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TWO NEW SPECIES OF FLABELLINIDAE (OPISTHOBRANCHIA: AEOLIDACEA) FROM BAJA CALIFORNIA

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ABSTRACT: Two new species of *Flabellina* are described from Baja California. *Flabellina bertschi* sp. nov. is widely distributed within the Gulf of California from Puerto Peñasco to the area north of La Paz. *Flabellina marcusorum* sp. nov. has been found on the Pacific and Gulf coasts of Baja California, as well as the coast of Brazil. This species was originally recorded from Brazil as *Coryphellina rubrolineata* O'Donoghue, 1929. However, when compared with Indo-Pacific material of *F. rubrolineata,* the presently described species is consistently distinct in its internal and external morphology. A preliminary phylogeny of the Flabellinidae supports the maintenance of *Flabellina* as a single, large, diverse genus.

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INTRODUCTION

The opisthobranch gastropod fauna of the Pacific and Gulf of California coasts of México has been extensively studied for much of the twentieth century (e.g., MacFarland 1924; Baker and Hanna 1927; Marcus and Marcus 1967; Keen 1971; Bertsch and Ferreira 1974; Bertsch 1977, 1978a, b, c; Gosliner and Behrens 1985). Although approximately 150 different species have been recorded from the region, many new records and taxa remain to be added to the fauna.

Seven species of the aeolidacean family Flabellinidae have been recorded from the Pacific coast of Baja California and the Gulf of California. The flabellinid nudibranch *Flabellina rubrolineata* (O'Donoghue, 1929), originally described from the Red Sea, has subsequently been reported from Japan (Baba 1949) and Australia (Willan and Coleman 1984). Marcus and Marcus (1961, 1970) recorded specimens of this species (as *Coryphellina* O'Donoghue, 1929) from the coast of Brazil and from Sonora, México. Recent investigations within the Gulf of California and from the Pacific coast of Baja California have yielded specimens of *Flabellina* Voigt, 1834, that are identical in their external morphology to material described by the Marcuses from México and Brazil. These animals are consistently different from Indo-Pacific specimens of *F. rubrolineata* (O'Donoghue) and are here described as a new species.

Other investigations into the opisthobranch fauna of the Gulf of California have yielded specimens of a second undescribed species of flabellinid, which is also described in this paper. This species has been collected from several different localities within the Gulf of California. Its anatomy is described and compared to other closely allied species.

DESCRIPTIONS

Flabellina bertschi sp. nov.

(Figs. 1A, 2, 3)

Flabellina telja Er. Marcus and Ev. Marcus, 1967:223, in part, specimen from Puerto Peñasco, collected by Mary Anne Hill, 18 June 1966.

TYPE MATERIAL.—Holotype, California Academy of Sciences, San Francisco, CASIZ 066760, in tide pool, among hydroids on *Sargassum* sp., Puerto Peñasco, Sonora, México, 23 July 1975, Hans Bertsch and P. Cook. Five paratypes, CASIZ 066761, same date and locality as holotype. One dissected paratype, CASIZ 066762, same date and locality as holotype. One paratype, CASIZ 066763, collected from hydroids on vertical wall, San Diego Reef (25°12′N, 110°42′W), s.e. of Isla San Diego, Gulf of California, México, 13 m depth, 24 July 1985, T. M. Gosliner.

DISTRIBUTION.—*Flabellina bertschi* is known within the Gulf of California from Puerto Peñasco, south to Isla San Diego.

ETYMOLOGY.—This species is named for our friend and colleague, Hans Bertsch, who first noted that this appears to be an undescribed species. Hans has contributed considerably to our knowledge of the Panamic molluscan fauna.

DESCRIPTION.—*External morphology*. The living animals (Fig. 1A) are thin and elongate (8–12 mm long). The body color is translucent white with an overlaying opaque white pigment on the distal two-thirds of the rhinophores and oral tentacles. The opaque white pigment covers most of the dorsal surface of the animal, except for an area of translucence immediately posterior to the rhinophores. Each translucent ceras contains a central red to red-brown digestive diverticulum and terminates in a large, opaque white cnidosac.

The rhinophores are smooth, without ornamentation, and are up to 2.5 mm in length. The oral tentacles are approximately as long as the rhinophores. The cylindrical cerata are of uniform diameter throughout most of their length. They (Fig. 2A) are arranged in discrete clusters that are inserted on slightly pedunculate mounds of notal tissue. The anteriormost cluster on either side is most pronounced in its elevation from the notum. The left and right anterior branches of the digestive tract each contain three or four rows of cerata with 1–4 cerata per row. The posterior digestive branch contains up to six clusters of cerata, each containing 1–3 rows of cerata. Each row is composed of 1–3 cerata. The anteriormost cluster contains more rows of cerata, with more cerata per row. The density of both rows per cluster and cerata per row decreases posteriorly.

The genital apertures are located on the right side of the body ventral to the first and second or second and third ceratal rows. The pleuroproctic anus is situated within the interhepatic space, below the notum, immediately anterior to the anteriormost cerata of the right digestive branch. The nephroproct is located immediately anterodorsal to the anus. The anterior border of the foot (Fig. 2B) bears elongate foot corners that are held perpendicular to the longitudinal body axis, when the animal is actively crawling. The foot narrows posteriorly and terminates in an acutely pointed tail.

Buccal cavity. The thin, ovoid jaws (Figs. 2C, 3A) occupy much of the muscular buccal mass. They bear several rows of minute denticles on their elongate masticatory margin. From the anterior end of the buccal mass, a pair of elongate, highly digitate oral glands extends posteriorly within the laterally elevated tissue of the notum. The posterior limit of the glands is at the anteriormost cluster of cerata of the posterior digestive branches. A pair of elongate strap-like salivary glands joins the posterior end of the buccal mass near its junction with the esophagus. The triseriate radula, also contained within the buccal mass, has a formula of 24–31 × 1.1.1., in five specimens examined. The rachidian teeth (Fig. 3C, D) bear 6–8 elongate denticles on either side of the elongate central cusp. The central cusp is depressed ventrally below the level of the adjacent denticles. The teeth are broadly curved and deeply incised posteriorly. The posterior limbs of each tooth terminate in a posteriorly extended tubercle. The lateral teeth (Fig. 3B) are broadly triangular and bear an elongate primary denticle. The inner masticatory margin bears 9–11 irregular denticles.

Reproductive system. The arrangement of organs (Fig. 2D) is androdiaulic. The narrow preampullary duct expands into the ampulla and divides into the oviduct and vas deferens distally. The oviduct immediately expands into the

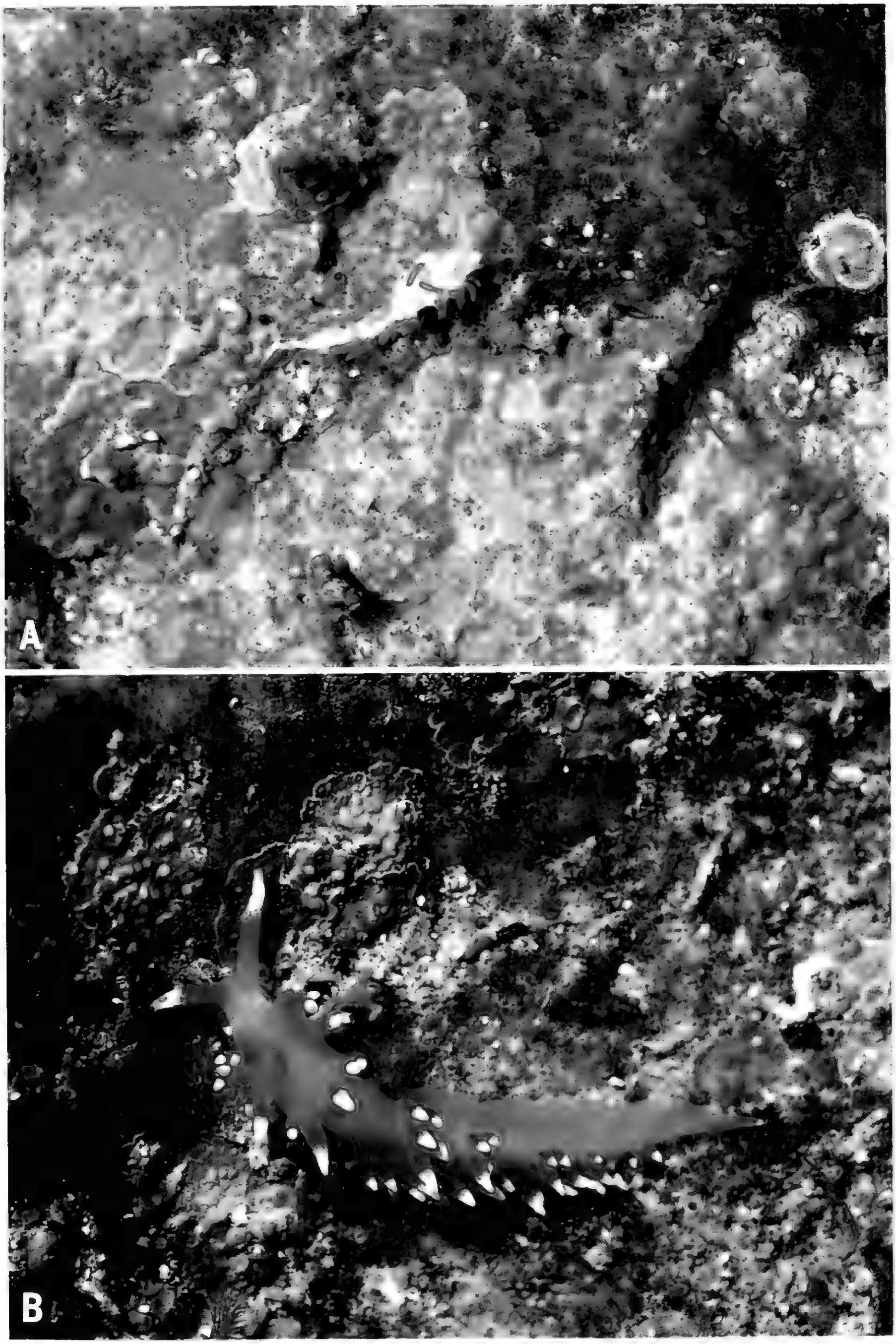

FIGURE 1. Living animals. A. *Flabellina bertschi* sp. nov., photograph of holotype. B. *Flabellina marcusorum* sp. nov., photograph of a paratype specimen from San Diego Reef, Baja California Sur, México.

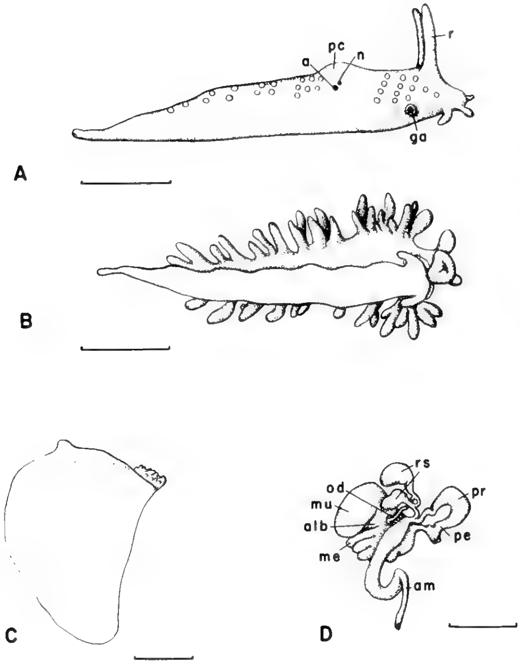

FIGURE 2. *Flabellina bertschi* sp. nov. A. Lateral view of holotype showing arrangement of cerata, a = anus; ga = genital aperture; n = nephroproct; pc = pericardial hump; r = rhinophore, scale = 1 mm. B. Ventral view of holotype, scale = 1 mm. C. Jaw, scale = 0.2 mm. D. Reproductive system, alb = albumen gland; am = ampulla; me = membrane gland; mu = mucous gland; od = oviduct; pe = penis; pr = prostate; rs = receptaculum seminis, scale = 0.5 mm.

two ovoid lobes of the receptaculum seminis. The oviduct again narrows and enters the albumen gland, situated between the larger membrane and mucous glands. The vas deferens expands into a simply curved prostatic portion that terminates in the indistinct, conical penial papilla, which is devoid of any armature. The nidamental and penial apertures are united into a short common genital atrium. A bursa copulatrix is absent in the three specimens examined.

DISCUSSION.—*Flabellina bertschi* is sympatric with five other species of Flabellinidae: *Flabellina telja* Marcus and Marcus, 1967; *F. stohleri* Bertsch and Ferreira, 1974; *F. iodinea* (Cooper, 1863); and *F. cynara* (Marcus and Marcus, 1967). All possess perfoliate rather than smooth rhinophores. *Flabellina marcusorum* has strongly papillate rhinophores. None of these species has a white body with red cerata.

Flabellina bertschi is similar to two western Atlantic species in its external morphology. *Flabellina dushia* (Marcus and Marcus, 1963) has smooth rhinophores, a whitish body, and orange-brown cerata, but it lacks an area of translucence posterior to the rhinophores, which characterizes all specimens of *F. bertschi* examined in this study. More significantly, the lateral radular teeth of *F. dushia* are thinner with a more acutely pointed cusp. Nothing is known about the reproductive anatomy of *F. dushia*. *Flabellina verta* (Marcus, 1970) also has smooth rhinophores, a whitish body, and brown digestive gland. However, it has opaque white lines on the oral tentacles that join and pass between the rhinophores, which are absent in *F. bertschi*. Its radula has only half as many rows of teeth as *F. bertschi*. Also, the reproductive system of *F. verta* lacks a receptaculum seminis, but has a bursa copulatrix adjacent to the genital atrium. In *F. bertschi*, there is a bilobed receptaculum seminis, but a bursa copulatrix is absent.

