolism in vernal pool *Isoetes* (Isoetaceae). Madroño, 28:167–171.

———. 1982. Distribution of diurnal acid metabolism in the genus *Isoetes*. American Journal of Botany, 69:254–257.

———, and G. Bowes. 1982. Gas exchange characteristics of the submerged aquatic crassulacean acid metabolism plant, *Isoetes howellii*. Plant Physiology, 70:1455–1458.

Munz, P. A. 1959. A California flora. University of California Press, Berkeley.

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A New Subspecies of *Chrysoperla externa* (Hagen) from Cocos Island, Costa Rica (Neuroptera: Chrysopidae)

The entomofauna of Cocos Island, an isolated oceanic island 500 kilometers west of Costa Rica, is at present under investigation in an effort coordinated by Charles L. Hogue, of the Natural History Museum of Los Angeles County, and Scott E. Miller, of the Santa Barbara Natural History Museum (Hogue and Miller 1981). The subspecies described below is of interest as it represents a morphologically differentiated population of a widespread and abundant mainland species.

Chrysoperla externa cocosensis, n. subsp.

Description.—Face short, eyes very prominent, genae red marked, often a red v-mark on vertex and red spots on occiput near eyes (Fig. 6). Maxillary palpi black-lineate, terminal palpomere fuscous. Scape short, unmarked, flagellum pale, segments slender, setae on basal segments pale, those near apex darker. Pronotum short, anterior corners lightly marked with brown on some specimens; each side bearing a patch of 40–50 pale trichobothrial setae with brown bases, and a few (about eight) normal dark setae, remainder of thoracic setae pale.

Wings slender, tips acute, venation pale, delicate, small dark marks on auditory organ; in forewing, base of Cu and a short interval of 2A dark. Setae sparse, dark, only weakly curved, their length equalling about half the width of a gradate cell. Third median cell moderately long, intramedian cell short, terminating well basad of the first crossvein from Rs. Venational pattern as in Figure 1.

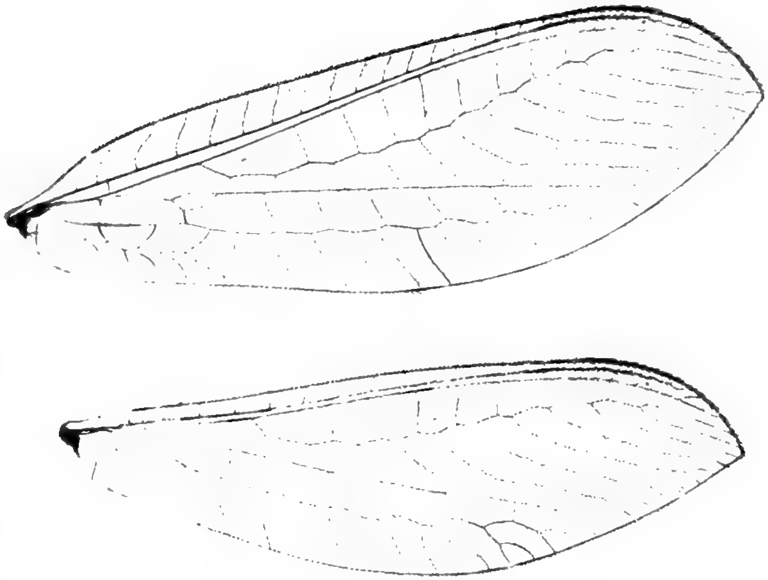


Fig. 1. *Chrysoperla e. cocosensis.* Wings of paratype male.

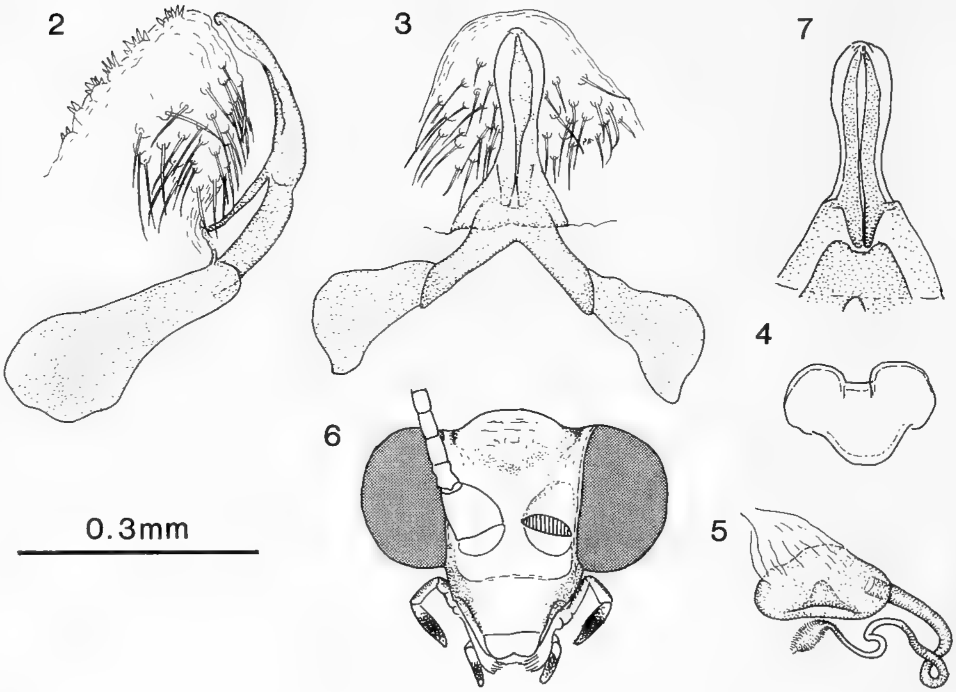
Abdomen pale, setae pale, those of terminal area brownish. Male ectoprocts and ninth sternite formed as usual in this genus. Tignum narrow with black spot on ligulate acumen. Mediuncus (Fig. 3) with a single median band, dark staining with chlorazol black e narrowed basally, and with thin lateral expansions. Gonosaccus with numerous long gonosetae dorsally, and ventrally with clumped spinellae bearing central scent pores. Female: subgenitale (Fig. 4) simple, broad, spermatheca (Fig. 5) short, vela not well tanned.

Measurements (millimeters, means in parentheses, N = 5 (males), = 8 (females)): antenna, ♂, 10.1–12.8 (11.3), ♀, 10.5–12.0 (10.9); forewing length, ♂, 10.0–11.9 (11.1), ♀, 10.7–12.2 (11.5), width, ♂, 3.3–3.8 (3.6), ♀, 3.4–3.8 (3.5).

Type material.—Costa Rica, Cocos Island, Wafer Bay, meadow, 9-III-1980, T. A. Sherry and T. K. Werner (in alcohol). Holotype male and three male, seven female paratypes in Los Angeles County Museum of Natural History; one male, one female paratype in Adams Collection.

Discussion.—As this material is preserved in alcohol, it is not possible to determine the body color. Some specimens retain red markings on the head as described.

This subspecies is very similar to typical *Chrysoperla externa* (Hagen) (new combination), differing principally in structure of the mediuncus. In *C. e. externa,* two distinct bands, dark staining, extend to the mediuncus tip, separated for their entire length by a non-staining area. In *C. cocosensis* it appears that the medial area is dark-staining, the lateral bands being desclerotized and displaced laterally. The wings, especially the forewing are somewhat more acute in *C. e. cocosensis* than in *C. e. externa.* Ecologically, the two subspecies appear to be similar in that the adults are often found associated with grass. I have collected *C. externa* by sweeping grass in Cuba and Central America, but have rarely encountered it on



Figs. 2–6. *C. e. cocosensis.* Fig. 2, gonarcus complex, lateral view; Fig. 3, same, dorsal view; Fig. 4, subgenitale, ventral view; Fig. 5, spermatheca, left lateral view; Fig. 6, head, anterior view. Fig. 7, *C. e. externa,* mediuncus, dorsal view. Scale for genitalic illustrations.

shrubs or trees. The guts of the Cocos Island specimens are filled with grass pollen, and they were collected in a meadow.

The western hemisphere species of *Chrysoperla* are for the most part widespread, and the number of species is low. In South America for example, only *C. externa* and *C. asoralis* Banks (new combination) are present, the range of *C. externa* extending from Chile and Argentina to the southeastern United States and Antilles. Such a range indicates good powers of dispersal, suggesting that *C. externa cocosensis* has originated from colonization by one or more individuals of *C. e. externa.*

Navás described several varieties of *C. externa,* based upon variation in coloration. I have examined types and Navás-determined specimens of most of the varieties and have not found genitalic differences. Except for the Cocos I. population, I have found the genitalia to be rather uniform in *C. externa.* While it is of course quite possible that the Cocos Island population may be a biologically distinct species. I do not consider that its relatively weak morphological differentiation warrants its taxonomic differentiation at the species level. Morphological differences in island populations of wide-ranging chrysopid species have been reported by Adams (1959) for *Mallada basalis* (Walker) and *M. alcestes* (Banks), and by Tjeder (1966) for *M. boninensis* (Okamoto).

I am grateful to C. L. Hogue for making the material available and for comments on the manuscript.

Literature Cited

Adams, P. A. 1959. Neuroptera: Myrmeleontidae and Chrysopidae. Ins. of Micronesia 8(2):13–33.

Hogue, C. L., and C. E. Miller. 1981. Entomofauna of Cocos Island, Costa Rica. Atoll Research Bull. 250:1–29.

Tjeder, B. 1966. The Lacewings of Southern Africa. 5. Family Chrysopidae. South African Animal Life 12:228–534.

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McWilliams, K. L. 1970. Insect mimicry. Academic Press, vii + 326 pp.

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

Brattstrom, B. H. 1969. The Condor in California. Pp. 369–382 *in* Vertebrates of California. (S. E. Payne, ed.), Univ. California Press, xii + 635 pp.

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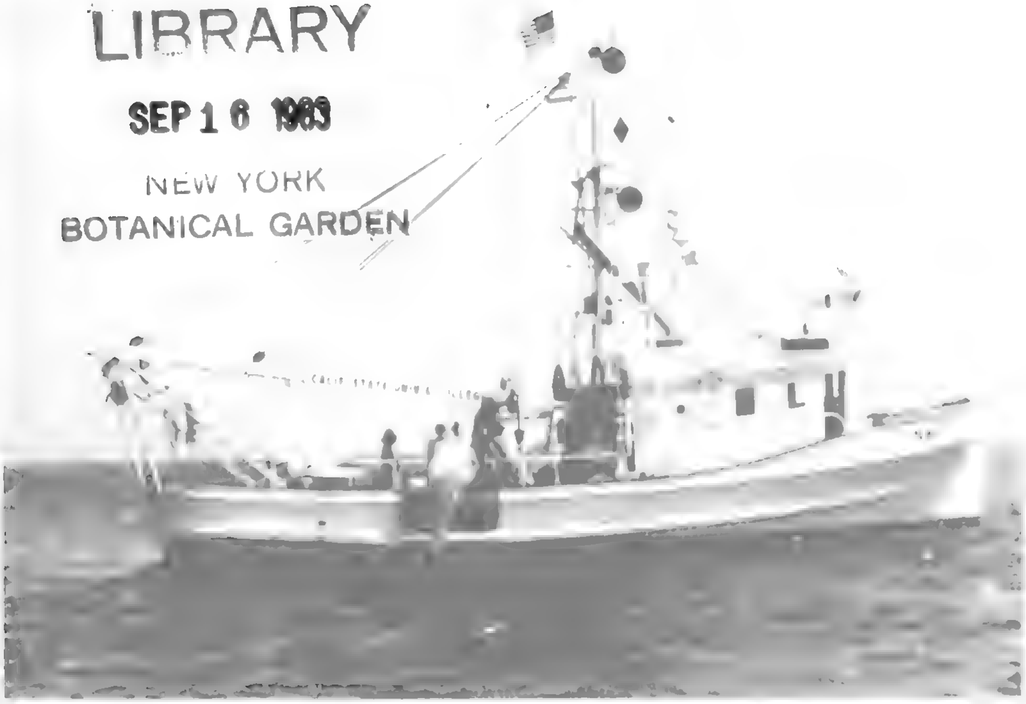
Research Notes

COVER: *Mancalla diegensis*. The skeleton of an extinct fossil auk-like flightless bird from San Diego, California. The photograph is provided through the courtesy of the Natural History Museum of Los Angeles County. The skeleton is on display in the Hildegarde Howard Cenozoic Hall at the Museum.

SOUTHERN CALIFORNIA ACADEMY OF SCIENCES

BULLETIN

Volume 82 Number 2



BCAS-A82(2) 47-102 (1983) AUGUST 1983

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Date of this issue 25 August 1983

Bull. Southern California Acad. Sci.
82(2), 1983, pp. 47–70

Structure and Seasonal Dynamics of the Fish Assemblage in the Cabrillo Beach Area of Los Angeles Harbor, California[1]

Larry G. Allen,[2] Michael H. Horn,[3] Frank A. Edmands II,[4] and
Carol A. Usui[5]

Abstract.—Structure and seasonal dynamics of the fish assemblage in the Cabrillo Beach area of Los Angeles Harbor, California by Larry G. Allen, Michael H. Horn, Frank A. Edmands II, and Carol A. Usui, *Bull. Southern California Acad. Sci.*, 82:47–70, 1983. Eggs, larvae, and juvenile-adult fishes were sampled monthly over a one-year period (February 1979–January 1980) in the Cabrillo Beach area, a relatively little altered section of Los Angeles Harbor. *Engraulis mordax* was the most abundant species of juvenile-adult fish while sciaenid eggs and *E. mordax* larvae dominated the ichthyoplankton samples. Both the juvenile-adult and egg and larval populations showed marked seasonal fluctuations in abundance. Quantitative clustering of juvenile-adult species in each sample produced five distinct groups of resident and periodic species. Temperature and depth (of capture) accounted for 76% of the variation in juvenile-adult abundances based on two canonical correlation axes. The Cabrillo Beach area contains a variety of habitats and supports a seasonally dynamic fish fauna characterized by a high proportion of juveniles.

Introduction

Artificial harbor environments have steadily replaced many natural bay and estuarine habitats in coastal waters of the United States in this century. In California alone, over 60% of the estuarine areas have either been highly modified into harbors or destroyed (Frey et al. 1970). The area now occupied by the Los Angeles-Long Beach (LA-LB) Harbor complex was initially a large estuary of the Los Angeles River system complete with marshlands, mudflats and expansive areas of marsh grasses (Reish et al. 1980). Changes have been extensive since 1872 and include the dredging of channels, filling of lowlands, constructing of breakwaters, and relocating of rivers (Reish et al. 1980).

Harbor ichthyofaunas within the Southern California Bight that have been studied include King Harbor, Redondo Beach (Stephens 1972; Terry and Stephens 1976; Stephens and Zerba 1981), Newport Harbor (Allen 1976; Allen and White in press) and LA-LB Harbor (see below). These investigations have found that, in general, harbor habitats contain diverse and abundant fish assemblages. The richness of these areas can probably be attributed to their protected nature, presumed high productivity and abundant food supply, variety of substrates, and adequate circulation (Stephens 1978). Adequate circulation and good water quality are unquestionably important to the health of harbor fish populations. Poor water quality apparently contributed to the very "poor condition" of many fishes trawled

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[1] Contribution No. 22 from the Southern California Ocean Studies Consortium.

(Young 1964) from LA-LB Harbor before pollution abatement was begun in 1968 (Reish et al. 1980).

Most investigations of juvenile-adult fishes in LA-LB Harbor have been of short duration and limited to one or two types of sampling gears or strategies (cf. Horn and Allen 1981a). Otter trawl studies (Stephens et al. 1974; Harbor Environmental Project-University of Southern California [HEP-USC] 1979) have adequately assessed the species composition and relative abundances of demersal fishes in the harbor during their respective sampling periods. However, fishes occupying other major habitats (e.g., water column, shorelines) within LA-LB Harbor have been largely overlooked.

Ichthyoplankton surveys (HEP-USC 1976; Southern California Ocean Studies Consortium [SCOSC] 1977; HEP-USC 1979) have produced useful information on species composition and relative abundances of fish eggs and larvae. Generalizations, however, are prevented by the wide separation of the studies in space and time. Only one previous attempt (SCOSC 1977) has been made to provide a simultaneous survey of the eggs, larvae and juvenile-adult fishes in an area of the harbor during both day and night periods. Unfortunately, this study encompassed only a three-month period.

The present study conducted in the Cabrillo Beach area of Los Angeles Harbor was designed to correct some of these limitations. The specific objectives were to (1) assess taxonomic composition, abundance, and diversity of all life history stages of fishes from the major subhabitats (bottom, water column, and sandy beach); (2) describe seasonal patterns of abundance of all life history stages; (3) determine the structure of the juvenile-adult fish assemblage based on species associations; (4) examine diel patterns in abundance of juvenile-adult and ichthyoplankton populations; and (5) identify the principal environmental factors that influence abundance and distribution of juvenile-adult fish species.

Methods

Study site.—Cabrillo Beach (Fig. 1) is located (33°43′6″N, 118°16′50″W) in the southwest corner of Los Angeles Harbor. This harbor environment represents the least altered section of the heavily modified Los Angeles Harbor complex. Cabrillo Beach contains an extensive sandy beach area and a series of rock jetties as well as a launching ramp, moorings, swimming areas and a fishing pier. Large boat dock systems (West Channel and Watchorn Basin) and a large oil tanker berth are in close proximity. The waters of the Cabrillo Beach site are shallow (generally <3 m) and largely protected from open ocean influences. An expansive bed of red algae (mainly *Gracilaria* sp.) persists year round (with a spring-summer peak in abundance) in the shallow subtidal waters along the sandy beach. Depth increases rapidly to more than 20 m on the eastern margin of the study area. The substrate changes to a clay-silt composition away from the sandy beach.

Sampling procedures.—Sampling was undertaken during day (1200–1700 h) and night (2000–0100 h) periods monthly from February 1979 through January 1980. Night sampling was initiated 1–2 h after sunset. The sampling program was designed to capture fishes in both inshore and offshore areas and from the bottom and water column habitats of the study site (Fig. 1).

The different types of gear and procedures used in the study are described below. A 15.2 × 1.8 m seine fitted with 1.8 × 1.8 × 1.8 m bag was used to collect juvenile

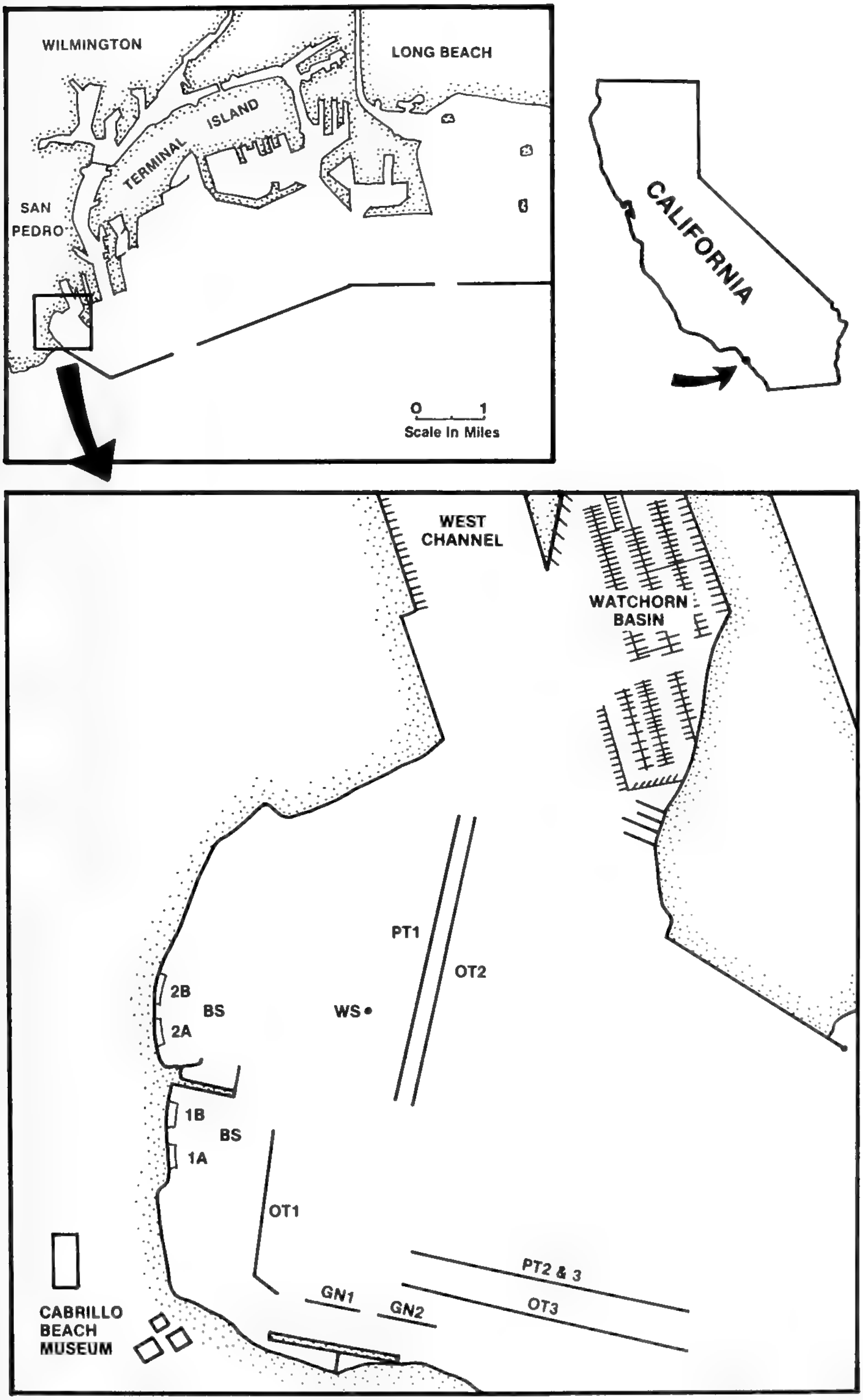

Fig. 1. Map of the Cabrillo Beach area of Los Angeles Harbor showing station locations (BS, bag seine; OT, otter trawl; PT, plankton tow; GN, gill net; WS, water station).

and adult fishes at shallow (<1–2 m) depths. Bar mesh size was 0.6 cm in the wings and 0.3 cm in the bag. The net was set 15 m from and parallel to shore. Each haul swept approximately 220 m^2 of bottom calculated as the area of a trapezoid with a 15.2 m base, an 11 m top and a 15 m height. A total of 96 hauls (four each day and each night period) was taken over the study period. An otter trawl with a 3.8 m headrope, 4.1 m wings of 2.0 cm (bar) mesh, a 2.6 cm codend of 0.8 cm (bar) mesh in the liner and 0.3 × 0.5 m doors was used to collect bottom-associated juvenile and adult fishes. Trawls, each of 5 min duration, were taken at three stations (Fig. 1) of 2, 3 and 6 m depths. A total of 72 trawls (three each day and each night period) was taken over the study period. Two 45.6 × 2.4 m monofilament gill nets were set in line of one another in 2–4 m of water (Fig. 1) to capture juvenile and adult fishes in the water column. Each net was composed of six panels of variable (bar) mesh with two panels each of 1.3–2.5 cm, 2.5–5.1 cm, and 6.4–7.6 cm mesh. Mean duration of each set was 3.9 h (range 3.1–5.8 h). A total of 48 samples (two each day and each night period) was taken over the study period. Two 0.5 m Hensen plankton nets of 0.505 mm nitex mesh were towed simultaneously (paired samples) at two locations (Fig. 1; PT1, PT2 surface tows; PT3 bottom tow) to collect fish eggs and larvae. Filtration volume was determined by a flow meter positioned in the mouth of each net. Each tow was of 5 min duration. A total of 144 samples (six each day and each night period) was taken over the study period.

Temperature, salinity, and dissolved oxygen values (Fig. 2) were obtained with Martek sensing devices at two depths (surface and bottom = 6 m) during the day and at night at a centrally located station (Fig. 1, Station WS). Temperature and salinity readings were also recorded at bag seine stations (Fig. 2).

Standard lengths (mm SL) and weights (g) of juvenile and adult fishes were recorded aboard ship for the entire catch or aliquots of the large catches. Specimens were returned (except for vouchers) to the water after measurements were taken. Plankton samples were fixed in 5% buffered formaldehyde-seawater solution aboard ship and returned to the laboratory. Fish eggs and larvae were sorted from the samples, identified to the lowest possible taxonomic level, and enumerated by taxon. All sorted specimens of eggs and larvae were stored in 5% buffered formaldehyde-seawater solution.

Data analysis.—Species clustering and simple correlation analysis of the data were performed at the University of Southern California Computer Center using the Ecological Analysis Package developed by R. W. Smith. Cluster analysis with flexible sorting determined species associations based on sample abundances. For this analysis, the Bray-Curtis index of dissimilarity (Clifford and Stephenson 1975) was utilized and allowed quantitative clustering without assuming normality in the sampled populations. Square root transformation of species abundances was used to counter the tendency of the index to overemphasize dominant species.

Canonical correlation analysis was performed using programs within the Statistical Analysis System (SAS). This method was used to determine the extent to which certain combinations of abiotic factors accounted for the variation in individual species abundances. This analysis tends (Clifford and Stephenson 1975) to maximize the correlation between linear combinations of abiotic factors and species abundances both in n-dimensional fields. The coefficient of determination (R^2) calculated for each axis represents the amount of variation in species abun-

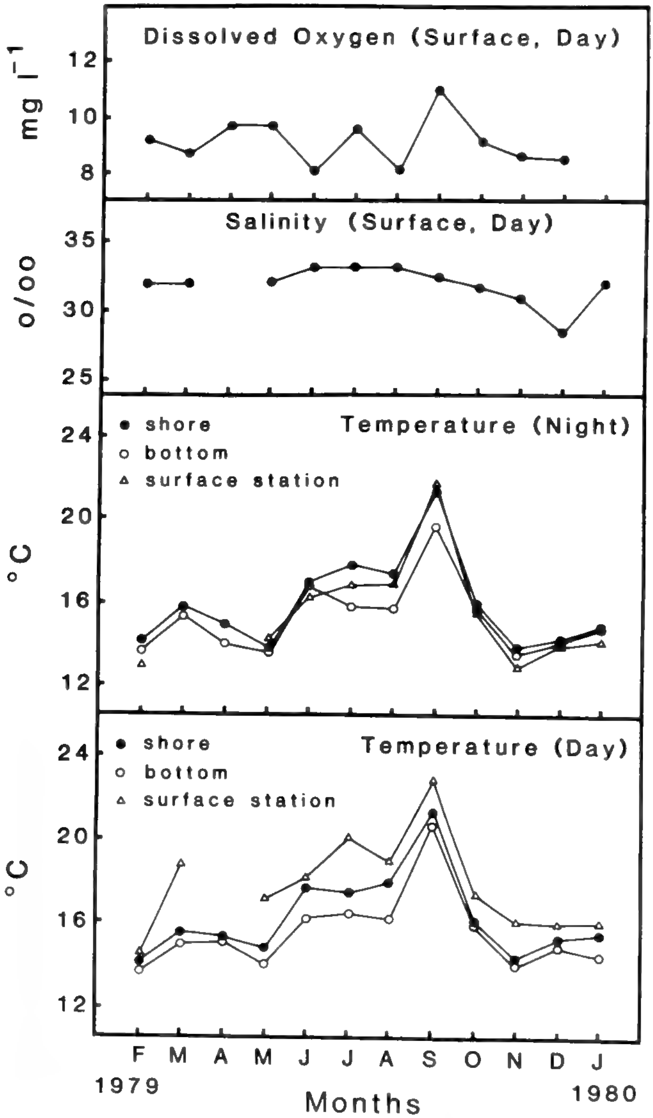

Fig. 2. Monthly variation (February 1979–January 1980) in dissolved oxygen (mg/l) and salinity (‰) during the daytime at the surface, and water temperature (°C) at surface, bottom, and shore stations during the day and night at the Cabrillo Beach site. (Nighttime salinities and dissolved oxygen concentrations were consistently similar to daytime values.)

dance accounted for by a set of abiotic factors. Abundance data (catch-per-unit effort) were log transformed, $\log_e(x + 1)$ to satisfy the assumption of linearity. Only those species with a minimum total abundance of ≥ 20 individuals and/or a minimum of ≥ 5 occurrences were used to avoid problems associated with inclusion of rare species. This procedure resulted in a total of 23 species.

The Shannon-Wiener information function (H′) (Shannon and Weaver 1949) was calculated from pooled monthly data for numbers of individuals and for biomass. Natural logs were used in the calculations.

A multiple-gear strategy was adopted since no single gear type could have adequately sampled the major subhabitats (shoreline, offshore bottom, and water column) in the Cabrillo Beach area. Data for the various methods were combined for two purposes. First, we combined all three of the above juvenile-adult sampling methods for total counts and weights within each month for month-to-month comparisons. We believe this procedure presented no important bias since sampling effort remained constant from month to month. Second, we included catches from the three types of gear for cluster and canonical correlation analyses. In mixing methods we made three assumptions: 1) each method employed was that most effective at sampling fishes from a particular subhabitat among the gears available; 2) catches reasonably reflected the relative abundances of species within the subhabitat at any one time and therefore; 3) each sample could be viewed as a discrete collection from a particular subhabitat. The principal bias introduced by this approach was that a certain gear type, especially the bag seine, may have overly influenced the analyses due to the relatively high abundances of some species collected with this gear. The impact of this unequal representation was minimized by square-root and log-transformations of abundance data prior to the clustering and canonical correlation analyses, respectively.

Results

Juvenile-adult fishes.—A total of 23,592 juvenile-adult fishes belonging to 65 species and weighing more than 463 kg was captured in 216 samples taken with three types of gear (bag seine, otter trawl, gill net) over the 12-month period (February 1979–January 1980) at the Cabrillo Beach site (Table 1). *Engraulis mordax* (northern anchovy) was the most abundant species comprising 58% of the total catch. The next four most abundant species, *Genyonemus lineatus* (white croaker), *Seriphus politus* (queenfish), *Leuresthes tenuis* (California grunion) and *Phanerodon furcatus* (white surfperch) accounted for over 26% of the total numbers. *Genyonemus lineatus* constituted 39% of the total biomass. Four other species, *Embiotoca jacksoni* (black surfperch), *Paralichthys californicus* (California halibut), *Phanerodon furcatus* and *Seriphus politus,* accounted for >26% of the total biomass. Total H′ diversity values for the study were 1.72 for numbers and 2.55 for biomass.

Considerable variation in abundance and diversity measures occurred during the 12-month study period (Fig. 3). Species richness (number of species) fluctuated moderately from a low in February to a high in November. H′ diversity for numbers was lowest in June and August, corresponding to the two months of greatest *Engraulis mordax* abundance, whereas higher, relatively uniform values were obtained for other months. H′ diversity for biomass remained relatively uniform throughout the year with a low in October and highest values in June and September. The number of individuals increased dramatically from a low in February to a moderate peak in June to a maximum level in August and then declined sharply in September remaining low through January. Biomass gradually increased from February through July then rose sharply in August, reached a peak in October and then declined markedly in December.

Bag seine hauls (Table 2) captured 77.9% of the total individuals and 14.4% of the total biomass. Of the 29 species captured during the day periods, *Engraulis mordax* accounted for over 77% of the individuals and more than 34% of the biomass. Nighttime collections were less dominated by a single species. *Micrometrus minimus* (dwarf surfperch), *Hyperprosopon argenteum* (walleye surfperch), *Seriphus politus, Genyonemus lineatus,* and *Embiotoca jacksoni* were the most abundant of the 29 species obtained during night bag seine collections. Overall, a much greater proportion of individuals (94.6%) was captured during the day, primarily due to the extremely large daytime catches of juvenile *Engraulis mordax.* A slightly greater biomass (55.1% of the total), however, was obtained during night periods indicating that, in general, larger fishes were collected at night. Daytime density estimates were 1.65 individuals/m^2 for numbers and 2.84 g/m^2 for biomass compared to nighttime values of 0.09 individuals/m^2 and 3.49 g/m^2.

Otter trawls (Table 2) captured 17.9% of the total individuals and 47.2% of the total biomass. Of the 30 species captured during the day periods, three species, *Genyonemus lineatus, Phanerodon furcatus,* and *Engraulis mordax,* accounted for over 70% of the individuals. *Genyonemus lineatus, Paralichthys californicus, Phanerodon furcatus,* and *Embiotoca jacksoni* comprised approximately 70% of the biomass. Nighttime hauls (36 species) were largely dominated by *G. lineatus* which accounted for over 59% of the numbers and more than 63% of the biomass. Overall, greater proportions of individuals (57.1%) and biomass (66.8%) were obtained during night periods. Daytime catch-per-unit-effort values were 50.4 individuals/trawl for numbers and 2020 g/trawl for biomass compared to nighttime values of 67.1 individuals/trawl and 4055 g/trawl.

Gill net sets (Table 2) collected 4.2% of the total individuals and 38.3% of the total biomass. *Genyonemus lineatus, Phanerodon furcatus, Seriphus politus,* and *Embiotoca jacksoni* were the most abundant of the 22 species captured during the day. The nighttime sets (27 species) were largely dominated, as were the nighttime otter trawls, by *G. lineatus. Seriphus politus* ranked second in numbers and *Mustelus californicus* (gray smoothhound) second in biomass. Overall, larger percentages of individuals (57.2%) and biomass (56.8%) were obtained during the day periods. Daytime catch-per-unit-effort values were 5.6 individuals/h for numbers and 1021 g/h for biomass compared to nighttime values of 5.0 individuals/h and 904 g/h.

A summary of the juvenile-adult fish collections by all three methods (Table 1) showed that the large majority (88%) of fishes were collected during day periods whereas a greater proportion (56%) of the biomass was obtained during night periods. The predominance of juvenile *Engraulis mordax* in the daytime bag seine hauls and the large nighttime catches of *Genyonemus lineatus* in the otter trawl and gill net contributed disproportionately to these diel differences. Four of the five most abundant species (comprising 85% of total individuals), *E. mordax, Seriphus politus, Leuresthes tenuis,* and *Phanerodon furcatus,* were caught in greater numbers during the day; only *G. lineatus* was more numerous at night. All five species, however, had greater mean weights in nighttime collections.

In most cases no significant differences were detected between daytime and nighttime samples taken with the three types of gear for numbers of species, numbers of individuals, or biomass (Wilcoxon signed-ranks test for paired values; all $P > 0.05$). The exceptions were nighttime otter trawl collections which had significantly greater ($P < 0.05$) numbers of individuals and biomass than daytime hauls.

Clustering of juvenile-adult species based on numerical abundance in each

Table 1. Number of individuals and biomass of juvenile-adult fish species collected by all methods during day (1200–1700 h), night (2000–0100 h) and combined periods over the 12-month study (February 1979–January 1980) at the Cabrillo Beach site (species ranked according to total number of individuals for combined day and night periods).

	Day		Night		Totals	
Species	No.	Biomass (g)	No.	Biomass (g)	No. (% total)	Biomass (g) (% total)
Engraulis mordax	13,824	11,614	33	173	13,857 (58.7)	11,787 (2.5)
Genyonemus lineatus	727	51,987	1725	128,164	2452 (10.4)	180,151 (38.9)
Seriphus politus	1576	10,540	405	13,450	1981 (8.4)	23,990 (5.2)
Leuresthes tenuis	906	749	21	116	923 (3.9)	865 (0.2)
Phanerodon furcatus	681	20,304	156	8211	837 (3.5)	28,515 (6.1)
Micrometrus minimus	287	3655	264	4551	551 (2.3)	8206 (1.8)
Clevelandia ios	380	17	—	—	380 (1.6)	17 (<0.1)
Symphurus atricauda	93	1366	205	3547	298 (1.3)	4913 (1.1)
Cymatogaster aggregata	174	1339	122	1482	296 (1.2)	2821 (0.6)
Hyperprosopon argenteum	48	4718	225	10,356	273 (1.1)	15,074 (3.2)
Embiotoca jacksoni	117	17,941	131	17,314	248 (1.0)	35,255 (7.6)
Atherinops affinis	127	621	63	556	190 (0.8)	1177 (0.2)
Atherinopsis californiensis	134	6237	36	4631	170 (0.7)	10,868 (2.3)
Paralichthys californicus	76	15,494	83	18,037	159 (0.7)	33,531 (7.2)
Lepidogobius lepidus	105	95	47	46	152 (0.6)	141 (<0.1)
Gibbonsia elegans	114	877	24	406	138 (0.6)	1283 (0.3)
Syngnathus californiensis	110	868	20	141	130 (0.5)	1009 (0.2)
Heterostichus rostratus	66	4866	38	2511	104 (0.4)	7377 (1.6)
Sebastes dallii	26	442	32	412	58 (0.2)	854 (0.2)
Paralabrax nebulifer	19	4734	38	4784	57 (0.2)	9518 (2.0)
Damalichthys vacca	27	8222	21	6160	48 (0.2)	14,382 (3.1)
Synodus lucioceps	17	4250	15	4387	32 (0.1)	8637 (1.9)
Leptocottus armatus	15	608	16	454	31 (0.1)	1062 (0.2)
Hypsopsetta guttulata	11	2358	9	2124	20 (<0.1)	4482 (1.0)
Paralabrax clathratus	17	166	—	—	17 (<0.1)	166 (<0.1)
Menticirrhus undulatus	8	2514	8	3650	16 (<0.1)	6164 (1.3)
Mustelus californicus	6	7702	8	9233	14 (<0.1)	16,935 (3.6)
Porichthys myriaster	2	720	11	2922	13 (<0.1)	3642 (0.8)
Pleuronichthys verticalis	9	1032	4	725	13 (<0.1)	1757 (0.4)
Sarda chiliensis	11	6820	—	—	11 (<0.1)	6820 (1.5)
Umbrina roncador	—	—	11	1100	11 (<0.1)	1100 (0.2)
Cheilotrema saturnum	6	2117	3	1040	9 (<0.1)	3157 (0.7)
Triakis semifasciata	4	2285	3	1970	7 (<0.1)	4255 (0.9)
Sphyraena argentea	5	1813	2	1360	7 (<0.1)	3173 (0.7)
Scorpaena guttata	3	345	3	578	6 (<0.1)	923 (0.2)
Pleuronichthys ritteri	2	158	4	395	6 (<0.1)	553 (0.1)
Syngnathus leptorhynchus	6	47	—	—	6 (<0.1)	47 (<0.1)
Myliobatis californica	4	2400	1	340	5 (<0.1)	2740 (0.6)
Xystreurys liolepis	3	785	2	400	5 (<0.1)	1185 (0.2)
Amphistichus argenteus	2	180	3	440	5 (<0.1)	620 (0.1)
Chilara taylori	—	—	5	470	5 (<0.1)	470 (0.1)
Peprilus simillimus	—	—	5	233	5 (<0.1)	233 (<0.1)
Acanthogobius flavimanus	2	58	3	23	5 (<0.1)	81 (<0.1)
Syngnathus exilis	4	32	1	5	5 (<0.1)	37 (<0.1)
Anchoa delicatissima	3	14	2	7	5 (<0.1)	21 (<0.1)
Ulvicola sanctaerosae	4	2	—	—	4 (<0.1)	2 (<0.1)
Ophidion scrippsae	—	—	3	270	3 (<0.1)	270 (<0.1)
Anchoa compressa	2	6	1	10	3 (<0.1)	16 (<0.1)

Table 1. *Continued.*

	Day		Night		Totals	
Species	No.	Biomass (g)	No.	Biomass (g)	No. (% total)	Biomass (g) (% total)
Parophrys vetulus	1	370	2	1	3 (<0.1)	371 (<0.1)
Sebastes serranoides	1	2	1	216	2 (<0.1)	218 (<0.1)
Citharichthys stigmaeus	2	12	—	—	2 (<0.1)	12 (<0.1)
Girella nigricans	1	830	—	—	1 (<0.1)	830 (0.2)
Scomber japonicus	—	—	1	346	1 (<0.1)	346 (<0.1)
Trachurus symmetricus	—	—	1	180	1 (<0.1)	180 (<0.1)
Porichthys notatus	—	—	1	160	1 (<0.1)	160 (<0.1)
Sebastes auriculatus	—	—	1	110	1 (<0.1)	110 (<0.1)
Paralabrax maculatofasciatus	—	—	1	100	1 (<0.1)	100 (<0.1)
Sebastes rastrelliger	—	—	1	100	1 (<0.1)	100 (<0.1)
Brachyistius frenatus	—	—	1	80	1 (<0.1)	80 (<0.1)
Gillichthys mirabilis	—	—	1	10	1 (<0.1)	10 (<0.1)
Cynoscion nobilis	—	—	1	5	1 (<0.1)	5 (<0.1)
Sebastes mystinus	1	<1	—	—	1 (<0.1)	1 (<0.1)
Mugil cephalus	1	<1	—	—	1 (<0.1)	1 (<0.1)
Ilypnus gilberti	—	—	1	<1	1 (<0.1)	1 (<0.1)
Rhacochilus toxotes	—	—	1	310	1 (<0.1)	310 (<0.1)
Totals	19,766	204,314	3826	258,803	23,592	463,117
No. species	50		56		65	

sample produced five distinct species groups (Fig. 4). The largest dichotomy (~160% distance) was between 10 species (Group I) captured almost exclusively by bag seine and the remainder of the species captured by other methods. The next largest dichotomy (~140% distance) was between species Groups II–IV and Group V. In general, dissimilarity values were high indicating the apparent distinctiveness of both the habitats within the area and the sampling methods employed. The 15 rarest species were not included in the cluster analysis.