The only other described species that are known to possess a bilobed receptaculum seminis but lack a bursa copulatrix are *F. pedata* (Montagu, 1815) (see Schmekel and Portmann 1982: fig. 7.50e) and *F. albomarginata* (Miller, 1971). In *F. pedata* the body color is purple rather than white. In *F. albomarginata* the rhinophores are covered with small tubercles, and an opaque white line is present around the margin of the foot.

Flabellina marcusorum sp. nov.

(Figs. 1B, 4, 5)

Coryphellina rubrolineata O'Donoghue, 1929:798; Marcus and Marcus 1961:224, figs. 1–10 (misidentification); Marcus and Marcus 1970:210, fig. 81 (misidentification).

Flabellina telja Marcus and Marcus, 1967:223; Ferreira and Bertsch 1972:414, fig. 1 (misidentification); Kerstitch 1989: 66, fig. 154 (misidentification).

TYPE MATERIAL.—Holotype, California Academy of Sciences, San Francisco, CASIZ 066151, San Diego Reef (25°12′N, 110°42′W), s.e. of Isla San Diego, Gulf of California, México, 13 m depth, 24 July 1985, T. M. Gosliner. Paratypes, CASIZ 066152, six specimens, same date and locality as holotype. Paratypes, CASIZ 066153, two specimens, one dissected, Los Islotes (24°36′N, 110°24′W), Gulf of California, México, 10 m depth, 20 May 1985, Lynne Dunne.

OTHER MATERIAL.—Fifteen specimens, CASIZ 066154, Sayulita (20°52′N, 105°29′W), Nayarit, México, intertidal, 24 Jan. 1975, Gary McDonald. Three specimens, CASIZ 066155, two dissected, São Sebastião, Brazil, Eveline Marcus. One specimen, Arroyo San Carlos, Isla Cedros, Baja California, México, 4 m depth, 31 Dec. 1985, Hans Bertsch.

DISTRIBUTION.—*Flabellina marcusorum* has been collected from the Atlantic coast of Brazil

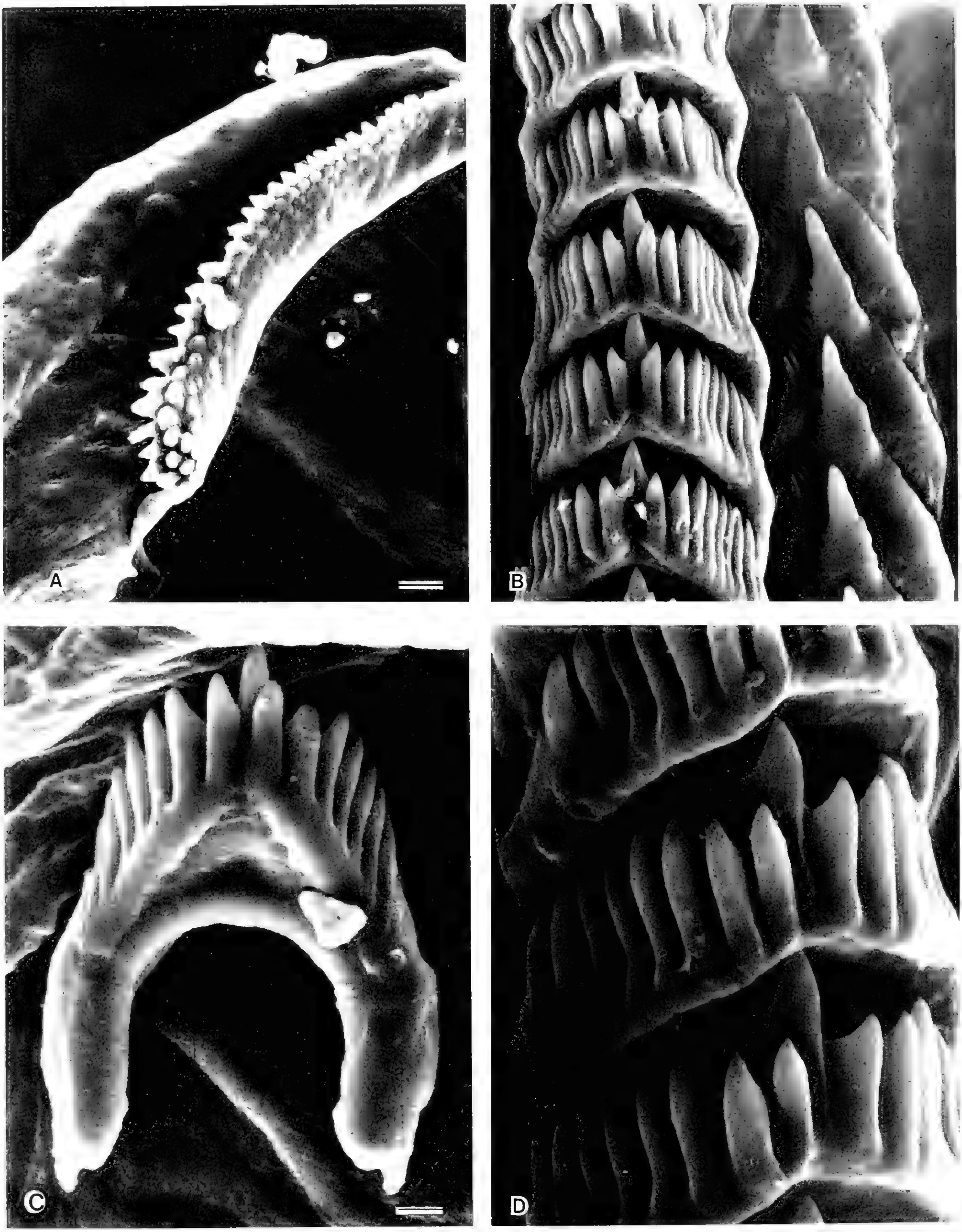

FIGURE 3. *Flabellina bertschi* sp. nov. Scanning electron micrographs of radula of a specimen from Puerto Peñasco. A. Masticatory border of jaw, scale = 10 μm. B. Rachidian and lateral teeth, scale = 4 μm. C, D. Rachidian teeth, scale = 4 μm.

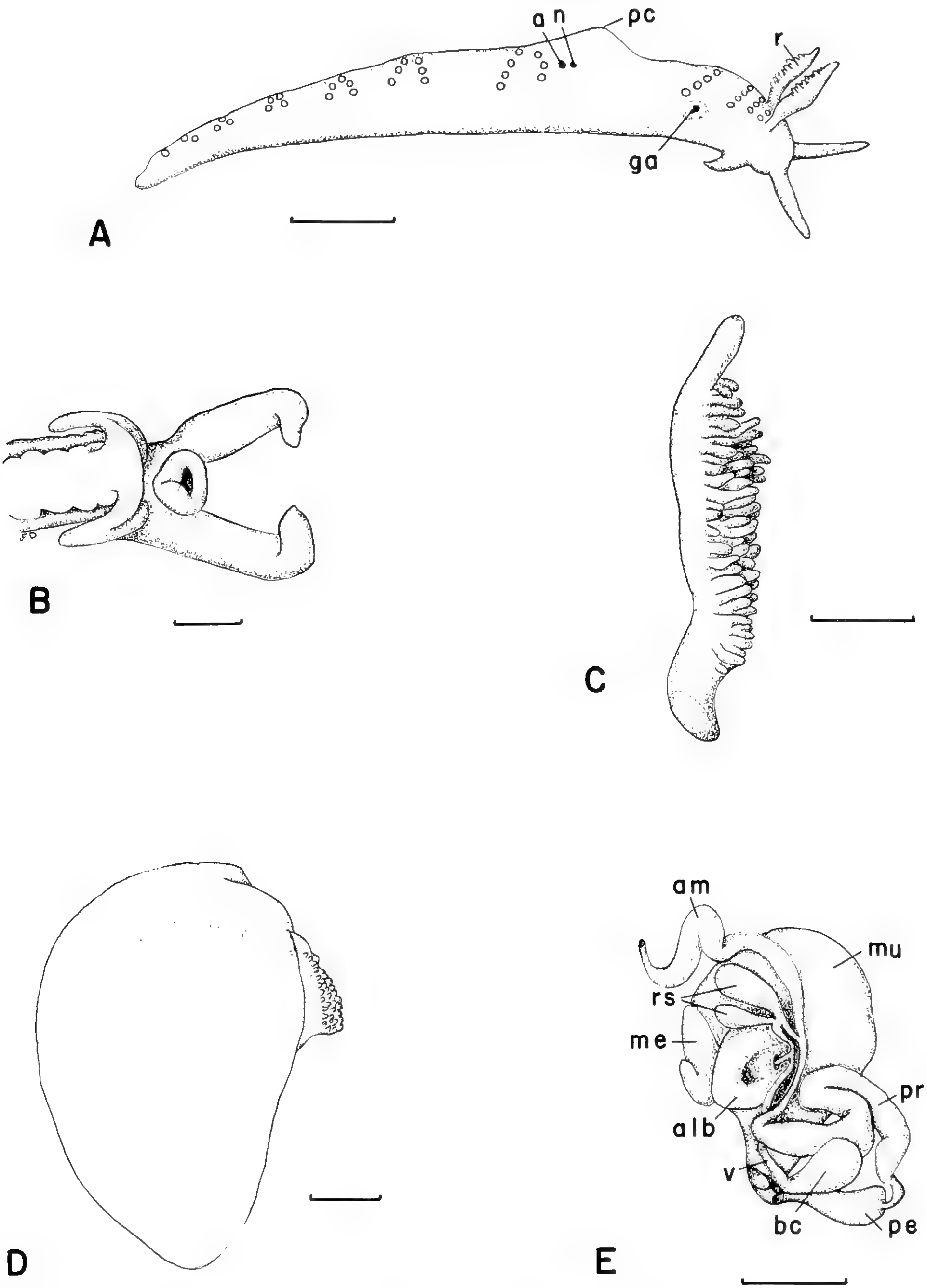

FIGURE 4. *Flabellina marcusorum* sp. nov. A. Lateral view, a = anus; ga = genital aperture; n = nephroproct; pc = pericardial hump; r = rhinophore, scale = 2 mm. B. Ventral view, scale = 1 mm. C. Rhinophore, scale = 0.5 mm. D. Jaw, scale = 0.2 mm. E. Reproductive system, alb = albumen gland; am = ampulla; bc = bursa copulatrix; me = membrane gland; mu = mucous gland; pe = penis; pr = prostate; rs = receptaculum seminis; v = vagina, scale = 1 mm.

(Marcus and Marcus 1961). On the Pacific coast of México, it has been found from Isla Cedros south to Sayulita, Nayarit (present study). Within the Gulf of California, it is known from San Agustín, Sonora, south to Los Islotes, north of La Paz, Baja California Sur.

ETYMOLOGY.—This species is named for Ernst Marcus and Eveline du Bois Reymond Marcus, who first recorded this species (as *Coryphellina rubrolineata*) from Brazil and the Gulf of California.

DESCRIPTION.—*External morphology.* The living animals (Fig. 1B) are 7–30 mm in length. The general body color is translucent rose pink. The oral tentacles, foot corners, rhinophores are rose basally, with purple pigment in their middle, and opaque white present on the apical portion. The oral tentacles have a wide band of purple, while the cerata bear only a narrow ring between the pink and white pigments. The pigment on the apices of the cerata may be yellowish rather than white, in some specimens. The rhinophores bear more purple pigment on their posterior face, where it covers most of the surface of the papillae. The anterior face of the rhinophores bears less purple pigment. The posterior end of the foot is also purple with an opaque white line or spot on its posterodorsal end. The digestive gland within the cerata is the same rose color as the rest of the body.

The rhinophores (Fig. 4C) are elongate (approximately 4 mm in length) and conical. They each bear approximately 100 long papillae on their posterior face. The papillae are approximately 0.5 mm in length and are arranged in somewhat indistinct rows, covering the middle two-thirds of the rhinophores. The oral tentacles are thin and elongate, tapering to a rounded apex. They are longer than the rhinophores.

The cerata are cylindrical and rounded apically immediately distal to the ovoid cnidosac. Within each ceras is a thin core of digestive gland that fills a variable portion of the diameter of the ceras. The cerata are arranged in distinct groups (Fig. 4A). Only the anterior cluster is slightly elevated from the notum. The anterior, precardiac cluster contains 3–5 rows of cerata on either side of the animal, with 2–4 cerata per row. The postcardiac cerata are arranged in 6–8 groups per side of the body. Generally, each group contains a pair of tightly packed rows with 2–4 cerata per row. Only the posteriormost 1–2 rows are unpaired and consist of a single row. The gonopore is situated on the right side of the body, ventral to the third and fourth ceratal rows of the precardiac cluster. The pleuroproctic anus is situated at the posterior end of the interhepatic space, just anterior to the first postcardiac ceratal row. The nephroproct is immediately anterodorsal to the anus.

The foot (Fig. 4B) is grooved anteriorly and possesses elongate, tentacular foot corners. Posteriorly, it tapers gradually to a narrow tail.

Buccal cavity. The buccal mass is short and muscular. Extending from the anteroventral portion of either side of the buccal mass is a large digitate oral gland, which extends into the widened portion of the notum in the region of the precardiac cerata. Within the buccal mass is a pair of large chitinous jaws (Fig. 4D). They are ovoid with an elongate masticatory margin (Fig. 5A). The margin bears several rows of denticles with 20–24 denticles on the outer row. The radular formula is 27–34 × 1.1.1. in six specimens studied. The rachidian teeth (Fig. 5B, C) are simply arched with 5–8 triangular denticles on either side of the elongate central cusp. The central cusp is approximately the same width as the adjacent denticles but is depressed ventrally from their level. The lateral teeth (Fig. 5B, D) are triangular in shape with a broad base extending towards the outer edge. There is a single prominent, acutely pointed apex. On the inner margin of the tooth is a series of 4–12 triangular denticles.

At the posterior limit of the buccal mass, near its junction with the esophagus, is a pair of elongate salivary glands that extend posteriorly on the dorsolateral surface of the stomach.

Reproductive system. The arrangement of reproductive organs is essentially triaulic (Fig. 4E). The ovotestis is a diffuse aggregation of distinct follicles. The female acini are distinct. The narrow preampullary duct widens into an ampulla consisting of two convolutions. The postampullary duct again narrows and passes between the lobes of the albumen and membrane glands. After a short distance it divides into the oviduct and vas deferens. After a short distance the oviduct joins a pair of receptacula seminis. The more proximal receptaculum is the larger of the two. The oviduct again narrows, and a short distance later enters the nidamental glands. At this branching point, a distinct, narrow vaginal duct continues towards the genital apertures. Imme-

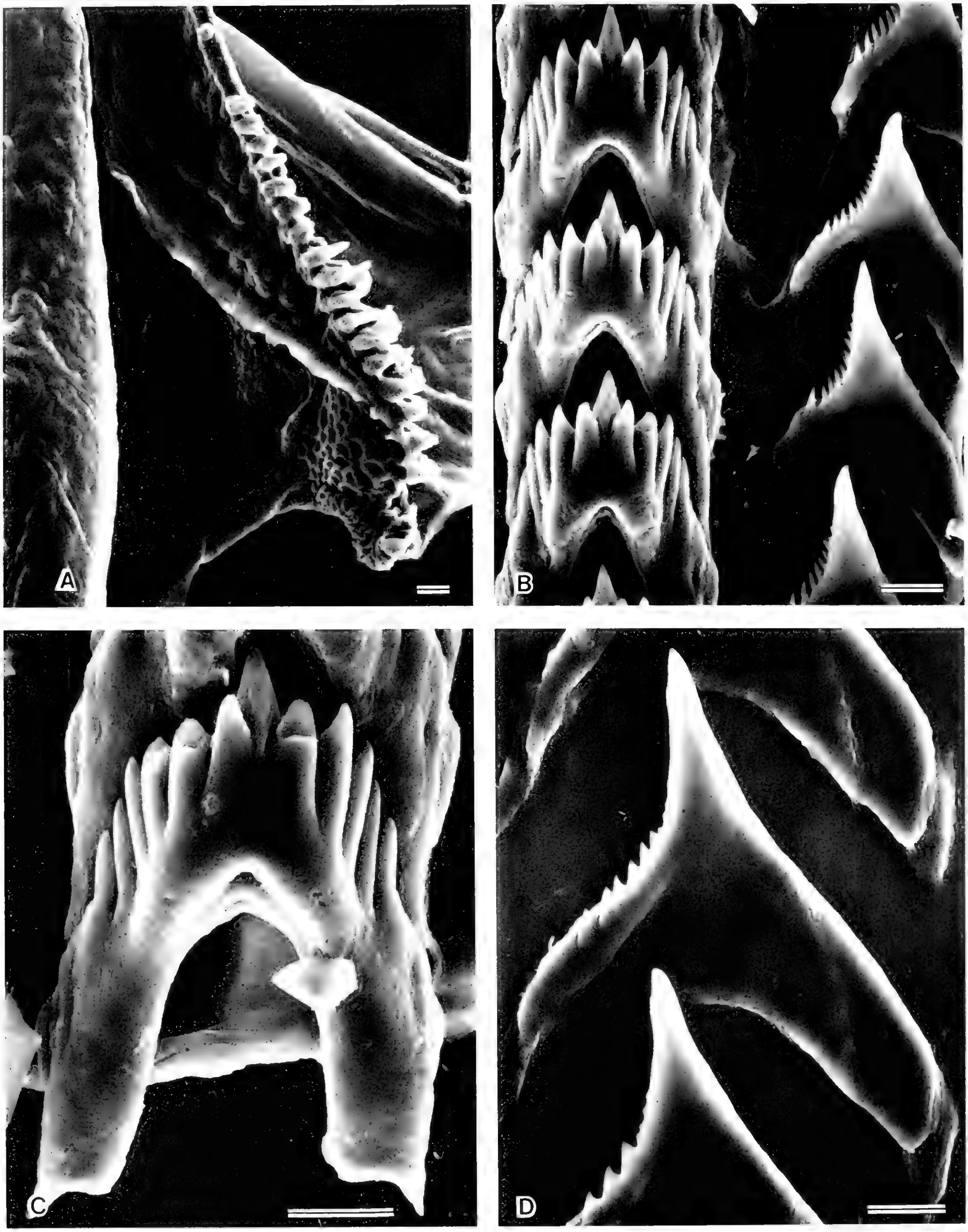

FIGURE 5. *Flabellina marcusorum* sp. nov. Scanning electron micrographs. A. Masticatory border of a specimen from San Diego Reef, Baja California Sur, México. B. Rachidian and lateral teeth of specimen from São Sebastião, Brazil. C. Rachidian tooth of specimen from São Sebastião, Brazil. D. Lateral tooth of specimen from San Diego Reef, Baja California Sur. Scales = 10 μm.

diately prior to emptying into its own genital pore, it joins with a large saccate bursa copulatrix. The bursa is thin walled and short stalked. The nidamental glands comprise the bulk of the reproductive system. The mucous gland is by far the largest portion, while the albumen and membrane glands are smaller. The nidamental glands empty via their own gonopore, ventral to the vaginal and penial apertures. The vas deferens is initially quite narrow and expands into a smooth prostatic portion, which is slightly convoluted. The vas deferens enters the short penial sac at its distal end. The penial papilla is tubular and thin with a slightly flared apex. There is no armature associated with the penial papilla.

DISCUSSION.—*Flabellina marcusorum* was originally described from Brazil (Marcus and Marcus 1961) as *Coryphellina rubrolineata* O'Donoghue, 1929. Marcus and Marcus (1970) also misidentified specimens from the Gulf of California as *C. rubrolineata*. *Flabellina marcusorum* has also been misidentified as *Flabellina telja* Marcus and Marcus, 1967 by Ferreira and Bertsch (1972) and Kerstitch (1989). The latter species differs from *F. marcusorum* in having perfoliate rather than papillate rhinophores, and in several other major details of its external and internal anatomy.

Flabellina marcusorum and *F. rubrolineata* differ in several consistent aspects of their coloration. In *Flabellina rubrolineata* there is a mid-dorsal and a pair of lateral red or purple lines along the length of the animal (O'Donoghue 1929; Baba 1955, pl. 13, fig. 37; Abe 1964, pl. 30, fig. 107; Willan and Coleman 1984, fig. 133; Tan, Pai, and Hsha 1987, fig. 52). These observations are confirmed by examination of specimens of *F. rubrolineata* from Aldabra Atoll and Madang, Papua New Guinea, in this study. Occasionally, the red or purple lines may be interrupted as in the case of the specimen illustrated by Willan and Coleman, but are present in all material observed. In *F. rubrolineata* the rhinophores are opaque white basally with apical purple pigment. The body color is a much deeper rose in *F. marcusorum*, and longitudinal lines are never present on the body. The rhinophores are purplish basally with an opaque white apex, the reverse of the colors in *F. rubrolineata*.

The number of radular rows and denticles on the radular teeth varies considerably in both species (Table 1). However, the shape of the rachidian teeth differs consistently between the two species. In *Flabellina marcusorum* the indentation of the posterior end of the tooth extends deeply, almost to the basal portion of the central denticles (Marcus and Marcus 1961; Fig. 5B, C). In *F. rubrolineata* (Fig. 6A–C), the indentation is rounded and does not extend as far forward, leaving a triangular chitinous area between the indentation and the basal portion of the denticles. The lateral teeth of *F. rubrolineata* (O'Donoghue 1929:fig. 219d; Fig. 6D) bear a series of striations along the middle of their outer edge, which are absent in all specimens of *F. marcusorum* that have been examined.

In their description of *Flabellina marcusorum* from Brazil, Marcus and Marcus (1961, as *Coryphellina rubrolineata*) depicted the reproductive anatomy in detail. Their specimens had a large spherical bursa copulatrix, but no receptaculum seminis. Our examination of Brazilian specimens provided by Eveline Marcus and from material collected from the Pacific coast of México indicates that all specimens do possess a bilobed receptaculum seminis near the branching of the oviduct. In addition, the reproductive system is entirely triaulic in all the material we examined. The only aspect of the reproductive anatomy of *F. rubrolineata* that has been described was the presence of an unarmed penis (O'Donoghue 1929). However, Dr. Kikutaro Baba provided dissection notes of a specimen of *F. rubrolineata* from Japan, and we dissected specimens from Papua New Guinea. Both species possess a triaulic arrangement of organs and two proximally situated receptacula seminis; however, their anatomy differs from that of *F. marcusorum* in two significant regards. The prostate of *F. marcusorum* is more elongate and convoluted than in *F. rubrolineata*. More importantly, the bursa copulatrix is small and sessile in *F. rubrolineata*, while it is well developed and stalked in *F. marcusorum*.

GENERIC DIVISION WITHIN THE FLABELLINIDAE

The genus *Coryphellina*, with *C. rubrolineata* as the type species, was placed in synonymy with *Coryphella* (Miller 1971). More recently Gosliner and Griffiths (1981) considered *Coryphella*, including *Coryphellina*, as a junior synonym of *Flabellina*. This view has been generally adopted

Table 1. Comparative morphology of *Flabellina rubrolineata* and *F. marcusorum.*

	Color	Ceratal arrangement	Radular formula	Denticles per side of rachidian	Receptaculum seminis	Bursa copulatrix	Locality	Reference
F. rubrolineata	3 longitudinal vermillion or crimson mid-dorsal lines	6–8 groups	30–32 × 1.1.1.	6–7	—	—	Red Sea	O'Donoghue 1929
F. rubrolineata	3 longitudinal red lines, cerata with purple bands	5 rows 5 arches	30 × 1.1.1.	7–9	bilobed	—	Japan	Baba 1955, personal communication
F. rubrolineata	3 longitudinal reddish purple lines, body variously colored	3 rows 4 arches	30 × 1.1.1.	6–8	bilobed	minute	Papua, New Guinea	present study
F. marcusorum	body orange, rhinophores & cerata with purple & opaque white	3 rows 7 arches	27 × 1.1.1.	5–8	absent, bilobed in present material	elongate stalk	Brazil	Marcus 1961, present study
F. marcusorum	body pink orange, tentacles, cerata rhinophores with purple rings	11 groups	34 × 1.1.1.	7	—	—	Gulf of California	Marcus and Marcus 1970
F. marcusorum	body pink, oral tentacles, rhinophores & cerata with purple & opaque white	3–5 rows 6–8 double rows	31 × 1.1.1.	6–8	bilobed	elongate stalk	Pacific Mexico, Gulf of California	present study

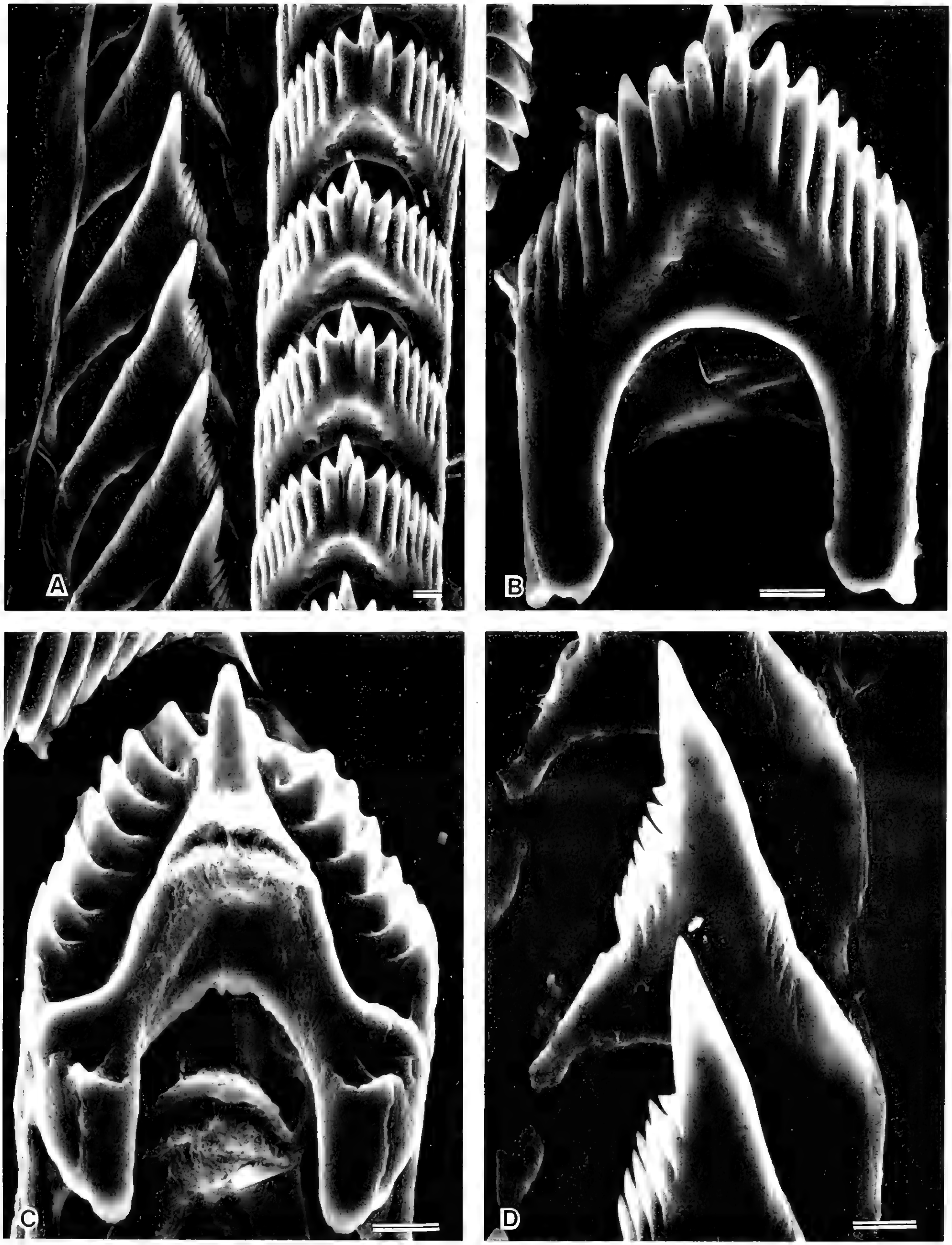

FIGURE 6. *Flabellina rubrolineata* (O'Donoghue, 1929). Scanning electron micrographs of specimen from Madang, Papua New Guinea. A. Dorsal view of half-row of radula. B. Dorsal view of rachidian tooth. C. Ventral view of rachidian tooth. D. Lateral tooth. Scales = 10 μm.