Group I was comprised primarily of resident or seasonal inshore species. The components of Subgroup A, *Gibbonsia elegans* (spotted kelpfish), *Syngnathus californiensis* (kelp pipefish), and *Heterostichus rostratus* (giant kelpfish), were species closely associated with the *Gracilaria* beds in the shallow water along the sandy beach. Subgroup B was composed of three species, *Micrometrus minimus*, *Hyperprosopon argenteum*, and *Atherinops affinis* (topsmelt), that were captured in greater numbers in nighttime hauls over the algal beds. Subgroup C consisted of two species, *Engraulis mordax* and *Leuresthes tenuis*, that were highly abundant in daytime samples during the spring and summer months. Two rare pipefishes, *Syngnathus leptorhynchus* (bay pipefish) and *S. exilis* (slim pipefish) were associated with the algal beds and comprised the markedly distinct (~135% distance) Subgroup D.

Group II was composed of common, resident, bottom-associated fishes including *Genyonemus lineatus*, *Seriphus politus*, *Phanerodon furcatus*, and seven other species that were primarily collected with otter trawl and gill net.

Group III consisted of four large, seasonal (mainly late summer and fall), predatory fishes that were captured exclusively in the gill nets. These species were

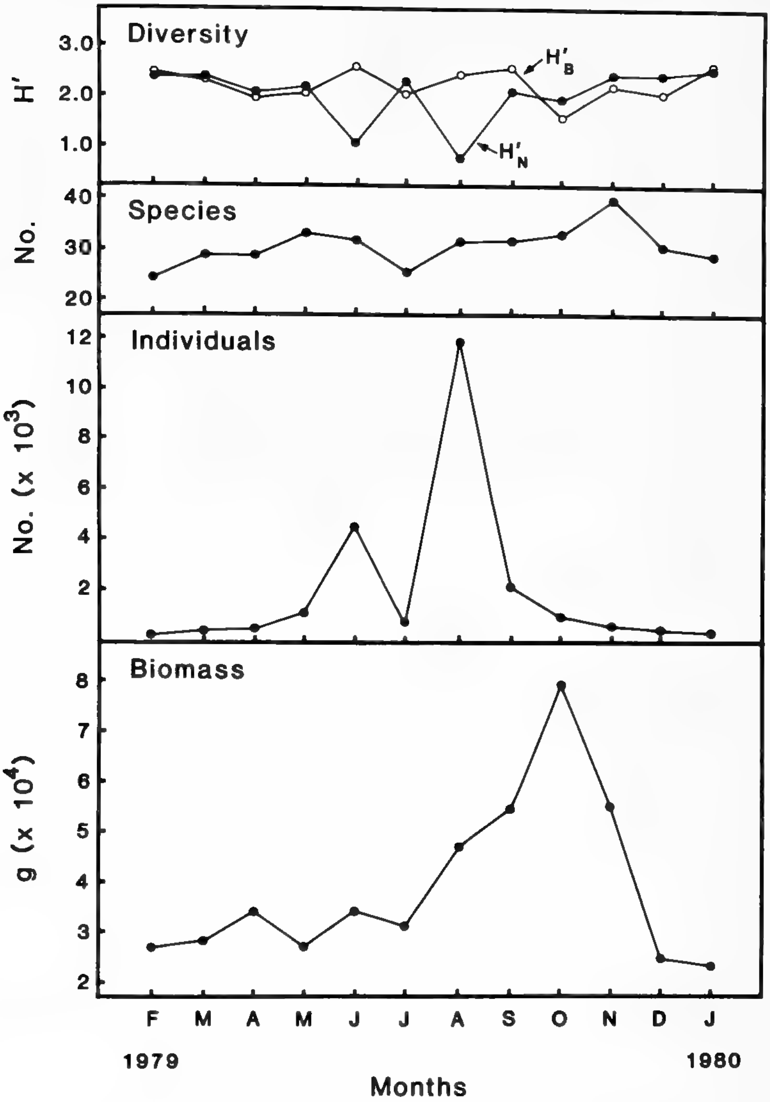

Fig. 3. Monthly variation (February 1979–January 1980) in diversity (H_N' for numbers, H_B' for biomass), number of species, number of individuals, and biomass (g) of juvenile-adult fishes collected by all methods at the Cabrillo Beach site.

Mustelus californicus, Sphyraena argentea (California barracuda), *Triakis semifasciata* (leopard shark), and *Sarda chiliensis* (Pacific bonito).

Group IV was made up of 16 relatively rare species that were captured in varying numbers by all three methods. Species in this group were periodic in occurrence either as juvenile or adult migrants or as newly recruited juveniles. None of these species remained as common members of the assemblage after their initial migration or recruitment into the study area.

Group V was composed of 10 species that were captured in the deeper portions

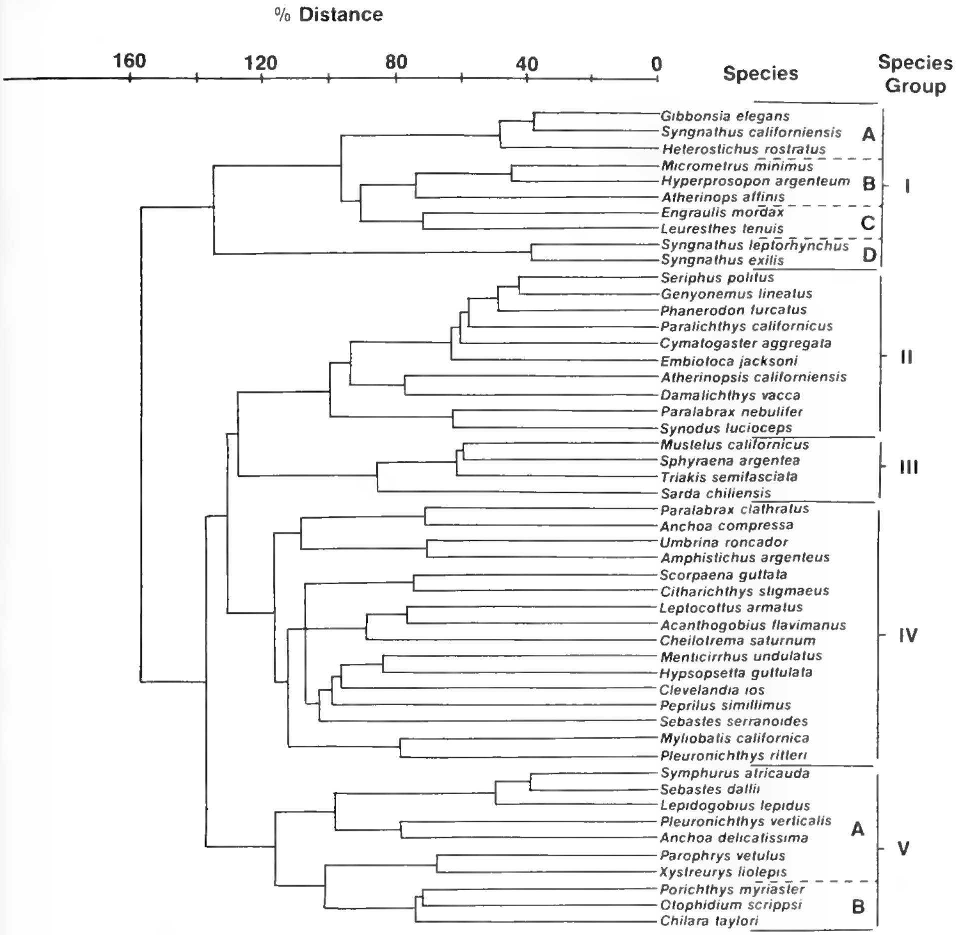

Fig. 4. Dendrogram of the clustering of juvenile-adult fish species based on abundance in samples taken by all methods at the Cabrillo Beach site. Five species groups (Roman numerals) are recognized according to the Bray-Curtis index of dissimilarity (% distance). Capital letters denote subgroups.

of the study area (Station OT3). The most common members of Subgroup A were *Symphurus atricauda* (California tonguefish), *Sebastes dallii* (calico rockfish), and *Lepidogobius lepidus* (bay goby). Subgroup B consisted of fishes that were collected only in nighttime trawls. These species were *Porichthys myriaster* (specklefin midshipman), *Ophidion scrippsae* (basketweave cusk-eel), and *Chilara taylori* (spotted cusk-eel).

Members of the species groups identified in the dendrogram (Fig. 4) are illustrated in profiles depicting occurrences in the Cabrillo Beach area during "cold" water months (November–April) when surface temperatures were generally < 16°C (Fig. 5) and "warm" water months (May–October) when temperatures generally exceeded 16°C (Fig. 6). Only species with ≥ 5 individuals during each time segment were included. These profiles illustrate both subhabitat affinity and seasonality within this fish assemblage.

Table 2. Number of individuals of juvenile-adult fish species collected by each of the three sampling methods during the 12-month study (February 1979–January 1980) at the Cabrillo Beach site (species ranked for each method according to numerical abundance for that method).

Bag Seine			Otter Trawl			Gill Net		
Species	No.	% of Total	Species	No.	% of Total	Species	No.	% of Total
Engraulis mordax	13,493	73.4	*Genyonemus lineatus*	2006	47.4	*Genyonemus lineatus*	332	33.9
Seriphus politus	1564	8.5	*Phanerodon furcatus*	489	11.6	*Phanerodon furcatus*	165	16.8
Leuresthes tenuis	923	5.0	*Engraulis mordax*	364	8.6	*Seriphus politus*	143	14.6
Micrometrus minimus	520	2.8	*Symphurus atricauda*	299	7.1	*Embiotoca jacksoni*	76	7.8
Clevelandia ios	380	2.1	*Seriphus politus*	274	6.5	*Atherinopsis californiensis*	47	4.8
Hyperprosopon argenteum	224	1.2	*Cymatogaster aggregata*	190	4.5	*Damalichthys vacca*	43	4.4
Atherinops affinis	189	1.0	*Embiotoca jacksoni*	136	3.2	*Hyperprosopon argenteum*	37	3.8
Phanerodon furcatus	183	1.0	*Paralichthys californicus*	121	2.9	*Paralichthys californicus*	27	2.8
Gibbonsia elegans	133	0.7	*Lepidogobius lepidus*	90	2.1	*Paralabrax nebulifer*	14	1.4
Syngnathus californiensis	131	0.7	*Sebastes dallii*	58	1.4	*Mustelus californicus*	14	1.4
Atherinopsis californiensis	123	0.7	*Paralabrax nebulifer*	37	0.9	*Sarda chiliensis*	11	1.1
Genyonemus lineatus	114	0.6	*Micrometrus minimus*	31	0.7	*Menticirrhus undulatus*	9	0.9
Cymatogaster aggregata	105	0.6	*Synodus lucioceps*	23	0.5	*Synodus lucioceps*	9	0.9
Heterostichus rostratus	95	0.5	*Pleuronichthys verticalis*	13	0.3	*Hypsopsetta guttulata*	7	0.7
Lepidogobius lepidus	62	0.3	*Hypsopsetta guttulata*	13	0.3	*Sphyraena argentea*	7	0.7
Embiotoca jacksoni	36	0.2	*Hyperprosopon argenteum*	12	0.3	*Triakis semifasciata*	7	0.7
Leptocottus armatus	30	0.2	*Heterostichus rostratus*	9	0.2	*Cheilotrema saturnum*	7	0.7
Paralabrax clathratus	15	0.1	*Pleuronichthys ritteri*	6	0.1	*Porichthys myriaster*	7	0.7
Paralichthys californicus	10	0.1	*Xystreurys liolepis*	5	0.1	*Peprilus simillimus*	4	0.4
Amphistichus argenteus	7	<0.1	*Scorpaena guttata*	5	0.1	*Scorpaena guttata*	1	0.1
Umbrina roncador	7	<0.1	*Chilara taylori*	5	0.1	*Scomber japonicus*	1	0.1
Menticirrhus undulatus	6	<0.1	*Porichthys myriaster*	5	0.1	*Rhacochilus toxotes*	1	0.1
Syngnathus leptorhynchus	4	<0.1	*Myliobatis californica*	4	0.1	*Amphistichus argenteus*	1	0.1
Ulvicola sanctaerosae	4	<0.1	*Anchoa delicatissima*	4	0.1	*Sebastes serranoides*	1	0.1
Acanthogobius flavimanus	4	<0.1	*Gibbonsia elegans*	4	0.1	*Trachurus symmetricus*	1	0.1
Syngnathus exilis	3	<0.1	*Damalichthys vacca*	3	0.1	*Porichthys notatus*	1	0.1
Anchoa compressa	3	<0.1	*Umbrina roncador*	3	0.1	*Brachyistius frenatus*	1	0.1
Cheilotrema saturnum	2	<0.1	*Ophidion scrippsae*	3	0.1	*Umbrina roncador*	1	0.1

Table 2. *Continued.*

Bag Seine			Otter Trawl			Gill Net		
Species	No.	% of Total	Species	No.	% of Total	Species	No.	% of Total
Damalichthys vacca	2	<0.1	*Syngnathus californiensis*	3	0.1	*Gibbonsia elegans*	1	0.1
Paralabrax nebulifer	2	<0.1	*Paralabrax clathratus*	2	0.1	*Girella nigricans*	1	0.1
Parophrys vetulus	2	<0.1	*Citharichthys stigmaeus*	2	0.1	*Myliobatis californica*	1	0.1
Mugil cephalus	1	<0.1	*Menticirrhus undulatus*	1	<0.1	*Atherinops affinis*	1	0.1
Sebastes mystinus	1	<0.1	*Parophrys vetulus*	1	<0.1	*Cymatogaster aggregata*	1	0.1
Porichthys myriaster	1	<0.1	*Amphistichus argenteus*	1	<0.1		980	
Cynoscion nobilis	1	<0.1	*Leptocottus armatus*	1	<0.1			
Anchoa delicatissima	1	<0.1	*Sebastes serranoides*	1	<0.1			
Ilypnus gilberti	1	<0.1	*Sebastes auriculatus*	1	<0.1			
	18,382		*Sebastes rastrelliger*	1	<0.1			
			Paralabrax maculatofasciatus	1	<0.1			
			Peprilus simillimus	1	<0.1			
			Acanthogobius flavimanus	1	<0.1			
			Gillichthys mirabilis	1	<0.1			
				4230				

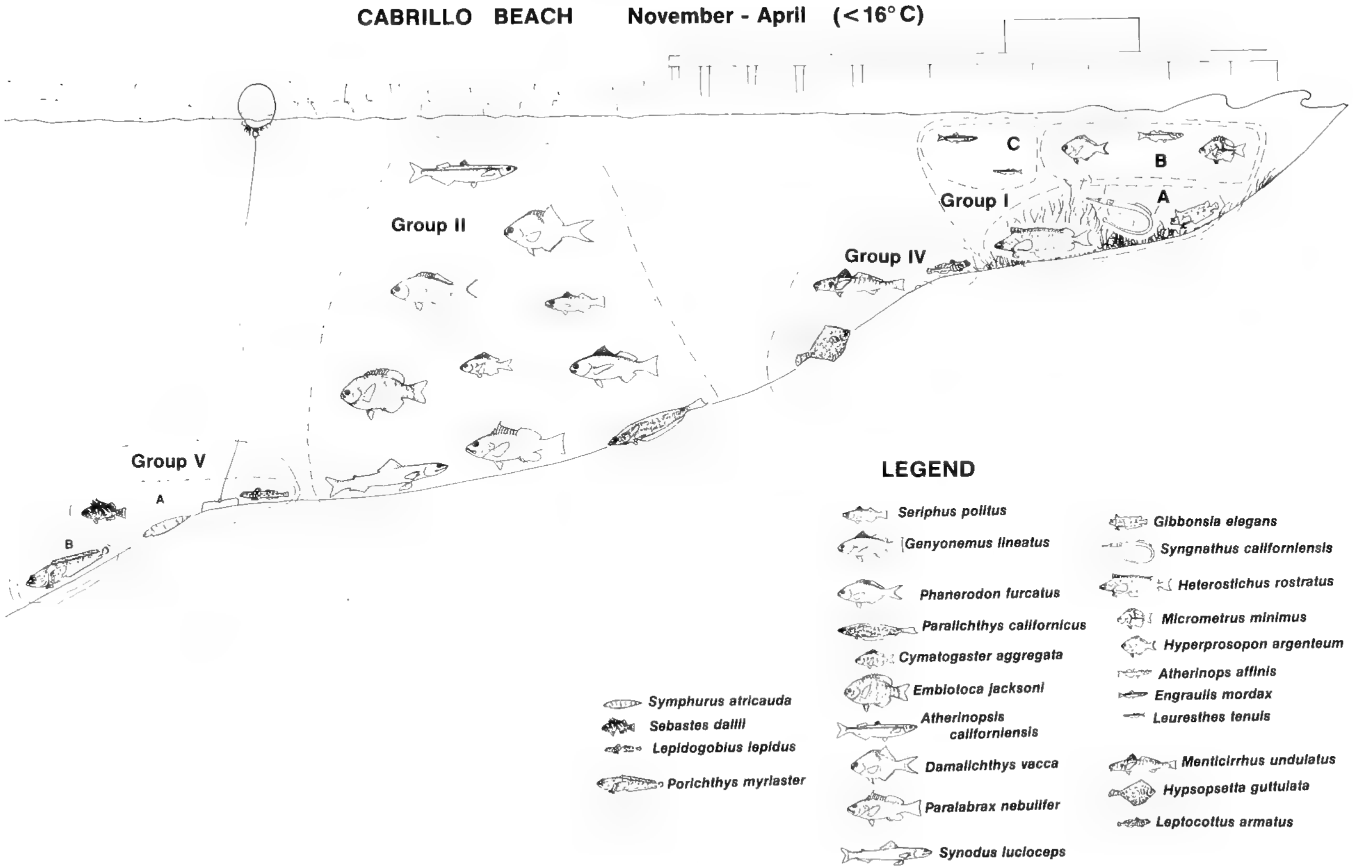

Fig. 5. Illustration of the principal juvenile-adult fish species present in the Cabrillo Beach area by subhabitat during the colder water (<16°C) months (February–April, November, and December 1979 and January 1980) of the study period. Inclusion of species limited to those with ≥5 individuals in the samples. Dashed lines enclose species groups derived from dendogram of Fig. 4.

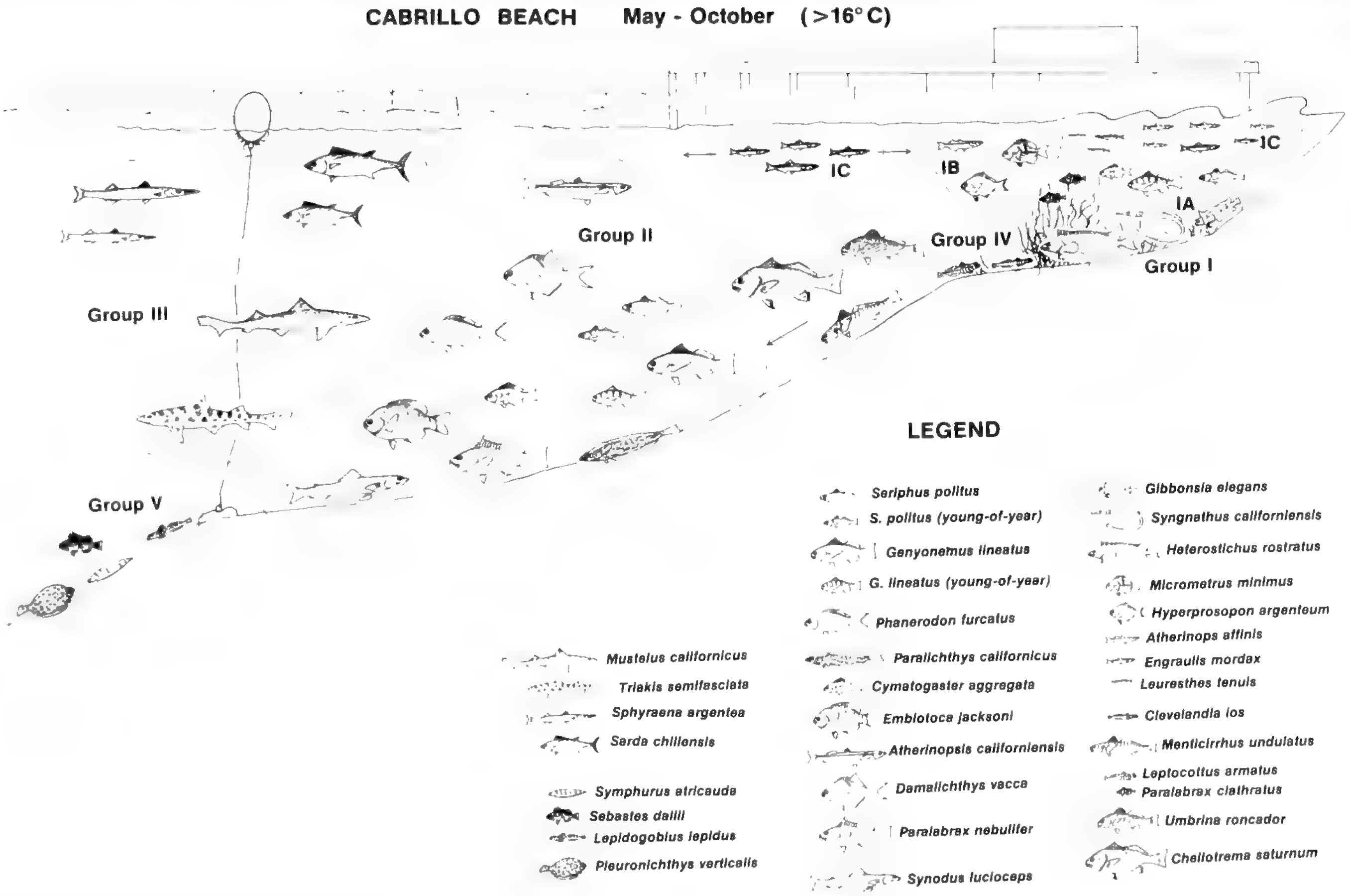

Fig. 6. Illustration of the principal juvenile-adult fish species present in the Cabrillo Beach area by subhabitat during the warmer water (>16°C) months (May–October 1979) of the study period. Arrows indicate inshore-offshore occurrence. Other information as in Fig. 5.

Table 3. Number of individuals of egg and larval taxa collected in paired plankton tows taken during day (1200–1700 h) and night (2000–0100 h) periods at the Cabrillo Beach Site.

	Day		Night		Totals	
Family Species	Larvae	Eggs	Larvae	Eggs	Larvae (% total)	Eggs (% total)
Engraulidae						
Engraulis mordax	361	1	1325	—	1686 (53.5)	1 (<0.1)
Gobiesocidae						
Gobiesox rhessodon	—	—	2	—	2 (<0.1)	—
Gobiesox sp.	1	—	3	—	4 (<0.1)	—
Atherinidae						
Atherinops affinis	—	—	58	—	58 (1.8)	—
Atherinopsis californiensis	7	—	44	—	51 (1.6)	—
Leuresthes tenuis	—	—	31	—	31 (1.0)	—
Syngnathidae						
Syngnathus californiensis	—	—	1	—	1 (<0.1)	—
Syngnathus leptorhynchus	1	—	3	—	4 (<0.1)	—
Scorpaenidae						
Sebastes sp.	15	—	14	—	29 (0.9)	—
Cottidae	—	—	1	—	1 (<0.1)	—
Clinocottus analis	2	—	3	—	5 (<0.1)	—
Cottid I	2	—	2	—	4 (<0.1)	—
Leptocottus armatus	—	—	2	—	2 (0.1)	—
Serranidae	—	296	—	42	—	338 (1.7)
Paralabrax clathratus	—	—	1	—	1 (0.1)	—
Sciaenidae						
Cheilotrema saturnum	1	—	—	—	1 (0.1)	—
Genyonemus lineatus	104	—	217	—	321 (10.2)	—
Seriphus politus	7	—	14	—	21 (0.6)	—
Blenniidae						
Hypsoblennius sp.	25	—	23	—	48 (1.5)	—
Clinidae						
Gibbonsia sp.	5	—	54	—	59 (1.9)	—
Heterostichus rostratus	10	—	8	—	18 (0.6)	—
Pholididae						
Ulvicola sanctaerosae	—	—	1	—	1 (<0.1)	—
Gobiidae	—	—	1	—	1 (<1.0)	—
Clevelandia ios	64	—	436	—	500 (15.9)	—
Gobiid I	40	—	183	—	223 (7.1)	—
Gobiid II	6	—	34	—	40 (1.3)	—
Gillichthys mirabilis	—	—	1	—	1 (<0.1)	—
Ilypnus gilberti	1	—	2	—	3 (<0.1)	—
Bothidae						
Citharichthys sp.	—	473	—	298	—	771 (3.8)
Hippoglossina stomata	—	—	—	2	—	2 (<0.1)
Paralichthys californicus	—	—	5	—	5 (0.1)	—
Pleuronectidae						
Hypsopsetta guttulata	2	16	6	36	8 (0.2)	52 (0.2)
Parophrys vetulus	—	—	1	—	1 (<0.1)	—
Pleuronichthys coenosus	—	7	—	14	—	21 (0.1)
Pleuronichthys decurrens	—	1	—	—	—	1 (<0.1)
Pleuronichthys ritteri	3	10	6	14	9 (0.3)	24 (0.1)
Pleuronichthys verticalis	—	6	2	81	2 (<0.1)	87 (0.4)

Table 3. *Continued.*

Family Species	Day		Night		Totals	
	Larvae	Eggs	Larvae	Eggs	Larvae (% total)	Eggs (% total)
Cynoglossidae						
Symphurus atricauda	1	—	—	—	1 (<0.1)	—
Unknown	2	105	6	445	8 (0.2)	550 (2.7)
Total Larvae	658	—	2492	—	3150	—
Total Eggs	—	8564	—	11,494	—	20,058

During the "cold" water months (November–April) the assemblage consisted mainly of resident species from Groups I, II, IV, and V in relatively low abundances. Members of Group I occupied the shallow, algal beds along the shore. Group II was widespread through the shallow to mid-depth (~2–4 m) offshore areas. Species comprising Group V inhabited the deeper portions of the study area on or near the bottom. Certain members of Group IV occurred irregularly in the shallows near the shore.

Abundances of all common species were substantially higher during the "warm" water months of May through October. Recruitment was especially pronounced in members of Groups I and II. A large portion of juveniles from each of Groups I, II, and IV occupied the shore zone during this period. The large predators (Group III) were also present at this time of high prey abundance. Group V occurred in the deeper areas, but not in appreciably greater abundance than in colder water months.

Ichthyoplankton.—A total of 20,058 eggs belonging to 10 taxa and an unknown category was collected in the 144 plankton tows taken over the 12-month period (February 1979–January 1980) (Table 3). Sciaenid eggs overwhelmingly dominated the catch making up over 90% of the total numbers. Eggs of *Citharichthys* sp. (sanddabs) ranked second followed by the unknown category and serranid (sea bass) eggs. A significantly larger number of eggs were collected during the night periods than during the day periods (Wilcoxon signed-ranks test for paired values, $P \leq 0.05$). Approximately 57% of the total eggs were taken in nighttime tows (Table 2). Marked variation in the number of taxa and density of eggs occurred over the 12-month period (Fig. 7). The largest numbers of taxa and individuals were obtained in February with a secondary peak of individuals occurring in January. Lowest values for both parameters were recorded in July and August. Overall, the mean egg density was 167/100 m^3 of water sampled.

A total of 3150 larvae belonging to 33 taxa (representing 15 families) and an unknown category was collected in the 144 plankton tows (Table 3). Larvae of *Engraulis mordax* were the most abundant comprising 53.5% of the total individuals. *Clevelandia ios* (arrow goby) and *Genyonemus lineatus* ranked second and third in abundance. A significantly greater number ($P \leq 0.05$, Wilcoxon's signed-ranks test) of taxa and of individuals were collected during the night periods than during the day periods. Approximately 79% of the larvae were obtained at night (Table 3). Overall, the mean larval density was 27 individuals/100 m^3 of water sampled. Diel period was significantly associated (Chi-square test, $P < 0.05$) with mean density values of the top 14 species combined.

The number of taxa and density of larvae varied over the 12-month period in

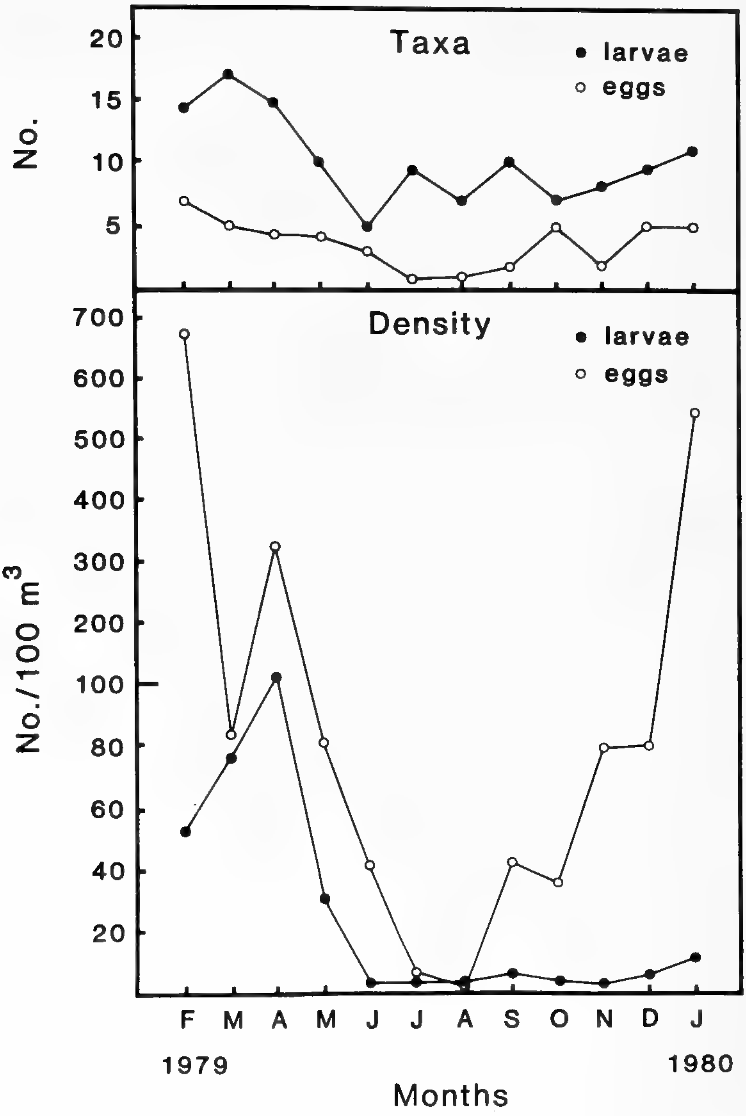

Fig. 7. Monthly variation (February 1979–January 1980) in number of taxa and density (No./100 m^3) of fish eggs and larvae collected at the Cabrillo Beach site.

a pattern similar to that for eggs (Fig. 7). The largest numbers of taxa and individuals were collected in March. The fewest taxa were obtained in June and the smallest number of individuals in August. Both parameters had increased noticeably by January 1980.

Life history stages.—Of the 70 taxa identified to species at the Cabrillo Beach site, 41 (58.6%) were represented by at least two life history stages, 15 (21.4%) by three or more stages and three species (4.3%) by all four (egg, larval, juvenile, and adult) life stages. The members of the last group were *Engraulis mordax, Pleuronichthys ritteri* (spotted turbot), and *P. verticalis* (hornyhead turbot).

Table 4. Percentage of juveniles in samples of the 20 most abundant fish species collected during the 12-month study (February 1979–January 1980) at the Cabrillo Beach site. Distinction of juvenile and adult stages based on information from the literature (primarily as summarized in Horn 1974) and/or on the condition (i.e., size class or gonadal state) of captured specimens.

Rank	Species	% Juveniles
1	*Engraulis mordax*	100
2	*Genyonemus lineatus*	29
3	*Seriphus politus*	75
4	*Leuresthes tenuis*	100
5	*Phanerodon furcatus*	62
6	*Micrometrus minimus*	35
7	*Clevelandia ios*	100
8	*Symphurus atricauda*	15
9	*Cymatogaster aggregata*	42
10	*Hyperprosopon argenteum*	62
11	*Embiotoca jacksoni*	17
12	*Atherinops affinis*	94
13	*Atherinopsis californiensis*	68
14	*Paralichthys californicus*	68
15	*Lepidogobius lepidus*	83
16	*Gibbonsia elegans*	64
17	*Syngnathus californiensis*	35
18	*Heterostichus rostratus*	18
19	*Sebastes dallii*	98
20	*Paralabrax nebulifer*	86

The total catch of juvenile-adult fishes using all methods consisted mainly of juveniles. Juveniles were present in the samples of approximately two-thirds (47) of the species. Of the 20 species that made up 98.5% of the total catch, juveniles comprised over 82% of the individuals. Percentages of juveniles ranged from 15% to 100% for individual species (Table 4). *Leuresthes tenuis* and *Clevelandia ios* were represented exclusively by juveniles. Most young fishes were caught primarily in the shallow, inshore locations with the bag seine. Bag seine collections accounted for 78% of the total individuals but only about 14% of the total biomass.

Relationship of abiotic factors to fish abundance and distribution.—In the canonical correlation analysis (Table 5) two abiotic factors, temperature and depth of capture, accounted for almost 50% ($R^2 = 0.47$) of the variation in individual

Table 5. Results of canonical correlation analysis using abiotic factors (temperature and depth of capture) and log-transformed abundances of the 23 most abundant juvenile-adult fish species.

Axis	Canonical R^2	Canonical R	df	F	*P*
1	0.47	0.69	46	2.61	0.0001*
2	0.29	0.54	22	1.83	0.0235*

Standardized Canonical Coefficients for Abiotic Variables

	V_1	V_2
Temperature	−0.3225	0.9532
Depth of capture	−0.9833	−0.2138

* Denotes significance, $P < 0.05$.

abundances of the top 23 species at the Cabrillo Beach site in the first canonical axis. Standardized canonical coefficients of the two abiotic variables indicated that depth contributed more to the first axis and temperature more to the second axis, both at statistically significant levels. The two axes together accounted for approximately 76% of the variability in species abundances.

Salinity values were not used in the canonical correlation analysis because they (1) varied little (28–33‰) over the study period and (2) were found to be significantly correlated with temperature. Dissolved oxygen concentrations were not included in the above analyses because they (1) varied only between 8 and 11 ppm and (2) were not measured at the bag seine stations.

Discussion

The Los Angeles-Long Beach Harbor complex is recognized (Environmental Quality Analysts-Marine Biological Consultants (EQA-MBC) 1976; HEP-USC 1976) as supporting diverse and abundant fish populations that are characterized by seasonal fluctuations in numbers and composition. *Engraulis mordax* and *Genyonemus lineatus* are two especially abundant planktivorous species (the latter as a juvenile); their numbers apparently reflect the nutrient enrichment within the harbor (Stephens 1978). The harbor fish fauna, in general, is characterized (Stephens 1978) by the seasonal occurrence of a large proportion of juvenile fishes.

The results of the present study show that the Cabrillo Beach area is substantially representative of the entire harbor in terms of habitat diversity and fish diversity and abundance. Of the 112 juvenile-adult species that have been recorded (Horn and Allen 1981a) in the harbor complex, 65 were collected at the Cabrillo Beach site. H′ diversity values for numbers at the Cabrillo Beach site equaled or exceeded the range of diversity values summarized by Allen and Horn (1975) for a number of bay-estuarine and harbor environments and are slightly higher than those obtained (0.65–2.08) by Stephens et al. (1974) in an otter trawl survey in outer Los Angeles Harbor. Higher values, however, are to be expected in the present study since three types of sampling gear were utilized during both day and night periods.

The fishes at Cabrillo Beach were characterized by seasonality in diversity, species richness and especially abundance. Diversity was generally inversely related to numerical abundance and biomass. Highest H′ values were recorded in the winter and early spring whereas greatest numbers and biomass were obtained from summer and early fall. This pattern was largely a result of the high abundance of juvenile *Engraulis mordax* in the inshore areas during the summer months. Based on trawl data, Stephens et al. (1974) and HEP-USC (1976) demonstrated a seasonal abundance pattern similar to that of the present study.

A unique feature of the Cabrillo Beach site was the sandy beach habitat and associated shallow subtidal algal bed. This area supported a rich and abundant fish assemblage that was comprised largely of juveniles. Not only were more than 75% of the total fishes of the study captured at this location, the habitat contained a distinct group of fish species that was clearly identified in the cluster analysis (Species Group I).

The cluster analysis delineated species groups that were linked to particular habitats and seasons of occurrence. Group I was essentially composed of resident clinids, embiotocids, syngnathids, and of the seasonally abundant juveniles of

Engraulis mordax and *Leuresthes tenuis.* Group II was a characteristic harbor assemblage captured mainly by otter trawl and was dominated numerically by *Genyonemus lineatus, Seriphus politus,* and *Phanerodon furcatus.* Group III consisted of a small number of seasonal predators, Group IV a set of periodic species and Group V a deep water unit of residents including some nocturnally-active species.

Nighttime collections at Cabrillo Beach enriched the numbers and species composition of juvenile-adult fishes in the samples. Although nighttime samples were significantly greater in abundance only for otter trawls, individual species varied greatly in their day versus night occurrence in the samples. Diel activity patterns, patchy distributions, and visually-mediated gear avoidance are probably all factors that contribute to the more abundant and species-rich catches at night.

The day-night differences in the catches, however, can most likely be attributed to the behavior patterns of the fishes. *Engraulis mordax* juveniles formed schools close to shore during the day. Hence, they were caught in large numbers by bag seine during this period. At night, these juveniles probably dispersed away from shore and were not accessible to the bag seine. Daytime schooling along the shore in the algal beds probably affords some protection from visual, diurnal predators (Hobson 1965) as well as providing warmer temperatures that promote growth. Nighttime dispersal is a well-recognized phenomenon among schooling planktivorous fishes (Loukashkin and Grant 1959; Shaw 1978) although the reason for such activity is not clear. Individuals of *Genyonemus lineatus* may be more active and more widely dispersed at night which could account for their higher abundance in nighttime samples (Allen and DeMartini in press). However, decreased net avoidance at night may also be important in this highly mobile species. Cusk-eels, *Chilara taylori* and *Ophidion scrippsae,* forage actively at night, but remain burrowed in the substrate during the day (Greenfield 1968); this behavior pattern most likely accounts for the greater nighttime catches of these two species in the Cabrillo Beach samples.

Seasonal fluctuations in composition and abundance of fishes occupying inshore habitats (including bays, estuaries, and harbors) may be related to several factors, but temperature frequently appears to be the major underlying factor (e.g., Allen and Horn 1975; Horn and Allen 1981b). Stephens et al. (1974) pointed out that since most temperate species spawn in spring and early summer, recruitment during these months would account for increased abundance. The winter months, just prior to recruitment, should represent the period when a species has been reduced to its lowest numbers. The fact that species richness also decreases in the winter indicates that some species probably leave the harbor during this period.

At Cabrillo Beach, temperature was not significantly correlated with total monthly values for species richness, number of individuals or biomass. However, the combination of temperature and depth of capture accounted for approximately 76% of the variation in individual species abundances and provided an environmental basis for the species groups recognized in the cluster analysis.

Results of the egg and larval sampling showed that the Cabrillo Beach area is used as a spawning and/or a nursery site (especially the latter) by a variety of fish species. The nursery function continues to be important into the juvenile stage as evidenced by the large proportion of juveniles in the juvenile-adult samples.

Egg samples were overwhelmingly dominated by sciaenids. Many of these eggs are probably those of *Genyonemus lineatus* or *Seriphus politus* since these two species are the most abundant sciaenids in the harbor. Sciaenid eggs collected in fall and winter months probably are those of *G. lineatus* and those from late spring and summer months probably *S. politus,* since *G. lineatus* spawns from October through April and *S. politus* from April through August in the Southern California Bight (Goldberg 1976; DeMartini and Fountain 1981). Eggs of *Citharichthys* sp. also contributed substantial numbers to the totals, especially in the fall and winter months. Low numbers of adult *Citharichthys stigmaeus* at the Cabrillo Beach site and in Los Angeles Harbor in general may be due to the limited combination of sandy substrate and cool water temperatures that are preferred by this species (Stephens 1978).

Larval samples were dominated by *Engraulis mordax* although 32 other taxa were identified. Brewer (HEP-USC 1976) also found *E. mordax* to be the most abundant larval form although it was less dominant numerically in his study. He emphasized the importance of *E. mordax* in the trophic structure of the harbor and the significance of the harbor as a nursery for young *E. mordax.* The abundance of larval and juvenile *E. mordax* at the Cabrillo Beach site supports the view of nursery function for the harbor. Thirteen of the 19 families represented by larvae in Brewer's study were collected at the Cabrillo Beach site.

The marked seasonality of both eggs and larvae at the Cabrillo Beach site is similar to that outlined by Brewer (HEP-USC 1976) for the entire harbor. The pattern of high abundance in winter and early spring followed by the low numbers in summer and early fall suggests that several abundant species in the Cabrillo Beach area spawn prior to the warm, productive spring months. Recruitment from these early spawnings can then occur at the onset of the spring pulse of productivity.