TABLE 2. Morphological diversity in *Flabellina*.

	peduncles	cerata	rhinophores	anus	oral glands	central cusp	receptaculum seminis	bursa copulatrix	foot corners	reproductive system	lateral teeth	number of laterals	rhinophoral papillae
hypothetical ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0
affinis	2	2	1	2	1	2	1	0	1	0	0	1	0
albomarginata	1	1	2	2	1	2	2	1	1	0	0	1	1
alisonae	2	2	3	2	1	1	1	0	1	0	0	1	0
babai	2	2	3	2	1	2	1	1	1	0	0	1	0
bertschi	1	1	0	2	1	2	2	1	1	0	0	1	0
browni	0	1	0	1	0	1	1	0	1	0	0	1	0
capensis	0	1	0	1	0	1	1	0	1	0	0	1	0
cynara	0	1	3	0	0	1	0	0	1	0	2	1	0
dushia	0	1	0	2	9	2	9	9	1	9	0	1	0
engeli	2	2	3	2	1	2	1	0	1	0	0	1	0
falklandica	0	0	0	0	9	1	9	9	1	9	0	1	0
funeka	2	2	1	2	1	2	1	0	1	0	0	1	0
fusca	0	0	1	1	0	1	1	0	1	9	0	1	0
gracilis	1	1	0	1	0	1	1	0	1	0	0	1	0
iodinea	1	2	3	1	0	1	3	0	1	0	2	1	0
islandica	0	0	0	1	0	0	0	0	0	0	0	0	0
lineata	0	1	0	1	0	1	1	0	1	0	0	1	0
marcusorum	1	2	2	2	1	2	2	1	1	1	0	1	2
nobilis	0	0	0	0	0	1	1	0	1	0	0	1	0
ornata	2	2	3	2	1	1	1	0	1	0	0	1	0
pedata	1	1	0	2	1	2	2	1	1	0	0	1	0
pellucida	1	1	0	2	1	2	2	1	1	0	1	1	0
poenicia	1	2	2	2	9	2	9	9	1	0	0	1	1
pricei	1	1	1	1	1	2	9	0	1	0	1	1	0
rubrolineata	1	2	2	2	1	2	2	0	1	1	0	1	2
salmonacea	0	0	0	0	2	0	3	0	0	0	0	1	0
telja	2	2	3	2	1	2	1	0	1	0	0	1	0
trilineata	1	1	1	1	1	1	1	0	1	0	0	1	0
verrucosa	0	0	0	1	0	1	1	0	1	0	0	1	0
verta	0	1	0	2	9	1	0	0	1	0	0	1	0
species 1	1	2	2	2	1	2	2	1	1	1	0	1	2
species 2	1	2	2	2	1	2	2	0	1	1	0	1	2
species 3	2	2	3	2	1	1	1	0	1	0	0	1	0

For all characters 9 = unknown

1. peduncles	0 = absent, 1 = present, 2 = well elevated
2. cerata	0 = congested, 1 = separate, 2 = single groups
3. rhinophores	0 = simple, 1 = annulate, 2 = papillate, 3 = perfoliate
4. anus	0 = posterior, 1 = middle of cluster, 2 = interhepatic space
5. oral glands	0 = absent, 1 = ramified, dorsal, 2 = simple, ventral
6. central cusp	0 = large, 1 = small, 2 = depressed
7. receptaculum seminis	0 = serial, 1 = semiserial, 2 = bilobed, 3 = multilobed
8. bursa copulatrix	0 = present, 1 = absent
9. foot corners	0 = rounded, 1 = tentacular
10. reproductive system	0 = diaulic, 1 = triaulic
11. lateral teeth	0 = denticulate, 1 = smooth, 2 = denticulate on outer edge
12. number of laterals	0 = 2–3, 1 = 1
13. rhinophoral papillae	0 = absent, 1 = short, 2 = elongate

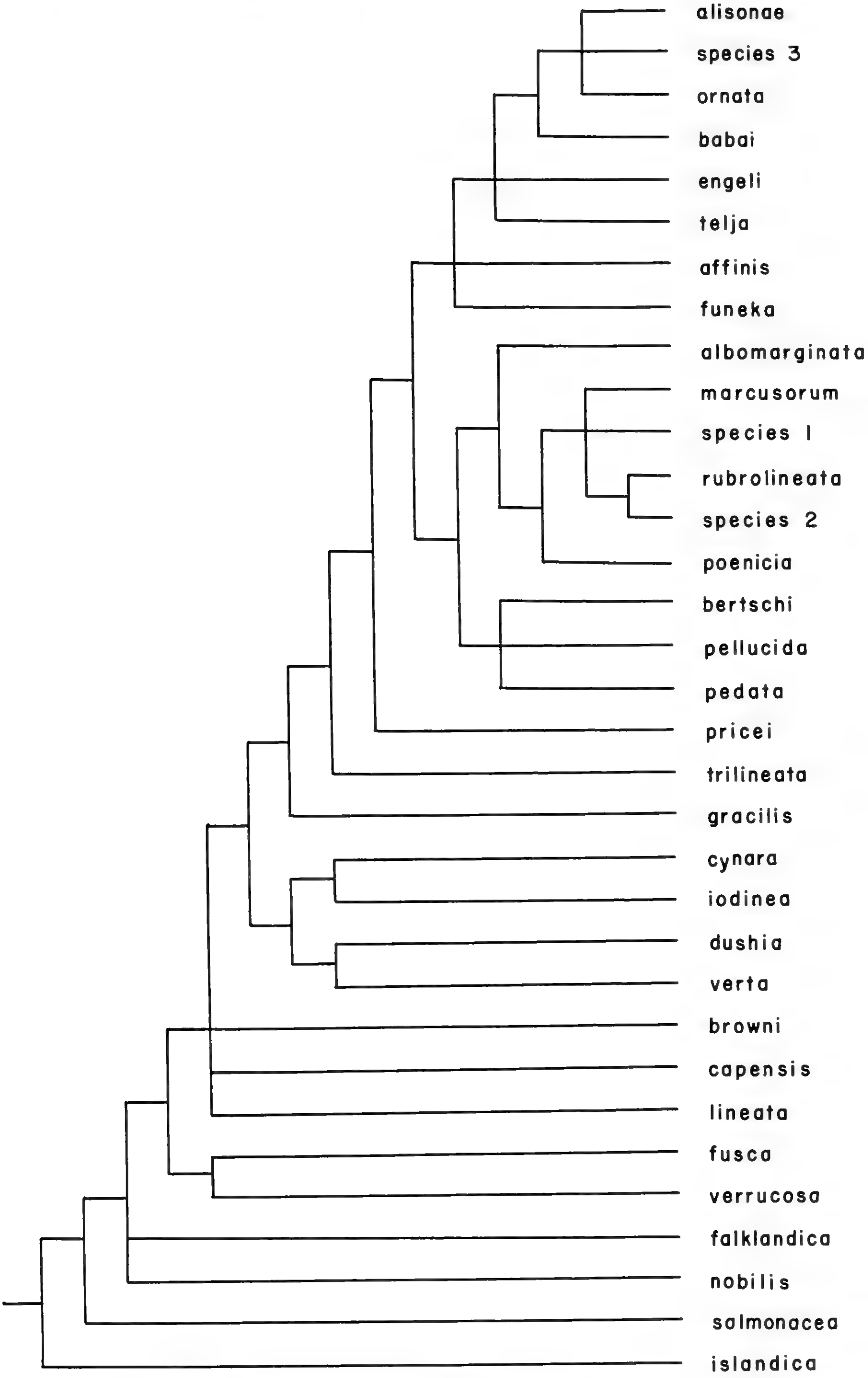

FIGURE 7. Cladogram depicting preliminary phylogeny of *Flabellina*.

by virtually all opisthobranch systematists. The Flabellinidae is a morphologically diverse assemblage, containing primitive and derived taxa. Subdividing the family into genera is problematic, as there is a continuum of gradually adding derived features, sometimes with poor correlation of these characters. Cladistic analysis, employing Phylogenetic Analysis Using Parsimony (PAUP, by David Swofford), was conducted on all 33 species of Flabellinidae for which adequate morphological data are known, including three undescribed species. Polarity of characters was ascertained by using the Notaeolidiidae as the outgroup of the Flabellinidae. Thirteen characters were considered for 33 taxa. The characters and their distributions are included in Table 2.

Subsequent cladistic analysis produced six equally parsimonious trees of similar configuration and a length of 37 and a consistency index of 0.568, one of which is presented here (Fig. 7). The other five trees differ only in the placement of one or two taxa. All of these cladograms demonstrate that genera such as *Flabellina* and *Coryphellina* cannot be maintained without rendering *Coryphella* paraphyletic. Maintenance of these genera as distinct requires the erection of many new monotypic genera and higher taxa for more primitive members of the family. There are no autapomorphic features to support many of these taxa. This is clearly counterproductive and provides no further resolution of the phylogeny and classification of the Flabellinidae. From this analysis, it is apparent that most plesiomorphic members of the Flabellinidae are restricted to polar environments, with more derived taxa inhabiting temperate and tropical waters. Little adaptive radiation and speciation has occurred within primitive members of the family. Most speciation has occurred in the two clades that possess either perfoliate or papillate rhinophores. Accumulation of morphological data for species that are not well known, including additional undescribed taxa, will provide needed data for future re-evaluation of the generic divisions within the Flabellinidae.

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Several individuals assisted in the successful completion of this project. Hans Bertsch, David Behrens, Jeff Hamann, the late Eveline Marcus, and Gary McDonald kindly provided specimens of the two species described in this paper. The collection of specimens of *Flabellina rubrolineata* in Madang, Papua New Guinea, was made possible by a fellowship from the Christensen Research Institute. Jean DeMouthe kindly prepared the ink drawings.

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A CHECKLIST AND KEY TO THE HERPETOFAUNA OF NEW CALEDONIA, WITH REMARKS ON BIOGEOGRAPHY

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ABSTRACT: A checklist and key to all amphibian and reptile species, terrestrial and marine, from New Caledonia and the Loyalty Islands are provided. Thirty-six of 68 extant amphibian and reptile species of the New Caledonian region are represented by 1,643 specimens in the collections of the California Academy of Sciences. Specimen lists and natural history and systematic notes of these taxa are presented. The reptile fauna of the New Caledonian mainland is largely endemic. Certain taxa, especially arboreal geckos and leaf-litter-dwelling skinks, are restricted to regions of lateritic soils and/or high rainfall within the island. Other faunal components include regional endemics (New Caledonia and Loyalty Islands and Vanuatu), pan-oceanic taxa, and known human introductions in historical times. The gekkonine geckos are generally easily transported and have colonized the region only after Vanuatu and the Loyalty Islands obtained their present configuration with respect to New Caledonia. The endemic diplodactyline geckos are most closely related to New Zealand and Australian forms and probably became isolated as a result of Mesozoic tectonic movements and sea-level changes. The zoogeography of most of the scincids remains obscure. Human activity in New Caledonia has likely been responsible for the extinction of additional reptile taxa representative of a once broader herpetofaunal diversity.

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INTRODUCTION

New Caledonia is unique among the islands of the tropical Pacific in possessing a speciose herpetofauna composed largely of endemic forms (Bauer 1988a). The native terrestrial herpetofauna, which consists only of geckos and skinks, remains poorly known as a consequence of the isolation of New Caledonia, its mountainous terrain, and large size (19,103 km²). Almost every major collecting trip to the region has revealed new species or rediscovered others not seen since their description. Recent systematic treatments of the skinks (Greer 1974; Böhme 1976; Sadlier 1986; Ineich and Sadlier 1990) and carphodactyline geckos (Bauer 1986, and in press; Sadlier 1989) of New Caledonia and its satellites, the Loyalty Islands, have provided useful information regarding distribution, morphology, and phylogeny. Nonetheless, most of the taxa remain poorly known, and new forms undoubtedly remain to be discovered.

In this paper we present a checklist and key to the herpetofauna of the New Caledonian region and summarize biological information for 36 of the 68 species inhabiting the New Caledonian area (33 of 53 terrestrial taxa). This information is derived primarily from specimens housed in the herpetological collections of the California Academy of Sciences (CAS).

The New Caledonian amphibians and reptiles in the CAS collection originate from several sources. The first eight specimens accessioned, including two paralectotypes, were obtained by exchanges from the Naturhistorisches Museum Basel, the repository of the large New Caledonian collections made by Fritz Sarasin and Jean Roux during the period 1911–1912. Until the last decade, Basel (NMBA) and Paris (MNHN) were the only major collections of reptile material from the island, although type specimens and smaller collections were housed in a number of other museums. Two of these collections, those of the Museu de Lisboa and the Musée de l'Ecole de Medécine Navale de Brest, are no longer extant, the former having been destroyed by fire and the latter dispersed or lost.

An important collection of 120 specimens was donated to the Academy by F. X. Williams in 1940, including material from the Ile des Pins. Unfortunately, there are no precise locality and collection data associated with some of this material, and the Academy's archives include no field notes or records from Williams's collecting trip. Other additions include sea snakes obtained through Stanford University (CAS-SU), a small collection from Ted Case (University of California, San Diego), and a specimen of *Leiolopisma steindachneri* obtained through exchange with the Australian Museum, now a leading repository of New Caledonian reptile specimens. The remainder of the California Academy of Sciences New Caledonian collection was built by material obtained by the senior author as a result of ongoing research on the systematics, morphology, and biogeography of the geckos of the southwest Pacific. These additions make the California Academy of Sciences a repository for one of the largest collections of New Caledonian reptile material in the world, with 1,643 specimens, including eight types.

MATERIALS AND METHODS

The standard abbreviations m (meters), mm (millimeters), mybp (million years before present), and SVL (snout–vent length) are used in the following text. Collection abbreviations follow Leviton et al. (1985). A checklist is provided listing original authors, representation in the CAS collection, and broad distributional patterns of all species in the region, including fossil taxa. An artificial key to the living taxa—using, when available, invariant characters easily determined from museum specimens—is also provided.

Species accounts are for those taxa represented in the CAS collections. Specimens examined include only those in the California Academy of Sciences (CAS and CAS-SU), although New Caledonian specimens from 17 additional institutions have been examined by the senior author (see Bauer 1986 for a complete listing of gekkonid specimens examined). Synonymies are limited to first description, junior synonyms (if applied to New Caledonian populations), and first or establishing usage of the currently employed combination. More complete synonymies are available in the literature for *Litoria aurea* (Duellman 1977; Cogger et al. 1983), sea turtles (Wermuth and Mertens 1977), geckos (Wermuth 1965; Bauer 1986; Ineich 1987; Sadlier 1989), *Ramphotyphlops braminus* (Robb 1966; McDowell 1974; Ineich 1987), *Candoia bibroni* Stimson (1969), and sea snakes (Stejneger 1907; Smith 1926; Gail and Rageau 1958). Unfortunately, complete synonymies more recent than Boulenger (1887) are not available for most New Caledonian skinks, although Sadlier (1986) provided partial synonymies. Remarks on natural history, diet, and reproduction are limited to CAS material, of which the authors have field knowledge, and are provided to supplement, confirm, or rectify information available in the literature. The basic biological data pertinent to the other large collections of New Caledonian material have already been presented (Roux 1913; Sadlier 1986, 1989). Summaries of the biology of some species may be found in Bavay (1869), Roux (1913), Meier (1979), Sadlier (1986, 1989), Bauer (1986), and Bauer and Devaney (1987). A comprehensive bibliography of New Caledonian herpetology was prepared by Bauer (1985b).

Localities represented by collected material are number coded and appear in Figure 1. Many of these localities were visited on several occasions during different seasons in an attempt to achieve a representative sample of the fauna. The coordinates, elevation, and basic vegetational characteristics of these sites are summarized below.

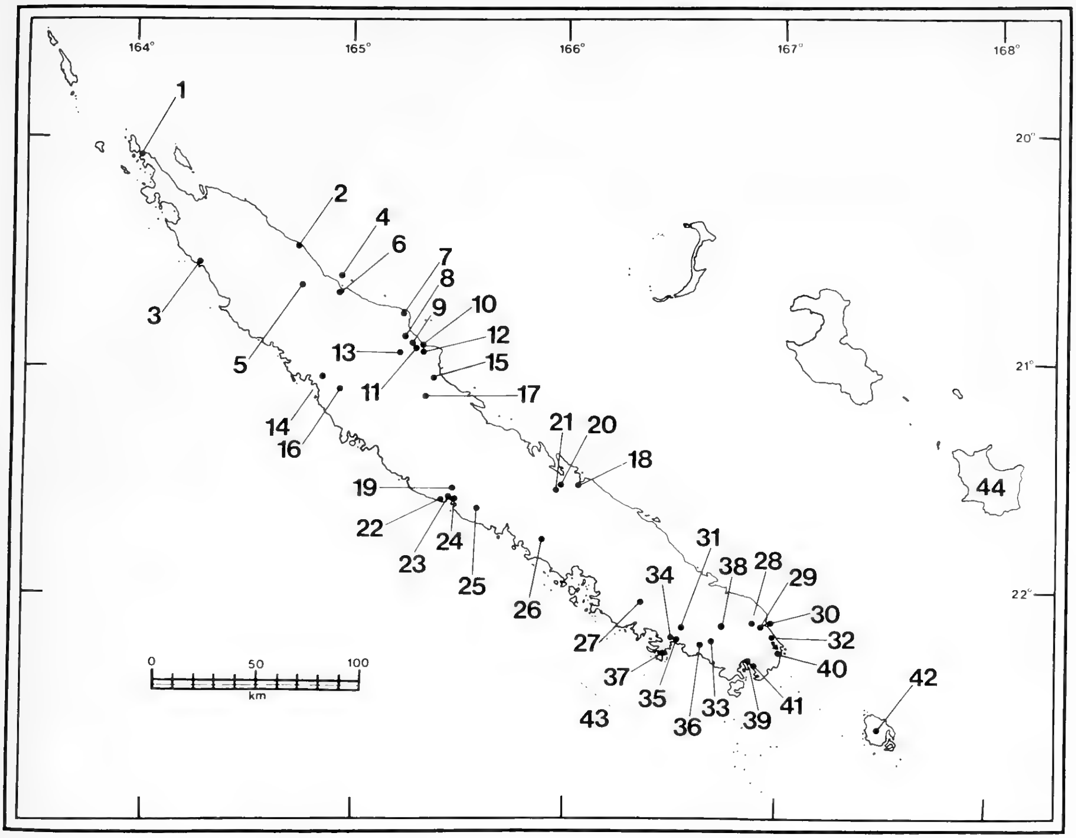

FIGURE 1. Map of New Caledonia showing collecting sites represented by specimens in the California Academy of Sciences. See text for key to numbered localities.

LOCALITIES REPRESENTED BY SPECIMENS IN THE CAS COLLECTIONS

Collection Dates: A = July–October 1940; B = March–April 1984; C = September–October 1984; D = May–June 1985; E = December 1985–January 1986; F = December 1986; and G = miscellaneous dates including exchanges.

LOCALITY 1: Boat Pass Beach (Pointe Narian), 20°05′S, 164°00′E, sea level (C). Northernmost point of mainland New Caledonia. White sandy beach bounded by mangrove vegetation.

LOCALITY 2: Cascade de Galarino, 20°30′S, 164°46′E, elevation 0–20 m (C). Base of large waterfall dropping steeply from southeast slopes of Mt. Colnett (1,505 m) to coast. Vegetation transitional from humid forest to narrow strand palm belt.

LOCALITY 3: Koumac Caves, 20°34′S, 164°17′E, elevation 20–100 m (E). Limestone outcrop in savanna/niaouli (*Melaleuca quinquenervia*, the dominant myrtaceous tree in drier areas of New Caledonia) mosaic. *Ficus* and other trees are invested within the outcrop itself.

LOCALITY 4: Ilot de Hiénghène, 20°38′S, 164°56′E, sea level (C). Small, flat, coralline island, 3.5 km off coast of Ouanpouès, near Hiénghène. Vegetation includes palms, *Ficus,* and variety of other trees and shrubs, excluding truly mesic forms.

LOCALITY 5: Campement Vanhalle, 20°40′S, 164°44′E, elevation ca. 800 m (C). Densely forested region between drainages of Hiénghène and Ouaième rivers. Characterized by mature humid forest, including tree ferns and *Agathis.* Traversed by several small, rocky streams. Forest clearings bounded by palms and cut by small, weed-choked brooks.

LOCALITY 6: Hiénghène, 20°41′S, 164°56′E, sea level (A and G). Town in region of large black limestone cliffs, crags, and caves. Vegetation in and around townsite highly disturbed, surrounding areas—including mountains behind the town (400–450 m)—covered in dense humid forest.

LOCALITY 7: Touho, 20°47′S, 165°14′E, elevation 0–50 m (C and E). Grassy field on hill overlooking Touho airport and adjacent forested region inland from the town center. Vegetation in townsite largely disturbed; inland forests typical humid types.

LOCALITY 8: North bank, Tiwaka River, 4 km W of Rte. 3, 20°54′S, 165°13′E, elevation 0–30 m (D). Hilly area, typified by humid forest vegetation, broken by small riverside plantations.

LOCALITY 9: Vallée d'Amoa, 0–1.0 km W of Rte. 3, 20°55′S, 165°17′E, sea level (C, E and F). Short transect along north bank of Amoa River. Vegetation of humid forest type broken by small family dwellings and plantations.

LOCALITY 10: Vallée d'Ina, 20°56′S, 165°19′E, elevation 10–20 m (C). Grassy pasture with scattered rocks in forest clearing near Ina River.

LOCALITY 11: Poindimié, 20°56′S, 165°20′E, elevation 0–20 m (B, C, D, E and F). Disturbed roadside vegetation, house and hotel walls, and sheets of corrugated metal in town.

LOCALITY 12: Mount Koyaboa, 20°57′S, 165°20′E, elevation 20–390 m (C, D, E and F). Lower slopes (to ca. 50 m) characterized by secondary-growth scrub and some primary and secondary mixed non-coniferous forest associations. Middle elevations (50–140 m) with fern scrub and niaouli. Above 140 m, vegetation primarily secondary growth with some primary humid-forest trees (see Bauer and DeVaney 1987 for detailed description of this site).

LOCALITY 13: St. Thérèse, Vallée d'Amoa, 20°59′S, 165°13′E, elevation 0–20 m (B). Densely forested region along Amoa River, some *Araucaria* (Araucariaceae, column pines) present.

LOCALITY 14: Koné, 21°04′S, 164°52′E, sea level (B and C). Sclerophyll forest, residential gardens, disturbed riverbanks, and banana grove.

LOCALITY15: Vallée de Nimbayes, 21°05′S, 165°21′E, elevation 0–30 m (C). Humid forest.

LOCALITY 16: 10 km E of Pouembout, 21°08′S, 164°59′E, elevation ca. 50 m (B). Sclerophyll forest with thick layer of leaf litter along banks of Pouembout River in area of forest/savanna mosaic.

LOCALITY 17: Creek crossing, 1 km NE of Mt. Aoupinie, 21°08′S, 165°21′E, elevation 500 m (G). Locality described by Sadlier (1986).

LOCALITY 18: Nakety, 21°22′S, 166°34′E, elevation ca. 350 m (C). Open grassy area in forest/savanna mosaic.

LOCALITY 19: 16 km NW of Plage de Poé, 21°34′S, 165°24′E, elevation ca. 120 m (C and E). Open sclerophyll forest bordered by cultivated fields. Traversed by dry creek beds, dead standing trees and thick leaf litter abundant.

LOCALITY 20: Cascade de Ciu, 21°34′S, 165°58′E, elevation ca. 270 m (C). Rocky pools at top of waterfall in disturbed area of shrubs and grass.

LOCALITY 21: Mt. Canala, 21°35′S, 165°56′E, elevation 100–1,051 m (G). Exact site unknown. Area of high rainfall with *Araucaria* stands and generally humid-forest vegetation.

LOCALITY 22: Plage de Poé, 21°37′S, 165°24′E, sea level (C, D and E). Grassy site bordering white sand beach. Roadsides bordered by water-filled ditches and tall grass.

LOCALITY 23: Baie de Gouaro, 21°37′S, 165°26′E, sea level (D). Beach wrack and grassy borders of white sand beach.

LOCALITY 24: Baie des Tortues, 21°37′S, 165°27′E, sea level (C and D). Beach wrack and vegetation along small seaside cliffs. Area of large coastal grove of *Araucaria columnaris.*

LOCALITY 25: 15 km S of Bourail on Rte. 1, 21°41′S, 165°35′E, elevation ca. 50 m (D). Grassy ditch on west side of highway in hilly area of forest/savanna mosaic.

LOCALITY 26: 63 km S of Bourail on Rte. 1, 21°47′S, 165°50′E, elevation ca. 40 m (D). Grassy ditch on west side of highway in area of savanna dotted with scattered naiouli.

LOCALITY 27: Mt. Mou, 22°04′S, 166°21′E, elevation ca. 500 m (F). Humid forest on the lower slopes of mountain. Area of very large trees and high canopy with abundant ground cover traversed by several small streams.

LOCALITY 28: ca. 5 km W of Yaté off Rte. 2, 22°09′S, 166°53′E, elevation ca. 500 m (F). Rocky, open area of edaphic scrub vegetation.

LOCALITY 29: Yaté (Waho), 22°09′S, 166°54′E, sea level (C). On main road through town in area of humid forest/maquis (mediterranean shrub vegetation) interface.