Greater numbers of eggs and larvae were consistently collected in the nighttime samples as compared to daytime samples at the Cabrillo Beach site. Differences in number of larvae may be due to a number of factors including daytime gear avoidance and diel vertical migration patterns of various species. The higher number of eggs at night may indicate dusk (or nocturnal) spawning in several species especially *Seriphus politus* (DeMartini and Fountain 1981).

The fish populations of upper Newport Bay, a relatively unaltered estuarine habitat in southern California, are similar (Horn and Allen 1981b) to those of Cabrillo Beach in terms of: 1) numerical dominance by low trophic level fishes, 2) a high degree of seasonality and 3) the influence of temperature and depth on species abundance and distribution. However, species composition and the chronological sequence of abundance peaks of both ichthyoplankton and juvenile-adult populations were markedly different. Both habitats contained a shallow-water species group associated with seasonally abundant algal beds. At Cabrillo Beach the algal beds were occupied by an atherinid-clinid-embiotocid-engraulid species group while the upper Newport Bay beds were dominated by an atherinid-cyprinodontid-gobiid association. Although artificial harbors provide habitat for a diverse array of coastal marine fishes, they do not support the unique assemblage of fishes found in estuarine environments such as upper Newport Bay and, therefore, do not substitute for estuaries as inshore fish habitats.

The Cabrillo Beach site, nevertheless, contains a variety of fish habitats including artificial rocky reef, sandy shore, algal substrate, soft bottom, and limited open water. The area is inhabited either on a permanent or periodic basis by fishes which reflect this habitat diversity. The sandy beach and associated subtidal algal bed support a distinct assemblage of fishes and a large number of juvenile forms. It is the presence of this habitat type that most clearly distinguishes the area from the remainder of Los Angeles Harbor.

The physical and biological features of the Cabrillo Beach area offer a lesson on harbor construction. If habitat diversity and water circulation are maintained and if pollution inflow is minimized, harbors can support abundant, rich and dynamic fish assemblages.

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Literature Cited

Allen, L. G. 1976. Abundance, diversity, seasonality and community structure of the fish populations in Newport Bay, California. M.A. Thesis, California State Univ., Fullerton, 108 pp.

———, and M. H. Horn. 1975. Abundance, diversity and seasonality of fishes in Colorado Lagoon, Alamitos Bay, California. Estuar. Coast. Mar. Sci., 3:371–380.

———, and E. E. DeMartini. *In press.* Temporal and spatial patterns of nearshore distribution and abundance of the pelagic fishes off San Onofre—Oceanside, California. Fish. Bull.

———, and W. S. White. *In press.* Ecological aspects of the ichthyoplankton and demersal fish populations of Newport Bay, California: 1974–1975. Contrib. Sci. Los Angeles Nat. Hist. Mus.

Clifford, H. T., and W. Stephenson. 1975. An introduction to numerical classification. Academic Press, xii + 229 pp.

DeMartini, E. E., and R. K. Fountain. 1981. Ovarian cycling frequency and batch fecundity in the queenfish, *Seriphus politus*: attributes representative of serial spawning fishes. Fish. Bull., 79: 547–560.

Environmental Quality Analysts and Marine Biological Consultants (EQA-MBC). 1976. Marine monitoring studies, Long Beach Generating Station. Prepared for Southern California Edison Company. Annual Report, 1975.

Frey, H. W., R. F. Hein, and J. L. Spruill. 1970. The natural resources of Upper Newport Bay and recommendations concerning the bay's development. Calif. Resources Agency, Dept. Fish and Game, 148 pp.

Goldberg, S. R. 1976. Seasonal spawning cycles of the sciaenid fishes *Genyonemus lineatus* and *Seriphus politus*. Fish. Bull., 74:983–984.

Greenfield, D. W. 1968. Observations on the behavior of the basketweave cusk-eel, *Otophidium scrippsi* Hubbs. Calif. Fish Game, 54:108–114.

Harbors Environmental Projects, University of Southern California (HEP-USC). 1976. Environmental investigations and analyses, Los Angeles-Long Beach harbors 1973–76. Final Report to U.S. Army Corps of Engineers, Los Angeles District, 737 pp.

———. 1979. The marine environment in Los Angeles and Long Beach harbors during 1978. Report on field research under contract with the City of Los Angeles and Port of Los Angeles.

Hobson, E. S. 1965. Diurnal-nocturnal activity of some inshore fishes in the Gulf of California. Copeia, 1965:291–302.

Horn, M. H. 1974. Fishes, Chapter 11, 124 pp. *In* A summary of knowledge of the southern California coastal zone and offshore areas. Vol. II, Biological environment. (Dailey, M. D., B. Hill and N. Lansing, eds.), South. Calif. Ocean Stud. Consort. for Division of Marine Minerals, Bureau of Land Management, Dept. Interior. Contract No. 08550-CT4-1.

———, and L. G. Allen. 1981a. A review and synthesis of ichthyofaunal studies in the vicinity of Los Angeles and Long Beach Harbors, Los Angeles County, California. Final Report to U.S. Fish and Wildlife Service, Ecological Services, Laguna Niguel, California, 96 pp.

———. 1981b. Ecology of fishes in Upper Newport Bay, California: seasonal dynamics and community structure. Calif. Dept. Fish Game, Mar. Res. Tech. Rep. No. 45, 102 pp.

Loukashkin, A. S., and H. Grant. 1959. Behavior and reactions of the Pacific sardine, *Sardinops caerulea* (Girard), under the influence of white and colored lights and darkness. Proc. Calif. Acad. Sci., 29:509–548.

Reish, D. J., D. F. Soule, and J. D. Soule. 1980. The benthic biological conditions of Los Angeles-Long Beach harbors: results of 28 years of investigations and monitoring. Helgoländer Meersunter. 34:193–205.

Shannon, C. E., and W. Weaver. 1949. The mathematical theory of communication. Univ. of Illinois Press, +117 pp.

Shaw, E. 1978. Schooling fishes. Am. Sci., 66:166–175.

Southern California Ocean Studies Consortium (SCOSC). 1977. Draft environmental impact report. Downtown marina. E-11-77. City of Long Beach.

Stephens, J. S., Jr. 1972. Bay and inshore fish. Pp. 18–21 *in* Proc. So. Calif. Coastal Zone Symp., Fullerton, California, March 17–18, 1972.

———. 1978. Breakwaters and harbors as productive habitats for fish populations—why are fishes attracted to urban complexes? *In* Proc. First So. Calif. Ocean Stud. Consort. Symp.—The Urban Harbor Environment (J. N. Baskin, M. D. Dailey, S. N. Murray, and E. Segal, eds.). South. Calif. Ocean Stud. Consort. Tech. Paper No. 1:i–viii + 95 pp.

———, C. Terry, S. Subber, and M. J. Allen. 1974. Abundance, distribution, seasonality and productivity of the fish populations in Los Angeles Harbor, 1972–73 *in* Marine Studies of San Pedro Bay, Part IV, Environ. Field Invest. (D. Soule and M. Oguri, eds.), Allan Hancock Foundation Pub. USC-SG-6-72:1-42.

———, and K. E. Zerba. 1981. Factors affecting fish diversity on a temperate reef. Env. Biol. Fish., 6:111–121.

Terry, C. B., and J. S. Stephens, Jr. 1976. A study of the orientation of selected embiotocid fishes to depth and shifting seasonal vertical temperature gradients. Bull. So. Calif. Acad. Sci., 75: 170–183.

Young, P. H. 1964. Some effects of sewer effluent on marine life. Calif. Fish Game, 50:33–41.

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New Range Information on Two West American Slugs (Gastropoda: Pulmonata: Arionidae)

Barry Roth and Peter H. Pressley

Abstract.—New range information on two West American slugs (Gastropoda: Pulmonata: Arionidae) by Barry Roth and Peter H. Pressley. *Bull. Southern California Acad. Sci.* 82(2):71–78, 1983. *Prophysaon dubium* Cockerell, 1890, occurs in rockslides in the vicinity of Big Bar, Trinity County, California. This is the first record of the species in California and a range extension south approximately 375 km from near Cheshire, Lane County, Oregon. *Hesperarion niger* (Cooper 1872) occurs at the same locality, a range extension north-northwest about 195 km from Williams, Colusa County, California. Seven localities in southern Monterey and northern San Luis Obispo counties, California, document the southern range of *H. niger* in the Coast Ranges; three new localities in the Sierra Nevada are added. The known distribution of *H. niger* is mapped.

From September 1980 to October 1981 we conducted field study in a portion of the Klamath Mountains, Trinity County, California. The distribution of all land mollusks was investigated in an area extending roughly from Ripstein Campground, north of Junction City (on the NE), Hawkins Bar (NW), Hyampom (SW), and Hayfork Summit (SE), with additional study along Hayfork Creek as far south as Natural Bridge. This is approximately 123°00′–123°30′W long. by 40°37.5′–40°52.5′N lat. and lies mainly within the Shasta-Trinity National Forest. All stations are in the watershed of the Trinity River and its tributary streams. Some sampling was performed during every month of the year.

This region, like the Klamath Mountains in general, has been very sparsely prospected for land mollusks in past times; 11 of the 22 species of land mollusks detected in our survey proved to be either new, problematical, or range extensions. Descriptions of the new taxa are in preparation. This paper records the occurrence of two slug species, *Prophysaon dubium* Cockerell, 1890, and *Hesperarion niger* (Cooper 1872), not previously known from this part of California.

Field work by the senior author and E. V. Coan in southern Monterey and northern San Luis Obispo counties, California, in the spring of 1982, resulted in the finding of *Hesperarion niger* at numerous localities in the southern Coast Ranges and additional southward range extension. The known distribution of *H. niger* is reviewed—based on museum specimens and accurate published localities—and plotted on a map for the first time.

Family Arionidae
Genus *Prophysaon* Bland and Binney, 1873
Subgenus *Prophysaon, sensu stricto*

Prophysaon (*Prophysaon*) *dubium* Cockerell, 1890

(Fig. 1)

Prophysaon coeruleum var. *dubium* Cockerell, 1890:112.
Prophysaon dubium Cockerell, Pilsbry 1948:694–695, fig. 379.—Webb 1959:23.

Rockslides on the north side of California Highway 299, 3.9 mi (6.8 km) by road west of the Trinity River bridge at Big Bar, investigated on 28 April 1981, yielded the following assemblage of mollusks: *Monadenia churchi* Hanna and Smith, 1933; *Helminthoglypta* sp., cf. *H. mailliardi* Pilsbry, 1927; an undescribed species of *Trilobopsis*; *Prophysaon dubium*; *Ariolimax columbianus* (Gould 1851); and *Hesperarion niger* (Cooper 1872). This constitutes a range extension for *P. dubium* south approximately 375 km from near Cheshire, Lane County, Oregon, where it was reported by Webb (1959). The other known localities, as reported by Pilsbry (1948) are as follows: WASHINGTON: Olympia (type locality); Home, Pierce County. OREGON: Oswego, Clackamas County; mushroom growth at the edge of a mountain meadow within a few feet of a stream, the first creek east of Cascade Locks, Hood River County. This is the first record of *P. dubium* in California.

Two specimens were taken; subsequent visits later in the year produced no additional specimens. The locality is a steep, south-facing cut bank in an open stand of mixed evergreen forest, elevation about 370 m. There is little immediate cover over the rockslides except for sparsely distributed shrubs of *Rhus diversiloba* and *Ceanothus.* The most common snail at this site in April was an undescribed species of *Trilobopsis* (Roth in prep.) related to *Trilobopsis roperi* (Pilsbry 1889) from the vicinity of Shasta Lake, Shasta County.

The two *Prophysaon dubium* agree in most particulars with Pilsbry's (1948: 694–695) redescription of the species. They are about 15 and 16 mm long, respectively, after preparation by drowning followed by transfer in stages to 75% ethanol. The body is purplish gray, the mantle irregularly marbled with black. The papillae on mantle and flanks are conspicuous; the summit of each papilla is light, surrounded by a rosette of darker pigment. A distinct constriction surrounds the body about 4 mm from the tail tip, posterior to the end of the visceral cavity, in the usual zone of abscission in tail-shedding species of *Prophysaon.* This feature was not described by Pilsbry in specimens from Cascade Locks, Oregon, but his enlarged figure of a living individual (1948:fig. 379A) shows a slight dorsal indentation 9 mm anterior to the tail tip that probably represents the abscission zone. In life the slugs were of an unusual matte appearance (in contrast to the typical moist gloss of most slug species) and stuck to the fingers without a copious discharge of mucus. As usual in the genus, the pedal furrows are deep and the sole of the foot shows no trace of tripartite division.

Genitalia of one specimen were dissected (Fig. 1). They closely resemble the dissections figured by Pilsbry (1948:figs. 379D, E), except that the epiphallus is not "over twice the length of the preserved animal," but about 17 mm long. The lobules of the ovotestis are black pigmented distally, as in Oregon specimens.

The material at hand offers no firm basis for taxonomic separation of the California specimens; length of the epiphallus is an unreliable systematic character in *Prophysaon.* The apparent gap in range from the Klamath Mountains to central Oregon may eventually be filled by more field work in the intervening area.

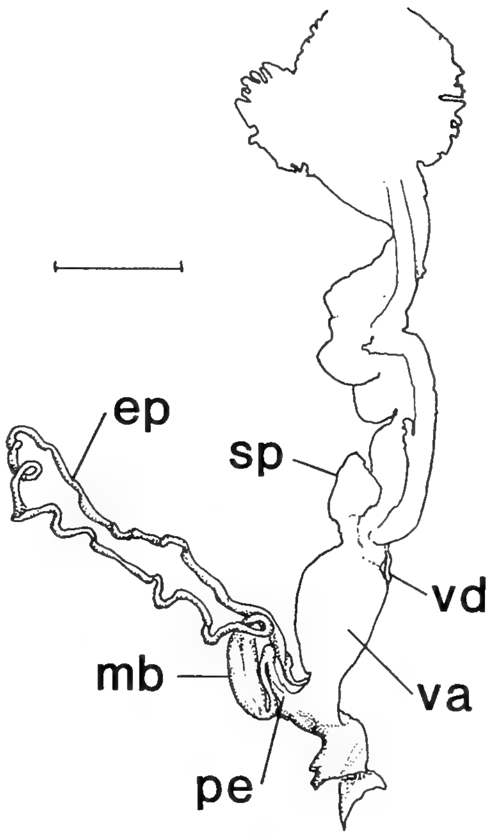

Fig. 1. Lower genital anatomy of *Prophysaon dubium*, CAS 028724. Scale line = 2 mm. ep, epiphallus; mb, muscular body of epiphallus; pe, penis; sp, spermatheca; va, vagina; vd, vas deferens.

Genus *Hesperarion* Simroth, 1891

Hesperarion niger (Cooper 1872)

(Fig. 2)

Ariolimax niger Cooper, 1871:151 (*nomen nudum*).—1872:147–148, pl. 3, figs. E1–4.—Binney 1878:234, fig. 133; pl. V, fig. D; pl. XII, fig. F.—Coan 1982: 168.

Hesperarion niger (Cooper), Mead 1943:699–702, pl. 2, figs. 6–7.—Gregg 1943a: 8.—1943b:5.—Lange 1944:37.—Gregg 1945:36.—Pilsbry 1948:723–726, figs. 388–390.—Ingram 1949:24–25.—Ingram and Lotz 1950:21–22.—Zilch 1959: 232, fig. 825.—Gregg 1961:85.—Webb 1961:35.

Ariolimax andersoni "J. G. Cooper," Binney 1878:235–236, figs. 135, 136; pl. V, fig. G; pl. XII, fig. E. *Non Arion? andersonii* Cooper, 1872.

The above synonymy is complete for references from 1943 to present; for earlier references, see Pilsbry (1948:723).

A single specimen of *Hesperarion niger* was found in rockslides on the north side of California Highway 299, 3.9 mi (6.8 km) by road west of the Trinity River bridge at Big Bar, 28 April 1981. Subsequent visits later in the year produced no additional specimens. The specimen is 37 mm long after drowning and preservation in 75% ethanol. It is smoky brown dorsally, with numerous small, irregular black spots scattered over the integument, some joining in an oblique reticulation along the mucus grooves of the flanks. The foot margin is light tan, conspicuously striped vertically with black. The sole is light tan, and unmarked. The specimen proved to be sexually immature.

Figure 2 plots the known occurrences of *H. niger* exclusive of unlocalized county records. Almost all reported occurrences seem to have been based on small samples—single or at most a few specimens. Cooper (1871) listed the still undescribed "*Ariolimax*" *niger* from "near San Francisco" (by present boundaries, either San Mateo or San Francisco county), Sausalito, Pescadero (San Mateo County), and "Mt. Diablo Range." Whether the latter refers to Mount Diablo proper (as interpreted by Coan 1982) or the more southern Diablo Range is not certain. The original description (Cooper 1872) does not include a type locality designation, citing only "a very young one from east of S[an]. F[rancisco]. Bay," and Cooper's surmise that a specimen mentioned by Gould (1852), questionably from Oregon, might be conspecific. Cooper (1876) recorded the species from near Cypress Point, Monterey, and near Oakland, "not in gardens but in uncultivated oak-groves on clay lands."

Binney (1878) added Bolinas, Marin County, and Santa Rosa and Healdsburg, Sonoma County; for the synonymous *Ariolimax andersoni,* his locality is "the mountains of Alameda County." Pilsbry and Vanatta (1898) added the localities Hayward, Santa Clara, near San Jose, and Stevens Creek Canyon, Santa Cruz Mountains, elevation 900 ft (270 m). Waste (1940 MS) recorded *H. niger* from Colusa, Napa, Marin, Alameda, San Mateo, Santa Clara, and Monterey counties, mostly documented by voucher specimens now in the California Academy of Sciences (CAS) collection. His most northern locality was 10 mi (16 km) west of Williams, Colusa County. Lange (1944) added Tehama, Lake, and San Benito counties to the record, but did not give specific localities or cite repositories for these specimens. Our attempts to locate the material have been unsuccessful. The finding of *H. niger* in Trinity County might be regarded as, indirectly, supporting Lange's Tehama County record; but since Tehama County extends from the inner Coast Range across the Sacramento Valley to the Sierra Nevada foothills, the citation is too vague to enter on the map. There is, however, the suggestion that *H. niger* may extend more or less continuously along the inner North Coast Ranges from the San Francisco Bay area to Trinity County. Ingram and Lotz (1950) reported specimens from Berkeley, Tilden Park (north of Berkeley), Happy Valley (near Lafayette, Contra Costa County), Napa, and San Mateo, in addition to several previously recorded localities.

Gregg (1945, 1961) presented the first definite Sierran localities: west of Poso Creek, about ½ mile (0.8 km) north of Glennville, Kern County, and along Arrastre Creek, about 3 miles (4.8 km) east of White River, Tulare County. Here we add three northern Sierran localities—Mormon Island, Sacramento County, and San Antonio Creek and West Point, Calaveras County—based on material in the CAS collection.

The finding of *Hesperarion niger* at several localities near Jolon and east of San Lucas, southern Monterey County, by K. Lucas and R. Hanson in May 1969 and

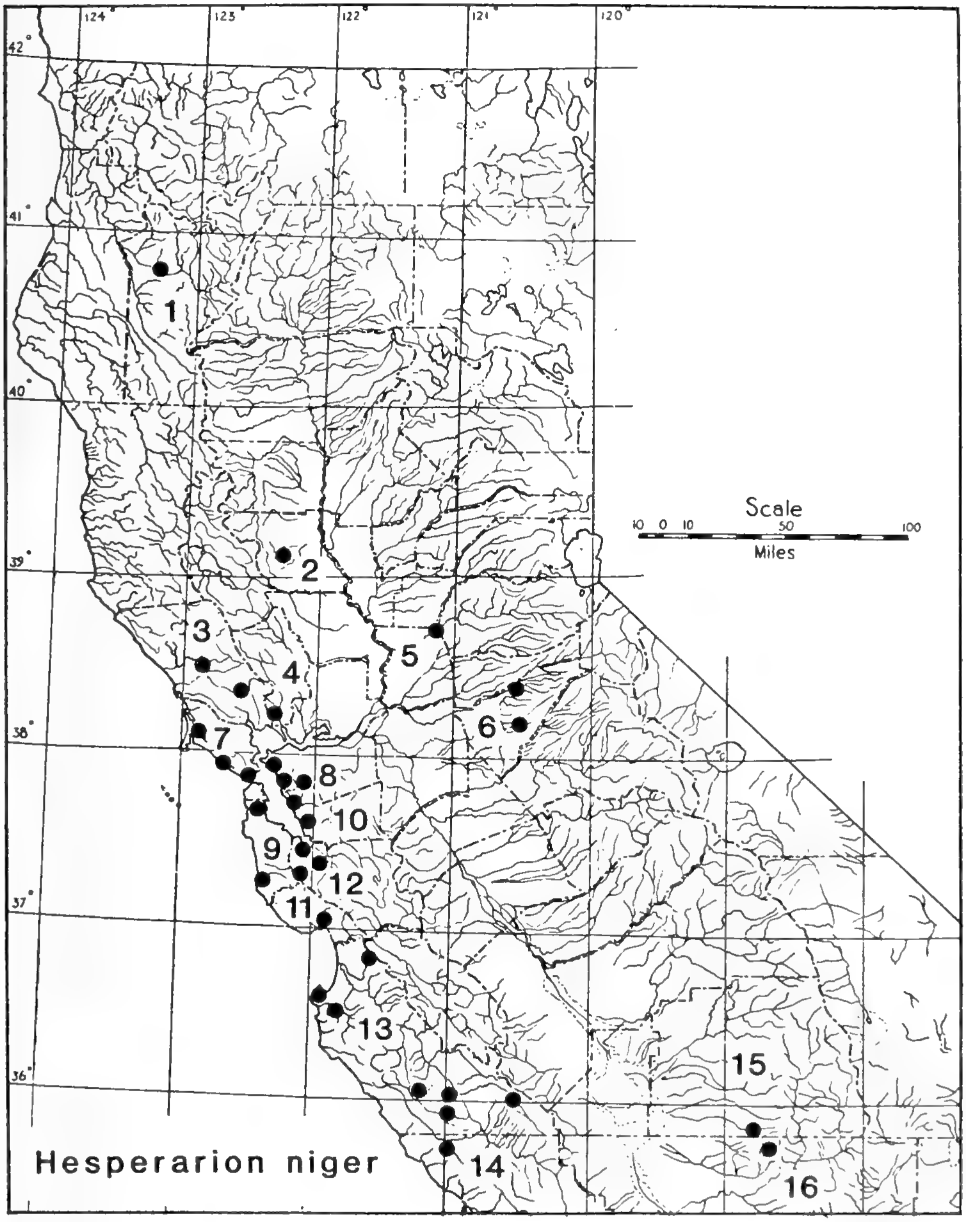

Fig. 2. Map of California showing distribution of *Hesperarion niger*, exclusive of unlocalized records. Data from Cooper (1871, 1872, 1876), Binney (1878), Pilsbry & Vanatta (1898), Gregg (1945, 1961), Ingram and Lotz (1950), and CAS collection localities described in text. Numbers designate counties: 1, Trinity; 2, Colusa; 3, Sonoma; 4, Napa; 5, Sacramento; 6, Calaveras; 7, Marin; 8, Contra Costa; 9, San Mateo; 10, Alameda; 11, Santa Cruz; 12, Santa Clara; 13, Monterey; 14, San Luis Obispo; 15, Tulare; 16, Kern.

by Roth and E. V. Coan in April 1982 extends the range southward in the Coast Ranges from the upper Carmel Valley, where it was recorded by Waste (1940 MS). The winter of 1981–1982 was exceptionally wet in northern California, with moist ground conditions lasting well into the spring months. Roth and Coan found *H. niger* in moderate numbers under and around oak deadfalls and branches on the ground in regions of Valley Oak Savanna and adjacent California Prairie (Küchler 1977) (specific localities in list that follows). Elevations range from about 240–360 m west of the Salinas Valley (CAS 029653, CAS 029656) to about 470 m east of the valley (CAS 029651).

The CAS collection contains material from the following localities:

TRINITY COUNTY: 3.9 mi (6.8 km) west of Trinity River bridge at Big Bar, rockslides on north side of California Highway 299, B. Roth coll. 28 April 1981, one specimen (CAS 028725). COLUSA COUNTY: 10 mi (16 km) west of Williams, on road to Lower Lake, G. D. Hanna coll. 1931, 3 specimens (CAS 029496). NAPA COUNTY: Archer Taylor Ranch, Mount La Salle, A. G. Smith coll. 3 April 1949, 3 specimens (CAS 029501). 8 mi (13 km) southwest of Napa, R. Holdenried coll. 4 February 1940, 2 specimens (CAS 029458). SACRAMENTO COUNTY: Mormon Island, A. G. Smith coll. 18 February 1931, one specimen (CAS 029495). CALAVERAS COUNTY: Near West Point, A. G. Smith coll. 2 May 1954, 3 specimens (CAS 029658). San Antonio Creek, near Sheep Ranch, A. G. Smith coll. 18 May 1952, 4 specimens (CAS 029503). MARIN COUNTY: Inverness, A. G. Smith coll. 24 February 1951, one specimen (CAS 029654). Bolinas, H. Hemphill coll., 7 specimens (CAS 029457). CONTRA COSTA COUNTY: 2 mi (3 km) south of Pinole, A. G. Smith coll. 12 January 1941, 2 specimens (CAS 029492). Happy Valley, near Lafayette, A. G. Smith coll. 22 March 1942, 4 specimens (CAS 029499). ALAMEDA COUNTY: Wildcat Canyon, Tilden Park, Berkeley, A. G. Smith coll. 1 February 1942, 2 specimens (CAS 029500). Wildcat Canyon, A. G. Smith coll. 10 March 1954, 2 specimens (CAS 029660). Garden at 3090 Buena Vista Way, Berkeley, in pile of loose bricks, A. G. Smith coll., one specimen (CAS 029502). SAN MATEO COUNTY: San Bruno Mountain, Radio Road turnoff, eucalyptus forest and blackberry, K. E. Lucas coll. 29 December 1970, 2 specimens (CAS 029494). [No more definite locality.] H. Hemphill coll., 4 specimens (CAS 029493). SANTA CRUZ COUNTY: 3.5 mi (5.6 km) up Soquel Creek, M. Sanfort coll. 10 April 1941, one specimen (CAS 029497). MONTEREY COUNTY: San Juan Grade Road southwest of San Juan Bautista, above creek tributary to Gabilan Creek, B. Roth & E. V. Coan coll. 17 April 1982, 2 specimens (cf. *niger*) (CAS 029659). Hastings Reservation, Carmel Valley, J. M. Linsdale coll. 24 January 1940, one specimen (CAS 029498). Upper Carmel Valley, J. M. Linsdale coll. 21 January 1940, 2 specimens (CAS 029456). Head of Jolon Valley on Jolon Road, B. Roth & E. V. Coan coll. 16 April 1982, 2 specimens (CAS 029656). West side of Jolon Valley 0.25 mi (0.40 km) south of Jolon Road-Sulphur Springs Road intersection, B. Roth & E. V. Coan coll. 16 April 1982, 6 specimens (CAS 029652). Espinosa Canyon, north of Lockwood, B. Roth & E. V. Coan coll. 17 April 1982, one specimen (CAS 029653). South end of Tule Canyon, south of Lockwood, B. Roth & E. V. Coan coll. 17 April 1982, 5 specimens (CAS 029650). Bank of Nacimiento River 0.5 mi (0.8 km) southwest of Bryson, K. Lucas & R. Hanson coll. 5 May 1969, 3 specimens (CAS 029657). Peach Tree Valley, east of San Lucas, B. Roth & E. V. Coan coll. 17

April 1982, 2 specimens (CAS 029651). SAN LUIS OBISPO COUNTY: Camp Roberts Military Reservation across county road from Chimney Rock. B. Roth & E. V. Coan coll. 17 April 1982, 2 specimens (CAS 029655).

In summary, presently documented records of *Hesperarion niger* indicate an extensive distribution in the North and South Coast Ranges, coastal and subcoastal in the Monterey and San Francisco Bay areas, entering the southern Klamath Mountains in the north, with two (possibly isolated) enclaves in the foothill belt of the Sierra Nevada. Additional field work will be necessary to determine whether the distribution is more nearly continuous through low elevations in the Sierras, in the inner North Coast Ranges, and possibly around the northern end of the Sacramento Valley.

Acknowledgments

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Literature Cited

Binney, W. G. 1878. The terrestrial air-breathing mollusks of the United States and the adjacent territories of North America, vol. V. Bull. Mus. Compar. Zool., 4:1–449.

Coan, E. V. 1982. James Graham Cooper: Pioneer western naturalist. Moscow, Idaho, University Press of Idaho.

Cockerell, T. D. A. 1890. New western slugs. The Nautilus, 3:111–113.

Cooper, J. G. 1871. On shells of the west slope of North America. Proc. California Acad. Sci., ser. 1, 4:150–154.

———. 1872. On new Californian Pulmonata, etc. Proc. Acad. Nat. Sci. Philadelphia, 24:143–154.

———. 1876. On shells of the west slope of North America. No. III. Proc. California Acad. Sci., ser. 1, 6:14–27.

Gould, A. A. 1852. Mollusca and shells. United States Exploring Expedition during the years 1839–1842 . . . , 12:i–xv, 1–510.

Gregg, W. O. 1943a. Notes on land slugs of southern California. Min. Conchol. Club So. California, 25:3–8.

———. 1943b. Other species of land slugs found in the Pacific Coast states. Min. Conchol. Club So. California, 27:3–9.

———. 1945. Southern record for *Hesperarion niger*. The Nautilus, 59:36.

———. 1961. Southern California slugs, additional locality records. The Nautilus, 75:84–85.

Ingram, W. M. 1949. A check list of the Limacidae, Endodontidae, Arionidae, Succineidae, Pupillidae, Valloniidae, Carychiidae, and Truncatellidae of California. Bull. So. California Acad. Sci., 48:19–34.

———, and C. Lotz. 1950. Land mollusks of the San Francisco Bay counties. J. Entomol. Zool., Pomona Coll., 42:20–39.

Küchler, A. W. 1977. The map of the natural vegetation of California. Pp. 909–939, map *in* Terrestrial vegetation of California. (M. G. Barbour and J. Major, eds.), New York, John Wiley and Sons.

Lange, W. H. 1944. Land slugs in California. Bull. So. California Acad. Sci., 43:33–40.

Mead, A. R. 1943. Revision of the giant west coast land slugs of the genus *Ariolimax* Moerch. Amer. Midl. Nat., 30:675–717.

Pilsbry, H. A. 1948. Land Mollusca of North America (north of Mexico). Acad. Nat. Sci. Philadelphia Monog. 3, 2(2):i–xlvii, 521–1113.

———, and E. G. Vanatta. 1898. Revision of the North American slugs: *Binneya, Hemphillia, Hesperarion, Prophysaon* and *Anadenulus*. Proc. Acad. Nat. Sci. Philadelphia, 50:219–261.

Waste, R. J. 1940 (MS). The land slugs of California. Unpublished M.S. thesis, Univ. California, Berkeley, 111 pp.

Webb, G. R. 1959. Two new northwestern slugs, *Udosarx lyrata*, and *Gliabates oregonia*. Gastropodia, 1:22–23.

———. 1961. The phylogeny of American land snails with emphasis on the Polygyridae, Arionidae, and Ammonitellidae. Gastropodia, 1:31–44.

Zilch, A. 1959. Gastropoda, Teil 2, Euthyneura. Lief. 2. Handbuch der Paläozoologie, 5:201–400.

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Seasonal Structure of a Central California Rocky Intertidal Community in Relation to Environmental Variations[1]

Michael H. Horn, Steven N. Murray, and Roger R. Seapy

Abstract.—Seasonal Structure of a Central California Rocky Intertidal Community in Relation to Environmental Variations by Michael H. Horn, Steven N. Murray, and Roger R. Seapy, *Bull. Southern California Acad. Sci.*, 82(2), 79–94, 1983. The overall abundance (% cover) of macrophyte populations from a central California rocky intertidal habitat near Piedras Blancas was greatest during summer and fall and least during winter. As with the macrophytes, total macroinvertebrate abundance (% cover and density) was lowest in winter. However, unlike the macrophyte pattern, macroinvertebrate abundance was highest in spring. Summer macrophyte standing stocks were characterized by increased abundances of the more delicate, rapidly growing and spatially unpredictable annual seaweeds. In contrast, the reduced winter macrophyte flora was dominated by populations of structurally tougher, slower growing and spatially predictable perennial species. High macrophyte standing stocks were associated with increased day length, reduced periods of aerial exposure due to daytime minus tides, low rainfall, and periods of infrequent storms. Conversely, low macrophyte standing stocks were associated with decreased day length, longer periods of aerial exposure, relatively high rainfall, and periods of frequent storms. The seasonal pattern of high summer/fall and low winter macrophyte standing stocks parallels that recently described for southern California rocky intertidal communities. However, the less complex, more uniform, and predictable environment of the central California coast appears to lead to more consistent and sharply defined patterns of biotic seasonality.

Introduction

Relatively few studies have quantitatively assessed the seasonal dynamics of rocky intertidal communities in temperate waters despite the fact that it is generally recognized that seasonal changes in the standing stocks of the biota occur at these latitudes. On the California coast, investigations of seasonality in rocky intertidal communities are recent and confined to the warm temperate waters of the Southern California Bight (Gunnill 1980; Littler 1980a, b; Seapy and Littler 1982). The marine biota of the central California coastline between Point Conception and Monterey Bay is relatively well known in terms of its taxonomy and natural history (e.g., Ricketts et al. 1968; Stephenson and Stephenson 1972; Smith and Carlton 1975; Abbott and Hollenberg 1976; Morris et al. 1980) and cold-water affinities (e.g., Valentine 1966; Horn and Allen 1978; Murray et al. 1980; Seapy and Littler 1980; Murray and Littler 1981). However, published ecological research has been limited to a study by Seapy and Littler (1978) on rocky intertidal community structure at Cayucos Point (35°26′45″N, 120°56′55″W) and a two-

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[1] Contribution No. 19 from the Southern California Ocean Studies Consortium.

year biotic survey by Burge and Schultz (1973) at Diablo Cove (35°12′44″N, 120°51′23″W) (Fig. 1). Neither of these studies included quantitative analyses of seasonal fluctuations in the abundances of the biota.

The lack of information on seasonal fluctuations of the standing stocks of the rich and diverse intertidal biota of the central California coast provided the main impetus for the present study. In the course of other work, we observed marked seasonal fluctuations in abundance of macrophytes occurring in the relatively uniform thermal environment of the intertidal zone near Piedras Blancas. Also, we were aware that Gislén (1943), based on an extensive series of observations, had described some important climatic differences between the shore environments of central and southern California. The primary purposes of this study were, then, to (1) quantitatively describe seasonality in species composition and standing stocks of macrophytes and macroinvertebrates near Piedras Blancas, (2) relate the observed abundance patterns to the environmental features of the region and (3) compare the seasonal patterns exhibited by central California rocky intertidal macroorganisms with those recently described for southern California shores.

The Study Area

Our rocky intertidal study site (35°39′55″N, 121°15′25″W) is located ~3 km southeast of Piedras Blancas, San Luis Obispo County, California (Fig. 1). The site is protected from waves originating from the northwest by Point Piedras Blancas and to a lesser degree from southerly waves by offshore rock masses. The shoreline lies at the base of an eroded coastal bluff and slopes gently seaward exposing a horizontal expanse of ~60 m during minus tides. The substrate consists mostly of large, stable rock masses and flattened benches, along with numerous small boulders that accumulate as rubble in the midintertidal zone. Periodically, sections of intertidal zone are partially buried by coarse-grained sand, which we found to range in cover from 1.6 to 3.2% during the study. A dense bed of *Macrocystis integrifolia* extends from the lower intertidal zone seaward. The study site is characteristic of the semi-protected rocky shores along this portion of the central California coastline and was selected for study because of its typical features and accessibility.

Materials and Methods

The distributions and abundances of macrophyte and macroinvertebrate populations were studied on 23–27 May 1978, 16–20 August 1978, 29 November–2 December 1978, and 23–26 February 1979. Two parallel transect lines were laid perpendicular to the shoreline (~130° magnetic). The origin of each line was determined haphazardly and marked securely with a metal eyebolt that was cemented into the substrate using marine epoxy. In addition, several bolts were similarly embedded into the substrate along each transect line to facilitate accurate relocation during subsequent visits. The transect lines were separated by a distance of ~10 m and traversed biological communities visually determined to be representative of the beach.

Rectangular (30 × 50 cm) 0.15 m^2 quadrats were placed at 2-m intervals along each transect line except where prohibited by substrate topography or in the flat

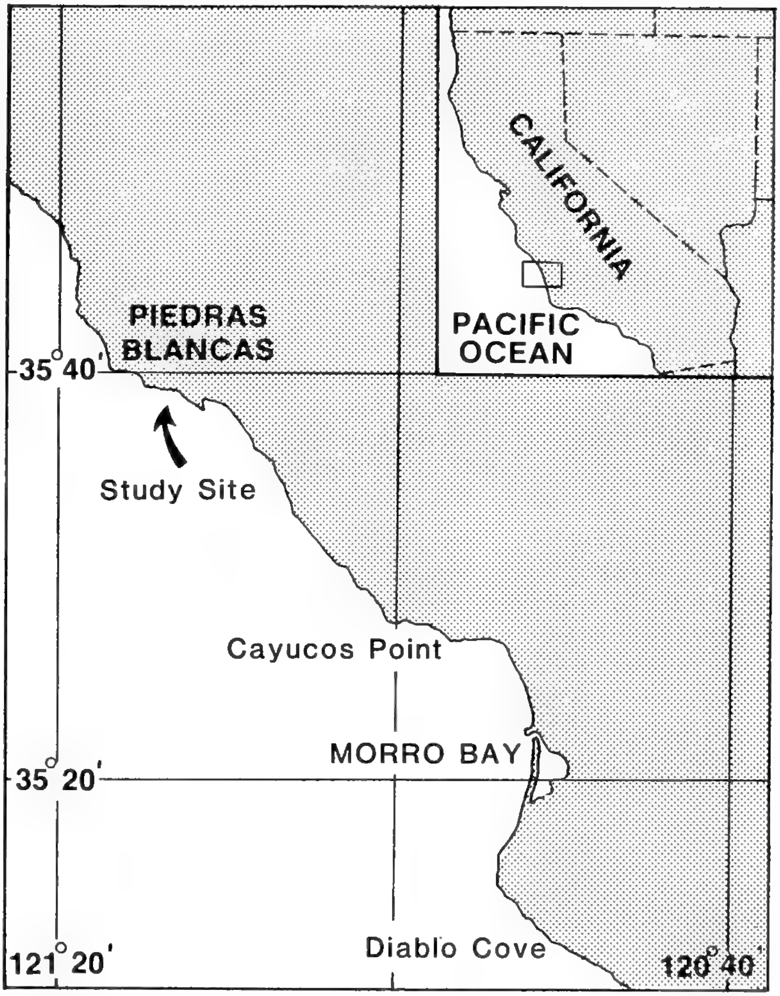

Fig. 1. Location of the rocky intertidal study site near Piedras Blancas, San Luis Obispo County, California.

and monotonous rubble habitat where samples were obtained at 4-m intervals. Additionally, two to three samples were taken at the extreme ends of the transect lines to increase sampling intensity on the upper and lower portions of the shore. This sampling regime provided a total of 35 permanently located plots for each seasonal quantification of the abundances of the macrophyte and macroinvertebrate populations.

Vertical tidal heights of the quadrats relative to 0 tidal datum at MLLW were determined with respect to a permanent reference point using standard surveying techniques. The height of the reference point was obtained using predicted low tides reported in the U.S. Department of Commerce Tide Tables (Anon. 1978a, 1979a). Independent determinations of the tidal height of the permanent reference point performed on successive days and during successive seasonal visits yielded a variation < ±0.1 m.

Macrophyte and Macroinvertebrate Abundance

Abundances of macrophytes and macroinvertebrates were determined for each quadrat using a photographimetric technique described in detail elsewhere (Littler 1980a). This technique provides for nondestructive sampling, a necessity where the same set of quadrats is to be reassessed on a seasonal basis. Quadrats were photographed at right angles to the substrate using Kodachrome color and Ektachrome infrared color slide film in 35-mm cameras equipped with electronic strobes. In cases where multilayered algal canopies occurred, which often resulted in greater than 100% total cover for any given quadrat, more than one photograph was taken to account for the organisms occupying different strata. In addition to photographs, the species composition of each quadrat was recorded in the field along with counts of macroinvertebrates and visual estimates of cover provided by macrophytes and macroinvertebrates. Only the macro-epibiota, those organisms that could readily be discerned in the field with the unaided eye, were included in the quadrat analyses. Quantification of microalgae (including the blue-green algae), small epifauna, and infauna was not attempted. The field notes were utilized along with the photographs in the laboratory to determine cover (percentage of the substrate covered by each species) for macrophytes and sessile macroinvertebrates and density (No. m^{-2}) for macroinvertebrate species other than sponges and colonial ascidians. Cover data were obtained by a point-intercept method where the color transparencies were projected onto paper containing a grid of dots. To facilitate the data analysis, a minimum cover value of 0.1% was assigned to all species occurring within a quadrat but not intercepted by a point.