LOCALITY 30: Islet next to Yaté [Ile Potino?], 22°09′S, 166°57′E, sea level (G). Exact locality uncertain (F. X. Williams locality—no field notes). Possibly Ile Potino, a small island in the mouth of the Yaté River typified by maquis vegetation.

LOCALITY 31: Mt. Koghis, 22°10′S, 166°32′E, elevation ca. 460–800 m (D, E and F). Dense, mixed humid forest with *Ficus* and, more rarely, tree ferns and *Araucaria*. Forest floor covered by stones and moist leaf litter.

LOCALITY 32: Touaourou, 22°11′S, 166°58′E, elevation 0–20 m (B, C, D, E and F). Open grassy areas and adjacent white sand beach, maquis forest along abandoned mining roads, and disturbed roadside habitats.

LOCALITY 33: 20 km SE of St. Louis, 22°12′S, 166°42′E, elevation ca. 200 m (C). Roadside maquis off highway.

LOCALITY 34: Border of Commune de Mont Dore, on Rte. 2 at intersection of Tina-sur-Mer road, 22°13′S, 166°29′E, sea level (F). Partially flooded, low-lying grassy and marshy areas near housing development.

LOCALITY 35: Vallée de Yahoué, 22°14′S, 166°30′E, elevation ca. 30 m (A and F). Small, dense forest patch along Yahoué River, interrupted by small banana plantations and habitations.

LOCALITY 36: Col de Mourirange, 22°14′S, 166°39′E, elevation 258 m (D). Area of short, shrubby maquis in hilly region of lateritic soils.

LOCALITY 37: Nouméa, 22°16′S, 166°27′E, sea level (A, C, D, E and F). Capital city of New Caledonia. Urban building walls, gardens, and beach front.

LOCALITY 38: Rivière Bleue, 22°18′S, 166°50′E, 50–100 m (D). Maquis vegetation.

LOCALITY 39: Prony Bay, 22°19′S, 166°49′E, sea level (A). Region of maquis vegetation. Exact collecting localities unknown.

LOCALITY 40: Goro, 22°19′S, 167°00′E, elevation 0–20 m (C, D, E and F). Area near Gite Wadiana, along coral flats and in adjacent grassy areas with scattered coconut palms; also in narrow belt of coastal forest with rocky substrate and along the margins of roadsides, in leaf litter, grass and rocks.

LOCALITY 41: Mt. L'Aiguillon, 22°21′S, 166°50′E, elevation ca. 200 m (D). Transitional zone between humid forest and maquis vegetation. Substrate rather rocky, traversed by several small streams.

LOCALITY 42: Ile de Pins (A). Exact location unknown.

LOCALITY 43: Marine environments off the coast of Nouméa (G).

LOCALITY 44: Maré, Loyalty Islands (G). Exact location unknown.

ARTIFICIAL KEY TO THE EXTANT REPTILES OF THE NEW CALEDONIAN REGION

1a. Limbs present ... 2
1b. Limbs absent (snakes) ... 53
2a. Carapace present, limbs modified as flippers (turtles) ... Family Cheloniidae ... 50
2b. No carapace, limbs unmodified (lizards) ... 3
3a. Body scales generally small, granular, juxtaposed ... Family Gekkonidae ... 4
3b. Body scales imbricate ... Family Scincidae ... 24
4a. Subdigital scansors present ... 5
4b. Subdigital scansors absent ... *Nactus pelagicus*
5a. Digit I of manus and pes clawless ... 6
5b. All digits clawed ... 8
6a. Digit I rudimentary, without scansors ... *Hemiphyllodactylus typus*
6b. Digit I small but well developed, with scansors ... 7
7a. Penultimate phalanx completely free from scansorial pad ... *Gehyra vorax*
7b. Penultimate phalanx partially subsumed in pad ... *Lepidodactylus lugubris*
8a. Digit I with apical plates ... 10
8b. Digit I without apical plates ... *Hemidactylus* ... 9
9a. Two pairs of enlarged post-mental chin shields contact infralabials ... *Hemidactylus frenatus*
9b. Second pair of enlarged postmentals excluded from infralabials by series of small scales ... *Hemidactylus garnotii*
10a. Subdigital scansors divided ... *Bavayia* ... 11
10b. Subdigital scansors undivided ... 17
11a. Claw of digit I situated medial to single terminal scansor ... 12
11b. Claw of digit I situated between halves of cleft apical scansor ... 13
12a. Lateral surface of hindlimb with distinct, contrasting pale spots on a dark background ... *Bavayia ornata*
12b. Lateral surface of hindlimb without pale spots, or spots indistinct ... *Bavayia sauvagii*
13a. Dorsal pattern with pale, broad vertebral strip ... 14

TABLE 1. Checklist of the recent and fossil* herpetofauna of New Caledonia.

Taxon	New Caledonian specimens in CAS collection	Distribution		
		New Caledonia	Loyalty Islands	Marine
Class Amphibia				
Order Anura				
Family Hylidae				
Litoria aurea (Lesson, 1830) [introduced]	70 (including 20 tadpoles)	X	X	
Class Reptilia				
Order Chelonia				
Family Cheloniidae				
Caretta caretta (Linnaeus, 1758)	—			X
Chelonia mydas (Linnaeus, 1758)	—			X
Eretmochelys imbricata (Linnaeus, 1766)	—			X
Lepidochelys olivacea (Eschscholtz, 1829)	—			X
Family Meiolaniidae				
**Meiolania mackayi* Anderson, 1925	—	(Walpole Is.)		
**Meiolania* sp. (see Gaffney et al. 1984)	—	X	X	
Order Crocodylia				
Family Mekosuchidae				
**Mekosuchus inexpectatus* Balouet and Buffetaut, 1987	—	X		
Order Squamata				
Suborder Lacertilia				
Family Gekkonidae				
Bavayia crassicollis Roux, 1913	1	X	X	
Bavayia cyclura (Günther, 1872)	62	X	X	
Bavayia montana Roux, 1913	1	X		
Bavayia ornata Roux, 1913	—	X		
Bavayia sauvagii (Boulenger, 1883)	299	X	X	
Bavayia septuiclavis Sadlier, 1989	—	X		
Bavayia validiclavis Sadlier, 1989	—	X		
Eurydactylodes symmetricus (Andersson, 1908)	—	X		
Eurydactylodes vieillardi (Bavay, 1869)	1	X		
Gehyra vorax Girard, 1857	—		X	
Hemidactylus frenatus Duméril and Bibron, 1836 [introduced]	28	X	X	
Hemidactylus garnotii Duméril and Bibron, 1836	4	X	X	
Hemiphyllodactylus typus Bleeker, 1860	2	X	X	
Lepidodactylus lugubris (Duméril and Bibron, 1836)	23	X	X	
Nactus pelagicus (Girard, 1857)	51	X	X	
Rhacodactylus auriculatus (Bavay, 1869)	38	X		
Rhacodactylus chahoua (Bavay, 1869)	4	X		
Rhacodactylus ciliatus (Guichenot, 1866)	—	X		
Rhacodactylus leachianus (Cuvier, 1829)	9	X		
Rhacodactylus sarasinorum Roux, 1913	1	X		
Rhacodactylus trachyrhynchus Bocage, 1873	—	X		
Family Scincidae				
Caledoniscincus atropunctatus (Roux, 1913)	16	X	X	
Caledoniscincus austrocaledonicus (Bavay, 1869)	727	X	X	
Caledoniscincus festivus (Roux, 1913)	8	X		
Caledoniscincus orestes Sadlier, 1986	—	X		
Cryptoblepharus novocaledonicus Mertens, 1928	5	X	X	
Emoia cyanura (Lesson, 1830)	—		X	
Emoia loyaltiensis (Roux, 1913)	—		X	
Geoscincus haraldmeieri (Böhme, 1979)	—	X		
Graciliscincus shonae Sadlier, 1986	1	X		
Leiolopisma greeri Böhme, 1979	—	X		

TABLE 1. Continued.

Taxon	New Caledonian specimens in CAS collection	Distribution		
		New Caledonia	Loyalty Islands	Marine
Leiolopisma nigrofasciolatum (Peters, 1869)	21	X	X	
Leiolopisma novaecaledoniae (Parker, 1926)	1	X		
Leiolopisma steindachneri (Bocage, 1873)	1	X		
Leiolopisma n. sp. Ineich and Sadlier	—	X		
Marmorosphax euryotis (Werner, 1909)	1	X		
Marmorosphax tricolor (Bavay, 1869)	95	X		
Nannoscincus gracilis (Bavay, 1869)	26	X		
Nannoscincus greeri Sadlier, 1986	12	X		
Nannoscincus mariei (Bavay, 1869)	35	X		
Nannoscincus rankini Sadlier, 1986	—	X		
Nannoscincus slevini (Loveridge, 1941)	1	X		
Phoboscincus bocourti (Brocchi, 1876)	—	X		
Phoboscincus garnieri (Bavay, 1869)	—	X	X	
Sigaloseps deplanchei (Bavay, 1869)	65	X		
Tropidoscincus aubrianus Bocage, 1873	—	X		
Tropidoscincus roehssii (Andersson, 1908)	15	X		
Tropidoscincus variabilis (Bavay, 1869)	2	X		
Family Varanidae				
**Varanus* sp. (see Gaffney et al. 1984)	—	X		
Suborder Serpentes				
Family Typhlopidae				
Ramphotyphlops angusticeps (Peters, 1878)	—	?		
Ramphotyphlops braminus (Daudin, 1803) [introduced]	7	X	X	
Ramphotyphlops willeyi (Boulenger, 1900)	—		X	
Family Boidae				
Candoia bibroni (Duméril and Bibron, 1844)	—		X	
Family Hydrophiidae				
Acalyptophis peronii (Duméril, 1853)	—			X
Aipysurus duboisii Bavay, 1869	—			X
Aipysurus laevis Lacépède, 1804	—			X
Disteira major (Shaw, 1802)	—			X[1]
Emydocephalus annulatus Krefft, 1869	—			X
Hydrophis gracilis (Shaw, 1802)	—			X[1]
Hydrophis coggeri (Kharin, 1984)	1			X
Hydrophis ornatus (Gray 1842)	—			X[1]
Laticauda colubrina (Schneider 1799)	8			X
Laticauda laticaudata (Linnaeus 1758)	3			X
Pelamis platurus (Linnaeus 1766)	—			X
Total species/species represented in CAS collection (extant taxa only)	68/36	48/33	20/12	15/3
Total specimens in CAS collection	1643	1629	2	12

[1] The occurrence of these taxa in New Caledonia has been reported in the literature, but specimens from the region were not recorded by Cogger (1975) nor have they been verified by the authors. The confusion surrounding the identification of *Hydrophis*-like New Caledonia sea snakes was discussed by Minton and Dunson (1985).

13b. Dorsal pattern composed of pale, transversely oriented blotches 15

14a. Preanal pores in 2 rows; supranasal generally separated by a single internasal scale .... *Bavayia validiclavis*

14b. Preanal pores in a single row, internasal region fragmented .... *Bavayia septuiclavis*

15a. First pair of infralabials usually contacting medially .... *Bavayia montana*

15b. First pair of infralabials usually separated 16

16a. Distinct bold, dark transverse bands bordering the pale, dorsal blotches .... *Bavayia cyclura*

16b. Pale dorsal blotches and dark bands obscure and poorly defined .... *Bavayia crassicollis*
17a. Body scales greatly enlarged, body compressed .... *Eurydactylodes* . . . 18
17b. Body scales small and granular or tubercular .... *Rhacodactylus* . . . 19
18a. Cruciform patch of raised, rounded scales on nape; continuous slit from angle of jaw to ear .... *Eurydactylodes symmetricus*
18b. No raised scales on nape, slit from angle of jaw to ear interrupted by skin fold .... *Eurydactylodes vieillardi*
19a. Body with loose folds of skin along throat and flanks, digits half-webbed 20
19b. Body without lateral folds, digits less than one third webbed 21
20a. Rostral contacts nostril .... *Rhacodactylus chahoua*
20b. Rostral excluded from nostril .... *Rhacodactylus leachianus*
21a. Paired, converging ciliated crests on dorsum .... *Rhacodactylus ciliatus*
21b. Dorsal scales generally homogeneous 22
22a. Head with raised bosses or rugosities 23
22b. Head smooth .... *Rhacodactylus sarasinorum*
23a. Snout rugose .... *Rhacodactylus trachyrhynchus*
23b. Raised orbital and aural bosses present, snout smooth .... *Rhacodactylus auriculatus*
24a. "Ablepharine eye" (completely fused brill) .... *Cryptoblepharus novocaledonicus*
24b. Brill not completely fused 25
25a. Ear opening minute or absent 26
25b. Ear opening not minute 31
26a. Body elongate, snout blunt and flattened; 5 supralabial scales .... *Graciliscincus shonae*
26b. Body elongate, snout pointed; 6 supralabial scales .... *Nannoscincus* . . . 27
27a. Ear opening absent . *Nannoscincus mariei*
27b. Ear opening minute 28
28a. Frontoparietals distinct, lower eyelid scaly 29
28b. Frontoparietals fused, lower eyelid with semi-translucent central area 30
29a. Forelimb pentadactyl .... *Nannoscincus gracilis*
29b. Forelimb tetradactyl .... *Nannoscincus slevini*
30a. Phalangeal formula for pes 2.3.4.5.4 .... *Nannoscincus greeri*
30b. Phalangeal formula for pes 2.3.4.4.3 .... *Nannoscincus rankini*
31a. Supranasal scales present 32
31b. Supranasal scales absent 35
32a. Lower eyelid scaly, limbs short, teeth recurved .... *Phoboscincus* . . . 33
32b. Lower eyelid with transparent disk, limbs overlap when adpressed; teeth not recurved .... *Emoia* . . . 34
33a. Supranasals broadly contacting; 32–34 midbody scale rows .... *Phoboscincus garnieri*
33b. Supranasals narrowly separated, 66 midbody scale rows .... *Phoboscincus bocourti*
34a. Mid-vertebral stripe present; 52–64 scale rows between parietal and tail base .... *Emoia cyanura*
34b. No vertebral stripe; 62–71 scale rows between parietal and tail base .... *Emoia loyaltiensis*
35a. Dorsal body scales smooth 36
35b. Dorsal body scales carinate 40
36a. Frontoparietals fused 37
36b. Frontoparietals distinct 38
37a. Enlarged nuchal scales; 22–27 lamellae beneath fourth toe .... *Sigaloseps deplanchei*
37b. No enlarged nuchal scales; 37–47 lamellae beneath fourth toe .... *Leiolopisma steindachneri*
38a. Lower eyelid scaly .... *Geoscincus haraldmeieri*
38b. Lower eyelid with central transparent disk 39
39a. Paravertebral scales 74; prefrontals contacting .... *Leiolopisma greeri*
39b. Paravertebral scales 82–96; prefrontals not contacting or contacting only at a point .... *Leiolopisma nigrofasciolatum*
40a. Ear with one much-enlarged anterior lobule .... *Leiolopisma novaecaledoniae*
40b. Ear with small lobules or no distinct lobules 41
41a. Supralabials excluded from lower eyelid by subocular row .... *Marmorosphax* . . . 42
41b. Supralabials not entirely excluded from lower eyelid 43
42a. Parietal scales bordered by uniform sized scales similar to dorsals .... *Marmorosphax euryotis*
42b. Parietal scales bordered by single upper secondary temporal and single enlarged nuchal scale .... *Marmorosphax tricolor*