Species diversity was expressed as richness (simple counts of taxa) and as indices derived from the abundance data, i.e., H' diversity (Shannon and Weaver 1949) and J' evenness (Pielou 1975). Natural logarithms were used in calculating H' and J'.

Macrophyte Biomass

In order to estimate macrophyte biomass, 18 quadrats were harvested to the substrate during each seasonal visitation. These samples were arbitrarily collected from macrophyte assemblages similar to those occurring in the undisturbed quadrats. Prior to harvesting, the percentage cover of the macrobiota was quantified by the photographimetric method. Harvested material was fixed in a 5–10% formaldehyde-seawater solution, returned to the laboratory, and sorted to species. Samples were then dried to constant weight at 50–60°C. For each species, this procedure provided percentage cover and dry biomass data pairs from each quadrat sample. Regression equations for each species were then calculated (sensu Littler 1979) from the entire data set where the dependent variable $\hat{Y}$ = dry biomass in g m^{-2} and the independent variable $\hat{X}$ = cover (%). Seasonal variations in dry biomass were then estimated for the macrophyte populations from the cover data generated from the undisturbed sampling program by using the regression equations.

Environmental Factors

We obtained records of air and sea temperature, rainfall and storm events for the Piedras Blancas region for 1978 and 1979 and calculated tidal exposure times and day lengths for comparison with our data on seasonal standing stocks of macrophytes and macroinvertebrates. Monthly rainfall data and mean monthly air temperatures for Morro Bay (~40 km south of the study site) were obtained from U.S. Department of Commerce Climatological Data (Anon. 1978b, 1979b). Mean monthly sea surface temperatures for Morro Bay were calculated from daily temperature records obtained from the Scripps Institution of Oceanography. Records of storm events occurring from November 1978 through 1979 were obtained from the Piedras Blancas Field Station (~3 km northwest of the study site) operated by the Fish and Wildlife Service (U.S. Department of the Interior). Day length (the number of hours of daylight per 24-h period) and periods of tidal exposure (the number of hours of daytime exposure to air for tidal levels < MLLW) were calculated from data obtained in U.S. Department of Commerce Tide Tables (Anon. 1978a, 1979a).

Results

Macrophyte and Macroinvertebrate Abundance

Total macrophyte mean cover (Table 1) averaged 117.2% during 1978–1979 and was greatest during August (125.7%) and November (129.2%) and least during February (101.2%). Total macroinvertebrate mean cover (7.0%) and mean density (471 m^{-2}) similarly reached minimal values during February (Tables 1, 2, Fig. 2A); maximal cover (12.3%) and density (621 m^{-2}) were achieved during May.

A total of eight taxa, including two species of brown algae, five red algae and a single spermatophyte species, accounted for nearly 70% of the macrophyte cover at the study site (Table 1). The spermatophyte *Phyllospadix scouleri*, contributed the greatest mean cover (21.0%) over the year, followed by the rhodophytes *Gigartina canaliculata* (12.3%), and *Gigartina papillata* (11.6%). The brown algae were represented by the rockweed *Pelvetia fastigiata* (8.6%) and intertidal stands of the large kelp *Macrocystis integrifolia* (5.4%); the latter was much more abundant in the shallow subtidal habitat immediately seaward of the study site. The fleshy red algae *Endocladia muricata* (7.8%) and *Rhodoglossum affine* (6.9%), which formed bushy, erect tufts, and the crustose Corallinaceae (7.5%) were also abundant macrophytes.

These eight most abundant macrophytes exhibited relatively high cover values during all four seasonal assessments (Table 1) and, therefore, represented persistent and conspicuous components of the biological environment. Nevertheless, most perennial species, including *Phyllospadix scouleri, Gigartina canaliculata, Gigartina papillata,* and *Macrocystis integrifolia,* reached greatest abundance in August and November, the months of greatest total macrophyte cover. In addition, annual seaweeds, such as the green alga *Ulva lobata* and the red algae *Smithora naiadum* and *Porphyra perforata,* reached maximal abundance during the summer and fall periods. In contrast, winter (February) was characterized by reduced cover of most of the abundant perennial macrophytes and extremely low abundances of the annual seaweeds. Consequently, winter represented the period of least macrophyte cover on the shore and also the period of least abundance for the thin, membranous annuals such as *U. lobata, S. naiadum* and *P. perforata.* These three seaweeds appear to contribute to macrophyte standing stocks only on a highly seasonal basis. Spring (May) was generally characterized by moderate to

Table 1. Seasonal cover (%) of the more abundant macrophytes and sessile macroinvertebrates from a rocky intertidal habitat near Piedras Blancas, San Luis Obispo County, California, May 1978 to February 1979.

	Cover (%)				
Taxa	May 1978	Aug 1978	Nov 1978	Feb 1979	Mean
Phyllospadix scouleri Hook.	16.8	19.9	27.4	19.7	21.0
Gigartina canaliculata Harv.	11.5	12.1	14.8	10.8	12.3
Gigartina papillata (C. Ag.) J. Ag.	11.3	14.4	13.9	6.8	11.6
Pelvetia fastigiata (J. Ag.) DeToni	9.4	9.2	7.6	8.3	8.6
Endocladia muricata (Post. & Rupr.) J. Ag.	7.9	4.5	7.0	11.8	7.8
Crustose Corallinaceae	8.0	6.9	7.4	7.6	7.5
Rhodoglossum affine (Harv.) Kyl.	7.4	5.5	7.3	7.5	6.9
Macrocystis integrifolia Bory	5.9	6.1	6.7	2.9	5.4
Ulva lobata (Kütz.) S.&G.	0.2	11.5	5.5	1.7	4.7
Peyssonelliaceae/Hildenbrandiaceae	3.4	1.8	6.7	6.1	4.5
Gelidium coulteri Harv. and *G. pusillum* (Stackh.) Le Jolis	3.9	3.3	4.1	3.5	3.7
Gastroclonium coulteri (Harv.) Kyl.	4.1	3.3	5.0	1.5	3.5
Iridaea flaccida (S.&G.) Silva	3.6	4.8	1.5	0.7	2.7
Fucus distichus ssp. *edentatus* (de la Pyl.) Pow.	1.7	2.8	2.7	1.2	2.1
Ralfsiaceae	2.7	0.5	1.2	3.9	2.1
Iridaea cordata var. *splendens* (S.&G.) Abb.	2.8	1.9	0.6	1.5	1.7
Corallina officinalis var. *chilensis* (Decne.) Kütz.	1.8	0.5	1.2	2.7	1.6
Prionitis lanceolata (Harv.) Harv.	2.4	1.1	1.3	0.3	1.3
Smithora naiadum (Anders.) Hollenb.	<0.1	2.7	1.5	<0.1	1.1
Hesperophycus harveyanus (Decne.) S.&G.	1.3	1.2	0.7	0.7	1.0
Ascidiacea	1.9	1.5	0.3	0.1	1.0
Gigartina leptorhynchos J. Ag.	1.2	0.3	0.7	0.4	0.7
Spirorbidae	0.8	1.0	0.9	0.2	0.7
Laurencia spectabilis var. *spectabilis* Post. & Rupr.	1.0	0.4	0.7	0.3	0.6
Porphyra perforata J. Ag.	0.2	1.5	0.1	0.1	0.5
Cryptosiphona woodii (J. Ag.) J. Ag.	0.6	0.3	0.4	0.1	0.4
Bossiella orbigniana ssp. *dichotoma* (Manza) Johans.	0.3	0.1	0.1	0.1	0.2
Microcladia coulteri Harv.	0.2	0.1	0.2	0.1	0.2
Anthopleura elegantissima (Brandt, 1835)	0.2	0.2	0.1	0.2	0.2
Chthamalus fissus Darwin, 1854 and *C. dalli* Pilsbry, 1916	0.2	<0.1	0.1	0.2	0.2
Demospongiae	<0.1	<0.1	0.2	0.2	0.2
Tetraclita rubescens Darwin, 1854	0.5	<0.1	<0.1	<0.1	0.2
Other macrophytes	3.0	9.0	3.0	0.8	
(No. taxa)	(14)	(14)	(13)	(6)	
Other macroinvertebrates	8.6	7.4	7.1	6.1	
(No. taxa)	(63)	(53)	(52)	(43)	
Total macrophyte cover	112.7	125.7	129.2	101.2	117.2
Total macroinvertebrate cover	12.3	10.4	8.7	7.0	9.6
Grand total cover	125.0	136.1	137.9	106.2	126.8

high cover of the abundant and persistent red and brown algae along with various fleshy rhodophytes including *Iridaea flaccida, Iridaea cordata* var. *splendens,* and *Gastroclonium coulteri.*

The most abundant of the sessile macroinvertebrates, based on cover (Table 1), were barnacles, ascidians, and spirorbid worms while the most abundant mobile forms, based on density (Table 2), were turban snails and hermit crabs.

Table 2. Seasonal densities (No. m^{-2}) of the more abundant macroinvertebrates from a rocky intertidal habitat near Piedras Blancas, San Luis Obispo County, California.

	Density (No. m^{-2})				
Taxa	May 1978	Aug 1978	Nov 1978	Feb 1979	Mean
Chthamalus fissus Darwin, 1854 and *C. dalli* Pilsbry, 1916	260	129	157	196	186
Tegula funebralis (A. Adams, 1855)	109	156	197	118	145
Tetraclita rubescens Darwin, 1854	53	28	13	6	25
Pagurus samuelis (Stimpson, 1857)	34	16	23	19	23
Tegula brunnea (Philippi, 1848)	20	10	13	24	17
Pagurus hirsutiusculus (Dana, 1851)	13	18	22	9	16
Alia carinata (Hinds, 1844)	24	15	11	10	15
Pagurus granosimanus (Stimpson, 1859)	7	13	9	13	11
Crepidula adunca Sowerby, 1825	7	9	10	9	9
Petrolisthes cinctipes (Randall, 1839)	5	4	10	11	8
Anthopleura elegantissima (Brandt, 1835)	6	6	7	8	7
Collisella asmi (Middendorff, 1847)	4	11	4	4	6
Littorina scutulata Gould, 1849	6	17	<1	1	6
Other Macroinvertebrates	72	62	65	43	
(No. taxa)	(51)	(40)	(40)	(31)	
Totals	621	495	542	471	532

Of the sessile macroinvertebrates, greatest mean annual cover was supplied by the ascidians (1.0%) followed by the Spirorbidae (0.7%). The small acorn barnacles *Chthamalus fissus/dalli* (186 m^{-2}) and the black turban snail *Tegula funebralis* (145 m^{-2}) contributed by far the greatest macroinvertebrate densities followed by the thatched barnacle *Tetraclita rubescens* (24 m^{-2}) and the hermit crab *Pagurus samuelis* (23 m^{-2}). Most of the macroinvertebrate taxa exhibited low cover values, and their density fluctuations did not suggest marked seasonal patterns; the barnacles and ascidians, however, appeared to reach greatest abundances during spring.

Macrophyte Biomass

Except for the crustose Corallinaceae, the same taxa that contributed the majority of the macrophyte cover similarly furnished most of the dry biomass (Table 3). Two species, *Phyllospadix scouleri* and *Pelvetia fastigiata*, accounted for more than one-half of the mean annual macrophyte standing stock. The brown algae and the more species-rich red algae each furnished ~30% of the total macrophyte biomass, values slightly less than the total (36.7%) supplied by *P. scouleri*, the single spermatophyte species. The green algae accounted for only ~1.0% of the yearly mean macrophyte dry biomass.

Macrophyte standing stock (Fig. 2A) was maximal during November (1128.8 g m^{-2}) and dropped precipitously to a minimal value by February (777.7 g m^{-2}), a pattern similar to that exhibited by the cover data. The winter decline was due primarily to reductions in the abundances of the kelp *Macrocystis integrifolia* and most species of perennial, fleshy red algae. Annual macrophytes such as *Ulva lobata* provided relatively little dry biomass during February and reached greatest standing stocks during August or November. Consequently, the dry biomass data

Table 3. Seasonal variations in dry biomass (g m^{-2}) of the more abundant macrophytes from a rocky intertidal habitat near Piedras Blancas, San Luis Obispo County, California. Regression equations have been utilized to generate dry biomass from cover data where $\hat{Y}$ = dry biomass (g m^{-2}) and $\hat{X}$ = cover (%); r = correlation coefficient.

	Dry Biomass (g m^{-2})						
Taxa	May 1978	Aug 1978	Nov 1978	Feb 1979	Mean	Regression Equation	r
Phyllospadix scouleri Hook.	268.4	330.3	474.4	327.2	350.1	$\hat{Y} = 2.92X - 20.97$	0.85
Pelvetia fastigiata (J. Ag.) DeToni	183.9	180.7	153.1	165.2	170.7	$\hat{Y} = 2.46X + 7.28$	0.81
Gigartina papillata (C. Ag.) J. Ag.	71.5	92.2	92.2	35.6	72.9	$\hat{Y} = 1.18X - 3.24$	0.90
Macrocystis integrifolia Bory	88.1	47.6	109.8	3.3	62.2	$\hat{Y} = 4.16X - 57.03$	0.47
Gigartina canaliculata Harv.	40.9	44.5	78.7	40.4	51.1	$\hat{Y} = 2.04X - 24.93$	0.88
Rhodoglossum affine (Harv.) Kyl.	35.1	28.3	34.6	35.4	33.4	$\hat{Y} = 0.52X + 1.40$	0.74
Endocladia muricata (Post. & Rupr.) J. Ag.	25.0	16.6	22.7	27.4	22.9	$\hat{Y} = 0.37X + 1.35$	0.69
Hesperophycus harveyanus (Decne.) S.&G.	21.4	20.9	14.8	14.8	18.0	$\hat{Y} = 1.59X + 5.83$	0.94
Iridaea flaccida (S.&G.) Silva	22.4	29.5	10.9	6.9	17.4	$\hat{Y} = 0.79X + 0.81$	0.79
Egregia menziesii (Turn.) Aresch.	<0.1	69.1	<0.1	0.0	17.3	$\hat{Y} = 7.23X - 21.79$	0.65
Corallina officinalis var. *chilensis* (Decne.) Kütz.	23.0	<0.1	5.2	40.3	17.2	$\hat{Y} = 3.61X - 6.55$	0.96
Gastroclonium coulteri (Harv.) Kyl.	19.7	14.5	24.0	4.9	15.8	$\hat{Y} = 0.87X - 0.99$	0.92
Fucus distichus ssp. *edentatus* (de la Pyl.) Pow.	9.2	22.2	18.9	6.9	14.3	$\hat{Y} = 2.13X - 7.41$	0.96
Gelidium coulteri Harv. and *G. pusilium* (Stackh.) Le Jolis	12.5	10.6	13.0	11.0	11.8	$\hat{Y} = 0.56X - 0.32$	0.96
Prionitis lanceolata (Harv.) Harv.	18.5	11.8	10.8	5.2	11.6	$\hat{Y} = 0.80X + 1.44$	0.80
Iridaea cordata var. *splendens* (S.&G.) Abb.	15.7	11.2	4.0	9.1	10.0	$\hat{Y} = 0.79X + 0.81$	0.79
Gigartina spinosa (Kütz.) Harv.	9.7	12.6	7.3	10.0	9.9	$\hat{Y} = 0.37X + 2.34$	0.81
Crustose Corallinaceae	9.9	8.2	9.2	9.2	9.1	$\hat{Y} = 0.24X - 0.49$[a]	0.39
Ulva lobata (Kütz.) S. & G.	2.2	17.7	9.2	4.2	8.3	$\hat{Y} = 0.20X + 0.36$	0.80
Other macrophytes	31.8	33.8	35.9	20.7	30.5		
(No. taxa)	(18)	(20)	(20)	(13)			
Totals	909.9	1002.4	1128.8	777.7	954.5		

[a] Derived from Littler (1979) data for Ralfsiacese.

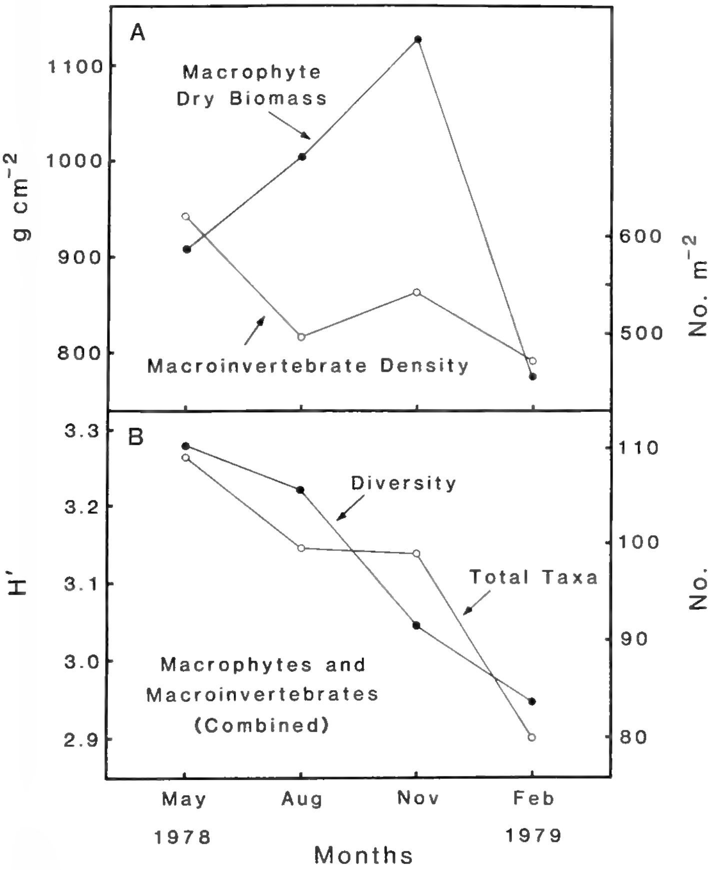

Fig. 2. Seasonal (quarterly) patterns of standing stock and diversity of the intertidal biota near Piedras Blancas, San Luis Obispo County, California, during 1978 and 1979: A. Macrophyte dry biomass (g m^{-2}) and macroinvertebrate density (No. m^{-2}); B. H′ diversity (based on combined macrophyte and macroinvertebrate cover) and total number of macrophyte and macroinvertebrate taxa.

coincide well with the seasonal patterns for cover, i.e., a steady increase in macrophyte standing stocks from spring to fall followed by a 20–30% decline by winter.

Macrophyte and Macroinvertebrate Diversity

Community diversity was greatest during May and least during February based on both counts of taxa (richness) and the H′ index (Fig. 2B). A total of 109 taxa (40 macrophytes and 69 macroinvertebrates) was obtained in quadrats assessed during May, but the number declined each quarter with the sharpest reduction registered from November to February when only 80 taxa (32 macrophytes and 48 macroinvertebrates) were recorded. H′ diversity (based on combined macrophyte and macroinvertebrate cover), exhibited the identical trend, falling from a high of 3.28 for May to a low of 2.94 for February. The evenness component of diversity (J′), however, remained relatively constant throughout the year, ranging only from 0.70 in May and August to 0.66 in November. Our data, therefore, serve to emphasize the distinctiveness of the intertidal community during the

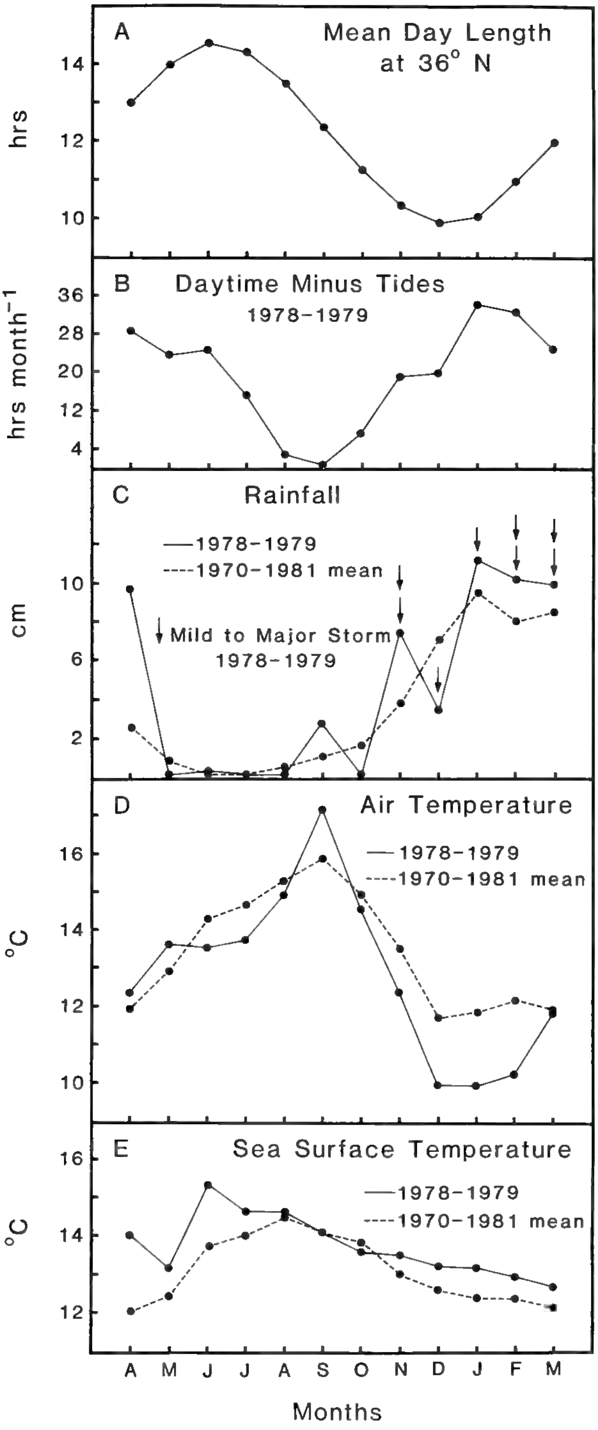

Fig. 3. Seasonal patterns of environmental factors on the central California coast: A. Mean monthly day length at 36°N; B. Total number of hours per month of daytime minus tides; C. Monthly rainfall and incidence of mild to major storms; D. Mean monthly air temperatures; E. Mean monthly sea surface temperatures.

winter, a season characterized by the annual minima for biotic cover, macrophyte biomass, and macroinvertebrate density as well as by the lowest species richness and H′ diversity.

Seasonality of Environmental Factors

Monthly records of some major abiotic factors for the central California coast (Fig. 3A–E) show that the seasons are characterized by distinctly different environmental conditions. Day length is more than 4 h greater in June than in December at the latitude of Piedras Blancas (Fig. 3A). The tidal cycles are such that minus tides resulting in extended aerial exposure of intertidal organisms occur primarily in the daytime during winter (especially January–February) and spring and primarily at night or early morning during the late summer and early fall (August–October) (Fig. 3B). A more even mixture of day and night minus tides occurs during other periods. Rainfall is also distinctly seasonal in this region with minimal amounts of precipitation generally occurring during summer and maximal amounts in winter (Fig. 3C). For 1978–1979, the pattern typical for this portion of the central California coast was apparent with rainfall occurring in small amounts from May through August and reaching greatest levels in January, February, and March. In addition, storms are prominent winter events along the central California coast resulting in high seas, strong southeast (usually) winds, and increased precipitation. Consistent with this pattern, greatest storm activity was recorded from November through March during our study (Fig. 3C). Air temperatures vary considerably and essentially follow the expected seasonal pattern for mid-temperate latitudes (Fig. 3D), i.e., highest temperatures during summer and lowest during winter.

Long-term records of surface seawater temperature are available for locations north and south of the study site. These data reveal that sea temperature fluctuates less markedly on a seasonal basis than air temperature, rainfall, or storm events. For Morro Bay, the area closest to the study site for which long-term temperature data are available, mean monthly surface temperatures showed only about a 2°C differential over the year (Fig. 3E). Although seawater temperatures were somewhat warmer than normal during most of 1978–1979, upwelling is known (Bolin and Abbott 1963; Burge and Schultz 1973) to occur and keep temperatures relatively low in spring and early summer (May–July).

In summary, there are sharp differences in environmental conditions between summer and winter months on the central California coast. During summer, the days are long and warm with little rainfall and minimal daytime aerial exposure in the intertidal zone; water temperatures are kept relatively low by pronounced upwelling. In contrast, the winter months are characterized by short, cool days but with long periods of aerial exposure and increased rainfall accompanied by frequent storms of varying intensity. Sea temperatures in winter tend to be uniformly cool.

Discussion

The biological features of our study site are similar to those previously described (Hewatt 1937; Ricketts et al. 1968; Stephenson and Stephenson 1972; Seapy and Littler 1978) for other central California rocky intertidal shores receiving protection from wave action. These features include the occurrence of an upper midintertidal fucoid zone, high densities of hermit crabs and turban snails, and the absence of a *Mytilus californianus* community along the middle shoreline (Ricketts et al. 1968). In addition, Stephenson and Stephenson (1972) recognized a number of low-growing, rhodophycean seaweeds that characteristically occupy sheltered shores of Monterey Bay near Pacific Grove. These red algae included *Endocladia muricata, Gelidium coulteri, Gelidium pusillum* (as *G. sinicola*), *Gigartina* spp., and *Rhodoglossum affine* which are also abundant components of the midintertidal communities near Piedras Blancas.

The distributions and abundances of the rocky intertidal macroorganisms near Piedras Blancas closely resemble the patterns identified by Seapy and Littler (1978) for a sheltered boulder beach at nearby Cayucos Point (Fig. 1). The upper mid-intertidal level at both sites was dominated by cover of fucoid brown algae, the wiry red alga *Endocladia muricata* and small acorn barnacles (*Chthamalus fissus/dalli*). Fleshy, erect (e.g., *Gigartina canaliculata* and *G. papillata*) and prostrate, encrusting (e.g., crustose Corallinaceae including *Hydrolithon decipiens*) perennial red algae were abundantly represented on the middle intertidal levels at both sites, as were the sea grasses (*Phyllospadix* spp.) and the larger, fleshy red algae on the lower shoreline. Turban snails (*Tegula brunnea* and *T. funebralis*) contributed high densities at both Cayucos Point and our study site. Grazing limpets (e.g., *Collisella limatula* and *C. scabra*), however, were much more abundant at Cayucos Point whereas hermit crabs (*Pagurus* spp.) occurred at greater densities at the Piedras Blancas site.

The marked seasonal changes in abundance, especially of macrophyte populations at Piedras Blancas, are not fully consistent with the patterns described for cold temperate rocky intertidal communities of eastern North Atlantic shores. The migration of mobile macroinvertebrates to lower levels in the intertidal zone (Newell 1979) and the decline of short-lived, ephemeral algae during the hot summer months (Lewis 1964) are recurring seasonal patterns for eastern North Atlantic biota. Although we did not directly investigate seasonal migrations of the mobile macroinvertebrates, our analysis of seasonal abundance data vs. tidal height did not provide evidence in support of seasonal movements of any of the more abundant populations. Furthermore, short-lived, ephemeral algae, such as *Porphyra perforata, Smithora naiadum* and *Ulva lobata* at our study site, reached greatest abundances during the summer in contrast to the pattern of decline described by Lewis (1964) for cold temperate British shores. These differences are perhaps due to the extended upwelling season that creates milder summer conditions along the central California coast.

In order to more fully analyze seasonality of the macrophyte communities, members of the intertidal flora near Piedras Blancas were categorized as either annuals or perennials according to Garbary's (1976) criteria. Annual algae included (1) species that are present throughout the year but undergo more than one generation and (2) short-lived, ephemeral species that occur during only one part of the year while spending the remainder in either a resting stage or as a microscopic vegetative form. Consequently, annual algae share the attributes of relatively short thallus life-spans and brief occupancy of an area (spatial unpredictability). In contrast, perennial algae included both erect and crustose species where the entire thallus persists for more than one year as well as those forms where only a portion of the frond persists over several years. Perennial algae, then, possess relatively long-lived thalli and persist as whole or partial fronds on essentially the same substrate throughout the year (spatial predictability). A total of 12 algal taxa were classified as having annual life forms according to these criteria (i.e., *Centroceras clavulatum, Ceramium* sp., *Cladophora* sp., colonial benthic diatoms, *Cryptopleura violacea,* Ectocarpaceae, *Microcladia coulteri, Polysiphonia* sp., *Porphyra perforata, Smithora naiadum, Spongomorpha coalita,* and *Ulva lobata*); the remainder of the macrophytes were categorized as perennials.

Abundance of annual algae at our study site was greatest during the summer (17.6% cover) and least during the winter (2.3% cover). The concomitant decrease in cover of most of the perennial seaweeds resulted in an impoverished winter macrophyte flora dominated by persistent, spatially predictable, and structurally tough species. The summer months, in contrast, were characterized by greater macrophyte standing stocks and increased abundances of delicate, rapidly growing and spatially unpredictable annual seaweeds.

The early descriptions of the central California coastal environment by Hewatt (1937) and Gislén (1943) give the general impression that the marine climate of this region is relatively uniform and that seasonal fluctuations in intertidal populations are slight. Although the extensive records now available (e.g., Fig. 3E) verify the low seasonal variation in sea surface temperatures of the central California coast, other environmental factors of the region vary noticeably with season and can be related to fluctuations in abundance and richness of the intertidal biota. We observed the period of greatest increase of macrophyte standing stocks to be characterized by long days with little daytime emergence time due to minus tides, negligible rainfall, and relatively warm air and sea temperatures. Conversely, the minimal values for macrophyte standing stock, macroinvertebrate densities, and total species richness recorded during February coincide with the short days but long periods of daytime aerial emergence and peak periods of rainfall and storms. These conditions are (arguably) adverse ones for growth and accumulation of biomass. The peak macroinvertebrate density and greatest species richness that we recorded for May are probably due to recruitment since favorable reproductive conditions develop during the spring. Subsequent increase in biomass by the dominant macrophytes probably results in a peak in macrophyte standing stock by late fall (November) and a simultaneous decline of subordinate species. Seawater temperature, because it varies so little over the course of the year, is most likely of little direct importance in influencing this pattern of seasonal change. The potentially adverse effects on the intertidal biota of increased summer and fall air temperatures during tidal emergence are ameliorated because the low tides occur at night or in the early morning hours. Conversely, in winter, cool air temperatures prevail when low tides occur primarily during afternoon hours.

Almost a half century ago, Gislén (1943) pointed out that, in general, southern California's shores are less favorable for marine life than the central California coast. He also recognized that in southern California greater amounts of sunshine and warmer air temperatures characterize the winters, periods when minus tides occur in the afternoon. Moreover, although there is greater cloud cover in the early summer in southern California, the humidity is always lower than in central California. These more highly desiccating conditions in southern California contrasted with the lower and more uniform seawater temperatures associated with upwelling on the central California coast led Gislén (1943) to conclude that the intertidal conditions were less harsh resulting in greater standing stocks of intertidal biota in central California.

The more highly variable environmental conditions in southern California as described by Gislén (1943) lead to the prediction that the intertidal communities in southern California exhibit more pronounced seasonal fluctuations than those in central California. However, our results demonstrate a strong seasonality in the central California biota paralleling those from studies (Gunnill 1980; Littler 1980a, b; Seapy and Littler 1982) of southern California intertidal macro-organisms. Gunnill (1980) recorded seasonal fluctuations in abundances of six species of macroalgae near La Jolla but concluded that the algae were responding independently to regional environmental factors that varied during their reproductive and recruitment periods. The dominant feature coinciding with algal recruitment at La Jolla was a spring-summer combination of frequent cloud cover, increasing day length, reduced daytime exposure to air, and rising water temperatures with high variability indicative of upwelling. On the other hand, fall and early winter were identified by Gunnill as periods of intense desiccation associated with daytime tidal emergence and declines in algal standing stocks. Similarly, Littler (1980b) and Seapy and Littler (1982) reported that many of the macrophytes on southern California shores increase in abundance throughout the late spring and summer, reach their peak in fall and then show a marked decline associated with the stressful daytime low tide periods of late fall and winter. Seapy and Littler (1982) found this decline to be exacerbated when strong, hot and dry ("Santa Ana") wind conditions prevailed and coincided with early afternoon low tides of late fall and winter.

Despite certain similarities in the pattern and apparent causes of fluctuations in abundance of the intertidal macrobiotas of central and southern California, there appear to be differences related to the degree of environmental uniformity and predictability. Littler (1980a, b) reasoned that the complex climatological and oceanographic regime of the Southern California Bight leads to a mosaic of physical and biological conditions. Local conditions in this region can overshadow and obscure broad climatic effects. In contrast, the less complex, more highly predictable, and more uniform environmental conditions of central California shores lead to the hypothesis that seasonal abundance patterns of the intertidal biota in this region are more sharply defined and less locally autonomous than in southern California. Longer term studies of central California intertidal systems are required to test this hypothesis.

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Literature Cited

Abbott, I. A., and G. J. Hollenberg. 1976. Marine algae of California. Stanford University Press, xii + 827 pp.

Anon. 1978a. Tide tables 1978. High and low water predictions. West coast of North and South America including the Hawaiian Islands. U.S. Dept. Commerce, National Ocean Survey, Rockville, MD, 222 pp.

———. 1978b. California 1978. Climatological data annual summary, 82 (13). U.S. Dept. Commerce, National Climatic Survey, Asheville, NC, 27 pp.

———. 1979a. Tide tables 1979. High and low water predictions. West Coast of North and South America including the Hawaiian Islands. U.S. Department Commerce, National Ocean Survey, Rockville, MD, 230 pp.

———. 1979b. California 1979. Climatological data annual summary, 83 (13). U.S. Dept. Commerce, National Climatic Survey, Asheville, NC, 27 pp.

Bolin, R. L., and D. P. Abbott. 1963. Studies on the climate and phytoplankton of the central coastal area of California, 1954–1960. CalCOFI Rep., 9:23–45.

Burge, R. T., and S. A. Schultz. 1973. The marine environment in the vicinity of Diablo Cove with special reference to abalones and bony fishes. Calif. Dept. Fish Game, Mar. Resourc. Tech. Rept. No. 19, 433 pp.

Garbary, D. 1976. Life-forms of algae and their distribution. Bot. Mar., 19:97–106.

Gislén, T. 1943. Physiographical and ecological investigations concerning the littoral of the northern Pacific. Sections I–IV. Lunds Univ. Årsskrift. N.F. Avd. 2, 39(5):1–63 and 40(8):1–91.

Gunnill, F. C. 1980. Recruitment and standing stocks in populations of one green alga and five brown algae in the intertidal zone near La Jolla, California during 1973–1977. Mar. Ecol. Prog. Ser., 3:231–243.

Hewatt, W. G. 1937. Ecological studies on selected marine intertidal communities of Monterey Bay, California. Am. Midl. Nat., 18:161–206.

Horn, M. H., and L. G. Allen. 1978. A distributional analysis of California coastal marine fishes. J. Biogeogr., 5:23–42.

Lewis, J. R. 1964. The ecology of rocky shores. Hodder and Stoughton, xii + 323 pp.

Littler, M. M. 1979. The distribution, abundance and community structure of rocky intertidal and tidepool biotas in the Southern California Bight. Bureau of Land Management, U.S. Department of the Interior, Washington, D.C.

———. 1980a. Southern California rocky intertidal ecosystems: methods, community structure and variability. Pp. 565–608 *in* The shore environment, Vol. 2 Ecosystems (J. H. Price, D. E. G. Irvine and W. H. Farnham, eds.), Academic Press, xx + 623 pp.

———. 1980b. Overview of the rocky intertidal systems of southern California. Pp. 265–306 *in* The California Islands: proceedings of a multidisciplinary symposium. (D. M. Power, ed.), Santa Barbara Museum of Natural History, vii + 787 pp.

Morris, R. H., D. P. Abbott, and E. C. Haderlie. 1980. Intertidal invertebrates of California. Stanford University Press, ix + 690 pp.

Murray, S. N., M. M. Littler, and I. A. Abbott. 1980. Biogeography of the California marine algae with emphasis on the Southern California Islands. Pp. 325–339 *in* The California Islands: proceedings of a multidisciplinary symposium. (D. M. Power, ed.), Santa Barbara Museum of Natural History, vii + 787 pp.

———, and M. M. Littler. 1981. Biogeographical analysis of intertidal macrophyte floras of southern California. J. Biogeogr., 8: 339–351.

Newell, R. C. 1979. Biology of intertidal animals, third edition. Ecological Surveys LTD, ix + 781 pp.

Pielou, E. C. 1975. Ecological diversity. John Wiley & Sons, viii + 165 pp.

Ricketts, E. F., J. Calvin, and J. W. Hedgpeth. 1968. Between Pacific tides, fourth edition. Stanford University Press, xiv + 614 pp.

Seapy, R. R., and M. M. Littler. 1978. The distribution, abundance, community structure, and primary productivity of macroorganisms from two central California rocky intertidal habitats. Pac. Sci., 32:293–314.

———, and M. M. Littler. 1980. Biogeography of rocky intertidal macroinvertebrates. Pp. 307–323 *in* The California Islands: proceedings of a multidisciplinary symposium. (D. M. Power, ed.), Santa Barbara Museum of Natural History, vii + 787 pp.

———, and M. M. Littler. 1982. Population and species diversity fluctuations in a rocky intertidal community relative to severe aerial exposure and sediment burial. Mar. Biol., 71:87–96.

Shannon, C. E., and W. Weaver. 1949. The mathematical theory of communication. University of Illinois Press, 117 pp.

Smith, R. I., and J. T. Carlton, eds. 1975. Light's manual. Intertidal invertebrates of the central California coast, third edition. University of California Press, xvii + 716 pp.

Stephenson, T. A., and A. Stephenson. 1972. Life between tidemarks on rocky shores. W. H. Freeman, xii + 425 pp.

Valentine, J. W. 1966. Numerical analysis of marine molluscan ranges on the extratropical northeastern Pacific shelf. Limnol. Oceanogr., 11:198–211.

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Research Notes

First Record of Jaguar from the Late Pleistocene of California

The jaguar, *Panthera onca,* has not been previously reported from the late Pleistocene (Rancholabrean) of California (Simpson 1941; Kurten 1973; Kurten and Anderson 1980). Examination of existing collections from the asphalt deposits of Rancho La Brea, Hancock Park, Los Angeles, has produced specimens referrable to the large extinct subspecies *P. onca augusta* (Simpson 1941). Jaguars are known from Irvingtonian deposits in northern California (Savage 1951; Kurten 1973) and have been reported historically in Arizona and eastern California (Merriam

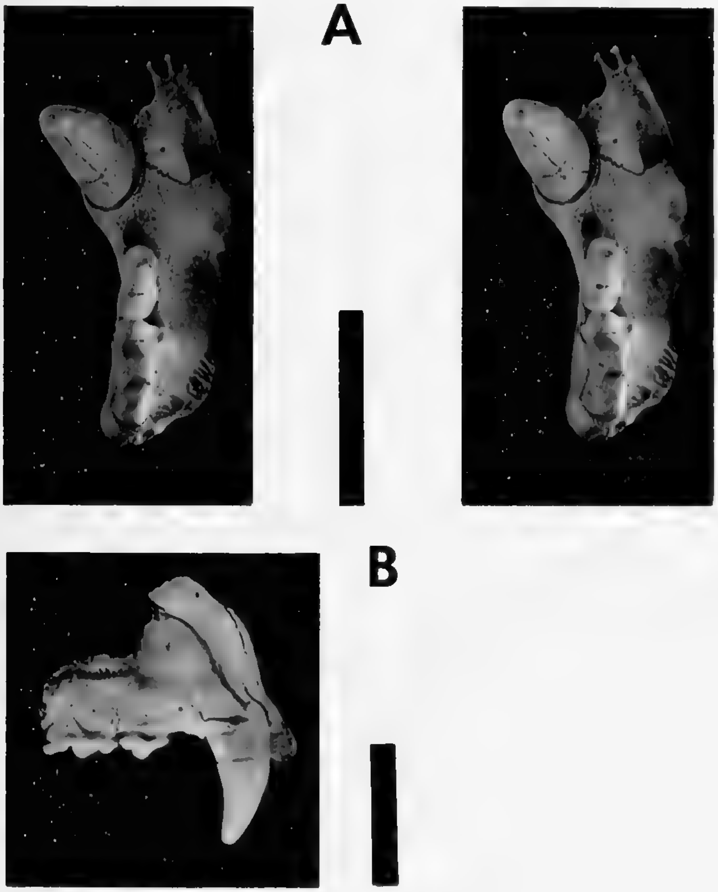

Fig. 1. A, LACM HC 1436 *Panthera onca* right maxilla and premaxilla (sterographic pair), scale bar 5 centimeters. B, lateral view of LACM HC 1436, scale bar 5 centimeters. Specimen coated with ammonium chloride.

Table 1. Measurements in millimeters of the upper dentition of *Panthera onca.* Abbreviations: N = number, OR = observed ranged, X = mean, S = standard deviation, L = greatest length, W = greatest width.

	N	OR	X	S
Panthera onca (modern)*				
L C-P4	9	66.0–82.1	76.0	6.76
L P3	9	16.0–19.4	17.4	1.19
W P3	9	8.0–10.2	9.4	0.70
L P4	9	23.4–27.7	26.0	1.45
W P4	9	12.5–15.3	14.0	0.99
P. o. (modern)**				
L C-P4	7	73.85–79.85	77.30	2.21
L P3	6	16.75–20.25	17.88	1.27
W P3	6	9.10–12.25	10.71	1.08
L P4	7	26.25–30.15	27.67	1.24
W P4	7	13.35–17.10	14.70	1.23
*P. o. augusta****				
L C	6	19.5–21.5	20.7	0.79
W C	6	16.1–18.8	17.1	1.04
L P3	5	16.9–22.3	19.4	1.95
W P3	7	9.2–11.8	10.4	0.96
L P4	5	28.8–33.5	30.8	3.01
W P4	5	13.1–16.7	15.3	1.44
LACM HC 1436				
L C-P4	1	80.11	—	—
L C	1	19.00	—	—
W C	1	15.03	—	—
L P3	1	18.90	—	—
W P3	1	9.90	—	—
L P4	1	26.79	—	—
W P4	1	13.88	—	—

* = measurement from Merriam and Stock (1932), ** = USNM specimens measured by the author, *** = measurements from Kurten (1973).

1919; Chalane 1960; Hall and Kelson 1969). The only Rancholabrean occurrences recorded west of the Rocky Mountains are Smith Creek Cave, Nevada and Fossil Lake, Oregon (Kurten 1973). Its presence at Rancho La Brea is a western extension within a larger known range.

Material.—Panthera onca is represented at Rancho La Brea by the following specimens: LACM HC 1436 (Los Angeles County Museum Hancock Collection), right and left premaxilla and maxilla with right C, P3-4 and left P3-4 (Fig. 1, Table 1); LACM HC X-8666, third thoracic vertebra; LACM HC X-8738, first sacral vertebra; LACM HC X-8424 and X-8475, right second ribs; LACM HC K-9927, right twelfth rib; LACM HC 6939, left second metacarpal (Table 2); LACM HC 6938, left third metacarpal (Table 2); LACM HC X-8848, right femur (see remarks below); LACM HC J-6362, right patella; and LACM HC X-7209, right tibia (Table 2). Tentatively referred to *P. onca* are LACM HC X-8773, xiphisternum; LACM HC 6943, first phalanx; and LACM HC 6941 and 6942, second phalanges.

Remarks.—All fossil forms of *Panthera onca,* which are known from early

Table 2. Measurements in millimeters of selected *Panthera onca* postcranial elements from Rancho La Brea. Abbreviations: MC = metacarpal, prox. = proximal, trans. = transverse, dia. = greatest diameter, dors.–vent. = dorsal–ventral, dist. = distal.

	MC II LACM HC 6939	MC III LACM HC 6938	Tibia LACM HC X-7209
Length	71.85	89.20	253.20
Prox. trans. dia.	15.40	21.40	63.40
Prox. dors.–vent. dia.	22.35	20.15	—
Mid-shaft dia.	11.30	13.55	—
Dist. trans. dia.	16.40	20.15	45.30

Irvingtonian through late Rancholabrean deposits, were regarded as a single subspecies, *P. onca augusta,* by Simpson (1941). He described it as being larger than most modern subspecies, falling within the range of the largest, *P. onca palustris.* Simpson distinguished *P. onca augusta* from all other subspecies on the basis of its distinctively larger P2/. Even though the Rancho La Brea specimen lacks this tooth (Fig. 1), the size of the alveolus for P2/ in LACM HC 1436 is relatively large, measuring 6.5 millimeters anteroposteriorly. The available dental measurements of LACM HC 1436 (Table 1) approach the size of the largest living jaguars, supporting its assignment to *P. onca augusta.* The metrics given for extant jaguars in Table 1 encompass a wide range of sizes including larger South American and smaller North American forms. Wisconsin specimens are 15 to 20% larger than modern forms and become progressively smaller through time (Kurten and Anderson 1980).

Merriam and Stock (1932) originally described and figured a complete right femur, LACM HC X-8848, and tentatively referred it to *Felis daggetti.* The affinities of this taxon, which is based on a left dentary, are not well understood. The size of LACM HC X-8848 is nearly identical to or larger than modern jaguar femurs. *Panthera onca* mandibles average 13% larger than the holotype of *F. daggetti.* LACM HC X-8848 is best assigned to *P. onca.* The remainder of the postcranial specimens differ from all other Rancho La Brea carnivores and, although large (Table 2), compare well with modern jaguar material, USNM (United States National Museum) specimen 49393.

A minimum number of five individuals are represented by the fifteen specimens, recovered from five different excavations (Pits) within Hancock Park. Bone collagen radiocarbon dates of specimens from levels in excavations which have yielded the *P. onca* material range in age from about 28.0 to 11.6 thousand years before present (Marcus and Berger in press).

Acknowledgments

The author wishes to thank R. W. Thorington Jr. of the Smithsonian Institution for providing the modern specimens, and William A. Akersten and Christopher A. Shaw of the George C. Page Museum for critically reading this manuscript.

Literature Cited

Chalane, J. H. 1960. The American Cats. Pp. 202–217 *in* Wild Animals of North America. (M. Severy, ed.), Nat. Geographic Soc., 400 pp.

Hall, E. R., and K. R. Kelson. 1969. The Mammals of North America. Poland Press Co., viii + 1083 pp.
Kurten, B. 1973. Pleistocene Jaguars in North America. Soc. Sci. Fennica, 62:1–23.
———, and E. Anderson. 1980. Pleistocene Mammals of North America. Columbia Univ. Press, xvii + 442 pp.
Marcus, L. F., and R. Berger. *In press.* The Significance of Radiocarbon Dates for Rancho La Brea. *In* Quaternary Extinctions (P. S. Martin and R. G. Klein, eds.), Univ. of Ariz. Press.
Merriam, C. H. 1919. Is the Jaguar Entitled to a Place in the California Fauna? Jour. Mamm., 1: 38–40.
Merriam, J. C., and C. Stock. 1932. The Felidae of Rancho La Brea. Carnegie Inst. Wash. Pub., 442:1–231.
Savage, D. E. 1951. Late Cenozoic Vertebrates of the San Francisco Bay Area. Univ. Calif. Press. Bull., Dept. of Geol. Sci., 28(10):215–314.
Simpson, G. G. 1941. Large Pleistocene Felines of North America. Am. Mus. Novitates, 1136: 1–26.

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A Fragment of Human Skull from Schuiling Cave, Mojave Desert, California

A fragment of right human temporal bone, including the glenoid region and the base of the zygomatic arch was recovered from late Pleistocene stream sediments in Schuiling Cave, Mojave Desert, California. The specimen is stratigraphically associated with the following extinct taxa: *Gymnogyps amplus, Equus, Hemiauchenia, Camelops hesternus,* and *Capromeryx minor.* A temporal and depositional hiatus separates the fossil assemblage from overlying, late prehistoric cultural remains.

Schuiling Cave was discovered by R. Sayles and W. Schuiling in 1953. A cooperative investigation and study was initiated by the San Bernardino County Historical Society, University of Southern California Geology Department, and the Vertebrate Paleontology Section of the Natural History Museum of Los Angeles County. Excavations were completed and the artifactual remains were described by 1955 (Smith 1955). The vertebrate fossils were deposited at the Natural History Museum of Los Angeles County (LACM) and described in 1959 (Downs et al. 1959). Schuiling Cave is located on the north east edge of the Newberry Mountains at an elevation of 658 m (meters) above sea level. It is 4 kilometers west of the 548 m shore line of pluvial Manix Lake (Jefferson 1968) on the U.S. Geological Survey Newberry Quadrangle in the SW1/4, NE1/4, Sec. 9, T8N, R3E. The cave is a relatively small opening, 5.5 by 3.9 m, situated 3 m above the floor of a dry wash which presently drains into Troy Lake playa. When discovered, the cave was almost completely filled with rhyolitic debris and fluvial sediment to a depth of about 1.8 m.

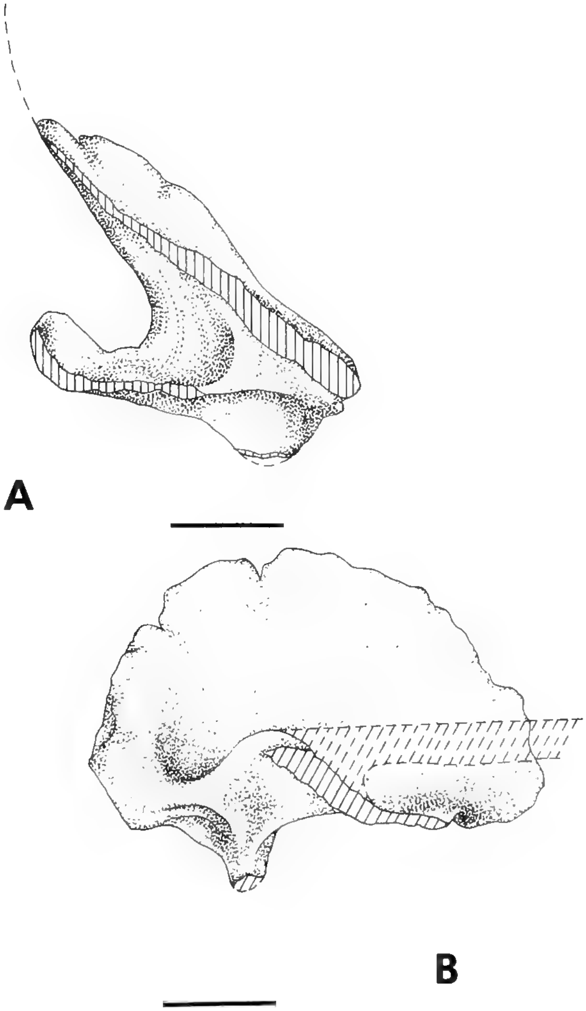

Fig. 1. LACM 47722, A. anterior and B. lateral views. Scale 1 cm.

About 20 years after the cave was excavated, a fragment of human skull was found in an unprepared and uncurated portion of the LACM collection. Apparently, because of encrusting matrix, the identity of the specimen was not recognized by previous investigators. The specimen was entirely coated and partially permineralized with calcium carbonate which contained fine to medium-grained particles of rhyolitic sand. All specimens of extinct taxa are similarly preserved and identical in color, light to moderate brown (5 YR 6 4 to 5 YR 4 4, standard Munsell colors).

Homo sapiens is represented by a nearly complete right temporal bone, LACM 47722 (Fig. 1). The specimen is relatively small measuring 43.9 mm (millimeters) anterior-posteriorly in the plane of the mandibular fossa. Superior to inferior margins measure 36.0 mm. No sutures are closed suggesting a sub-adult individual. The base of the zygomatic process is present, but the thin anterior portion is

Table 1. Revised faunal list. A double asterisk indicates extinct forms. Not previously reported taxa are indicated with a single asterisk.

Taxon	Common Name
Gopherus agassisi	desert tortoise
Sauromalus obesus	chuckwalla
Crotalus cf. *atrox*	rattlesnake
Anas cf. *platyrhynchos*	mallard duck
Anas cf. *carolinensis*	green-winged teal
Mareca americana?	baldpate duck
Nyroca cf. *americana*	redhead duck
Oxyura jamaicensis	ruddy duck
Mergus merganser	American merganser
*Gymnogyps amplus***	ancestral California condor
Aquila chrysaetos	golden eagle
Buteo jamaicensis	red-tailed hawk
Fulica americana	coot
Recurvirostra americana	avocet
Zenaidura macroura	mourning dove
Otus cf. *asio**	screech owl
*Bubo virginianus***	horned owl
Colaptes cafer	flicker
Corvus corvax	raven
*Homo sapiens**	human
Lepus sp.*	jack rabbit
Sylvilagus sp.*	cotton-tail rabbit
Citellus?*	ground squirrel
Thomomys?*	gopher
Perognathus sp.	pocket mouse
Dipodomys?*	kangaroo rat
Neotoma sp.	wood rat
Canis cf. *lupus*	wolf
Urocyon sp.	gray fox
Procyon?*	raccoon
Taxidea cf. taxus	badger
Lynx sp.*	bob-tailed cat
Felis cf. *concolor**	mountain lion
Equus sp. (small)**	small horse
Equus sp. (large)**	large horse
Hemiauchenia sp.**	llama-like camel
Camelid (?*Camelops hesternus*)**	large camel
*Capromeryx minor***	small antelope
Ovis sp.	mountain sheep

missing. Both the petrosal and mastoid portions are missing. The mandibular fossa and all but the ventral edge of the articular tuberculum are present. Parietal and sphenoidal margins are damaged to the base of the suture, but the anterior ventral portion of the sphenoidal suture is present. The medial temporal sulcus is weakly developed.

Original, handwritten excavation notes found in the museum collection with the specimen and several limb bone fragments from large mammals give their location as "various depths 3′ to 5′" within the deposit. Remains of all of the extinct taxa are restricted to this depth range. The upper .5 m of the deposit yielded two concentrations of cane shafts, fiber and two flaked stone artifacts (Smith 1955), most probably late prehistoric in age. Concerning the stratigraphic occurrence of these artifacts and the extinct vertebrate assemblage, Downs et al. (1959) state:

> ". . . , but the striking zonation of a lower horizon of extinct vertebrate remains and definitely higher horizon of identifiable cultural remains strongly indicates that there was a time difference in these occurrences in this cave assemblage."

All of the extinct taxa except *Capromeryx minor* are known from the Manix Lake beds (Jefferson 1968) and Fossil Lake, Oregon (Elftman 1931). The Rancho La Brea (Stock 1930) assemblage as well as that from McKittrick (Schultz 1938) include all forms except the small horse. Over one-half of the avian taxa from Schuiling Cave are water birds like the Fossil Lake and Manix Lake faunas. Seven out of the fifteen minimum number of individual birds from Schuiling Cave are taxa shared with the Manix Lake avifauna. Because of the high degree of mammalian as well as avian taxonomic similarity, these assemblages are considered Rancholabrean in age.

Schuiling Cave appears to have originally formed as a gas pocket in rhyolitic lava of probable Miocene age. Erosion following the (?Pliocene) uplift of the Newberry Mountains cut into and exposed the pocket in the side of a wash. Subsequent fluvial deposition during aggrading stream conditions filled the wash and buried the cave under approximately 3 m of sediment. Reduced stream velocities across the mouth of the cave at this time may have caused it to act as a trap for less dense animal bone and plant debris. Aggradation occurred in response to the latest filling of Manix Lake which established basin base level at the 548 m shore line (Jefferson 1968). Radiocarbon dates (Bassett and Jefferson 1971) associated with this level are no younger than about 19,000 BP (before present). If the dates are correct and the cave accumulation is related to the 548 m shore line, the fossil vertebrate remains including the human skull fragment must be on the order of 20,000 years or older.

It is not known whether the down cutting and erosion which resulted in the present wash configuration began with the draining of Manix Lake or was initiated by vegetational changes (Mehringer 1966) which occurred at the end of the Wisconsin about 10,000 BP. However, during this period of erosion the upper 2 feet of cave fill was removed. This situation provided a site for caching the younger artifactual materials and for the accumulation of wood-rat midden debris.

Acknowledgments

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Literature Cited

Bassett, A., and G. T. Jefferson. 1971. Radiocarbon Dates of Manix Lake, Central Mojave Desert, California. Geol. Soc. Amer., Abs. with Programs (Cordilleran Sec.), 3(2):79–80.

Downs, T. D., H. Howard, T. Clements, and G. A. Smith. 1959. Quaternary Animals from Schuiling Cave in the Mojave Desert, California. Los Angeles Co. Mus., Contrib. in Sci., 29:1–21.

Elftman, H. O. 1931. Pleistocene Mammals of Fossil Lake, Oregon. Am. Mus. Novitates, 481:1–21.

Jefferson, G. T. 1968. The Camp Cady Local Fauna from Pleistocene Lake Manix, Mojave Desert, California. Unpub. Thesis, Univ. California, Riverside.

Mehringer, P. J. 1966. Some Notes on the Late Quaternary Biogeography of the Mojave Desert. Geochron Lab. Univ. Arizona. Interm. Res. Rept., 11:1–17.

Schultz, J. R. 1938. A Late Quaternary Mammalian Fauna from the Tar Seeps of McKittrick, California. Carnegie Inst. Washington. Pub., 487:118–161.

Smith, G. A. 1955. Preliminary Report of the Schuiling Cave, Newberry, California. Quart. San Bernardino Co. Mus. Assoc., 3(2):2–19.

Stock, C. 1930. Rancho La Brea, A Record of Pleistocene Life in California. Los Angeles Co. Mus. Nat. Hist. Sci. Ser., 20:1–81.

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The BULLETIN is published three times each year (April, August, and November) and includes articles in English in any field of science with an emphasis on the southern California area. Manuscripts submitted for publication should contain results of original research, embrace sound principles of scientific investigation, and present data in a clear and concise manner. The current AIBS *Style Manual for Biological Journals* is recommended as a guide for contributors. Consult also recent issues of the BULLETIN. Authors should strive for directness and lucidity, achieved by use of the active voice. Special attention should be given to consistency in tense, unambiguous reference of pronouns, and logically placed modifiers.

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It is strongly recommended that, before submitting a paper, the author ask qualified persons to review it. The author is requested to submit *at least two additional copies with the original* on 8½ × 11 opaque nonerasable paper, double spacing the entire manuscript. ***Do not break words at right-hand margin anywhere in the manuscript.*** Footnotes should be avoided. **Manuscripts which do not conform to the style of the BULLETIN will be returned to the author.**

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The literature cited: Entries for books and articles should take these forms.

McWilliams, K. L. 1970. Insect mimicry. Academic Press, vii + 326 pp.

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

Brattstrom, B. H. 1969. The Condor in California. Pp. 369–382 *in* Vertebrates of California (S. E. Payne, ed.) Univ. California Press, xii + 635 pp.

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Research Notes

COVER: R V Nautilus, operated by the Southern California Ocean Studies Consortium of the California State University, at work in the Cabrillo Beach area of Los Angeles Harbor, September 1979. (see page 47).

Photograph by Michael H. Horn, Department of Biological Science, California State University, Fullerton.

SOUTHERN CALIFORNIA ACADEMY OF SCIENCES

BULLETIN

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Date of this issue 29 December 1983

Bull. Southern California Acad. Sci
82(3), 1983, pp. 103–114

Bat Fleas (Siphonaptera: Ischnopsyllidae) of California

Glenn E. Haas, Albert J. Beck, and P. Quentin Tomich

Abstract.—Bat fleas (Siphonaptera: Ischnopsyllidae) of California by G. E. Haas, A. J. Beck, and P. Q. Tomich. *Bull. Southern California Acad. Sci.*, 82(3):103–114, 1983. A key is given for *Sternopsylla distincta texana, Nycteridopsylla vancouverensis, Myodopsylla palposa, M. collinsi,* and *M. gentilis*; synonymy is given. Additional records total two, seven, 27, eight, and 52, respectively. Maps show *M. gentilis* has the widest distribution. Associations with 12 species of bats are tabulated; *S. d. texana* preferred molossids; *N. vancouverensis, Myotis californicus; Myodopsylla palposa, Antrozous pallidus; Myodopsylla collinsi, Myotis lucifugus*; and *Myodopsylla gentilis, Myotis yumanensis. Myodopsylla gentilis* had the most records (61), specimens collected (459), and the highest average per bat examined (3.0).

Introduction

In the past 50 years the large bat fauna of California attracted many investigators, some of whom managed to collect fleas from these mammals. Our enthusiasm in pursuing this long-term study of bat fleas is due in part to the activities of these early students of California bats. Today 23 species of bats are known for the state (Hall 1981), and fleas representing five taxa are recorded from 12 of these species. Future studies are likely to add at least one more flea. The purpose of our study is to collate all published records and the 96 additional ones that we obtained from our own field work and studies of museum and personal collections.

Methods

Field studies were initiated in 1941 by Tomich, along with collation of information from early publications and collections. New material was gathered from several counties in central California and a major study site at Calaveras Dam in Alameda County. This work was suspended in 1946, but some incomplete data were published (Holdenried et al. 1951). Beck was a principal in new studies begun in 1956 and these continued, with some interruption, until 1973. Field operations were then wide ranging but concentrated at several bat roosts in Colusa, Napa, Yolo, and Yuba Counties. Haas assumed a leading role in the studies in 1972, following up with the intensive research required for integration and completion of the entire long-term project.

Bats were collected by shooting, netting, and by hand. Different species were bagged separately, and fleas were later removed and preserved in 70% ethanol. All flea specimens were mounted on slides. Nearly all those obtained on loan were already permanently mounted. Our unmounted specimens were routinely treated in 10% KOH solution, dehydrated in ethanol, and cleared in oil of cloves before being mounted in Canada balsam. For identification of the fleas, the illustrated publications of Holland (1949), Hopkins and Rothschild (1956), and Smit (1958) were especially valuable. Our key uses morphological characters that are illustrated in Hopkins and Rothschild, although not necessarily for the same taxa.

For each of the five taxa of fleas, host associations are summarized in Table 1, and collecting localities are mapped in Figs. 1A, B, and C to show distributions in the state. In the separate accounts of each flea are synonymy in California, total ranges reported in the literature, and additional California records in full. The numbers of bats examined and infested are not listed as the data are not usually available. For selected surveys of *Myodopsylla palposa* (Rothschild) and *M. gentilis* Jordan and Rothschild, however, we discuss the average number of fleas per bat examined.

Most specimens collected by the authors are in their personal collections, but some were deposited in other collections. The names of the museums and persons whose collections provided material listed among the additional California records were abbreviated and listed parenthetically. The corresponding names of collections and abbreviations are Albert J. Beck (AJB); California Academy of Sciences (CAS); Center for Disease Control, USPHS, Fort Collins (CDCFC); California Department of Health, Division of Vector Control (CDHVC); Deane P. Furman (DPF); E. W. Jameson, Jr. (EWJ); Frank J. Radovsky (FJR); Gorgas Memorial Laboratory (GML); Los Angeles County Museum of Natural History (LACM); P. Quentin Tomich (PQT); and Stanford University Museum of Natural History (SUMNH).

Results and Discussion

Morphology

The keys to the species of bat fleas in the Rothschild Collection (Hopkins and Rothschild 1956) include all five bat fleas recorded for California. Our key uses combinations of characters that we found most useful for the identification of these five forms. A species that probably occurs in California, i.e., *Nycteridopsylla intermedia* Lewis and Wilson, has the same characters as given for *N. vancouverensis* Wagner, but the illustrated key of Lewis and Wilson (1982) indicates that the head is rounded rather than flattened and has a shorter row of spiniform bristles. Lewis (1978) revised the key to species of *Myodopsylla* by Hopkins and Rothschild (1956) to include *M. borealis* Lewis from Minnesota and Montana, *M. globata* Holland (male unknown) from southern Mexico, and *M. setosa* Johnson from Peru. Méndez and Lemke (1979) followed with the description of *M. tropica* from Colombia. Additional collections of these four species are likely to include localities closer to California but probably not within its boundaries.

Key to the Bat Fleas of California

1. Pale band on frons 3
   No pale band on frons 2
2. A single unmodified antepygidial bristle . . . . 1. *Sternopsylla distincta texana*
   A false comb of a number of short, spiniform antepygidial bristles . . . . 2. *Nycteridopsylla vancouverensis*
3. False combs on abdominal terga I–II 4
   No false combs on abdominal terga . . . . 3. *Myodopsylla palposa*

Table 1. Flea-bat associations in California.

	Bat Host											
Flea	1. *Myotis lucifugus*	2. *Myotis yumanensis*	3. *Myotis velifer*	4. *Myotis evotis*	5. *Myotis thysanodes*	6. *Myotis volans**	7. *Myotis californicus*	8. *Eptesicus fuscus*	9. *Plecotus townsendii*	10. *Antrozous pallidus*	11. *Tadarida brasiliensis*	12. *Eumops perotis*
1. *Sternopsylla distincta texana*											X	X
2. *Nycteridopsylla vancouverensis*					X		X		X			
3. *Myodopsylla palposa*		X						X	X	X		
4. *Myodopsylla collinsi*	X	X	X							?		
5. *Myodopsylla gentilis*	X	X		X	X					X	X	

**One unidentified flea recorded by Dalquest and Ramage (1946).*

4. False combs of abdomen only well developed on terga I and II; preoral tuber with slight, indistinct bend; ♂ 1 large and 1 small, thickened, shortened bristles (spiniforms) on acetabular projection; ♀ sternum VII with prominent, usually truncate dorsal lobe; anal stylet usually less than 2.5 times as long as broad .... 4. *Myodopsylla collinsi*
False combs of abdomen well developed on several terga in addition to terga I and II; preoral tuber usually with noticeable bend; ♂ 2 long and 1 short unmodified bristles on acetabular projection; ♀ sternum VII without well-developed dorsal lobe; anal stylet 2.5 or more times as long as broad .... 5. *Myodopsylla gentilis*

Synonymy, Records, and Notes

1. *Sternopsylla distincta texana* (C. Fox 1914)

(Fig. 1A)

Ischnopsyllus texanus C. Fox, 1914, U.S. Pub. Hlth. Hyg. Lab. Bull. 97:16, 17 (1 ♀, Pecos, Texas, from *Nyctinomus mexicanus*).

Sternopsylla texana (C. Fox). Augustson, 1943, Bull. So. Calif. Acad. Sci. 42:87 (City of Los Angeles, from *Eumops perotis californicus* and *Tadarida mexi-*

cana). Hubbard, 1943, Pacif. Univ. Bull. 39(8):7. Hubbard, 1947, Fleas of Western North America, pp. 379 (Fig. 235), 380, 386, 508. Hopkins & Rothschild, 1956, Catalogue of the Rothschild Collection of Fleas in the British Museum (Natural History), Vol. II, p. 221 (1 ♀, Los Angeles, from *Eumops perotis californicus*). Jellison & Senger in Taylor & Clark, 1976, Papers in Honor of Jerry Flora, p. 120 (1 ♂, San Jose, from *Tadarida mexicana*).

Sternopsylla distincta texana (C. Fox). Johnson, 1957, Mem. Ent. Soc. Wash. No. 5:100, 101. Lewis, 1974, J. Med. Ent. 11:531.

Total range.—Alabama, Arizona, California, Florida, Georgia, New Mexico, Oklahoma, South Carolina, Texas, Utah, México (D.F., Michoacán, Nuevo León).

Additional California records.—San Benito County, Idria, 6.4 km N (Silver Creek): one ♀, *Eumops perotis,* 9.IX.1945, S. B. Benson, det. Prince (PQT). Santa Clara County, San Jose: one ♀, *Tadarida mexicana,* no date, J. W. Anderson (SUMNH).

Host synonymy.—Nyctinomus mexicanus = *Tadarida brasiliensis. Tadarida mexicana* = *T. brasiliensis.*

Although this bat flea ranges widely in North America (Lewis 1974) and has been collected in large numbers, especially from *Tadarida brasiliensis* and its caves (Jellison and Senger 1976), it is relatively poorly known in California. Published records pertain to only two counties (Los Angeles and Santa Clara) and identify only two hosts (Table 1). We could add only one more county, with a locality between the two already published (Fig. 1A). Some collection dates are missing. The only months recorded are March and September. Both recorded hosts are molossid bats. Johnson (1957) indicated that all three subspecies of *S. distincta* (Rothschild) are associated with molossid bats.

2. *Nycteridopsylla vancouverensis* Wagner 1936
(Fig. 1A)

Nycteridopsylla vancouverensis Wagner, 1936, Z. Parasitenk. 8:658 (4 ♂♂, 4 ♀♀, Vancouver, British Columbia, from *Lasionycteris noctivagans*).

Eptescopsylla vancouverensis (Wagner). Holdenried, Evans & Longanecker, 1951, Ecol. Monogr. 21:14 (2 ♀♀, Alameda County, Calaveras Dam, from *Corynorhinus rafinesquii,* fleas det. P.Q.T.).

Nycteridopsylla vancouverensis Wagner. Hopkins & Rothschild, 1956, Catalogue of the Rothschild Collection of Fleas in the British Museum (Natural History), Vol. II, p. 235 (2 ♂♂, 2 ♀♀, Plumas County, Quincy, from *Myotis californicus*). Jellison & Glesne, 1967, Index to the Literature of Siphonaptera of North America Suppl. 2, p. 225. Lewis, 1974, J. Med. Ent. 11:530. Jellison & Senger in Taylor & Clark, 1976, Papers in Honor of Jerry Flora, p. 98 (1 ♀, San Jose, from *Plecotus townsendii*). Lewis & Wilson, 1982, J. Med. Ent. 19:613 (published records for Alameda, Plumas, and Santa Clara Counties listed; map with three localities in California).

Total range.—California, Nevada (?), Oregon, Washington, Canada (British Columbia).

Additional California records.—Colusa County, Wilbur Springs: one ♀, *Plecotus townsendii,* 14.I.1965, A.J.B. (AJB). Napa County, Angwin, 0.8 km S: one ♀, *Myotis thysanodes,* 1.IV.1946, W. W. Dalquest (PQT). Plumas County, Quincy:

all from *Myotis californicus,* one ♂, three ♀♀, 12.II.1949; one ♂, 30.XII.1949; one ♀, 15.III.1951, E. W. Jameson, Jr. (EWJ). Yolo County, Capay: one ♀ (gravid), *M. californicus,* 19.XII.1963, A.J.B. (AJB). Unknown locality: one ♀, *M. californicus,* 24.I.1962, C. J. Parkinson, det. A. J. Beck (AJB).

Host synonymy.—Corynorhinus rafinesquii = Plecotus townsendii.

This West Coast bat flea occurs on its hosts, chiefly *Myotis californicus* and secondarily *Plecotus townsendii,* only in the cooler months. Since the recent description of *N. intermedia* Lewis and Wilson (1982) from three interior localities including Virginia City, Nevada (only 31 km from California) and Big Bend National Park, Texas, the record of *N. vancouverensis* from the Nevada Test Site (Beck and Allred 1966) seems questionable. In fact, we suspect that *N. intermedia* ranges from Nevada into the drier parts of California that border on the Great Basin.

The Plumas County specimens of *N. vancouverensis* recorded by Hopkins and Rothschild (1956) came from the series presently in the Jameson Collection.

3. *Myodopsylla palposa* (Rothschild 1904)
(Fig. 1B)

Ceratopsylla palposus Rothschild, 1904, Novit. Zool. 11:652, 653 (2 ♀♀, Cowichan, near Duncan, Vancouver Island, British Columbia, from *Vespertilio fuscus*).

Myodopsylloides piercei Augustson, 1941, Bull. So. Calif. Acad. Sci. 40:104, 105, 107 (Pl. 7) (4 ♂♂, 3 ♀♀, Santa Barbara County, Santa Cruz Island, from *Antrozous pallidus pacificus* and 1 ♂, same locality, from *Corynorhinus rafinesquii intermedius*). Augustson, 1943, Bull. So. Calif. Acad. Sci. 42:86, 87 (added Los Angeles County, San Gabriel Mountains, Soledad Canyon and Santa Clara County, San Jose, from *Antrozous pallidus pacificus*). Hubbard, 1943, Pacif. Univ. Bull. 39(8):7. Costa Lima & Hathaway, 1946, Monogr. Inst. Oswaldo Cruz No. 4:171, 354.

Rhinolophopsylla palposa Rothschild. Hubbard, 1943, Pacif. Univ. Bull. 39(8):7.

Myodopsylloides palposa (Rothschild). Hubbard, 1947, Fleas of Western North America, pp. 376–378, 385, 508, 520, Fig. 233. Orr, 1954, Proc. Calif. Acad. Sci. 28:234, 235 (three specimens, San Luis Obispo County, from *Antrozous pallidus*).

Myodopsylloides palposus (Rothschild). Holland, 1949, Proc. Ent. Soc. B. C. 45: 13. Holland, 1949, The Siphonaptera of Canada, pp. 181, 182. Augustson & Wood, 1953, Bull. So. Calif. Acad. Sci. 52:49, 50, 56 (1 ♀, Madera County, San Joaquin Experimental Range, from *Myotis yumanensis sociabilis,* and 3 ♂♂, 1 ♀, same locality, from *Antrozous pallidus pacificus*). Jellison, Locker & Bacon, 1953, Index to the Literature of Siphonaptera of North America Suppl. 1, p. 129. Jellison, Locker & Bacon, 1953, J. Parasitol. 39:618.

Myodopsylla palposa (Rothschild). Hopkins & Rothschild, 1956, Catalogue of the Rothschild Collection of Fleas in the British Museum (Natural History), Vol. II, p. 240 (1 ♂, Los Angeles County, Soledad Canyon, and 1 ♀, Santa Clara County, San Jose, both from *Antrozous pallidus pacificus* and det. by Augustson as *Myodopsylloides piercei*). Jellison & Glesne, 1967, Index to the Literature of Siphonaptera of North America Suppl. 2, p. 212. Lewis, 1974, J. Med. Ent. 11: 530. Jellison & Senger in Taylor & Clark, 1976, Papers in Honor of Jerry Flora, p. 95 (1 ♂, 1 ♀, Alameda County; 1 ♀, Monterey County; and 1 ♂, 1 ♀, unknown locality, all from *Antrozous* sp. [=*A. pallidus*]; 3 ♂♂, San Jose [Santa Clara County], and 1 ♀, Tuolumne County, both collections from *Antrozous pallidus pacificus*). Lewis & Wilson, 1982, J. Med. Ent. 19:605. Lewis, 1978, J. Parasitol, 64:524–527.

Ceratopsylla palposus Rothschild. Smit & Wright, 1978, A List of Code Numbers of Species and Subspecies of Siphonaptera, pp. 8, 26.

Total range.—California, Canada (British Columbia).

Additional California records.—All from *Antrozous pallidus* except for two collections from *Eptesicus fuscus* indicated below. Alameda County, Livermore: one ♂, one ♀, 1.III.1943, B. E. Sagal (DPF). Colusa County, Wilbur Springs: one ♂, one ♀, 16.V.1964, A.J.B. (AJB). Kern County: two ♂♂, 6.VI.1948, collector?, det.H. E. Stark 1949 (CDCFC). Madera County, Knowles: one ♀, 12.VII.1952, Keith Murray, det. B. K. (?Keh) (CDHVC). Marin County, Tomales Bay, Marshall: two ♀♀, *Eptesicus fuscus,* 10.IX.1944, J. C. Couffer, det. L. C. Ryan (LACM). Napa County, Pope Valley (Store): one ♂, one ♀, 2.VI.1964, A.J.B. (AJB); St. Helena, 0.8 km S (Bourne Estate): one ♂, one ♀, 28.VII.1955, K. F. Murray, det. A. M. Barnes 1956 (CDHVC). Sacramento County, Folsom, 3.2 km NW: three ♂♂, nine ♀♀, 24.VI.1941, P.Q.T., det. F. M. Prince 1946 (PQT, but one ♂, one ♀, CDCFC); Sloughhouse (A. V. Signoretti Ranch): one ♀, 18.IX.1964 and one ♀, 7.X.1964, A.J.B. (AJB). San Luis Obispo County, Paso Robles: one ♀, *E. fuscus,* 23.VI.1945, S. B. Benson, det. F. M. Prince 1946 (PQT); Shandon, 7.2 km NE, 396 m elev.: one ♀, 20.IX.1947, R. T. Orr, det. H. E. Stark 1949 (CAS); (Granger Ranch): one ♂, two ♀♀, 15.IV.1949, collector?, det. H. E. Stark 1949 (CDCFC). Siskiyou County, Montague (Hart Ranch): two ♀♀, 15.V.1964 and one ♂, 20.VII.1964, A.J.B. (AJB). Tuolumne County, Long Barn: one ♂, one ♀, 29.V.1939, R. T. Orr, det. Prince & Good (N. E. Good). Yolo County, Capay (Capay School): two ♀♀ (one gravid), 21.IV.1964; one ♂, one ♀, 13.V.1964; two ♂♂, three ♀♀ (two gravid), 25.VI.1964; one ♂, 25.VIII.1964; and one ♂, one ♀, 25.IX.1964, A.J.B. (AJB); Davis (Univ. Calif.): one ♂, one ♀, 29.II.1964 and one ♀ (gravid), 30.V.1964, A.J.B. (AJB); Woodland, 8 km NW: two ♀♀, 16.V.1963, A.J.B. (AJB). Yuba County, Smartville, 1.6 km E: two ♂♂, three ♀♀, 8.VI.1964; one ♂, one ♀ (gravid), 31.VIII.1964; and one ♀, 29.X.1964, A.J.B. (AJB).

Host synonymy.—Corynorhinus rafinesquii intermedius = Plecotus townsendii. Vespertilio fuscus = Eptesicus fuscus.

In California *M. palposa* ranges widely on *Antrozous pallidus* (pallid bat) (Fig. 1B, except Marin County). In southern British Columbia, however, *Eptesicus fuscus* (big brown bat) was the only host recorded for six collections listed by Holland (1949) and Hopkins and Rothschild (1956). Only three female specimens were collected from the big brown bat in California. Also the female from *Myotis yumanensis* and the male from *Plecotus townsendii* are obviously strays from *A. pallidus* (see especially Augustson and Wood 1953). Some published records do not specify sex (Orr 1954) and number of specimens (Augustson 1943, cf. Hopkins and Rothschild 1956), but at least 13 males, nine females, and three unknowns have been collected from *A. pallidus.* These data plus our records from the pallid bat total 84 specimens (47 females) indicating that in California *M. palposa* prefers *A. pallidus.* The fleas were not numerous on the bats, however. The maximum average number of *M. palposa* specimens per pallid bat examined during the study

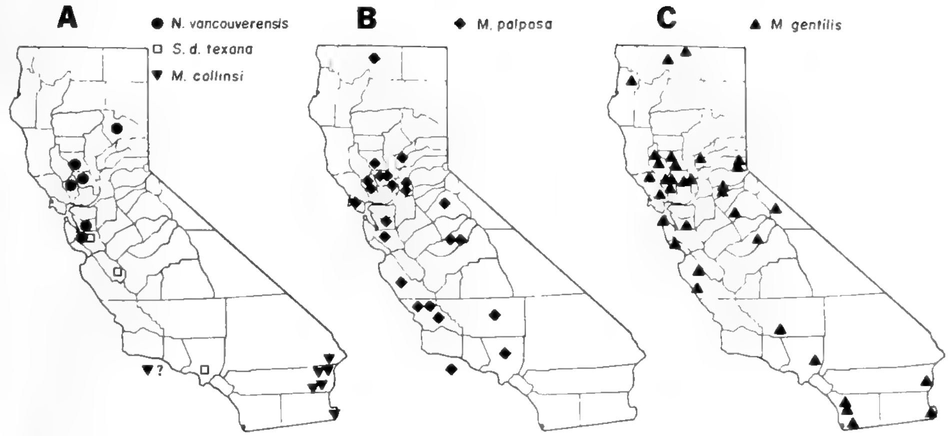

Fig. 1. Collecting localities in California of—(A) *Nycteridopsylla vancouverensis* Wagner, *Sternopsylla distincta texana* (C. Fox), and *Myodopsylla collinsi* Kohls.—(B) *Myodopsylla palposa* (Rothschild).—(C) *Myodopsylla gentilis* Jordan & Rothschild.

of 1962–1964 was <0.6. This was from a sample of nine bats taken from a bridge over a small stream at Smartville on 8 June 1964. Our new records include collections from *A. pallidus* in all months but January, November, and December. Orr (1954) discussed pallid bat collecting data for the months of January, March, and December that indicated this bat remains in California in winter and moves into hibernacula. Gravid fleas were found on pallid bats in April, May, June, and August.

In Fig. 1B the symbols in Kern and Monterey Counties signify records that lack known localities.

4. *Myodopsylla collinsi* Kohls 1937
(Fig. 1A)

Myodopsylla collinsi Kohls, 1937, J. Parasitol. 23:300–302, Figs. 1, 2 (3 ♂♂, 4 ♀♀, Madera Canyon, Santa Rita Mountains, Santa Cruz County, Arizona, from bats).

Myodopsylla [?collinsi]. Stager, 1939, J. Mamm. 20:228.

Myodopsylla collinsi Kohls. Stager, 1943, J. Mamm. 24:198 (Lower Colorado River Valley in the vicinity of Blythe, from *Myotis occultus,* flea det. Kohls). Augustson, 1943, Bull. So. Calif. Acad. Sci. 42:86 (Riverside Mountains, Colorado River, from *Myotis velifer velifer,* Stager coll.). Hubbard, 1943, Pacif. Univ. Bull. 39(8):7. Hubbard, 1947, Fleas of Western North America, pp. 376, 383, 508. Hopkins & Rothschild, 1956, Catalogue of the Rothschild collection of Fleas in the British Museum (Natural History), Vol. II, p. 247 (1 ♂, 2 ♀♀, Riverside Co., Riverside Mountains, from *Myotis v. velifer,* Stager coll.). Lewis, 1974, J. Med. Ent. 11:530. Jellison & Senger in Taylor & Clark, 1976, Papers in Honor of Jerry Flora, p. 94 (1 ♀, Santa Cruz Is., from *Antrozous pallidus* [stray or catalogue error? Same locality, host, and date as most type specimens of *M. piercei* Augustson, 1941]; 1 ♂, 1 ♀, Blythe, from *Myotis occultus*; 2 ♂♂, 2 ♀♀, Riverside Co., from *Myotis velifer*; eight specimens, Laguna Dam, from

Myotis yumanensis). Lewis & Wilson, 1982, J. Med. Ent. 19:605. Lewis, 1978, J. Parasitol., 64:524–527.

Myodopsylla collensi (sic) Kohls. Ubelaker, 1966, Amer. Midland Nat. 75:201.