43a. Prefrontal scales contacting or narrowly separated 44
43b. Prefrontal scales well separated *Caledoniscincus* . . . 47
44a. Prominent postnasal suture present *Tropidoscincus* . . . 45
44b. Postnasal suture absent *Leiolopisma* n. sp.
45a. Scales on posterior aspect of thighs overlapping and evenly decreasing in size ventrally 46
45b. Scales on posterior aspect of thighs small and juxtaposed, sharply demarcated from large, overlapping scales of dorsum of thigh *Tropidoscincus variabilis*
46a. Midbody scale rows 32–34 *Tropidoscincus aubrianus*
46b. Midbody scale rows 36–40 *Tropidoscincus roehssii*
47a. Tail with dark, transversely aligned chevrons 48
47b. Tail without chevrons, rostral scale always without dark median streak *Caledoniscincus atropunctatus*
48a. Dorsum with either vertebral or lateral pale striping or both 49
48b. Dorsum without vertebral or lateral striping, dark median rostral streak always present *Caledoniscincus festivus*
49a. Dorsum with pale vertebral stripe only, dark median rostral streak always present *Caledoniscincus orsetes*
49b. Dorsum with either vertebral or lateral pale striping, or both; dark median rostral streak variably present *Caledoniscincus austrocaledonicus*
50a. Four costal shields on each side of carapace 51
50b. Five or more costal shields on each side of carapace 52
51a. One pair of prefrontal scales present *Chelonia mydas*
51b. Two pairs of prefrontal scales present *Eretmochelys imbricata*
52a. Four enlarged inframarginals on bridge *Lepidochelys olivacea*
52b. Three enlarged inframarginals on bridge *Caretta caretta*
53a. Tail laterally compressed, marine Family Hydrophiidae . . . 57
53b. Tail rounded in cross-section, terrestrial 54
54a. Head distinct, body large, scales keeled Family Boidae . . . *Candoia bibroni*
54b. Head indistinct, body extremely thin, scales smooth Family Typhlopidae . . . 55
55a. Nasal cleft contacts preocular scale *Ramphotyphlops braminus*
55b. Nasal cleft not contacting preocular scale 56
56a. Nasal cleft contacts first supraorbital scale *Ramphotyphlops angusticeps*
56b. Nasal cleft contacts second supraorbital scale *Ramphotyphlops willeyi*
57a. Ventral scales at least three times as wide as adjacent scales 58
57b. Ventral scales barely twice width of adjacent scales 62
58a. Nasals contact one another 60
58b. Nasals separated by internasal scales *Laticauda* . . . 59
59a. Scale rows at midbody 19 *Laticauda laticaudata*
59b. Scale rows at midbody 21 or more *Laticauda colubrina*
60a. Supralabial scales 3 *Emydocephalus annulatus*
60b. Supralabial scales 6 or more *Aipysurus* . . . 61
61a. Head shield regular, larger than scales of neck *Aipysurus laevis*
61b. Head shield irregular, roughly equal in size to scales on neck *Aipysurus duboisii*
62a. Head scutes small, irregular; supraoculars without tubercles or spines *Acalyptophis peronii*
62b. Head scutes enlarged, regular, supraoculars without tubercles of spines 63
63a. Mental groove absent *Pelamis platurus*
63b. Mental groove present 64
64a. Anterior chin shields reduced, excluded from mental groove by first infralabials *Disteira major*
64b. Anterior chin shields large, bordering mental groove *Hydrophis* . . . 65
65a. Posterior ventrals all divided *Hydrophis gracilis*
65b. Posterior ventrals mostly undivided 66
66a. Scale rows at midbody 29–35 *Hydrophis coggeri*
66b. Scale rows at midbody 39–59 *Hydrophis ornatus*

SPECIES ACCOUNTS

AMPHIBIA

ANURA

FAMILY HYLIDAE

Litoria aurea (Lesson)

Rana aurea Lesson, 1830:60. Type locality: "Macquarie River, Bathurst, New South Wales, Australia." Lectotype locality: "Port Jackson" [New South Wales, Australia] (designated by Roux-Estève 1979).

Litoria aurea Tyler, 1971:352.

MATERIAL EXAMINED (50 adults; 20 tadpoles).—Locality 5: 6 Oct. 1984 (CAS 157654); Locality 8: 6 June 1985 (CAS 158555); Locality 9: 15 Dec. 1986 (CAS 162169); Locality 11: 10–11 Oct. 1984 (CAS 157655–6); Locality 14: 29 Mar. 1984 (CAS 157104–5), 1 Oct. 1984 (CAS 157652–3); Locality 19: 20 Oct. 1984 (CAS 157658–73); Locality 20: 17 Oct. 1984 (CAS 157674, lot of 20 tadpoles); Locality 21: 27 May 1985 (CAS 158311–20, 159025–8); Locality 32: 17 Oct. 1984 (CAS 157657), 4 Jan. 1986 (CAS 159569), 20 Dec. 1986 (CAS 162174–5); Locality 34: 17 Dec. 1986 (CAS 162170–3); Locality 35: 23 Dec. 1986 (CAS 162176); Locality 40: 5 Jan. 1986 (CAS 159570–1).

REMARKS.—The date of introduction of this Australian species into New Caledonia is unknown. Specimens referenced by Copland (1957) and Moore (1961), however, indicate that *Litoria aurea* has been present for over a century. By the time of Sarasin and Roux's expedition (1911–1912), this frog was widely distributed across the mainland of New Caledonia (Sarasin 1925), whence it was introduced into the New Herbrides [=Vanuatu] (Tyler 1976, 1979). The few specimens in early collections, however, suggest that *L. aurea* was not abundant until quite recently. Although it is now found in almost all habitats, *L. aurea* is most common in disturbed lowland sites such as gardens and ditches.

Specimens from areas of native forest were typically found singly, with males calling from the ground or from low branches. The species is carnivorous (Cogger et al. 1983) and even cannibalistic (Cogger 1986), and in Australia it has been known to take large vertebrate prey, including elapid snakes (Tyler 1976). One individual collected at Locality 34 disgorged a *Caledoniscincus austrocaledonicus.*

The presence of both calling males and free-swimming tadpoles in October is consistent with the reported breeding period of *L. aurea* in New Zealand (Bell 1982) and its native Australia (Barker and Grigg 1977). Tadpoles were collected from small rock pools at the top of a waterfall, but were also observed in slow-flowing creeks and vegetation-choked ponds from sea-level to 800 m (Campement Vanhalle—Locality 5).

REPTILIA

SQUAMATA

Family GEKKONIDAE

Bavayia crassicollis Roux

Bavayia cyclura crassicollis Roux, 1913:89. Type locality: "Maré: Netché, Rô, Pénélo; Lifou: Quépénée; Ouvéa: Fayaoué." Lectotype locality: "Maré, Loyalty Insel" (restricted by Kramer 1979).

Bavayia crassicollis Sadlier, 1989:365.

MATERIAL EXAMINED (1 specimen).—Locality 4: 13 Oct. 1984 (CAS 157695).

REMARKS.—One large specimen (70 mm SVL) was collected under loose bark of a dead standing tree on Ilot de Hiénghène, a tiny coralline island off the coast of Hiénghène. The species may be sympatric with other *Bavayia* in forest clearings (Sadlier 1989), but appears to be most common in the coastal lowland forest and mangroves on New Caledonia and the Loyalty Islands (Roux 1913).

Bavayia cyclura (Günther)

Peripia cyclura Günther, 1872:422. Type locality: "New Caledonia."

Lepidodactylus neocaledonicus Bocage, 1873a:206. Type locality: "Nouvelle Calédonie."

Hemidactylus (Peripia) Bavayi Sauvage, 1879:71. Type locality: "Nouvelle-Calédonie."

Bavayia cyclura Roux, 1913:88.

MATERIAL EXAMINED (62 specimens).—Locality 9: 1 Jan. 1986 (CAS 159546, 159550–1), 8 Jan. 1986 (CAS 165877), 14–15 Dec. 1986 (CAS 162203–9, 162219–21); Locality 11: 7 Apr. 1984 (CAS 165878–9), 10 Oct. 1984 (CAS 157696), 1–2 June 1985 (CAS 158549–50); Locality 12: 6 June 1985 (CAS 158548); Locality 19: 20–21 Oct. 1984 (CAS 157697–704, 165884–7), 13 Jan. 1986 (CAS 165861–74); Locality 35: July–Aug. 1940 (CAS 80842, 80849–50, 80853), 23 Dec. 1986 (CAS 162237–9); Locality 37: July–Oct. 1940 (CAS 80864–71); Locality 39: July–Aug. 1940 (CAS 80863).

REMARKS.—Although widely distributed on New Caledonia and all of the Loyalty Islands, *Bavaya cyclura* is restricted to the vicinity of trees and rotten or hollow logs. Only in the Forêt de Yahoué (Locality 35) were specimens of this species found to be syntopic with *B. sauvagii.* In this area, specimens of both species were collected from the trunks of trees at heights of 1–3 m. At Mt. Koyaboa (Locality 12) *B. cyclura* were found only at higher altitudes than *B. sauvagii*

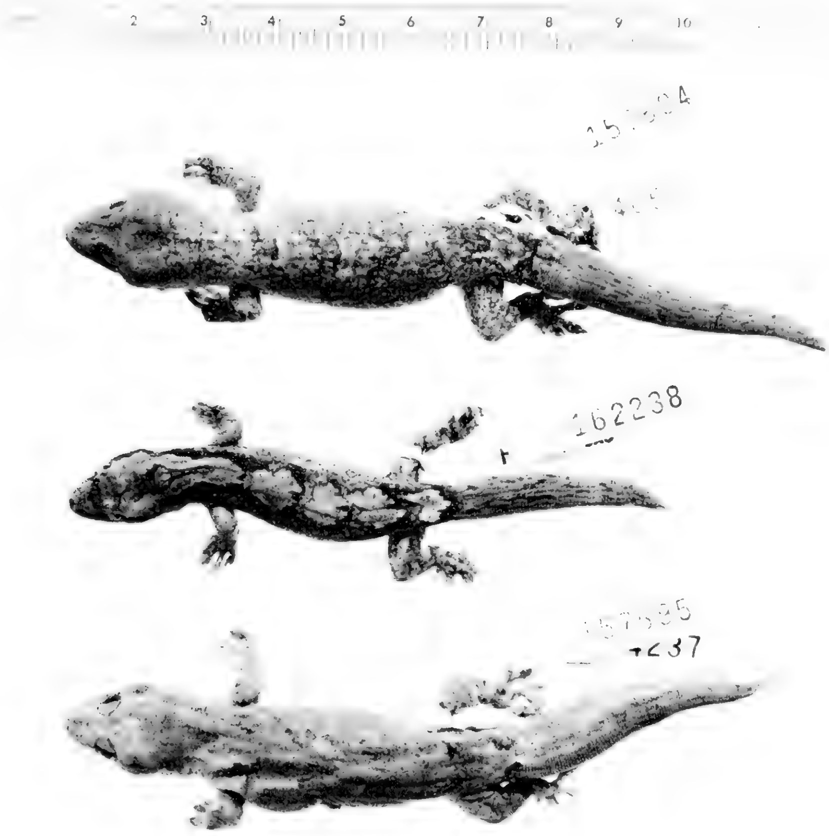

FIGURE 2. Variation in color and body proportion in *Bavayia* species. Specimens (bottom to top): *B. crassicollis* from Ilot de Hiénghène (Locality 4); *B. cyclura* from Vallée de Yahoué (Locality 35); and *B. montana* from Mt. Koyaboa (Locality 12).

and in conjunction with logs, rather than stones, as hiding places. A few individuals were found in association with human habitation. *Bavaya cyclura* is generally more gracile and boldly patterned than are *B. crassicollis* and *B. montana* (Fig. 2). A striped individual (CAS 165885) was collected with many typically patterned ones—we thus doubt that this pattern is of significance. The largest individual examined (from Locality 19) was 72 mm SVL.