Total range.—Arizona, California, Kansas, Oklahoma, Texas, México (D.F., México, Michoacán, Morelos), Guatemala.

Additional California records.—Riverside County, Blythe: one ♀, *Myotis lucifugus,* 3.VIII.1947, J. McSwain, T. Fisher & R. Smith, det. V. J. Tipton (CDHVC) and two ♂♂, six ♀♀, same data but Acc. No. 2097 (GML); 24 km SW: six ♂♂, seven ♀♀, *M. lucifugus,* same date and collectors, det. Traub (DPF); ? km SW (abandoned mine): one ♂, one ♀, Bat, same date and collectors, det. Traub (DPF); 24 km SW (Mule Mountains): two ♂♂, three ♀♀, *M. lucifugus,* same date and collectors but Acc. No. 2097 (GML); W. Riverside Mountains, Mountaineer Mine: one ♀, *Myotis velifer,* 27.VIII.1958, [?A.J.B.], det. E. W. Jameson 1960 (CDHVC) and one ♀, same data but A. Beck coll. (FJR). San Bernardino County, Vidal, 3.2 km SW: one ♀, *M. velifer,* 30.VII.1961, A.J.B. (AJB).

Host synonymy.—*Myotis occultus* = *Myotis lucifugus occultus.*

Lewis (1974) concluded from reviewing literature on *M. collinsi* that it mainly parasitizes bats of the genus *Myotis,* usually *M. velifer.* This bat ranges as far west as southern California along the Colorado River (Stager 1939, Hall 1981). The leading host of *M. collinsi* in California, with 29 flea specimens recorded (only 10 from *M. velifer*) is *Myotis lucifugus occultus,* another bat that reaches its western limit in California near the Colorado River (Findley and Jones 1967, Hall 1981). Furthermore, there is only one collection from *Myotis yumanensis,* again along the Colorado River (Jellison and Senger 1976). Therefore, the record of one female from *Antrozous pallidus* on Santa Cruz Island (Jellison and Senger 1976; also see synonymy above) is anomalous for both its host (Table 1) and its geography (Fig. 1A). The pallid bat ranges widely in the Southwest (Hall 1981), and Orr (1954) indicated a lack of evidence that it seasonally migrates long distances.

5. *Myodopsylla gentilis* Jordan & Rothschild 1921
(Fig. 1C)

Myodopsylla gentilis Jordan & Rothschild, 1921, Ectoparasites 1:152 (4 ♂♂, 4 ♀♀, Okanagan Landing, British Columbia, from bat).

Myodopsylla gentilis Jordan & Rothschild. Stager, 1943, J. Mamm. 24:198 (Lower Colorado River Valley in the vicinity of Blythe, from *Myotis occultus,* fleas det. Kohls). Augustson, 1943, Bull. So. Calif. Acad. Sci. 42:86 (Riverside County, Blythe, Palo Verde Valley, Colorado River, from *M. occultus,* S. F. Wood coll.). Hubbard, 1943, Pacif. Univ. Bull. 39(8):7 (Lower Klamath Lake). Hubbard, 1947, Fleas of Western North America, pp. 374, 375, 508 (1 ♂, 1 ♀, Siskiyou County, Lower Klamath Lake, from *Myotis yamanensis* (sic) *sociabilis*). Holdenried, Evans & Longanecker, 1951, Ecol. Monogr. 21:11, 14 (up to 28 per collection, Alameda County, Calaveras Dam, from *Myotis yumanensis,* fleas det. P.Q.T.). Augustson & Wood, 1953, Bull. So. Calif. Acad. Sci. 52:49 (4 ♂♂, 10 ♀♀, Madera County, San Joaquin Experimental Range, from *M. yumanensis sociabilis*). Krutzsch, 1955, J. Mamm. 36:457 (one specimen, San Diego County near lower Otay Dam from *M. y. sociabilis*). Hopkins & Rothschild, 1956, Catalogue of the Rothschild Collection of Fleas in the British Museum (Natural History), Vol. II., p. 251 (1 ♀, Kern County, Fort Tejon, from *M. y. sociabilis*).

Smit, 1958, Proc. Ent. Soc. Wash. 60:176 (map with five localities in California). Jellison & Glesne, 1967, Index to the Literature of Siphonaptera of North America Suppl. 2, p. 209. Jellison & Senger in Taylor & Clark, 1976, Papers in Honor of Jerry Flora, pp. 94, 95 (2 ♂♂, 2 ♀♀, Blythe, from *M. occultus* [cf. Stager, 1943]; 7 ♂♂, 4 ♀♀, Alameda Co., from *M. yumanensis saturatus*; 12 ♂♂, 19 ♀♀, Laguna Dam, from *M. y. yumanensis*). Lewis & Wilson, 1982, J. Med. Ent. 19:605.

Total range.—Alaska, California, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon, South Dakota, Texas, Utah, Washington, Wyoming, Canada (British Columbia), México (D.F.).

Additional California records.—All from *Myotis yumanensis* except for one collection each from *M. evotis* and *T. brasiliensis,* two collections each from *M. thysanodes* and *A. pallidus,* and three collections from unidentified species as indicated below. Alameda County, Calaveras Dam: two ♂♂, 26 ♀♀, 16.VI.1943; two ♂♂, two ♀♀, 9.VII.1943; four ♂♂, four ♀♀, 10.VIII.1943; one ♂, two ♀♀, 9.IX.1943; four ♀♀, 13.IX.1943; and four ♂♂, four ♀♀, 9.III.1946, P.Q.T. (PQT, part); one ♂, one ♀, 16.VIII.1943; six ♂♂, 14 ♀♀, 24.VIII.1944; eight ♂♂, 20 ♀♀, 26.VIII.1944; and four ♂♂, eight ♀♀, 10.VI.1945, D. S. Longanecker. Amador County, Martell (Winton Lumber Co.): two ♂♂, one ♀, 22.VII.1964, A.J.B. (AJB); Plymouth, 9.7 km W: one ♀, 19.VII.1941, P.Q.T. (PQT). Colusa County, Wilbur Springs: one ♂, four ♀♀, 16.VIII.1960, Garcia & Radovsky, one ♀ det. Poorbaugh 1960 (CDHVC, other specimens FJR); two ♂♂, five ♀♀ (four gravid), 27.IV.1963; six ♂♂, 15 ♀♀ (nine gravid), 25.IV.1964; three ♂♂, 17 ♀♀ (three gravid), 16.V.1964; one ♂, four ♀♀ (one gravid), 29.VI.1964; one ♂, 11 ♀♀ (five gravid), 14.VIII.1964; and one ♀ (gravid), 12.IX.1964, A.J.B. (AJB); 10.4 km SE: five ♂♂, one ♀, 23.IX.1945, S. B. Benson. Humboldt County, [Hoopa Valley] Indian Reservation: one ♀, *Myotis* sp., 13.X.1953, R. Talmadge (GML). Lake County, Lucerne, Clear Lake: one ♀, 1.XII.1945, S. B. Benson; Sulfur Bank Mine, Sulfur Bank Pen., Clear Lake: two ♂♂, eight ♀♀, 24.VI.1964, A.J.B. (AJB). Los Angeles County, Azusa: one ♀, 5.IX.1942, D. G. Constantine, det. Augustson (LACM). Mono County, Mono Lake: one ♂, two ♀♀, 3.VIII.1961, and one ♂, two ♀♀, 22.VIII.1964, A.J.B. (AJB). Monterey County, Lucia, 3.2 km S (Limekiln Creek mouth): two ♀♀, 25.VI.1945, W. W. Dalquest; Soledad, 6.4 km S (Arroyo Seco Wash): one ♂, one ♀, *A. pallidus,* 25.VII.1936, J. C. VonBloeker (LACM). Napa County, Angwin, 0.8 km S: two ♀♀, *M. thysanodes,* 1.IV.1945, W. W. Dalquest; Calistoga, 3.2 km N & 1.6 km W (Tubbs Ranch): seven ♀♀, 30.VII.1955, K. F. Murray, det. A. M. Barnes 1956 (CDHVC no. 1950); 3.2 km N & 7.2 km W: two ♂♂, one ♀, *M. thysanodes,* 20.V.1955, K.F.M., det. A.M.B. 1956 (CDHVC no. 1840); and 5.6 km SE: one ♂, *Myotis evotis,* 21.V.1955, K.F.M., det. A.M.B. 1956 (CDHVC no. 1853); Pope Valley: one ♂, two ♀♀, 2.VI.1964, A.J.B. (AJB). Placer County: one ♂, one ♀, 21.IX.1945, S. B. Benson (CDCFC); Homewood, Lake Tahoe: 25 ♂♂, 21 ♀♀, 21.IX.1945, S.B.B., det. P.Q.T. 1945 (five ♂♂, five ♀♀, PQT & one ♂, one ♀, CDCFC); Tahoe City: one ♂, one ♀, bat, 3.VIII.1946, J. Kitley, det. P.T.J. (?Johnson) 1949 (CDHVC). Riverside County: one ♂, one ♀, *Myotis* sp.,—II.1951, R.W., det. E. Méndez 1953 (GML). San Diego County, Escondido: two ♀♀, 9.VI.1946, Krutzsch & Dixon, det. Traub (DPF); Lake Hodges: same data but one ♂, one ♀. San Francisco County, Golden Gate Park: two ♂♂, three ♀♀, 6.VII.1958 (per R. T. Orr) (CAS); San Francisco Zoo: two ♀♀, 6.VI.1958 and two ♀♀ (gravid), 10.VI.1958, A.J.B. (AJB). Santa Cruz County, Big Basin, 6.4 km SW (Waddell Creek fork): 19 ♂♂, 35 ♀♀, 10.IX.1945, S. B. Benson, det. P.Q.T. (five ♂♂, five ♀♀, PQT). Siskiyou County, Lower Klamath Lake: one ♂, one ♀, 4.VII.1937, C. A. Hubbard (CAS); Montague (Hart Ranch): four ♂♂, two ♀♀, 20.VII.1964, A.J.B. (AJB). Sonoma County, Cloverdale: two ♂♂, four ♀♀, *A. pallidus,* 25.VII.1927, F. Tose & J. Mailliard, det. Prince & Good (one ♂, one ♀, N.E. Good & one ♂, three ♀♀, CAS); Glen Ellen, 0.8 km S: one ♀, *Tadarida* [*brasiliensis*], 1.VIII.1955, K. F. Murray, det. A. M. Barnes 1956 (CDHVC no. 1939-49). Tuolumne County, Jacksonville, 4 km ESE: four ♂♂, six ♀♀, 17.IX.1945, S. B. Benson, det. P.Q.T. (three ♂♂, five ♀♀, PQT). Yolo County, Capay, 11.2 km SW (Salt Creek): one ♂, 7.X.1964, A.J.B. (AJB); Woodland, 8 km N: one ♀, 28.IV.1961, A.J.B. (AJB). Yuba County, Smartville, 1.6 km E: one ♂, one ♀, 11.IX.1963 and one ♂, nine ♀♀ (gravid), 8.VI.1964, A.J.B. (AJB).

Host synonymy.—Myotis occultus = M. lucifugus occultus.

The western bat flea *M. gentilis* conspicuously leads all bat fleas of California in collections, specimens, and average numbers per bat examined. In addition, it has the widest distribution in the state (cf. Figs. 1A, B, and C). The most frequently recorded host was *Myotis yumanensis* (Yuma myotis), but along the Colorado River two (?three) collections were from *M. lucifugus* and one from the Yuma myotis. Bats of other genera (Table 1; also see records for Monterey and Sonoma Counties) are accidental hosts. The Yuma myotis is seldom observed in California in winter (Dalquest 1947). Consequently, *M. gentilis* was not recorded from this bat in January, February, and November, and only single collections were recorded in March (Alameda Co.), October (Yolo Co.), and December (Lake Co.). The majority of collections (such as 36 of the 43 additional records) of this flea from *M. yumanensis* occurred in June, July, August, and September.

The sample of 30 Yuma myotis (26 adult females) taken in a mine tunnel at Wilbur Springs, April to June 1964, was infested with an average of >1.5 specimens of *M. gentilis.* While the bats were being collected, some fleas became so agitated that they escaped, thereby depressing the calculated average infestation value. The roost area was heated by springs to over 30°C, and relative humidity was 85–95%. Gravid *M. gentilis* (23 of 53 females collected) occurred on the bats at Wilbur Springs throughout the collecting period, i.e., from late April to mid-September.

At Calaveras Dam 10 collections from 16 June 1943 to 9 March 1946 yielded 117 specimens of *M. gentilis* from a minimum of 87 Yuma myotis examined. That is, 85 bats were recorded, but totals for collections of 16 August 1943 and 10 June 1945 were not. Collections of 24 and 26 August 1944 were recorded in full (but not published) and yielded an average of 3.0 fleas per bat examined (n = 16). The bats roosted beneath the tile roof of the chlorine house. Full data for four of the six collections at Calaveras Dam incompletely reported by Holdenried et al. (1951) are included in the additional records. Collection dates are 16 June and 10 August 1943, 24 and 26 August 1944.

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Literature Cited

Augustson, G. F. 1943. Preliminary records and discussion of some species of Siphonaptera from the Pacific Southwest. Bull. So. Calif. Acad. Sci., 42:69–89.

———, and S. F. Wood. 1953. Notes on California mammal ectoparasites from the Sierra Nevada foothills of Madera County. Bull. So. Calif. Acad. Sci., 52:48–56.

Beck, D E., and D. M. Allred. 1966. Siphonaptera (fleas) of the Nevada Test Site. Brigham Young Univ. Sci. Bull., Biol. Ser., 7(2):1–27.

Dalquest, W. W. 1947. Notes on the natural history of the bat, *Myotis yumanensis,* in California with a description of a new race. Amer. Midland Nat., 38:224–247.

———, and M. C. Ramage. 1946. Notes on the long-legged bat (*Myotis volans*) at Old Fort Tejon and vicinity, California. J. Mamm. 27:60–63.

Findley, J. S., and C. Jones. 1967. Taxonomic relationships of bats of the species *Myotis fortidens. M. lucifugus,* and *M. occultus.* J. Mamm. 48:429–444.

Hall, E. R. 1981. The mammals of North America. 2nd ed. Vol. I. John Wiley & Sons, 600 pp. + 90 pp.

Holdenried, R., F. C. Evans, and D. S. Longanecker. 1951. Host-parasite-disease relationships in a mammalian community in the central Coast Range of California. Ecol. Monogr., 21:1–18.

Holland, G. P. 1949. The Siphonaptera of Canada. Can. Dep. Agric. Tech. Bull. 70, 306 pp.

Hopkins, G. H. E., and M. Rothschild. 1956. An illustrated catalogue of the Rothschild Collection of fleas (Siphonaptera) in the British Museum (Natural History). Vol. II. Brit. Mus. (Nat. Hist.), xi + 445 pp.

Jellison, W. L., and C. M. Senger. 1976. Fleas of western North America except Montana in the Rocky Mountain Laboratory Collection. Pp. 55–136 *in* Papers in honor of Jerry Flora. (H. C. Taylor, Jr., and J. Clark, eds.), Western Wash. State College.

Johnson, P. T. 1957. A classification of the Siphonaptera of South America with descriptions of new species. Mem. Ent. Soc. Wash. No. 5, 299 pp.

Lewis, R. E. 1974. Notes on the geographical distribution and host preferences in the order Siphonaptera Part 5. Ancistropsyllidae, Chimaeropsyllidae, Ischnopsyllidae, Leptopsyllidae and Macropsyllidae. J. Med. Ent., 11:525–540.

———. 1978. A new species of *Myodopsylla* Jordan and Rothschild 1911, from northern United States, with a key to the genus (Siphonaptera: Ischnopsyllidae). J. Parasitol., 64:524–527.

———, and N. Wilson. 1982. A new species of *Nycteridopsylla* (Siphonaptera: Ischnopsyllidae) from southwestern United States, with a key to the North American species. J. Med. Ent., 19:605–614.

Méndez, E., and T. O. Lemke. 1979. Description of a new species of bat flea from Colombia (Siphonaptera: Ischnopsyllidae). Proc. Ent. Soc. Wash., 81:657–662.

Orr, R. T. 1954. Natural history of the pallid bat, *Antrozous pallidus* (LeConte). Proc. Calif. Acad. Sci., Ser. 4, 28:165–246.

Smit, F. G. A. M. 1958. Differences, in the female sex, between two North American bat-fleas. Proc. Ent. Soc. Wash., 60:175–177.

Stager, K. E. 1939. Status of *Myotis velifer* in California, with notes on its life history. J. Mamm., 20:225–228.

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Drainage Density of Southern California Desert Mountains

Wayne N. Engstrom

Abstract.—Drainage density of southern California desert mountains by Wayne N. Engstrom, *Bull. Southern California Acad. Sci.,* 82(3):115–124, 1983. Measurements made in a systematic fashion from topographic maps reveal that the drainage density of 68 third order drainage basins located in three mountain ranges in the deserts of southern California averages 14.6 km/km^2. The drainage density of the El Paso Mountains is significantly lower than that of the Bullion and Chemehuevi Mountains. A preliminary inquiry suggests that variations in climate/vegetation conditions and in relief age may be linked to this difference. Relief ratio does not appear to significantly influence drainage density in the study ranges but the possible influence of rock type needs to be assessed.

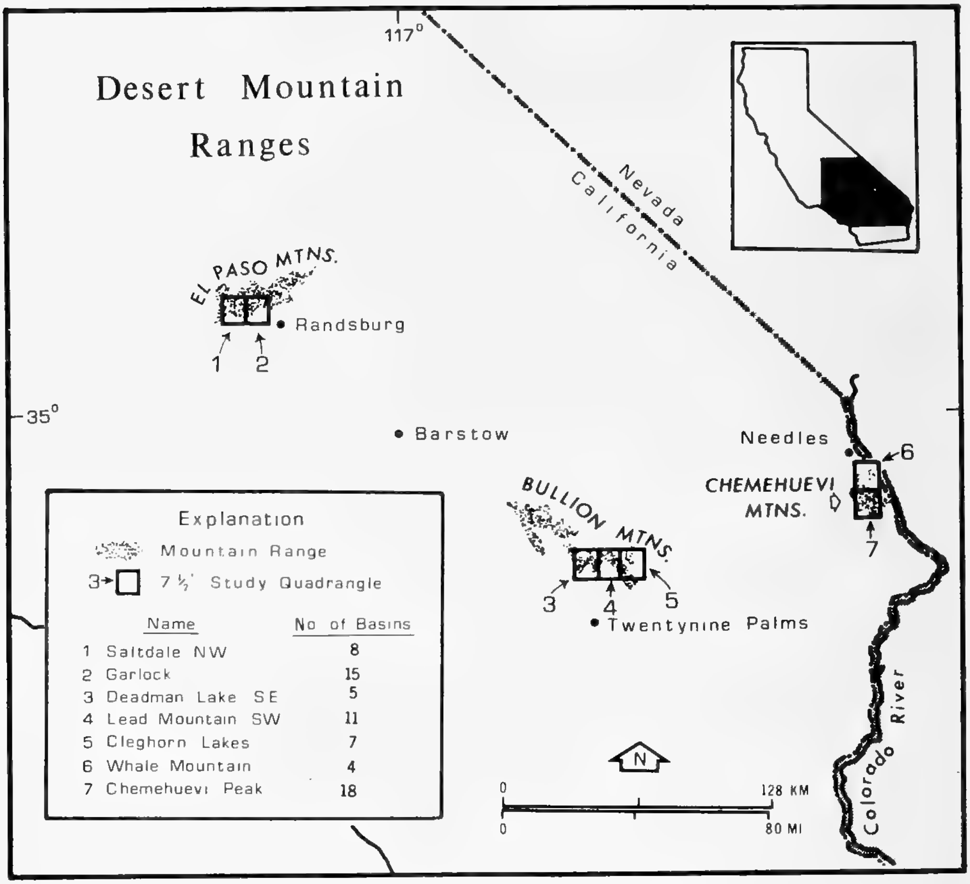
Introduction

Drainage density, a measure of landscape dissection, constitutes one of the most fundamental properties of fluvially eroded terrain. Commonly expressed in kilometers of stream channel per square kilometer, the drainage density of mountain ranges in southern California has attracted little attention. Providing exceptions to this generalization is the work of Maxwell (1967) and Bauer (1980) in the San Dimas area of the San Gabriel Mountains. Farther east in the deserts of southern California, other morphological aspects of mountain ranges have been investigated by Lustig (1969) and by Bull and McFadden (1977). An earlier paper (Engstrom 1981) provides information on the quantitative geomorphology of 68 third order drainage basins in three desert mountain ranges but the details concerning drainage density remain to be discussed. The purpose of this paper is to both supply information on the drainage density of these ranges and to try to provide an explanation for the variations in drainage density among the ranges that emerged during the course of the study.

Study Ranges

Three ranges, the El Paso, Bullion, and Chemehuevi Mountains, were selected because they all contain areas of well-dissected granitic rock which have been topographically mapped at a scale of 1:24,000 (Fig. 1). The ranges rise from 900 to 1000 m above surrounding lowlands. A sparse coverage of xerophytic shrubs, such as the creosote bush (*Larrea divaricata*), constitutes the vegetation cover of all three ranges and, consequently, much of the surface is bare.

Located immediately north of the Garlock Fault, the El Paso Mountains are found in the far southwestern corner of the Great Basin physiographic province (Oakeshott 1971). Structurally, the range is a tilt block. A prominent fault scarp forms a nearly straight mountain front along its southeastern flank, rising abruptly above the El Paso Fault. Dibblee (1952) believes that the El Paso Mountains reached their present height during the late Pleistocene. Gravels of probable mid-



	Name	No. of Basins
1	Saltdale NW	8
2	Garlock	15
3	Deadman Lake SE	5
4	Lead Mountain SW	11
5	Cleghorn Lakes	7
6	Whale Mountain	4
7	Chemehuevi Peak	18

Fig. 1. Location of the three study ranges.

dle or late Pleistocene age have been elevated by this tectonic event to form the highest terrace in the range. At the same time, a middle Pleistocene erosion surface experienced renewed erosion and major south-flowing streams cut narrow, deep canyons (Dibblee 1952). Several of these topographic characteristics have been associated with active tectonism by Bull and McFadden (1977). Intrusive igneous rocks of Jurassic age, largely quartz diorites (Dibblee 1952), outcrop in the central portion of the southeastern mountain front where all of the sample basins were collected.

Both the Bullion and the Chemehuevi Mountains are located in the Mojave Desert, although some writers would place the Chemehuevi Mountains in the Colorado Desert (Mazzucchelli 1967). Generalizations about the physiographic character of the subdivisions of the Basin and Range province usually suggest that the "older" ranges of the Mojave Desert have suffered considerably more erosion than the comparatively "younger" ranges, such as the El Paso Mountains, which lie north of the Garlock Fault in the Great Basin (Thornbury 1965; Lustig 1969). There is some topographic evidence that both the Bullion and the Chemehuevi Mountains conform with this generalization.

Situated in the central Mojave Desert, the Bullion Mountains are an areally extensive and topographically complex range. Broken into a number of ridges that trend northwesterly, the range has experienced strike-slip faulting since the middle or late Miocene. These primarily horizontal movements, however, ". . . failed to produce well-defined linear ridges as did the predominately vertical movements in the Great Basin farther north." (Garfunkel 1974, p. 1933). Sample basins, drawn from a wide area within the southern part of the range, are restricted to Mesozoic granitic rocks, mainly granite and quartz monzonite (Bishop 1964; Dibblee 1967; Rogers 1969). Following Bull and McFadden (1977), the topographic characteristics of this area suggest less vertical tectonic activity than that associated with the southeastern flank of the El Paso Mountains. Faults occasionally trace the base of abrupt scarps, but more commonly the mountain fronts are sinuous and pediments flank some of the individual ridges.

The Chemehuevi Mountains are also viewed as probably being less tectonically active than the southeastern flank of the El Paso Mountains. Only one fault parallels any of the mountain fronts and it lies at some distance from the abrupt northern flank of the range (Bishop 1964). Like the Bullion Mountains, irregular mountain fronts are commonplace. A rather extensive pediment flanks the southern side of the range. Sample basins were drawn from the portion of the range where granitic rocks of probable Precambrian age (Bishop 1964) are exposed.

Methods

Using seven 1:24,000 U.S.G.S. topographic maps, a random sample of 68 third order drainage basins was selected from the study ranges (Fig. 1). The Strahler system of stream ordering was employed to delimit the study basins. Designed to eliminate basins incised into alluvial fans and pediments, only basins in areas of well-dissected terrain above the mountain front were sampled. After the topographic maps were enlarged to a scale of 1:6000, the crenulation method was used to extend the blue line network to the last crenulated contour, completing the drainage network. Drainage networks delimited on the basis of contour crenulations are perhaps best referred to as valley networks (Gregory 1976) and can serve as a good measure of landscape dissection. Although a limited field reconnaissance was undertaken, no systematic effort was made to correct the mapped networks from field observations. Precluding such an effort is the large number of basins being investigated and the rugged character of the study ranges. Nevertheless, the drainage density values derived from the mapped networks are useful for comparative purposes in which the emphasis falls on regional variation (Gardiner 1974).

Differences in drainage density emerging from this study are not likely to arise from operator variance, variations in map scale or contour interval, or from significant variations in map reliability. Zakrzewska (1967), Chorley and Dale (1972), Gardiner (1974), and Gregory and Walling (1973) have all drawn attention to these considerations. All of the topographic maps used possess identical scales, experienced the same degree of enlargement, and have the same (12.2 m) contour interval. Faced with this rather large contour interval, the single operator inserting the drainage network took a somewhat liberal but consistent view as to the crenulation configurations indicative of a stream valley. Map reliability is judged to be uniformly good because limited field checking in each range indicates that the mapped drainage networks are a good approximation to the actual drainage networks. However, some first order valleys failed to appear on the enlarged maps. Published between 1955 and 1971, inclusive, all of the maps were compiled from aerial photographs of sparsely vegetated terrain, perhaps accounting for the generally close agreement between the actual networks and the networks indicated by the contour crenulations.

Several morphometric properties were measured in each study basin. Basin area was measured with a polar planimeter and the total stream length in each basin was measured with a map measurer. Drainage density was then calculated by dividing the total stream length in each basin by the area of the basin. The basin relief ratio was determined by dividing the basin relief by the basin length or diameter, measured with an engineer's scale, in a manner similar to that introduced by Schumm (1956). Basin relief was determined by subtracting the elevation of the basin mouth from the maximum elevation along the basin perimeter. The location of the basin length or diameter line was determined by using criteria established by Maxwell (1967).

Statistical analysis of the data was primarily accomplished by analysis of variance and correlation analysis, using the 0.05 confidence level. Initially, the normality of the variable distributions was checked by using the Kolomogorov-Smirnov Test. All of the distributions were found not to differ significantly from the normal distribution at the 0.05 level and so were not transformed with the exception of the distribution of all 68 basin areas which required a log transformation to achieve normality. Because the homogeneity of variances assumption was not violated at the 0.05 level, a pooled estimate of the variance was used. The method of a priori contrasts was used after a significant difference in drainage density was identified among the study ranges, permitting the nature of the difference to be determined (Nie et al. 1975).

Results and Discussion

Numerical analysis of the drainage density data reveals that the mean drainage density for all 68 third order basins is 14.6 km/km^2. A small but statistically significant difference was detected by analysis of variance between the mean drainage density of the basins in the El Paso Mountains (13.2 km/km^2) and the mean drainage densities of the basins in both the Bullion Mountains (15.3 km/km^2) and the Chemehuevi Mountains (15.4 km/km^2). These values fall within the range of those reported for deserts by Gregory and Gardiner (1975). With statistically significant differences in drainage density established, it remains to attempt explanations for these differences. An underlying assumption in what follows is that channel initiation in the study ranges, where soil mantles are thin and vegetation cover is quite limited, occurs primarily where overland flow is sufficiently deep to erode and maintain a channel. Other mechanisms, such as spring flow, are assumed to be less important to channel initiation (Abrahams 1980).

Basin Characteristics

Drainage density frequently shows a correlation with the area of the drainage basin and the relief ratio of the drainage basin. The relationship between drainage density and basin area, which is typically inverse in nature, has recently attracted considerable attention in the literature (Pethick 1975; Gardiner et al. 1977; Richards 1978). The geomorphic significance of the relationship, however, still remains to be firmly established. As reported earlier (Engstrom 1981), drainage density and basin area are negatively correlated when all 68 study basins are considered ($r = -0.32$) and when the basins in the El Paso Mountains ($r = -0.67$) are treated separately. These correlations are significant at the 0.05 level. However, this association fails to materialize when the mean basin areas and mean drainage densities for each range are compared. The drainage basins of the Bullion and Chemehuevi Mountains, despite their comparatively high mean drainage density, are larger (0.26 km^2 and 0.18 km^2, respectively) on the average than those of the El Paso Mountains (0.17 km^2) where a comparatively low drainage density exists.

Of the numerous drainage basin topographic characteristics, the relief ratio of the basin is usually considered to be the characteristic having the greatest controlling influence on drainage density. The mean relief ratio for all 68 study basins is 0.34. Greater relief ratios mean steeper basin slopes which should encourage a greater amount of overland flow, thereby promoting landscape dissection and high drainage densities. Several workers have detected this relationship in a variety of environments, including Schumm (1956), Morisawa (1962), Doornkamp and King (1971), and Roberts (1978). Correlation analysis, however, failed to yield a single positive correlation coefficient between relief ratio and drainage density which is significant at the 0.05 level. On these results, it must be concluded that the relief ratio of the basins does not significantly influence drainage density in the study ranges.

Rock Type

Variations in rock type, using the phrase in its broadest sense, are known to be associated with variations in drainage density as work by Johnson (1933), Smith (1950), Melton (1957), and Gregory and Gardiner (1975) have demonstrated. The study basins were all drawn from areas of granitic rock to minimize lithologic controls on drainage density. However, Thomas (1976), in his review of the characteristics of granitic rock that are geomorphically relevant, indicates that such rocks are quite variable in character. It would therefore be premature to dismiss variations in rock type as a possible cause of the observed variations in drainage density without detailed field study in the 68 study basins. It is possible that differences in joint density, infiltration rate, and surface erodability among the rocks may be great enough to account for the variations in drainage density.

Relief Age

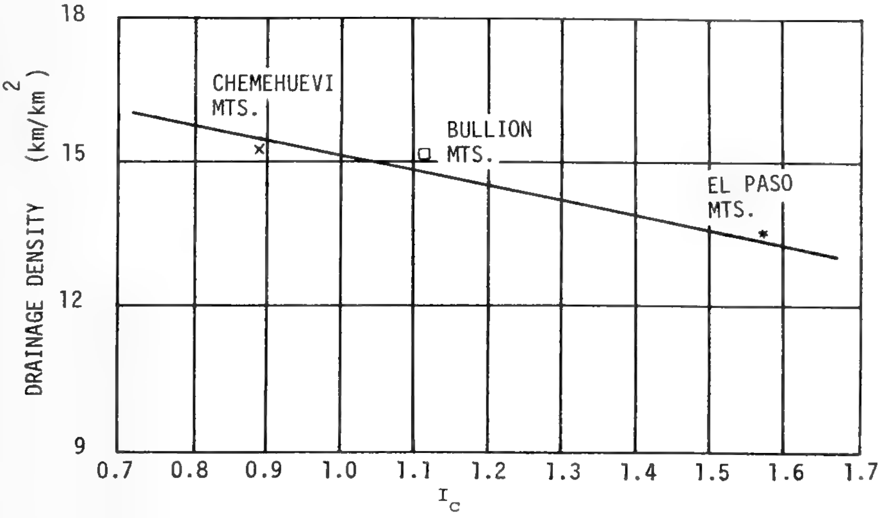
Attempts have been made for some time to link drainage density to the stage of fluvial erosional development. In the present context, the stage of fluvial erosional development of a drainage basin in a mountain range is considered to be primarily a function of the relief age of the portion of the range where the drainage basin is located. Relief age has been defined by Lustig (1969) as the time span since topographic expression was achieved. Some evidence, largely of a topographic nature, was presented earlier which implies that the southeastern flank of the El Paso Mountains has a younger relief age than that generally characteristic of the Bullion and Chemehuevi Mountains. These differences in relief age may be partly responsible for the variations in drainage density among the study ranges.

Suggested by early workers such as Glock (1931) and Smith (1950), there is perhaps a general consensus that drainage density increases through the early stages of erosional development. Evidence collected by Schumm (1956) at a site near Perth Amboy, New Jersey and by Roberts (1978) from drift sheets of varying age is in agreement with this idea. Additional support for this notion, as well as refinements, is provided by Schumm and his colleagues who employed hardware models (Schumm 1977). It may be that the lower drainage density of the basins along the southeastern flank of the El Paso Mountains is a reflection of the comparatively young relief age of that part of the range. Should this be the case, Lustig (1969, p. D68) would presumably classify the El Paso Mountains as one of the more recently uplifted ranges of the Basin and Range province where ". . . complete equilibrium between the drainage systems and their respective host ranges may not yet be achieved." It would follow that the higher drainage densities of the Bullion and Chemehuevi Mountains may be a reflection of the comparatively greater relief ages of the ranges.

Climate and Vegetation

The effect of climate and vegetation on the drainage density of the study ranges must be examined. In the drier climates, the prevailing view seems to be that drainage densities are low in deserts, rise to a maximum in semi-arid climates, and then decline in the more humid climates (Peltier 1962; Schumm 1969, 1977; Gregory and Gardiner 1975). Semi-arid climates are linked with high drainage densities because of a favorable mix of adequate precipitation and limited vegetation cover which tends to maximize the amount of overland flow, leading to vigorous dissection. In deserts, lower drainage densities prevail, despite a limited vegetation cover, presumably because of the rarity of precipitation events capable of generating enough overland flow for channel initiation and maintenance. Chorley (1957) was able to synthesize these notions and also to consider the impact of precipitation intensity by devising a climate/vegetation index. The amount of vegetation cover, estimated by Thornthwaite's Precipitation-Effectiveness (P-E) Index, is divided by the product of mean annual precipitation and some measure of precipitation intensity to yield the index. As he anticipated, Chorley found that drainage density in his study areas was inversely related to the index. Overland flow and landscape dissection would presumably tend toward maximum values in environments characterized by low values for the index.

Drainage densities in the study ranges appear to be influenced by climate and vegetation in the manner postulated by Chorley since an inverse relationship exists between mean drainage density and the climate/vegetation index for the ranges (Fig. 2). Calculation of the climate/vegetation index was achieved by using climatic data from Randsburg, Twentynine Palms, and Needles which predates the oldest of the topographic maps used in this analysis (U.S. Weather Bureau 1964). Precipitation amounts for the two year, 24 hour storm provided the necessary precipitation intensity values (Miller et al. 1973). Values for the index decline eastward across the desert, reflecting the increase in precipitation intensity and the decline in the P-E index in that direction. Although the drainage density values conform to Chorley's model based on contemporary climatic data, it may be unwise to assume that the drainage networks are a direct consequence of contemporary desert processes.



$$I_c = \frac{I}{P \times Q_s}$$

I_c = Chorley's climate/vegetation index

I = Thornthwaite's P-E index

P = Mean annual precipitation

Q_s = Precipitation intensity

Fig. 2. The relationship between mean drainage density and Chorley's climate/vegetation index for the three study ranges.

The distinction between fluvial landforms created by contemporary processes and those created by former processes is often a difficult one to draw in deserts. Contributing to this general difficulty is the limited vegetation cover and the associated slow recovery time of the landscape after a significant fluvial event (Wolman and Gerson 1978). For example, work by Ongley in arid Australia demonstrates that drainage networks can have a long and complex history in dry environments. His study indicates that the contemporary drainage network of the Cobar Pediplain began to be incised as early as the late Tertiary, was reactivated during the most recent pluvial climatic regime, and is presently moribund (Ongley 1974). Finally, this distinction is an especially difficult one to draw in the drainage networks being examined here because the networks are incised into resistant granitic rocks which change rather slowly in response to changes in geomorphic process type and/or intensity. As Ritter (1978, p. 299) remarks: "Granites in an arid climate may require imponderable time spans before their external form reflects an adjustment between processes and geology."

It is possible that the drainage networks under investigation are relict from an earlier climatic episode. Support for this notion is provided by the rather frequent incidence of channels choked with colluvium or aeolian sand noted during field reconnaissance. Reports of aeolian sand mantling fluvial features elsewhere in the Mojave Desert have been supplied by Burke et al. (1970) and by Bull and McFadden (1977). In addition, Blackwelder (1954) has identified relict channels in the California desert.

Late Tertiary and Quaternary climatic shifts in the California deserts, primarily involving semi-arid/arid climatic shifts, are known from botanical evidence (Axelrod 1958; Wells and Berger 1967; Van Devender 1977). One such change is believed to have triggered widespread erosion in the western Mojave Desert (Oberlander 1972). Another has been linked to cut and fill episodes in the granitic Argus Range (Bull and McFadden 1977). The drainage density/climate literature implies that drainage densities may have increased during the semi-arid climatic episodes, as Melton (1965) has suggested for some Arizona ranges, and may have decreased during the arid climatic episodes.

In summary, although the drainage densities of the study ranges appear to be related to contemporary climate/vegetation conditions, the distinct possibility exists that the drainage networks are not the direct consequence of contemporary desert processes but rather are relict. Faced with much the same question, albeit in a humid environment, Chorley and Morgan (1962) provide a useful discussion. If the networks are indeed relict, it may be that very similar climate/vegetation indexes prevailed during the climatic episode during which the networks were incised, accounting for the observed relationship. Such a circumstance would seem to require that subsequent changes in climate were in the same direction and of a similar magnitude throughout the California deserts. Continued study is necessary to determine if the drainage networks under investigation are relict as no evidence of a chronological nature was collected during the course of this study.

Conclusions

Measured from topographic maps, the drainage densities of third order drainage basins in three widely separated mountain ranges in the deserts of southern California average 14.6 km/km^2. The mean drainage density of the El Paso Mountains (13.2 km/km^2) was found to be significantly lower than the mean drainage density of both the Bullion Mountains (15.3 km/km^2) and the Chemehuevi Mountains (15.4 km/km^2). Only maps of uniform scale and contour interval were used in this analysis. Variations in map reliability or the method of drainage network delimitation that may exist are not believed to significantly influence the drainage density values.

No final conclusions can be reached concerning the causes of drainage density variations among the study ranges, although differences in relief age and climate/vegetation conditions may be linked to these variations. Differences in relief ratio appear to be unrelated to the variations in drainage density. Fieldwork in each of the study basins is required to assess the possibility that variations in rock type contribute significantly to the variation in drainage density. A complicating factor is the distinct possibility that the drainage networks may be of considerable antiquity. Further inquiry may shed some light on these matters but the task is a difficult one. As Ongley (1974, p. 290) concludes after his discussion of the drainage density of the arid Cobar Pediplain, such an inquiry may be "... doomed to entirely inferential and perhaps unwarranted assumptions concerning climatic, tectonic, and geomorphic history of the area."

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Literature Cited

Abrahams, A. D. 1980. Channel link density and ground slope. Annals, Association of American Geographers, 70:80–93.

Axelrod, D. I. 1958. Evolution of the Madro-Tertiary geoflora. Botanical Review, 24:433–509.

Bauer, B. 1980. Drainage density—an integrative measure of the dynamics and the quality of watersheds. Zeitschrift für Geomorphologie, 24:261–272.

Bishop, C. C. (compiler) 1964. Geologic map of California, Needles sheet. California Department of Conservation.

Blackwelder, E. 1954. Pleistocene Lakes and Drainage in the Mojave Region, Southern California. Pp. 35–40 *in* Geology of Southern California: Geomorphology. (R. H. Jahns, ed.), Division of Mines Bulletin 170, California Department of Natural Resources.

Bull, W. B., and L. D. McFadden. 1977. Tectonic Geomorphology North and South of the Garlock Fault, California. Pp. 115–138 *in* Geomorphology in Arid Regions. (D. O. Doehring, ed.), State University of New York at Binghampton, 272 pp.

Burke, J. D., R. G. Brereton, and P. M. Muller. 1970. Desert stream channels resembling lunar sinuous rilles. Nature, 225:1234–1236.

Chorley, R. J. 1957. Climate and morphometry. Journal of Geology, 65:628–638.

———, and P. F. Dale. 1972. Cartographic problems in stream channel delineation. Cartography, 7:150–162.

———, and M. A. Morgan. 1962. Comparison of morphometric features, Unaka Mountains, Tennessee and North Carolina, and Dartmoor, England. Geological Society of America Bulletin, 73:17–34.

Dibblee, T. W., Jr. 1952. Geology of the Saltdale Quadrangle, California. Division of Mines Bulletin 160, California Department of Natural Resources.

———. 1967. Geologic map of the Deadman Lake Quadrangle, San Bernadino County, Ca. Miscellaneous Geological Investigations Map I-488, United States Geological Survey.

Doornkamp, J. C., and C. A. M. King. 1971. Numerical analysis in geomorphology. St. Martin's Press, 372 pp.

Engstrom, W. N. 1981. Quantitative geomorphology of some desert mountain drainage basins. Zeitschrift für Geomorphologie, 25:383–390.

Gardiner, V. 1974. Drainage basin morphometry. British Geomorphological Research Group Technical Bulletin 14, Geo-Abstracts.

———, K. J. Gregory, and D. E. Walling. 1977. Further notes on the drainage density-area relationship. Area, 9:117–121.

Garfunkel, Z. 1974. Model for the Late Cenozoic tectonic history of the Mojave Desert, Ca. and its relation to adjacent regions. Geological Society of America Bulletin, 85:1931–1944.

Glock, W. S. 1931. The development of drainage systems: a synoptic view. Geographical Review, 21:475–482.

Gregory, K. J. 1976. Drainage Networks and Climate. Pp. 289–310 *in* Geomorphology and Climate, (E. Derbyshire, ed.), John Wiley and Sons, 512 pp.

———, and V. Gardiner. 1975. Drainage density and climate. Zeitschrift für Geomorphologie, 19: 287–298.

———, and D. E. Walling. 1973. Drainage basin form and process. Halsted Press, 456 pp.

Johnson, D. 1933. Available relief and texture of topography. Journal of Geology, 41:293–305.

Lustig, L. K. 1969. Trend surface analysis of the Basin and Range Province and some geomorphic implications. United States Geological Survey Professional Paper 500-D, United States Geological Survey.

Maxwell, J. C. 1967. Quantitative Geomorphology of Some Mountain Chaparral Watersheds of Southern California. Pp. 108–226 *in* Quantitative Geography Part II: Physical and Cartographic Topics. (W. L. Garrison and D. F. Marble, eds.), Department of Geography, Northwestern University, 324 pp.

Mazzucchelli, V. G. 1967. The southern limits of the Mojave Desert, California. California Geographer, 8:127–133.

Melton, M. A. 1957. An analysis of the relations among elements of climate, surface properties, and geomorphology. Technical Report 11, Department of Geology, Columbia University.

———. 1965. The geomorphic and paleoclimatic significance of alluvial deposits in southern Arizona. Journal of Geology, 73:1–38.

Miller, J. F., R. H. Frederick, and R. J. Tracey. 1973. Precipitation-frequency atlas of the Western United States: California. Volume 11, United States Department of Commerce.

Morisawa, M. E. 1962. Quantitative geomorphology of some watersheds in the Appalachian Plateau. Geological Society of America Bulletin, 73:1025–1046.

Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent. 1975. Statistical package for the social sciences (second edition). McGraw-Hill Book Company, 675 pp.

Oakeshott, G. B. 1971. California's changing landscapes. McGraw-Hill Book Company, 388 pp.

Oberlander, T. M. 1972. Morphogenesis of granitic boulder slopes in the Mojave Desert, California. Journal of Geology, 80:1–20.

Ongley, E. D. 1974. Fluvial morphometry on the Cobar Pediplain. Annals, Association of American Geographers, 64:281–292.

Peltier, L. C. 1962. Area sampling for terrain analysis. Professional Geographer, 14:24–28.

Pethick, J. S. 1975. A note on the drainage density-area relationship. Area, 7:117–121.

Richards, K. S. 1978. Yet more notes on the drainage density-basin area relationship. Area, 10:344–348.

Ritter, D. F. 1978. Process geomorphology. William C. Brown, 603 pp.

Roberts, M. C. 1978. Drainage density on the morainic landscapes of northeastern Indiana. Zeitschrift für Geomorphologie, 22:462–471.

Rogers, T. H. (compiler) 1969. Geologic map of California, San Bernadino sheet. California Department of Conservation.

Schumm, S. A. 1956. Evolution of drainage systems and slopes in badlands at Perth Amboy, New Jersey. Geological Society of America Bulletin, 67:597–646.

———. 1969. Geomorphic Implications of Climatic Change. Pp. 202–211 *in* Introduction to Fluvial Processes. (R. J. Chorley, ed.), Methuen, 218 pp.

———. 1977. The fluvial system. John Wiley and Sons, 338 pp.

Smith, K. G. 1950. Standards for grading texture of erosional topography. American Journal of Science, 258:655–668.

Thomas, M. F. 1976. Criteria for the Recognition of Climatically Induced Variations in Granite Landforms. Pp. 411–445 *in* Geomorphology and Climate. (E. Derbyshire, ed.), John Wiley and Sons, 512 pp.

Thornbury, W. D. 1965. Regional geomorphology of the United States. John Wiley and Sons, 609 pp.

U.S. Weather Bureau. (reprinted 1964). Climatic summary of the United States—supplement for 1931 through 1952, California. United States Department of Commerce, 153 pp.

Van Devender, T. R. 1977. Holocene woodlands in the southwestern deserts. Science, 198:189–192.

Wells, P. V., and R. Berger. 1967. Late Pleistocene history of coniferous woodland in the Mohave Desert. Science, 155:1640–1647.

Wolman, M. G., and R. Gerson. 1978. Relative scales of time and effectiveness of climate in watershed geomorphology. Earth Surface Processes, 3:189–208.

Zakrzewska, B. 1967. Trends and methods in land form geography. Annals, Association of American Geographers, 57:128–165.

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A New Species of Spider Crab of the Genus *Libinia* from Perú, and the First Known Male of *Delsolaria enriquei* Garth, 1973 (Crustacea, Brachyura, Majidae)

John S. Garth and Matilde Méndez G.

Abstract.—A new species of spider crab of the genus *Libinia* from Perú, and the first known male of *Delsolaria enriquei* Garth, 1973 (Crustacea, Brachyura, Majidae), by John S. Garth and Matilde Méndez G., *Bull. Southern California Acad. Sci.*, 82(3):125–130, 1983. A new species of spider crab, genus *Libinia,* and the first known male of another species, *Delsolaria enriquei,* from among IMARPE (Instituto del Mar del Perú) collections from northern Perú are described and illustrated. The former belongs to an amphi-American genus having north and south temperate anti-tropical cognates; the latter is a Peruvian endemic. The new *Libinia* species is most closely related to *L. mexicana* Rathbun of the Gulf of California. *Delsolaria,* as shown by the male first pleopod of *D. enriquei,* is allied with *Libidoclaea* Milne Edwards and Lucas, an austral American genus of the subfamily Pisinae.

Resumen.—Se describen e ilustran una nueva especie de cangrejo araña, *Libinia peruana,* y el macho de *Delsolaria enriquei,* no conocido anterioramente. Los ejemplares corresponden a colecciones efectuadas en el norte del Perú por una embarcación arrastrera langostinera y durante el Crucero 7008–09 del Barco Científico SNP-1 del IMARPE (Instituto del Mar del Perú). La primera especie pertenece a un género que se distribuye en ambas costas de América, la segunda especie es endémica del Perú. *Libinia peruana* se relaciona estrechamente con *L. mexicana* Rathbun, que habita el Golfo de California. *Delsolaria,* por la forma del primer pleópodo del macho de *D. enriquei,* se relaciona con *Libidoclaea* Milne Edwards, un género austral americano de la subfamilia Pisinae.

Introduction

In an earlier paper (Garth 1973) the senior author described and illustrated four new species and one new genus of brachyuran crabs obtained by E. M. del Solar, technical adviser to IMARPE (Instituto del Mar del Perú), from shrimp trawlers off northern Perú. Unfortunately, three of these, including the new genus *Delsolaria,* were represented by females only, making it impossible to describe and illustrate the diagnostic male first pleopods.

A few years ago, while curating the IMARPE collections, the junior author discovered a male specimen of *Delsolaria enriquei,* collected at the same locality as, and at an even earlier date than, the unique female holotype. She also recognized as a *Libinia* species other than the only previously known species from Perú, *L. rostrata* Bell (1835), a specimen collected by Ulario Peréa and given to Dr. del Solar. In the absence of comparative material, this specimen was forwarded to the senior author for study and has since been presented to the Allan Hancock

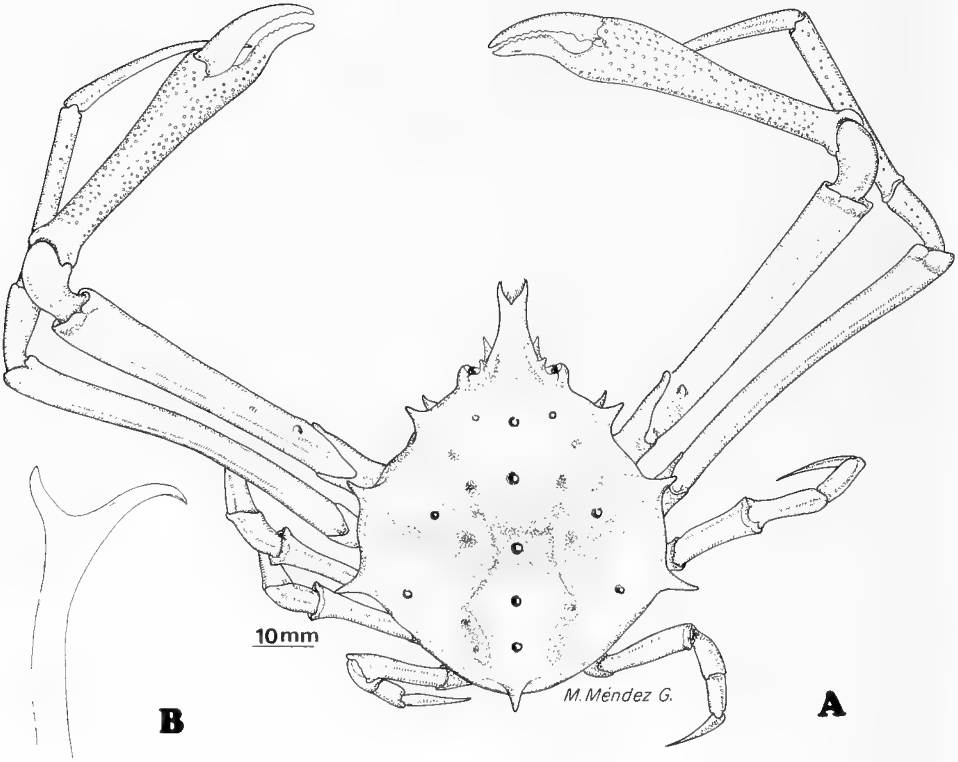

Fig. 1. *Libinia peruana,* new species, male holotype: A, dorsal view; B, first pleopod.

Foundation. Acknowledgment is made to Dr. Ulario Peréa and Dr. Enrique del Solar. This paper is Allan Hancock Foundation Contribution No. 399.

Libinia peruana, new species
Figure 1, A–B

Type: Male holotype, AHF Cat. No. 726, from Caleta Cruz, Perú, March 1972, from shrimp trawler, Dr. Ulario Peréa, collector, Dr. Enrique M. del Solar, donor.

Measurements (in millimeters): Length, including rostrum, 68.0; rostrum 12.5; width at level of branchial spines 58.8 with (48.5 without) spines; width at level of hepatic spines 33.8 with (31.1 without) spines; cheliped (basis-ischium-merus 66.4, carpus-propodus 72.8) 139.2; chela 61.0; dactyl 20.4; height of palm 12.6.

Diagnosis: Carapace with 6 median and 3 lateral spines, 2 branchial spines, and 1 hepatic spine. Rostrum elongate, horizontal, sides parallel. One spine on basal antennal article. Cheliped and first walking leg of adult male greatly elongated, manus widening distally, fingers gaping broadly at base. Tip of male abdomen rounded. Male first pleopod with tip and keel both slender and acuminate.

Description: Carapace smooth, narrowly pyriform, width less than postfrontal length. Rostrum horizontal, narrow, tubular, sides parallel, tip bifurcate, cleft triangular, tips fringed with hair, forming with antennae an excurrent channel.

Median spines six: two gastric, one genital, two cardiac, and one intestinal; two dorsal branchial spines, making an oblique line with lateral gastric spine; all but intestinal spine reduced in adult to tubercles. Three lateral marginal spines, one hepatic and two branchial, latter long, slender, upward and forward curving, as is intestinal spine. A prominent preocular spine, a pterygostomian spine with a tubercle behind it, a minute subbranchial tubercle. A spine at anteroexternal angle of basal antennal article; a small spine just behind outer margin of that segment.

Chelipeds and first ambulatory legs considerably longer than remaining pairs, merus of cheliped smooth, a stout spine at base, a tubercle in advance of it (on left side of type specimen only). Manus finely granulate, widening distally, not appreciably compressed, fingers widely gaping at bases. First walking leg as long as cheliped, merus smooth, dactylus very long and slender; remaining legs short, stout, and hairy, their dactyli overreaching their propodi.

Male abdomen 7-segmented, widest opposite segment 3, segment 4 narrowing distally, segments 5 and 6 with sides parallel, segment 7 broadly rounded. Male first pleopod with a slender, curving, grooved tip, keel arising from a broad base set well back but, unlike that of *L. mexicana,* narrowing abruptly, rather than toward tip.

Remarks: Had not the adult pair of *Libinia mexicana* Rathbun, originally described from a young specimen from the Gulf of California, México, already been described and illustrated (Garth 1958, p. 326, pl. 37, fig. 1), the male from Caleta Cruz, Perú, might have been mistaken for the adult of that species. Indeed, the same criteria may be used to separate the Peruvian specimen from *L. setosa* Lockington of the west coast of Baja California, México, that were used to separate *L. mexicana* from that species (Rathbun 1925, p. 311, key to *Libinia*). For, like *L. mexicana,* the carapace and rostrum of *L. peruana* are slender, the median spines are reduced from 8 to 6, there is but one hepatic spine, the cheliped is compressed and the fingers of the male gape widely, and the tip of the male abdomen is rounded.

The adult male from the Gulf of California, indubitably *L. mexicana,* makes it possible to differentiate the adult male from Perú, of which the young are unknown, from Rathbun's species. The rostrum of *L. peruana* is even more slender, the marginal spines of the carapace, namely, the paired hepatic, two paired branchial, and unpaired intestinal, are salient and not reduced to tubercles with age, and there is a cylindrical spine at the base of the merus of the cheliped that is not present in *L. mexicana.* Moreover, *L. mexicana,* like *L. setosa,* is a hairy species, while the type of *L. peruana,* although dried and coated with shellac, appears glabrous.

Genus *Delsolaria* Garth

Delsolaria Garth 1973, p. 5; type species *D. enriquei* Garth 1973.

Description (as emended to include the male sex): Chelipeds of male more robust and longer than walking legs, manus swollen, crested above and below, walking legs longer than those of female, diminishing in length from first to last.

Abdomen of male seven-segmented; male first pleopod terminating in a pointed tip and a blunt lobe.

Relationship: Placement of the genus in the subfamily Pisinae of the family Majidae is sustained by the configuration of the male first pleopod, which very closely resembles that of *Libidoclaea granaria* Milne Edwards and Lucas 1843, as illustrated in Garth (1958, pl. P, figs. 7, 8).

Delsolaria enriquei Garth
Figure 2, A–H

Delsolaria enriquei Garth 1973, pp. 5–7, fig. 3a–f.

Previous record: One female, holotype, north side of Banco de Mancora, Perú, 35 m, gravel, 9 December 1970, E. M. del Solar, collector.

Material examined: One male, topotype, Colección IMARPE-C-307-A-895-A, from Banco de Mancora, Lat. 3°30′S, Long. 81°06′W, 125 m, 1 September 1970, Ship SNP-1, E. M. del Solar, V. Alamo, collectors.

Measurements (in millimeters): Length, including rostrum, 54.2; rostrum 11.9; width at level of branchial spines 42.6; at level of posterolateral margin 38.4; cheliped (ischium-merus 31.6, carpus-propodus 44.3) 75.9; chela 36.0; dactyl 17.2; height of palm 16.5.

Diagnosis: Gastric, cardiac, and branchial regions swollen and tuberculate, lateral branchial tubercle prominent. Rostral, preorbital, and antennal spines of like size and sharpness. Maxilliped distally fringed with clavate setae. Male first pleopod ending in a pointed tip and a blunt lobe separated by a double fold.

Description of male: Carapace ovate-triangular, narrower than female (female one and one-quarter times longer than wide; male one and one-half times longer than wide), highly convex medially and laterally; rostrum 4.6 times length of carapace (in the female 6.0 times), front bifid, horn sharp, cleft shallow, U-shaped, sides slightly concave, a double row of curled setae on each; frontal, antennal, and preorbital spines of comparable size and sharpness. Preorbital spine with outer margin concave, separated by a narrow slit from postorbital cup into which eye retracts, leaving but a fraction of cornea visible from above, a slight constriction behind postorbital cup. Gastric region broad, swollen, surmounted by 16 or more small tubercles of which three are median, remainder paired; epibranchial regions surmounted by a large tubercle and some small ones; mesobranchial regions with three large tubercles forming a triangle; cardiac region most elevated, with four tubercles in a diamond; sides of hepatic and branchial regions each with one or two small tubercles; subhepatic regions with two rows of 3 or 4 small tubercles; intestinal region low, pinched, marked by a single median spine, posterior margin thin, broadly rounded, slightly sinuous, a notch marking off a small lobe at base of second walking leg. Outer maxilliped like that of female.

Chelipeds much more robust and longer than walking legs, merus with anterior and external margins cristate, outer crest with a subterminal spine, carpus tuberculate; manus more or less swollen, crested above and below, fingers long, slender, pointed, downcurving, incurving, ribbed, and multidenticulate; walking legs longer than those of female, diminishing in length from first to last, merus tuberculated on proximal end; carpi tuberculated; dactyli robust, setose.

Male abdomen with seven free segments, with a low median tubercle on each. Male first pleopod long and slender, reaching to last segment of abdomen; flaring distally; pointed tip and opposite blunt lobe separated by a fold continued on both sides of opening to base of tip, entire area provided with many minute spinules.

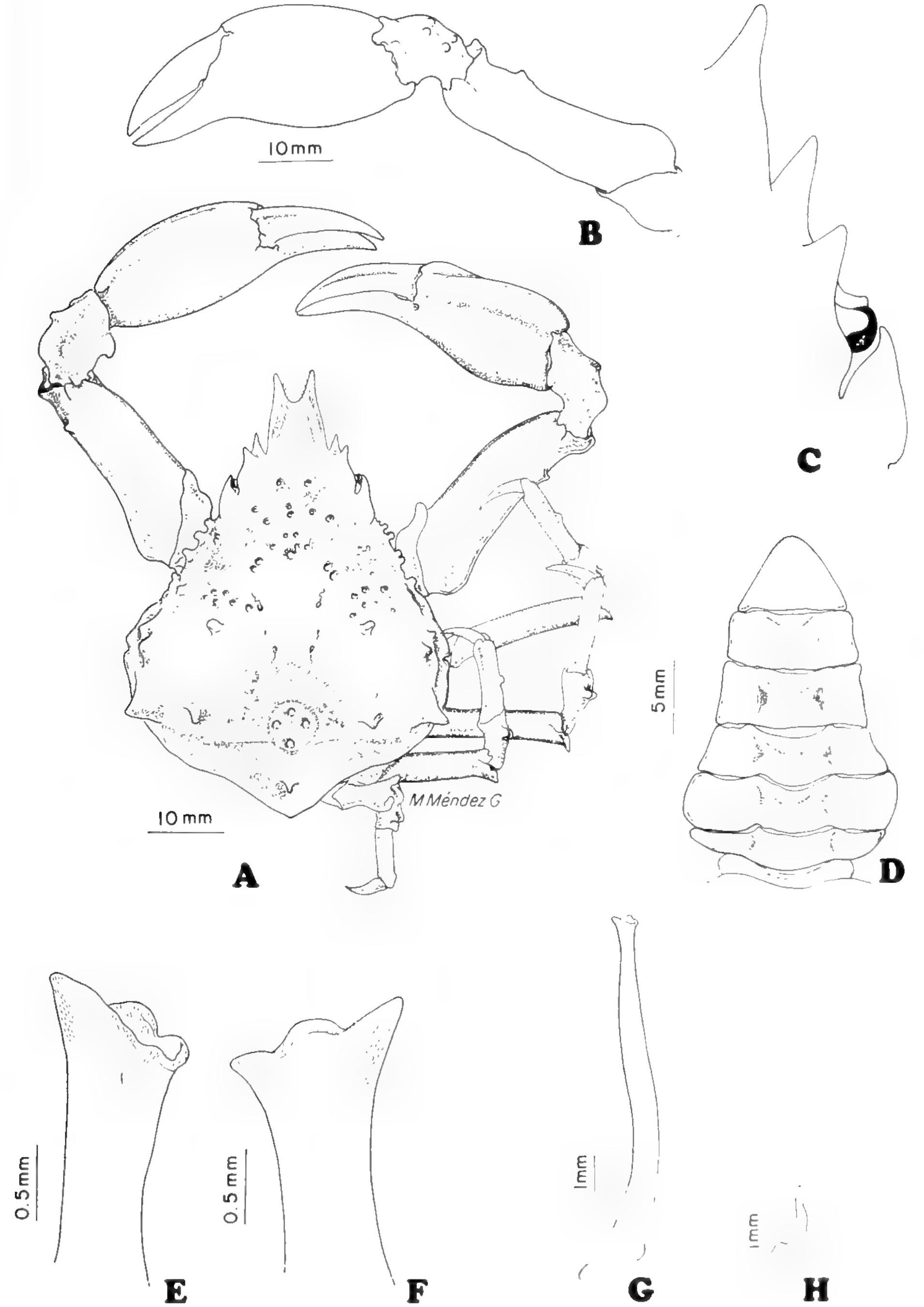

Fig. 2. *Delsolaria enriquei* Garth 1973, male topotype: A, dorsal view; B, left chela, outer view; C, rostrum and orbit, dorsal view (partial); D, abdomen; E, first pleopod, ventral view; F, first pleopod, dorsal view; G, first pleopod, entire; H, second pleopod.

Remarks: The discovery by the junior author among IMARPE collections of a male specimen collected at the same locality as the unique female holotype and at an even earlier date makes possible the description and illustration of the opposite sex, including the diagnostic first pleopod, and the placement of the genus *Delsolaria,* erected to receive it, in the subfamily Pisinae, a matter previously in doubt. It further permits emending the generic description to include the sexually dimorphic abdomen, chelipeds, and walking legs of the first two pairs of the male sex. Had the recently discovered specimen been known to the senior author at the time *Delsolaria enriquei* was first described (Garth 1973), it undoubtedly would have been selected as the holotype; under the circumstances of subsequent recognition, however, it does not qualify as a paratype, not having been present at the time the original description was written. Notwithstanding, its importance in establishing the systematic position of the new genus and species cannot be overestimated. The bathymetric range of the species is extended from 35 to 125 m.

Literature Cited

Garth, J. S. 1958. Brachyura of the Pacific Coast of America. Oxyrhyncha. Allan Hancock Pacif. Exped., 21:1–854, pls. A–Z_2, 1–55, text-figs. 1–9.

———. 1973. New taxa of brachyuran crabs from deep water off western Perú and Costa Rica. Bull. S. Calif. Acad. Sci., 72:1–12, text-figs. 1–5.

Rathbun, M. J. 1925. The spider crabs of America. Bull. U.S. Nat. Mus., 129:1–613, pls. 1–283, text-figs. 1–153.

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Leptarctus ancipidens (White) (Carnivora: Mammalia) from the Punchbowl Formation, Cajon Pass, California

Hugh M. Wagner and Robert E. Reynolds

Abstract.—*Leptarctus ancipidens* (White) (Carnivora: Mammalia) from the Punchbowl Formation, Cajon Pass, California by Hugh M. Wagner and Robert E. Reynolds. *Bull. Southern California Acad. Sci.*, 82(3):131–137, 1983. A maxillary fragment of the mustelid carnivore *Leptarctus ancipidens* from the Punchbowl Formation exposed in Cajon Pass, San Bernardino County, California is the first record of the species from California, and compares favorably with specimens from the type locality in Florida which produces the Thomas Farm Local Fauna. That local fauna was previously known to be correlated with the Hemingfordian North American Land Mammal age and this specimen re-affirms the previously published Hemingfordian age of the Punchbowl Formation at the locality where this specimen was recovered.

Introduction

Leptarctus Leidy, 1856 is a mustelid carnivore in the subfamily Leptarctinae. Remains of leptarctines are not common, but are recorded in Miocene deposits scattered across the United States. The specimen of *Leptarctus ancipidens* (White, 1941), San Bernardino County Museum, SBCM A500-1665, from the Punchbowl Formation exposed in Cajon Pass in San Bernardino County is a new record of the taxon at this locality and extends the geographic range of the species to California. The only other leptarctine material known from California is a P_4, University of California Museum of Paleontology, UCMP 33708, here identified as *L. wortmani* Matthew, 1924, that was recovered from the Black Hawk Ranch Local Fauna (Macdonald 1948) of Clarendonian age. Previously published records of *L. ancipidens* are from deposits of medial Hemingfordian age from the Thomas Farm Local Fauna of Florida (White 1941; Olsen 1957, 1958, 1959). The occurrence of *L. ancipidens* from deposits of late Hemingfordian age in the Punchbowl Formation (Woodburne and Golz 1972) is in approximate temporal agreement with the occurrence of this taxon in the Thomas Farm Local Fauna.

Locality and Stratigraphy

The specimen of *L. ancipidens*, SBCM A500-1665, was recovered from the Dip Slope locality, SBCM 1.103.8 (= RV 6988 = UCMP 3146) located in the NW½ of the SW¼ of the NW¼ of the SW¼ of section 36, T. 3 N., R. 6 W., San Bernardino Base and Meridian, as shown on the U.S.G.S. Cajon 7½ minute topographic map 1956, revised 1968 and 1973. The locality is 1350 feet (405 meters) South 10° West of the mapped Historical Marker, and is on the north side of the Atchison Topeka and Santa Fe railroad tracks (Fig. 1).

The specimen was collected by San Bernardino County Museum paleontologic monitors during the realignment of the Santa Fe railroad right-of-way in Cajon

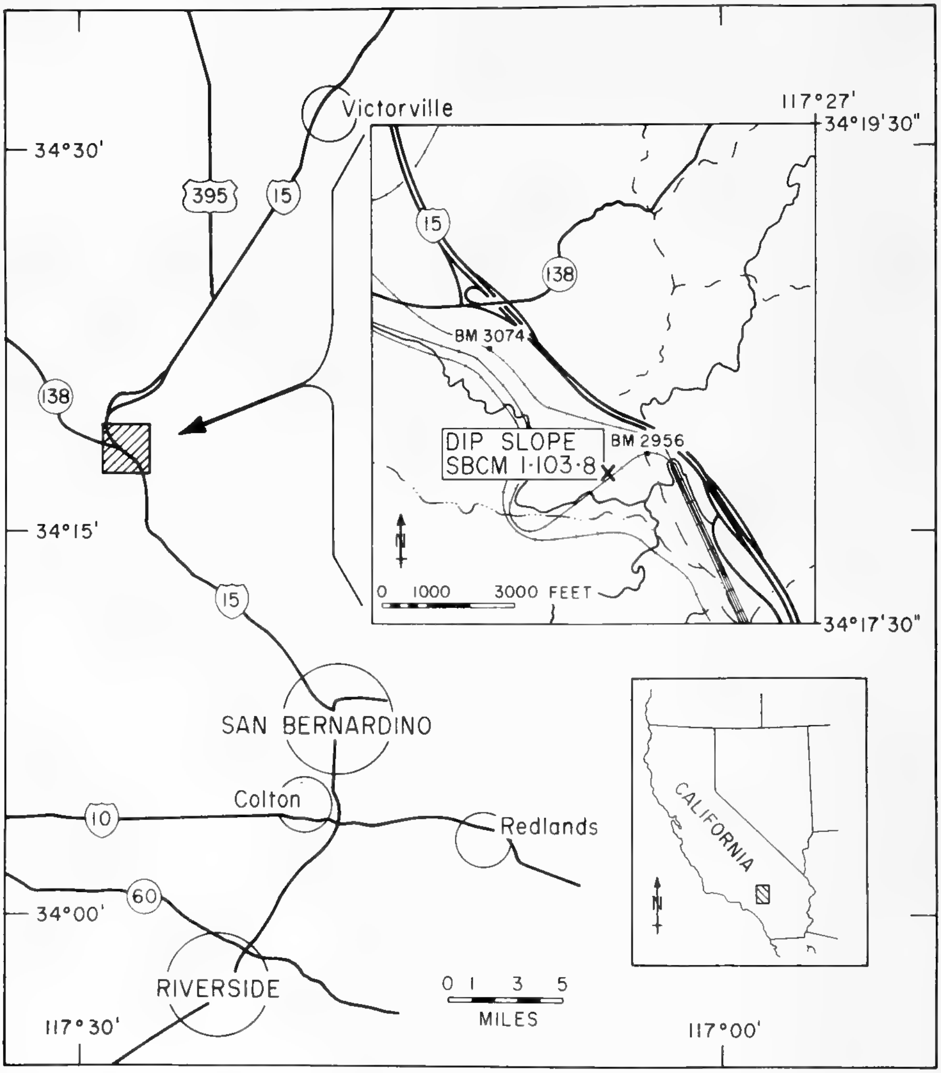

Fig. 1. The palate fragment of *Leptarctus ancipidens,* SBCM A500-1665 was recovered from SBCM loc. 1.103.8, Dip Slope, in Cajon Pass, San Bernardino County, southern California, designated with an X.

Pass. The bone-bearing horizon was located during excavation. Blocks of matrix containing specimens were brought to the museum for preparation.

The specimen was located *in situ* with the disarticulated remains of other large mammals. Gnaw marks by rodents suggest that the bones had lain exposed prior to burial. The *L. ancipidens* specimen was located in deeply-weathered red and brown arkosic sandstone of the Punchbowl Formation, Unit Tp^3, as described by Woodburne and Golz (1972, pp. 23–27). The locality is one-half mile northeast of the measured section described by Woodburne and Golz (p. 44) and is situated approximately 250 feet (75 meters) above the basal contact between Unit Tp^3

and Unit Tp^2 and approximately 650 feet (195 meters) below the contact between Unit Tp^3 and the overlying Unit Tp^5.

Methods

Abbreviations used in this report include AMNH—American Museum of Natural History; ANSP—Academy of Natural Sciences of Philadelphia; CM—Carnegie Museum; FGS—Florida Geologic Survey; LACM—Los Angeles County Museum of Natural History; MCZ—Museum of Comparative Zoology, Harvard; RV—Riverside Vertebrate Locality, University of California, Riverside; SBCM—San Bernardino County Museum; UCMP—University of California Museum of Paleontology, Berkeley.

All measurements are in millimeters.

Systematic Paleontology

Order CARNIVORA Bowdich, 1821
Family Mustelidae Swainson, 1835
Subfamily Leptarctinae Gazin, 1936
Genus *Leptarctus* Leidy, 1856
Leptarctus ancipidens (White, 1941)

Mephititaxus ancipidens, White, 1941. Proc. New England Zool. Club, Vol. 18: 91–98.
Mephititaxus ancipidens, Olsen, 1957. Jour. Mammalogy, Vol. 38:452–454.
Leptarctus ancipidens, Olsen, 1957. Amer. Mus. Novit. no. 186:1–7.

Referred material.—SBCM A500-1665, palate fragment with broken left and right P^4.

Stratigraphic and geographic range.—Deposits of medial and late Hemingfordian age, early middle Miocene from California and Florida.

Description and Comparison

SBCM A500-1665 (Fig. 2) is a palate fragment composed of the posterior portion of the left and right maxilla. The right maxilla has an alveolus for the posterior root of P^3. In the left maxilla, this alveolus is also preserved. The right P^4 is approximately 9.10 mm in length and 8.33 mm in width across the protocone. Anterolabial to the paracone is a low cingulum that extends lingually onto the anterior surface of the protocone. There is a small parastyle on this cingulum just anterior to the paracone. The protocone is large and well developed. On the lingual shelf, posterior to the protocone, there is a prominent hypocone. The hypocone is situated on the lingual margin of this shelf. The postero-labial portion of both P^4's have been damaged so that the exact height of this portion of the tooth is not known. This portion of the tooth has been restored on the right P^4 in Figure 2A.

On the left maxilla, posterior to the P^4, three alveoli for the roots of M^1 are preserved. Only the anterior labial alveolus is present just posterior to P^4. The two lingual alveoli are well-developed and are 9.30 mm apart, indicating that the M^1 had four roots and was a large, broad tooth (Fig. 2B) with the same number of roots as *L. ancipidens* from the Thomas Farm Local Fauna.

The morphology and size of the P^4 in SBCM A500-1665 closely resembles the

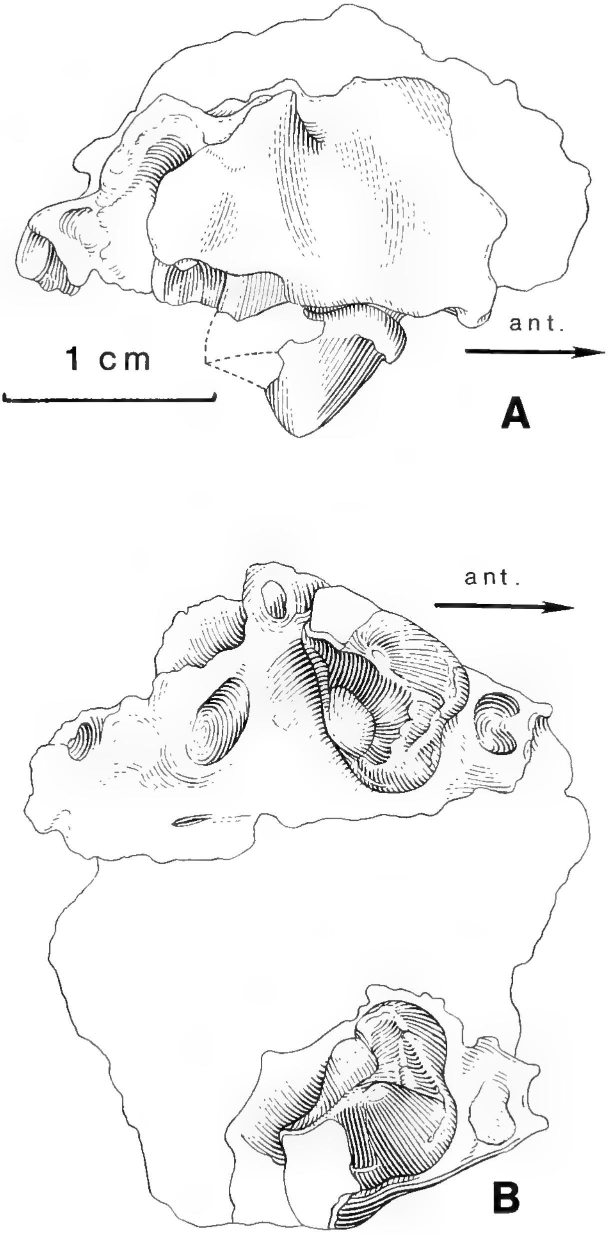

Fig. 2. *Leptarctus ancipidens* (White), SBCM A500-1665, SBCM loc. 1.103.8, partial palate with left and right P^4, A, right lateral view; B, occlusal view: scale indicated.

P^4's of specimens of *L. ancipidens* from the Thomas Farm Local Fauna. The only noticeable difference between the Thomas Farm and Cajon Pass material is the smaller size of the hypocone on the specimen from the Punchbowl Formation relative to the overall tooth size. The overall size of the P^4 is close to the Thomas Farm material (Table 1).

Table 1. Comparative measurements of the P^4 in various species of *Leptarctus*.

L. ancipidens	SBCM A500-1665	FGS V-5697	MCZ 3659	MCZ 3658
P^4 anteroposterior diameter	9.10	10.04	9.60	10.30
transverse diameter across protocone	8.33	8.55	7.18	8.00
L. primus	ANSP 11293	AMNH 18241		
P^4 anteroposterior diameter	7.20*	7.20		
transverse diameter across protocone	6.80*	5.65		
L. oregonensis	LACM(CIT) 206			
P^4 anteroposterior diameter	6.60			
transverse diameter across protocone	5.05			
L. bozemanensis	CM 9574			
P^4 anteroposterior diameter	8.4			
transverse diameter across protocone	6.2			
L. wortmani	UCMP 27130			
P^4 anteroposterior diameter	8.84			
transverse diameter across protocone	8.20			

* Approximate.

The palate and P^4 of *L. ancipidens* is larger than most other species of *Leptarctus. L. primus* Leidy, 1857, *L. oregonensis* Stock, 1930, and *L. bozemanensis* (Dorr, 1954) are significantly smaller in size than *L. ancipidens* (Table 1) and these species also have a proportionately larger hypocone relative to the overall size of the P^4 than does *L. ancipidens. L. wortmani* is a larger form than *L. ancipidens* and has a P^4 with a much larger hypocone.

Biostratigraphy

The specimen of *L. ancipidens* recovered from the Dip Slope locality in the Tp^3 unit of the Punchbowl Formation (Woodburne and Golz 1972) was found associated with the following other vertebrate taxa at this locality: Testunididae, Sciuridae, *Merychippus* cf. *M. carrizoensis* (Dougherty), Rhinoceratidae, *Dyseohyus* sp., *Bouromeryx* cf. *B. milleri* (Frick), and Antilocapridae. Unit Tp^2 and the lower portion of the overlying Tp^3 of the Punchbowl Formation in Cajon Pass contain a faunal assemblage of late Hemingfordian age, while the upper part of Tp^3 contains fossil taxa considered elsewhere in southern California to have an early Barstovian character (Woodburne and Golz 1972, pp. 15, 16). The Dip Slope locality occurs in the lower portion of the stratigraphic section of Tp^3 that contains fossil mammalian taxa considered to be late Hemingfordian in age. Taxa recovered from other localities in the Tp^3 unit of the Punchbowl Formation at Cajon Pass are *Hypolagus* sp., *Sciuropterus* sp., *Archaeohippus* sp. and *Brachycrus buwaldi* (Woodburne and Golz, pp. 15, 52). The presence of *L. ancipidens* at this locality may be slightly later in time than its occurrence in the medial Hemingfordian Thomas Farm Local Fauna of Florida. Temporally correlative late Hemingfordian faunas are the Red Division Local Fauna of the Barstow Formation (Woodburne and Tedford 1982), faunas from the Alvord and Cady Mountains, and the Phillips Ranch Local Fauna of the Mojave Desert, California (Woodburne, Miller, and Tedford 1982), and the fauna from the Sheep Creek Formation of Nebraska (Woodburne and Golz 1972).

Discussion

The genus *Leptarctus* differs from *Craterogale* Gazin, 1936 (a more primitive leptarctine) in the presence of a hypocone on P^4 which is absent in *Craterogale. Leptarctus ancipidens* appears to be the most primitive known species of this genus as the hypocone on the P^4 is smaller than that found on the other species of *Leptarctus. L. ancipidens* is found in rocks of Hemingfordian age, while the other species of *Leptarctus* are known from younger deposits of Barstovian and Clarendonian age, suggesting that the smaller, less developed hypocone on the P^4 in *L. ancipidens* is the primitive condition. The slightly smaller size of the hypocone on *L. ancipidens* from the Punchbowl Formation, when compared with the material of this species from the Thomas Farm Local Fauna, may indicate that the California form was slightly more primitive. However, the smaller hypocone is probably best attributed to individual variation within *L. ancipidens.*

Acknowledgments

We express our appreciation to Michael O. Woodburne for providing information concerning the age of the Dip Slope locality in Cajon Pass. The illustrations were drawn by Jaime P. Lufkin and Linda K. Jankov. We also thank the curators of the University of Florida, Gainesville, the Museum of Comparative Zoology, Harvard, and the Los Angeles County Museum of Natural History for the loan and use of comparative material.

Literature Cited

Macdonald, J. R. 1948. The Pliocene carnivores of the Black Hawk Ranch fauna. Univ. Calif. Publ. Dept. Geol. Sci., Bull. 28:53–80.

Olsen, S. J. 1957. The lower dentition of *Mephititaxus ancipidens* from the Florida Miocene. Jour. Mammalogy, vol. 38:452–454.

———. 1957. Leptarctines from the Florida Miocene (Carnivora: Mustelidae). Amer. Mus. Novit., 1861:1–7.

———. 1958. The skull of *Leptarctus ancipidens* from the Florida Miocene. Flor. Geol. Surv., Spec. Publ. no. 2, Cont. Flor. Vert. Pal., no. 2:1–11.

———. 1959. The middle ear of the Miocene mustelid *Leptarctus*. Jour. Paleontology, vol. 3:451–452.

White, T. E. 1941. Additions to the Miocene fauna of Florida. Proc. New England Zool. Club, vol. 18:91–98.

Woodburne, M. O., and D. J. Golz. 1972. Stratigraphy of the Punchbowl Formation Cajon Valley, southern California. Univ. Calif. Publ. Geol. Sci., Bull. 92:1–57.

———, S. T. Miller, and R. H. Tedford. 1982. Stratigraphy and geochronology of Miocene strata in the central Mojave Desert, California. Pp. 47–64 *in* Geologic excursions in the California desert. GSA Guidebook, Cord. Sect., 78th Ann. Meeting.

———, and R. H. Tedford. 1982. Litho- and biostratigraphy of the Barstow Formation, Mojave Desert, California. Pp. 65–76 *in* Geologic excursions in the California desert. GSA Guidebook, Cord. Sect., 78th Ann. Meeting.

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Plesionika sanctaecatalinae: a New Species of Deep-sea Shrimp from the Eastern Pacific (Caridea: Pandalidae)

Mary K. Wicksten

Abstract.—*Plesionika sanctaecatalinae:* a new species of deep-sea shrimp from the eastern Pacific (Caridea: Pandalidae) by Mary K. Wicksten. *Bull. Southern California Acad. Sci.*, 82(3):138–143, 1983. *Plesionika sanctaecatalinae* n. sp. is the only mesopelagic pandalid shrimp known off southern California. The species ranges from southern California to Peru at depths of 812–3877 m. It resembles *P. gracilis,* but can be distinguished from that species by its fewer dorsal rostral spinules and its 15–18 segments in the carpus of the second pereopod.

During 1960–69, collections of midwater animals were made off southern California and Baja California using an Isaacs-Kidd midwater trawl. Among the specimens taken were some large, bright red pandalid shrimp. These shrimp were placed in the collections of the Allan Hancock Foundation (AHF), University of Southern California.

Many of the shrimp were broken in the trawl. The specimens were preserved in unbuffered 10% formalin, which damaged many of them. When first examined, they were identified as *Plesionika* sp., then as *P. martia semilaevis* Bate (Wicksten 1978). However, closer inspection has revealed them to belong to an undescribed species. An additional specimen was obtained from the Instituto del Mar del Perú. The new shrimp is described herein.

Plesionika sanctaecatalinae new species
Figs. 1–3

Plesionika sp.: Ebeling, Ibara, Lavenberg, and Rohlf 1970:12.
Plesionika martia semilaevis: Wicksten 1978:85, fig. 1.—Méndez 1981:104, pl. 18, figs. 316–317.
Not *Plesionika semilaevis* Bate, 1888:644, pl. 113, figs. 3a–3b.

Diagnosis.—Rostrum longer than scaphocerite, with two minute dorsal spines and 8–12 ventral teeth. Abdominal segments without sharp points or spines, sixth abdominal somite about 2× length of fifth. Second pereopods equal, with 15–18 carpal segments. Third–fifth pereopods extremely long and thread-like.

Description.—Rostrum exceeding scaphocerite, with two minute dorsal spines and 8–12 ventral teeth. All ventral teeth on distal half of rostrum, proximal half with fine setae on ventral margin. One–3 spinules on dorsal midline of carapace posterior to rostrum in some individuals.

Carapace with minute punctae. Dorsal midline slightly raised posterior to rostrum for about 0.5–0.6× length of carapace. Small antennal and branchiostegal spines present. Ventral margin curved, posterior margin bluntly angled.

Abdomen lightly punctate. Posterior margin of third somite overhanging fourth somite on dorsal margin in some individuals. Pleura of segments 1–2 rounded,

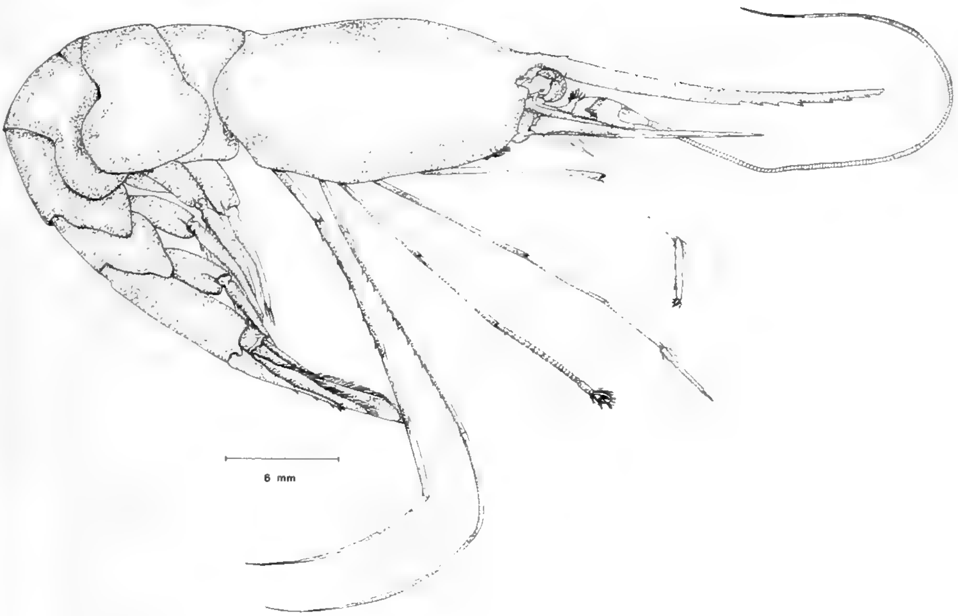

Fig. 1. *Plesionika sanctaecatalinae,* n. sp. Male, carapace length 18.3 mm. 25 miles from Pyramid Head, San Clemente Island, California, 1846–1938 m, *Velero IV* sta. 12390-68. Entire animal in lateral view. Rostrum broken, fifth pereopods missing.

pleuron of third segment subquadrate, pleura of fourth and fifth segments narrowly rounded. Sixth segment about 2× length of fifth segment, posteroventral angle with minute tooth. Telson shorter than sixth segment and uropods, with three pair small dorsolateral spines and two pair terminal spines.

Eye large, rounded and pigmented, without ocellus. Cornea not reaching end of first segment of antennular peduncle.

First segment of antennular peduncle the longest. Stylocerite longer than cornea of eye, with strong, blunt lateral hook at base. Second and third segments about equal in length. All segments with long, fine setae. Flagella long and slender.

Basicerite of second antenna with sharp point on lateral margin. Carpocerite reaching first segment of antennular peduncle. Scaphocerite 6.5× as long as wide, with lateral spine exceeding blade; mesial margins fringed with setae. Flagellum at least as long as body of shrimp, but usually broken when collected.

Mandible with 6–8 incisor teeth; molar process with teeth and ridges, palp with three segments. First maxilla with narrow proximal endite, broad distal endite and bilobed palp. Second maxilla with lower endite reduced, upper endite well developed and incised; palp and scaphocerite well developed. First maxilliped with endites of basis and coxa distinctly separated, palp well developed, exopod large, with distinct flagellum and caridean lobe, epipod large and bilobed. Second maxilliped with well developed exopod, epipod and podobranch. Third maxilliped exceeding scaphocerite, with exopod and epipod, its distal segment slightly shorter than penultimate segment, penultimate segment shorter than antepenultimate segment.

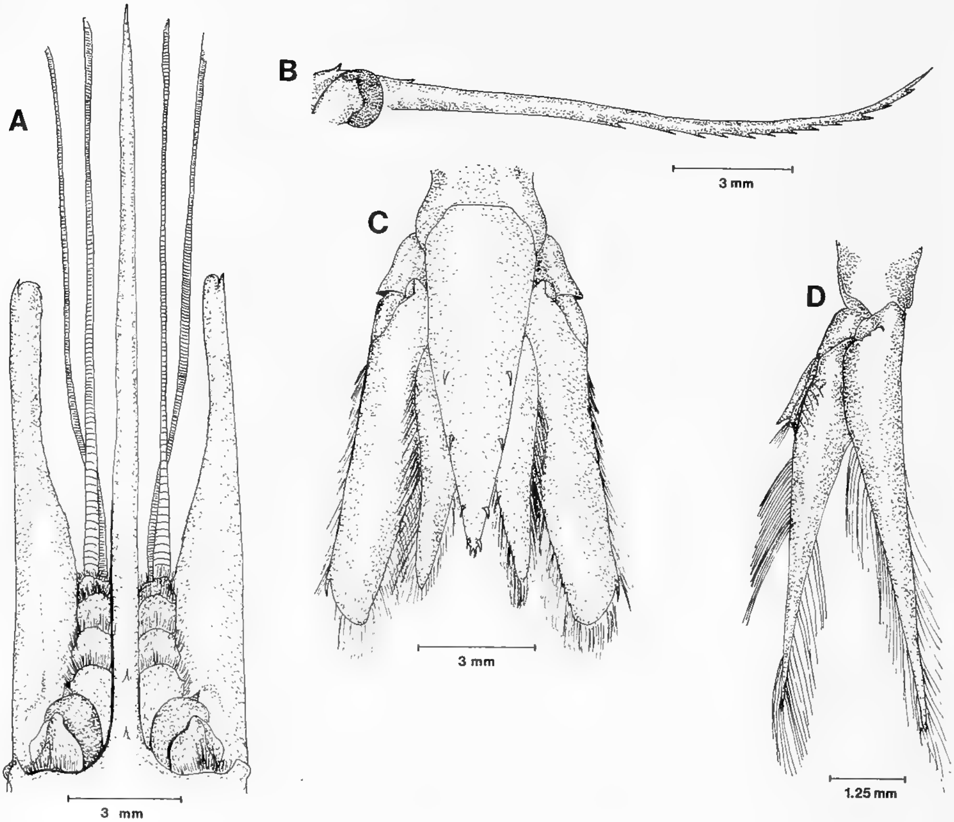

Fig. 2. *Plesionika sanctaecatalinae.* Male, carapace length 14.6 mm, 19.25 miles from Pyramid Head, San Clemente Island, 1680–1865 m, *Velero IV* sta. 11703-67. A, rostrum and frontal region in dorsal view; B, rostrum in lateral view; C, tail fan; D, second pleopod.

First pereopod as long as third maxilliped, minutely chelate. Propodus about equal in length to dactyl, carpus 2.5× length of propodus, merus 2× length of propodus, ischium about 0.3× length of merus, all segments with scattered long setae. Epipod present.

Second pereopods about equal in length. Dactyl about equal in length to palm of chela, fingers of chela with tufts of setae. Thick tuft of setae at propodal-carpal articulation. Carpus with 15–18 segments, the most distal segment the longest; distal segments more distinct than proximal segments. Merus about 0.75× length of carpus. Ischium about equal to merus. Epipod present.

Third–fifth pereopods broken in all specimens. Propodus and dactyl long, thread-like, exceeding length of carapace but broken in all specimens. Carpus about equal to 0.5× merus. Third merus with 10–14 ventral spines, fourth merus with 6–11 spines, fifth merus with 4–7 spines; spines usually occurring singly but occasionally in pairs. Ischium much shorter than merus, without terminal spine. Epipods lacking from third-fifth pereopods.

Endopod of first pleopod short and oval in female, blunt and paddle-shaped in male. Second pleopod with appendix interna; in males, also with appendix mas-

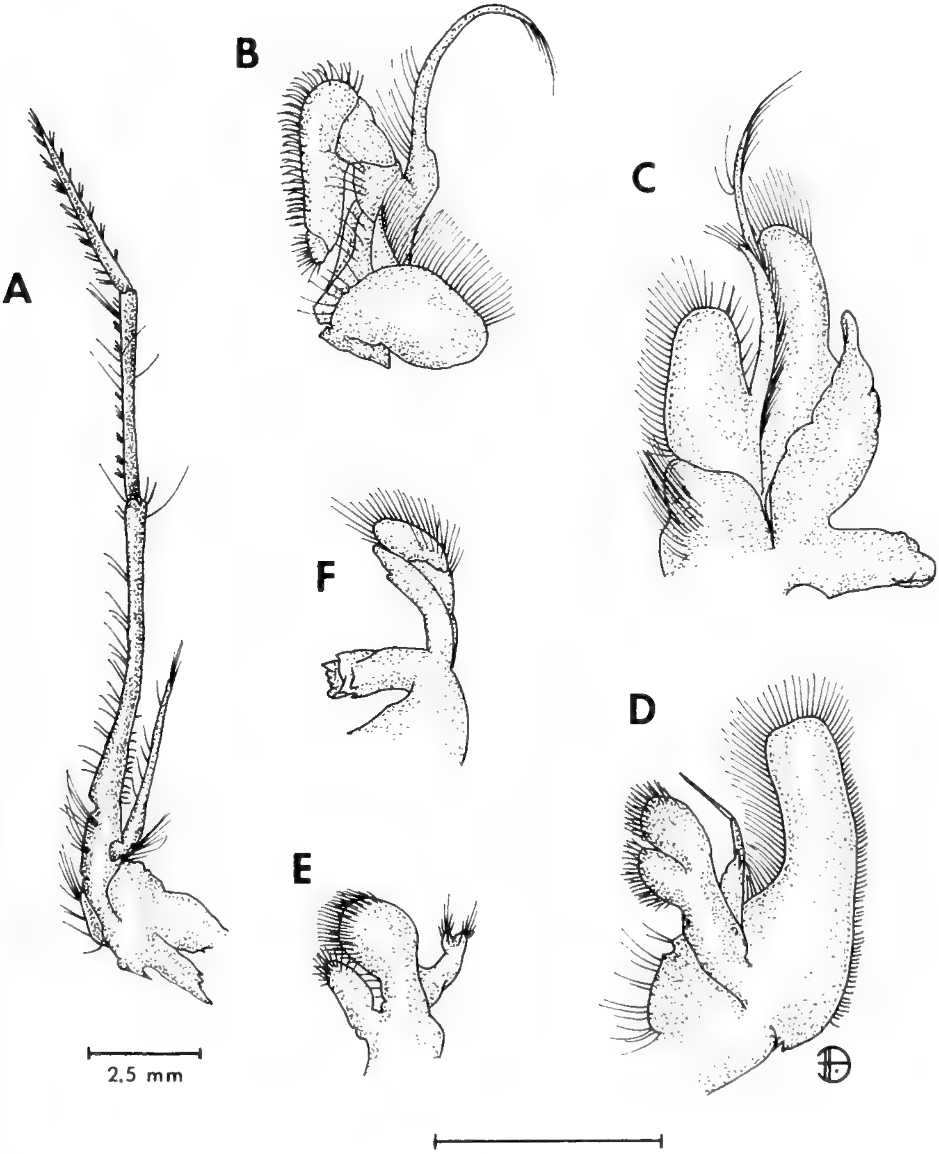

Fig. 3. *Plesionika sanctaecatalinae*. Broken specimen collected 5.7 miles from Ship Rock, Santa Catalina Island, 846–864 m, *Velero IV* sta. 7299-61. A, third maxilliped; B, second maxilliped; C, first maxilliped; D, second maxilla; E, first maxilla; F, mandible.

culina. Eggs small and numerous. Uropods slender, outer branch exceeding inner; small tooth on distolateral margin of outer branch; movable spine mesial to this tooth; both branches fringed with setae.

Holotype.—Male, postorbital carapace length (CL) in millimeters 19.0; 7.3 miles, 17° true from Long Point Light, Santa Catalina Island, California (33°33′29″N, 118°20′42″W–33°30′12″N, 118°17′28″W), 886 m, 29 June 1960, *Velero IV* station 7059-60, AHF type number 6053.

Paratypes.—Male, CL 13.2, off Santa Catalina Island (33°38′03″N, 118°32′39″W–33°25′48″N, 118°16′48″W), 846–864 m, 24 Feb. 1961, *Velero IV* sta. 7299-61, U.S. National Museum of Natural History (Smithsonian Institution). Male, CL 15.7, off Santa Catalina Island (33°26′54″N, 118°18′04″W–33°33′12″N, 118°27′24″W), 857–882 m, 28–29 June 1961, *Velero IV* sta. 7373-61, California Academy of Sciences. Female, ovigerous, CL 14.3, off Cortez Bank (31°57′30″N, 120°20′00″W–31°42′00″N, 120°16′00″W), 3822–3877 m, 25 August 1965, *Velero IV* sta. 10661-65; Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands. Male, CL 14.4, off coast of Perú (between 12° and 18°S), depth not recorded, drag sample, 1972, cruise 7201, Instituto del Mar del Perú. Also 57 specimens from 34 stations: off Ship Rock, Santa Catalina Island (about 33°N, 118°W) to off North Point, Guadalupe Island, México (about 29°N, 118°W); also off Santa Barbara Island, San Clemente Island, and Cortez Bank, California; and off Cabo Punta Banda and Islas Todos Santos, Baja California, México; 812–3877 m, AHF. Further data on all specimens is available in the records of the Allan Hancock Foundation.

Size distribution.—Males: 5–10 mm CL: 1; 10–15 mm: 10; 15–20 mm: 10.—Females: 5–10 mm: 10; 10–15 mm: 16; 15–20 mm: 9. (Sex of 6 specimens not determined due to breakage).

Depth distribution.—500-1000 m: 17; 1000–1500 m: 20; 1500–2000 m: 10; 2000–2500 m: 5; 2500–3000 m: 1; 3000–3500 m: 6; 3500–4000 m: 2. (The average depth is recorded for specimens taken at stations sampled over a great range of depths. Depth was not recorded for the specimens from Perú).

Etymology.—The species is named after Santa Catalina Island, California, off which many specimens were collected.

Remarks.—*Plesionika sanctaecatalinae* closely resembles *P. gracilis* Borradaile, 1917. In *P. gracilis,* the rostrum has two strong teeth on a crest over the eye and eight spinules. *Plesionika sanctaecatalinae* has two weak spines and 1–3 spinules. The eyestalk of *P. gracilis* bears a distinct ocellus. There are nine segments in the carpus of the second pereopod in *P. gracilis* instead of 15–18, as in *P. sanctaecatalinae. Plesionika gracilis* inhabits the western Indian Ocean, not the eastern Pacific.

Little is known about the natural history of *P. sanctaecatalinae.* Ebeling *et al.* (1970) included it in their numerical analysis of ecological groupings of midwater animals of the San Pedro Basin. The shrimp was associated with "rare, lower mesopelagic species of mixed origins." The animal is colored red in life (J. C. Yaldwyn unpublished data). A juvenile pandalid, carapace length 3.9 mm, taken at station 10975 (off Cortez Bank, 3230–3729 m), may be this species.

Plesionika sanctaecatalinae is the only mesopelagic pandalid known from California. *Plesionika mexicana* Chace rarely occurs at lesser depths on the bottom off southern California, ranging south to Perú. *Plesionika beebei* Chace has been collected off México and Perú; *P. trispinus* Squires and Barragan has been taken off Colombia and northern Perú. A key to the eastern Pacific species of *Plesionika* and illustrations of the species are available in the book by Méndez (1981).

Acknowledgments

John C. Yaldwyn, Donald Gin, and Manuel Murillo originally sorted many of the specimens and identified them to genus. Fenner A. Chace, Jr., Smithsonian Institution, helped confirm the identity of the shrimp as a new species, and reviewed early drafts of the manuscript. Matilde Méndez and Enrique del Solar, Instituto del Mar del Perú, sent the specimens from Perú. The drawings are by Paula Walker and Helen Finney, Texas A&M University.

Literature Cited

Bate, C. S. 1888. Report on the Crustacea Macrura collected by the H.M.S. *Challenger* during the years 1873–76. Rep. Sci. Results Voy. H.M.S. *Challenger*. Zool. 24. 942 pp.

Borradaile, L. A. 1917. On Carides from the western Indian Ocean. The Percy Sladen Trust Expedition to the Indian Ocean in 1905, under the leadership of Mr. J. Stanley Gardiner. Trans. Linn. Soc. London, Zool. Series 2, Vol. 17, pp. 397–412.

Ebeling, A. W., R. M. Ibara, R. J. Lavenberg, and F. J. Rohlf. 1970. Ecological groups of deep-sea animals off southern California. Bull. Los Angeles Co. Mus. Nat. Hist. No. 6. 43 pp.

Méndez, M. 1981. Claves de identificación y distribución de los langostinos y camarones (Crustacea: Decapoda) del mar y ríos de la costa del Perú. Bol. Inst. Mar Perú Vol. 5. 170 pp.

Wicksten, M. K. 1978. The species of *Plesionika* from California and western México (Natantia; Pandalidae). Bull. So. Calif. Acad. Sci. 77(2):84–87.

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Research Notes

The First Record of *Boccardia ligerica* (Polychaeta: Spionidae) from Imperial County, California

The genus *Boccardiella* Blake and Kudenov, 1978, was erected for species of *Boccardia* Carazzi, 1893, having branchiae from setiger 2, and both a superior dorsal fascicle of capillary setae and a single kind of modified spine on setiger 5. The six described species of *Boccardiella* are listed by Blake and Kudenov (1978: 264), and a seventh is reported from Japan as *Boccardiella* sp. (=*redeki sensu* Okuda, 1937; see Blake and Woodwick 1971:32).

The purpose of this paper is to report the first record of *Boccardiella ligerica* Ferroniere, from Imperial County, California, where it inhabits freshwater rivers, and to confirm its presence in the coastal marine fauna of southern California (previously queried by Light 1977:68; 1978:145). The systematic importance of the occipital cirrus of polydorid spionids is also briefly discussed. All materials on which this paper is based are deposited in the Allan Hancock Foundation, University of Southern California, Los Angeles, California.

Boccardiella Blake and Kudenov
Boccardiella ligerica (Ferronière)

Boccardia ligerica Ferronière, 1898:109, pl. 6, fig. a–i; Blake and Woodwick 1971: 32, fig. 1 [synonymy]; Light 1977:67 [synonymy]; 1978:144 [synonymy].
Polydora redeki Horst, 1920:111. *Fide* Blake and Woodwick 1971:32.
Not ?*Boccardia redeki* Hartman, 1941:304, pl. 48, figs. 44–45; 1969:97, figs. 1–3.
Boccardia uncata: Hartman, 1941:304 [in part]; 1969:97, figs. 1–5 [in part]; *not* Berkeley, 1927. *Fide* Light 1978:144.
Boccardia nr. *uncata:* Hartman 1954:9; *not* Berkeley, 1927. *Fide* Light 1978:144.
Polydora uncata: Filice 1958:170, 190; *not Boccardia uncata* Berkeley, 1927. *Fide* Light 1978:144.

Material examined.—CALIFORNIA, Imperial County, Westmoreland, New River; Outlet, Alamo River, 19–20 June 1979, coll. J. G. Setmire (15 specimens); San Francisco Bay, San Pablo Channel, several specimens identified as *Boccardia* nr. *uncata* by Hartman, 1954 (AHF N10173–75); Newport Bay, shelly sand at entrance to inner yacht harbor, 10 December 1935, coll. O. Hartman (AHF N1442, includes one specimen identified as *Boccardia uncata* by Hartman 1941); ARGENTINA, Mar Chiquita, Canal No. 7, with *Mercierella enigmatica,* coll. J. Orensanz, identified by J. A. Blake (20 specimens).

Remarks.—Specimens of *B. ligerica* from Imperial County agree with previous descriptions, except that they have an *occipital cirrus. Boccardiella ligerica* was originally described as lacking such a structure. The presence or absence of an occipital cirrus in polydorid spionids is widely considered to a specific criterion (Light 1978). However, Rice and Simon (1980) found that 22.2% of a population of *Polydora ligni* from Fort DeSoto, Florida, lacked an occipital cirrus, 76.7% had a single cirrus, and 1.1% had 2 cirri. Considerable variability also existed in the number of eyes, caruncle size, morphology of the major spines of setiger 5, and in the size and shape of the pygidium of *P. ligni*. *Boccardiella ligerica* from Imperial County exhibits little, if any, morphological variations in other primary characters. It is suggested, therefore, that the presence of an occipital cirrus is of minor systematic importance in eurytopic polydorids such as *B. ligerica* (Kudenov 1982). It seems reasonable to consider the divergent morphology of *B. ligerica* from Imperial County to be the result of geographic isolation coupled with founder effects (Rice and Simon 1980).

This is the first report of *B. ligerica* from Imperial County, where it inhabits freshwater rivers. This species has previously been reported from San Francisco Bay and freshwater habitats in San Joaquin County (Light 1977:67; 1978:144). This species is present, in fact, as part of the marine fauna of southern California, although it was previously identified as *Boccardia uncata* by Hartman (1941:301 in part) and later synonymized with *Boccardia hamata* by Blake (1966). The presence of *Boccardiella* (*Boccardia*) *ligerica* in southern California was originally questioned by Blake and Woodwick (1971:32) and Light (1977:68; 1978:144). The former authors suggested that all previous records of *Boccardia uncata* most probably were referable to *Boccardia hamata*. An examination of Hartman's original material generally confirms their suggestion, although it did reveal the presence of a single specimen of *B. ligerica* included in a sample of *B. hamata* from Newport Bay (AHF N1442).

Acknowledgments

I am grateful to J. A. Blake, Battelle Laboratories, Boston, Massachusetts, for commenting on this paper and for depositing specimens of *B. ligerica* in the Allan Hancock Foundation, and to D. J. Reish, California State University, Long Beach, California, for critically reading this paper.

Literature Cited

Berkeley, E. 1927. Polychaetous annelids from the Nanaimo district. 3. Leodocidae to Spionidae. Contrib. Canad. Biol. n.s., 3(17):407–422.

Blake, J. A. 1966. On *Boccardia hamata* (Webster), new combination (Polychaeta: Spionidae). Bull. So. Calif. Acad. Sci., 65:176–184.

———, and J. D. Kudenov. 1978. The Spionidae (Polychaeta) from southeastern Australia and adjacent areas with a revision of the genera. Mem. Nat. Mus. Vic., 39:171–280.

———, and K. H. Woodwick. 1971. A review of the genus *Boccardia* Carazzi (Polychaeta: Spionidae) with descriptions of two new species. Bull. So. Calif. Acad. Sci., 70:31–42.

Ferronière, G. 1898. Contribution à l'étude de la faune de la Loire-inférieure (Polygordiens, Spionidiens, Nemertien). Bull. Soc. Sci. Nat. l'Ouest France 8:101–115.

Filice, F. P. 1958. Invertebrates of the estuarine portion of the San Francisco Bay. Wasmann J. Biol., 16:159–211.

Hartman, O. 1941. Some contributions to the biology and life history of Spionidae from California. Allan Hancock Pacif. Exp., 7:289–324.

———. 1954. The marine annelids of San Francisco Bay and its environs, California. Allan Hancock Fdn. Publ. Occ. Pap., 15:1–20.

———. 1969. Atlas of the Sedentariate Polychaetous Annelids from California. Allan Hancock Fdn., Univ. So. Calif., Los Angeles. 812 pp.

Horst, R. 1920. Polychaeta anneliden uit het Alkmaarder Meer door Dr. R. Horst. Zool. Meded. Leiden 5:110–111.

Kudenov, J. D. 1982. Redescripton of the major spines of *Polydora ligni* Webster (Polychaeta: Spionidae). Proc. Biol. Soc. Wash., 95:571–574.

Light, W. J. 1977. Spionidae (Annelida: Polychaeta) from San Francisco Bay California: A revised list with nomenclatural changes, new records and comments on related species from the northeastern Pacific ocean. Proc. Biol. Soc. Wash., 90:66–88.

———. 1978. Spionidae Polychaeta Annelida. Invertebrates of the San Francisco Bay Estuary System. The Boxwood Press, Pacific Grove, California. 211 pp.

Rice, S. A. and J. L. Simon. 1980. Intraspecific variation in the pollution indicator polychaete *Polydora ligni* (Spionidae). Ophelia 19:79–115.

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Sebastodes atrorubens Gilbert, 1898, a Junior Synonym of *Sebastes atrovirens* (Jordan and Gilbert, 1880), with Notes on Individual Variation in the Species

In a paper on the 'sebastoid fishes' from the coast of California, Jordan and Gilbert (1880) described seven new species and discussed generic relationships; two genera, *Sebastodes* and *Sebastichthys,* were recognized for the then known 20 species of Californian rockfishes. In their paper, *Sebastichthys atrovirens* was described as new and its similarity to *Sebastichthys rastrelliger* (also described as new) noted: "Externally it [*atrovirens*] resembles *S. rastrelliger* most, but it may be known at once from the latter species by the long gill rakers and narrow pectorals." In reference to coloration, it was stated that *atrovirens* was "usually olive-green, marbled with darker; belly pale yellowish green; fins olivaceous. Sometimes this species is quite dark, but it never shows red tints either on body or fins." Eighteen years later in Jordan and Evermann's "The Fishes of North and Middle America" (1898, Part 2, p. 1796), the description of *Sebastodes atrorubens* appeared and was attributed to Charles Gilbert. It was noted that *atrorubens* was "Most nearly related to *S. atrovirens* . . . . It differs most conspicuously in its red color, strong protruding lower jaw, and very long slender gill rakers." The species was known from a single example, the type, a San Francisco market specimen, "probably from Monterey." The type-locality for *S. atrovirens* has also been intimated as Monterey.

In the most recent faunal list of California fishes, Hubbs, Follett, and Dempster (1979) included *S. atrorubens* as one of 62 species comprising the genus *Sebastes* known for the state. Besides the type of *atrorubens,* only one other specimen has been reported on, by Carl Hubbs (1921); it "was secured by the writer from a Chinese fisherman, who caught it near the southern end of Monterey Bay . . . ." Jordan, Evermann, and Clark (1930) included *atrorubens* in their "Check List," placing it in the genus *Zalopyr*; 16 genera were recognized for the rockfishes at this time. Phillips (1957), placing all Californian rockfishes in the genus *Sebastodes,* listed *atrorubens* as a synonym of *atrovirens* but failed to comment on or justify his action. Since a certain amount of confusion surrounds the relationship and validity of these two nominal species, it was felt that a report on their status was warranted (see Bailey et al. 1970 and Robins et al. 1980).

Coloration was noted for 358 freshly speared or caught (hook-and-line) specimens from the central coast of California (Monterey Bay to San Simeon). Five color variants or morphs were distinguished to note chromatic variation: tan, brown (=kelp brown), green, black (=black-brown), and red (=brick red) (Table 1). Meristic data were taken from approximately 120 of these specimens (Table 2).

Of the three characters emphasized as being significant in Gilbert's description of *atrorubens,* none was found to fall outside the range of normal variation for *S. atrovirens.* "Strong protruding lower jaw" and "very long slender gill rakers," are both character states consistent with the concept of *S. atrovirens.* "Red color," herein considered a low frequency morph, accounted for eight percent of the *S. atrovirens* examined (Table 1). Furthermore, all counts, measurements, and mor-

Table 1. Variation in coloration for 358 *Sebastes atrovirens.*

Color morph	Number	Percentage
Tan	49	14
Brown	168	47
Green	77	22
Black	34	09
Red	30	08

Table 2. Meristic characters for *Sebastes atrovirens.*

	Dorsal fin rays				Anal fin rays		
Count	12	13	14	15	6	7	8
Frequency	1	14	94*	12	8	112*	2

Pectoral fin rays

	Unbranched				Total		
	6	7	8	9	16	17	18
Left	—	19	102*	2	12	110*	1
Right	1	18	99*	5	9	110*	4
Σ	1	37	201	7	21	220	5

Gill rakers

	Upper limb			Lower limb				
	9	10	11	21	22	23	24	25
Left	42	71*	1	2	20*	52	35	5
Right	50	61	1	1	19	55	31	6
Σ	92	132	2	3	39	107	66	11

Total rakers

	30	31	32	33	34	35	36
Left	1	13	29*	39	27	4	1
Right	—	12	38	32	25	5	—
Σ	1	25	67	71	52	9	1

Lateral line pores (Left)

40	41	42	43	44	45	46	47	48
1	2	9	7	6*	1	1	0	1

* Counts from holotype of *Sebastodes atrorubens.*

phological features from the type of *S. atrorubens* (CAS-SU 1873) are typical of *S. atrovirens.*

In conclusion, I find no justification for recognizing *S. atrorubens* as a distinct and valid species. Therefore, *Sebastodes atrorubens* Gilbert *in* Jordan and Evermann 1898, is treated as a junior subjective synonym of *Sebastichthys atrovirens* Jordan and Gilbert, 1880. *Sebastes atrovirens* (Jordan and Gilbert) is the binomen in current usage and kelp rockfish, the accepted vernacular.

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helped with the analysis of material and discussed various aspects of the study. Reeve M. Bailey (University of Michigan) and Donald J. Stewart (Field Museum of Natural History) checked ther respective collections for the Hubbs 1921 specimen of *Sebastodes atrorubens.* William N. Eschmeyer (California Academy of Sciences) made the type of *Sebastodes atrorubens* available for examination.

Literature Cited

Bailey, R. M., J. E. Fitch, E. S. Herald, E. A. Lachner, C. C. Lindsey, C. R. Robins, and W. B. Scott. 1970. A list of common and scientific names of fishes from the United States and Canada (Third Ed.). Am. Fish. Soc. Spec. Publ. No. 6. 150 pp.

Hubbs, C. L. 1921. Notes on Sebastodes. Copeia. 93:27–28.

———, W. I. Follett, and L. J. Dempster. 1979. List of the fishes of California. Occas. Pap. Calif. Acad. Sci., No. 133. 51 pp.

Jordan, D. S., and B. W. Evermann. 1898. The fishes of North and Middle America. Bull. U.S. Nat. Mus. No. 47. Pt. 2. i–xxx, 1241–2183.

———, ———, and H. W. Clark. 1930. Check list of the fishes and fishlike vertebrates of North and Middle America north of the northwestern boundary of Venezuela and Colombia. Rept. U.S. Comm. Fisheries (1928). 670 pp.

———, and C. H. Gilbert. 1880. Description of seven new species of sebastoid fishes, from the coast of California. Proc. U.S. Nat. Mus. 3:287–298.

Phillips, J. B. 1957. A review of the rockfishes of California (Family Scorpaenidae). Calif. Dept. Fish and Game, Fish Bull. 104:1–158.

Robins, C. R., R. M. Bailey, C. E. Bond, J. R. Brooker, E. A. Lachner, R. N. Lea, and W. B. Scott. 1980. A list of common and scientific names of fishes from the United States and Canada (Fourth Ed.) Am. Fish. Soc. Spec. Publ. No. 12. 174 pp.

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Temporal Feeding Patterns and Interspecific Aggression of Anna's and Allen's Hummingbirds

The breeding distributions of Anna's hummingbird (*Calypte anna*) and Allen's hummingbird (*Selasphorus sasin*) overlap along coastal California from San Francisco Bay south to Ventura County (Grinnell and Miller 1944). Several studies have examined ecological relationships of these two species; differences in habitat selection were reported (Pitelka 1951; Legg and Pitelka 1956; Yeaton and Laughrin 1976). Resource use by hummingbirds also may be related to factors such as time of day (Wheeler 1980) and interspecific aggression (Stiles and Wolf 1970). The purpose of this study was to compare temporal feeding patterns and interspecific aggression of Anna's and Allen's hummingbirds.

The study was conducted on 20 April and 4, 11, and 18 May 1974 at a hummingbird feeder located 5 km southwest of Napa, Napa County, California. The

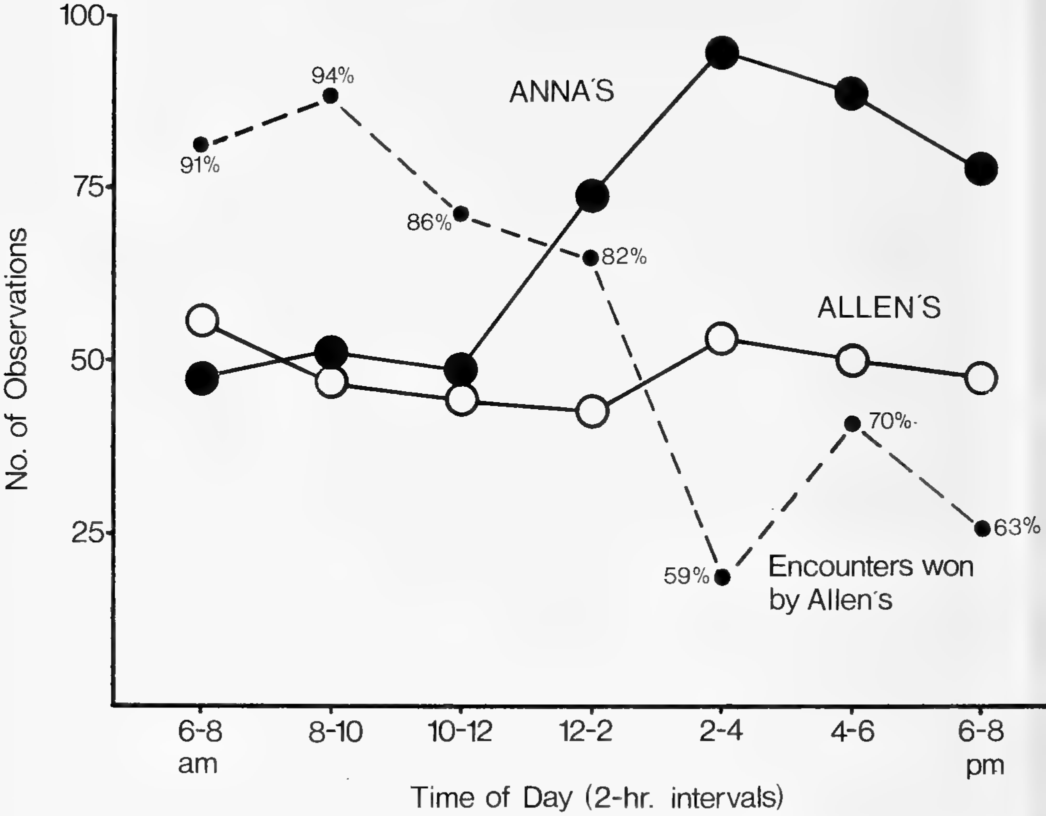

Fig. 1. Solid lines indicate number of observations per two-hour interval of Anna's and Allen's hummingbirds at a feeder near Napa, California. Superimposed on this graph, the dashed line shows the percentage of aggressive encounters per two-hour interval that were won by Allen's hummingbirds.

feeder had been in place for the preceding five years and was kept filled with 30% sucrose solution. At least 10 individual hummingbirds, 5 Anna's and 5 Allen's, used the feeder regularly during the study. Natural nectar sources were abundant in the vicinity, and each hummingbird seemed to include the feeder as part of a "trapline" of flowers. Individal hummingbirds rarely attempted to exclude other birds from the feeder for more than a few minutes before departing.

From 0600 to 2000 (PDT) each day, all feeding visits by hummingbirds to the feeder were recorded by species and then summed into two-hour intervals; data from the four days were averaged. Interspecific aggressive encounters were noted and a "win" assigned to the species that ended the encounter as pursuer. The weather was clear and sunny throughout the study.

I recorded 1906 visits by Anna's hummingbirds and 1367 visits by Allen's hummingbirds. Use by Allen's was relatively constant through the day, averaging just under 50 visits per two-hour interval (Fig. 1). Use by Anna's, however, increased as the day progressed, from about 50 visits per two-hour interval in the morning to almost twice that in the afternoon. Patterns of visitation by the two species were consistent over the four days. Wheeler (1980) found a contrasting pattern for Anna's hummingbirds at a feeder in the Sierra Nevada, where the birds fed primarily in the morning and frequency of use decreased after 0930. The Sierra Nevada site was outside the range of Allen's hummingbird.

Allen's hummingbird was the behaviorally dominant species during the study, winning 79% of the 214 aggressive encounters observed between the two species. The degree of dominance, however, was not constant throughout the day; the percentage of encounters won by Allen's during each two-hour interval was highest in the morning and lowest in the afternoon (Fig. 1). The average number of encounters per two-hour interval was higher before 1200 (37.0) than after 1200 (25.8), indicating that the decrease in dominance of Allen's was not caused by the "swamping" effect of increased feeder visitation by Anna's during the afternoon. Data from other studies on aggressive encounters between the two species are scarce and inconsistent. Stiles (1973) reported that Anna's hummingbirds were dominant in 37 of 52 (71%) encounters with Allen's in the Santa Monica Mountains. Pitelka (1951) reported three instances of displacement of Anna's from territories by Allen's in Alameda County. Trousdale (1954) indicated that Allen's typically were dominant to Anna's at another location in Alameda County.

Both the temporal feeding activity of Anna's hummingbird and dominance relationships with Allen's hummingbird seem to vary greatly with geographic location and associated ecological conditions. Different feeding patterns for Anna's at the Sierra Nevada and Napa County sites may have resulted from different patterns of nectar availability from natural sources near each feeder. Another possible cause of different feeding patterns was interspecific aggression by Allen's present at the Napa County site; Anna's were most active in the afternoon, when the dominance by Allen's was weakest and access to the feeder for Anna's presumably was increased. A relationship between feeder defense and accessibility by subordinate species was reported for three hummingbird species in Arizona (Pimm 1978); when the dominant species reduced time spent defending the feeder, feeder visitation by two subordinate species increased.

Literature Cited

Grinnell, J., and A. H. Miller. 1944. The distribution of the birds of California. Pac. Coast Avifauna, 27:1–608.

Legg, K., and F. A. Pitelka. 1956. Ecologic overlap of Allen and Anna hummingbirds nesting at Santa Cruz, California. Condor, 58:393–405.

Pimm, S. L. 1978. An experimental approach to the effects of predictability on community structure. Am. Zool., 18:797–808.

Pitelka, F. A. 1951. Ecologic overlap and interspecific strife in breeding populations of Anna and Allen hummingbirds. Ecology, 32:641–661.

Stiles, F. G. 1973. Food supply and the annual cycle of the Anna hummingbird. Univ. Calif. Publ. Zool., 97:1–109.

———, and L. L. Wolf. 1970. Hummingbird territoriality at a tropical flowering tree. Auk, 87:467–491.

Trousdale, B. 1954. Copulation of Anna hummingbirds. Condor, 56:110.

Wheeler, T. G. 1980. Experiments in feeding behavior of the Anna hummingbird. Wilson Bull., 92: 53–62.

Yeaton, R. I., and L. Laughrin. 1976. Fall resource division in Santa Cruz Island hummingbirds. Wilson Bull., 88:272–279.

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Brattstrom, B. H. 1969. The Condor in California. Pp. 369–382 *in* Vertebrates of California. (S. E. Payne, ed.), Univ. California Press, xii + 635 pp.

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COVER: The brown pelican, *Pelecanus occidentalis*, in Florida. This photograph was taken by the outstanding authority on pelicans, Dr. Ralph W. Schreiber, Curator of Ornithology, Natural History Museum of Los Angeles County.