Bavayia montana Roux

Bavayia cyclura montana Roux, 1913:88. Type locality: "Mount Ignambi, altit. 700–800 m, près Tao, altit. 400 m, Mont Canala, altit. 700 m, Coindié, altit. 250 m, Ni, altit. 250 m."

Lectotype locality: "Mount Ignambi, 700–800 m, Neu-Kaledonien" (restricted by Kramer 1979).
Bavayia montana Sadlier, 1989:365.

Material examined (1 specimen).—Locality 12: 3 Oct. 1984 (CAS 157694).

Remarks.—One individual (Fig. 2) was collected inside a moist log at about 200 m elevation on Mt. Koyaboa. In life the specimen displayed pale speckling over the basic pattern of indistinct dorsal blotches, and had a canary-yellow venter.

Bavayia sauvagii (Boulenger)

Lepidodactylus sauvagii Boulenger, 1883:122. Type locality: New Caledonia by implication (the original description seems to refer to the species now recognized as *Bavayia sauvagii*; however, the purported holotype is conspecific with *B. cyclura* and possibly is not the specimen designated by Boulenger).
Bavayia sauvagei Roux, 1913:91.

Material examined (299 specimens).—Locality 5: 6 Oct. 1984 (CAS 157706, 157711–4); Locality 11: 4 Oct. 1984 (CAS 157705, 157707–10); Locality 12: 3–5 Oct. 1984 (CAS 157914–61), 8 Oct. 1984 (CAS 165903–10), 11–12 Oct. 1984 (CAS 157962–70, 165881–3, 165888–9, 165893–4), 17 Oct. 1984 (CAS 165880), 1–9 June 1984 (CAS 158430–508, 165875–6), 29 Dec. 1985 (CAS 159513–25), 1 Jan. 1986 (CAS 159528–43), 8–9 Jan. 1986 (CAS 159555–61, 159566–7), 13–15 Dec. 1986 (CAS 162193–200, 162213–8); Locality 27: 11–12 Dec. 1986 (CAS 162186–92); Locality 31: 25 May 1985 (CAS 158378), 15–16 Jun. 1985 (CAS 158379–83), 11 Dec. 1986 (CAS 162184–5); between localities 32 and 39: 21 Oct. 1984 (CAS 157715); Locality 35: July–Aug. 1940 (CAS 80823–36, 80838–41, 80843–8, 80851–2, 80854–8), 17 Dec. 1986 (CAS 162225), 23 Dec. 1986 (CAS 162240–3); Locality 39: July–Aug. 1940 (CAS 80859–62); Locality 40: 18–20 Oct. 1984 (CAS 157716–8), 19–22 May 1985 (CAS 158321–31), 15 June 1985 (CAS 158332), 4 Jan. 1986 (CAS 159552–3), 18–20 Dec. 1986 (CAS 162228–32, 162235); Locality 41: 30 May 1985 (CAS 158386–8); Locality 43: exch. from NMBA, 1914 (CAS 38826). CAS 80837 exchanged to G. Pasteur.

Remarks.—Like *Bavayia cyclura, B. sauvagii* is extremely variable in pattern, and to a lesser extent, body form. In general, the specimens from the west coast of New Caledonia are larger (max. SVL 62 mm, CAS 162184) than those from the east coast. Most specimens were collected during daylight hours from under rocks in humid forest (Bauer and DeVaney 1987), although some were collected at night on bushes and trees. The species is broadly insectivorous with crickets making up the bulk of the diet on Mt. Koyaboa (Bauer and DeVaney 1987). *Bavayia sauvagii* is broadly sympatric and syntopic with *Nactus pelagicus* throughout the range of the former and is also frequently found in association with *Marmorosphax tricolor.*

Eurydactylodes vieillardi (Bavay)

Platydactylus Vieillardi Bavay, 1869:10. Type locality: "Houagape" [=Wagap, Nouvelle-Calédonie].
Eurydactylodes vieillardi Wermuth, 1965:30.

Material examined (1 specimen).—Locality 36: 10 May 1985 (CAS 158556).

Remarks.—Little is known about this arboreal species. It occurs in the southern lateritic region of New Caledonia and in regions of edaphic vegetation throughout the remainder of the island.

Hemidactylus frenatus Duméril and Bibron

Hemidactylus frenatus Duméril and Bibron, 1836:366. Type locality: "l'Afrique australe, et . . . tout l'archipel des grandes Indes" (restricted to "Java" by Loveridge 1947).

Material examined (28 specimens).—Locality 11: 10 Oct. 1984 (CAS 157738–40), 2–4 June 1985 (CAS 158551–2); Locality 14: 1 Oct. 1984 (CAS 157737); Locality 37: 27 Sept. 1984 (CAS 157727–36), 16 May–16 June 1985 (CAS 158289, 158294–303); Locality 38: June 1985 (CAS 172736).

Remarks.—These geckos are extremely common in urban habitats in New Caledonia. They are also present in much lower densities in areas of native vegetation. This species was not recorded by Roux (1913), nor was it collected by F. X. Williams in 1940. As in other parts of the Pacific, *Hemidactylus frenatus* has spread swiftly in recent years. It was not listed among the Hawaiian fauna by Oliver and Shaw in 1953, but it has established itself since being introduced in the 1950s (Hunsaker 1966; Hunsaker and Breese 1967). By 1978 it was the most common gecko in the islands, supplanting *H. garnotii* from both urban and native habitats (McKeown 1978). Likewise, *H. frenatus* was not recorded in Fiji by Pernetta and Watling (1978), but by 1985 it had displaced *H. garnotii* in edificarian habitats (Gibbons 1985). In New Caledonia, as in Hawaii, its introduction may have been associated with troop movement during World War II (Hunsaker and Breese 1967), and has certainly been facilitated by increased post-war contact with neighboring islands. *Hemidactylus frenatus* is approximately the same size as *H. garnotii* (max. SVL 60 mm [CAS 158552] vs. 61 mm [CAS 162223] for *H. garnotii*) and appears to outcompete it in natural and disturbed situations (Hunsaker and Breese 1967). In the Pacific the two species are known to be sympatric only in Hawaii, the Marquesas, and New Caledonia, and it appears likely that the spread of *H. frenatus,* especially on smaller islands, may cause local extinctions of *H. garnotii.*

Hemidactylus garnotii Duméril and Bibron

Hemidactylus Garnotii Duméril and Bibron, 1836:368. Type locality: "l'île de Taïti."

MATERIAL EXAMINED (4 specimens).—Locality 9: 15 Dec. 1986 (CAS 162222–3); Locality 37: July–Aug. 1940 (CAS 80876, 80878).

REMARKS.—Although formerly widespread in New Caledonia (Bavay 1869; Roux 1913), *Hemidactylus garnotii* appears to have retreated in the face of expansion by *H. frenatus.* Extensive searches in Nouméa indicate that the species has become extinct in the area since F. X. Williams's visit in 1940. The specimens collected in 1986 were active at night on forest tree trunks along with *Nactus pelagicus* and *Lepidodactylus lugubris.* The patchy distribution of this species in the Pacific (Ineich 1982; Blanc et al. 1983; Crombie and Steadman 1988) suggests that its spread has been mediated by human movements, and that its success on small islands is dependent on the absence of competitors, particularly *H. frenatus.*

Hemiphyllodactylus typus Bleeker

Hemiphyllodactylus typus Bleeker, 1860:327. Type locality: "Agam, Sumatra" [Indonesia] (see Kluge 1968 for a discussion of the type locality).
Platydactylus crepuscularis Bavay, 1869:8. Type locality: Nouvelle-Calédonie by implication.

MATERIAL EXAMINED (2 specimens).—Locality 38: June 1985 (CAS 172739–40).

REMARKS.—Little is known about the biology of this species in New Caledonia. It is rarely encountered and appears to be restricted to areas of undisturbed vegetation.

Lepidodactylus lugubris (Duméril and Bibron)

Platydactylus Lugubris Duméril and Bibron, 1836:304. Type locality: "l'île d'Otaïti."
Lepidodactylus lugubris Fitzinger, 1843:98.
Gymnodactylus Caudeloti Bavay, 1869:13. Type locality: "Nouvelle-Calédonie, surtout dans le Nord."

MATERIAL EXAMINED (23 specimens).—Locality 9: 10–12 Oct. 1984 (157741–6), 14–15 Dec. 1986 (CAS 162210, 162224); Locality 11: 6 June 1985 (CAS 159498), 8 June 1985 (CAS 158553–4), 8 Jan. 1986 (CAS 159511), 13–15 Dec. 1986 (CAS 162201–2, 162211); Locality 37: July–Aug. 1940 (CAS 80872–5, 80877), 17 May 1985 (CAS 158290); Locality 38: June 1985 (CAS 172737–38).

REMARKS.—*Lepidodactylus lugubris* is the most widely distributed gecko in the Pacific Basin. In New Caledonia it is common in and around houses and in lowland vegetation including humid forest and palm stands. In situations of cooccurrence with *Hemidactylus frenatus,* the smaller *L. lugubris* (max. SVL 44 mm, CAS 162201) is relatively secretive, foraging near shelter and on the periphery of the area of *Hemidactylus* activity. This situation parallels that seen in areas of sympatry in Hawaii (Hunsaker and Breese 1967). As in most areas of its range (Cuellar and Kluge 1972; Ineich 1982, 1988), the New Caledonian populations of *L. lugubris* appear to be all female. Adults collected in October contained enlarged ovarian or oviductal eggs, and communal egg clutches of up to nine eggs were observed under bark in December 1986. All specimens, regardless of date of collection, possessed enlarged extracranial endolymphatic sacs clearly visible through the skin.

Nactus pelagicus (Girard)

Gymnodactylus Arnouxii Duméril, 1851:44. Type locality: "Nouvelle-Zélande" (sic) (see Kluge 1983 for a discussion of probable locality).
Heteronota pelagica Girard, 1857:197. Type locality: "Feejee and Navigator Islands" [=Fiji and Samoa].
Nactus pelagicus Bauer and DeVaney, 1987:353.

MATERIAL EXAMINED (51 specimens).—Locality 9: 11 Oct. 1984 (CAS 157769), 1 Jan. 1986 (CAS 159544–5, 159547–9), 8 Jan. 1986 (CAS 159562–5); Locality 12: 3–11 Oct. 1984 (CAS 157758–67), 2–9 June 1985 (CAS 158509–21, 158543), 1 Jan. 1986 (CAS 159526–7), 8 Jan. 1986 (CAS 159554), 15 Dec. 1986 (CAS 162212); Locality 30: 25 Oct. 1940 (CAS 80882–3, 80885–6); Locality 40: 18 Oct. 1984 (CAS 157768), 20 May 1985 (CAS 158333–4), 11 June 1985 (CAS 158335), 18–20 Dec. 1986 (CAS 162226–7, 162233–4, 162236). CAS 80884 exchanged to G. Pasteur.

REMARKS.—Kluge (1983), when erecting the genus *Nactus,* placed *N. pelagicus* into the synonymy of *N. arnouxii.* However, the use of the older but unused name *arnouxii* disrupts stability and causes confusion in usage (Zug 1985a, 1989). We therefore use the specific epithet *pelagicus. Nactus pelagicus* (max. SVL 69 mm, CAS 158520) is widespread in New Caledonia but rather secretive. It was collected under stones during the day, frequently in dry streambeds (Bauer and DeVaney 1987), and low (<1 m) on the trunks of trees at night. The species has a broad insectivorous diet, similar in most respects to that of sympatric *Bavayia sauvagii.* All adult specimens in the collection are female, and Moritz (1987) has demonstrated that the same is true of populations from southern Vanuatu and the eastern Pacific, suggesting a parthenogenetic species (2N = 35) of hybrid origin.

Rhacodactylus auriculatus (Bavay)

Platydactylus auriculatus Bavay, 1869:6. Type locality: "Mont d'Or" [=Mont Dore, Nouvelle Calédonie].
Ceratolophus hexaceros Bocage, 1873a:205. Type locality: "Nouvellé Calédonie."
Rhacodactylus auriculatus Boulenger, 1883:127.

Material examined (38 specimens).—Locality 29: 19 Oct. 1984 (CAS 157684); Locality 32: 18–19 Oct. 1984 (CAS 157679, 157681–2), 20 May 1985 (CAS 158923), 11 June 1985 (CAS 158925); on road between localities 32 and 39: 18–21 Oct. 1984 (CAS 157676–8, 157680, 157683, 165858–9, 165892, 165901), 18–20 May 1985 (CAS 158919–20, 158922), 4 Jan. 1986 (CAS 159512), 20–22 Dec. 1986 (CAS 162179–83); Locality 33: 19 Oct. 1984 (CAS 165891); Locality 40: 20 May 1985 (CAS 158921, 158924), 12–14 June 1985 (CAS 165860, 165902), 2–5 Jan. 1986 (CAS 165895–900), 19 Dec. 1986 (CAS 162178); Locality 41: 30 May 1985 (CAS 158389–90).

Remarks.—*Rhacodactylus auriculatus* is endemic to southern New Caledonia. Within this region it has been collected widely. By night the animals are active in trees (generally at heights of <3 m) and on the ground. Most CAS specimens were collected along dirt roads from dusk until about 2100 hr. The diet of this species includes flowers (Bavay 1869), lizards (Bauer and DeVaney 1987), and probably insects and fruits as well. Females with shelled eggs were collected in October, December–January, and May–June; in captivity *R. auriculatus* breeds year round. This is the smallest species of *Rhacodactylus*; the largest specimen examined, CAS 162181, was a female of SVL 118 mm.

Rhacodactylus chahoua (Bavay)

Platydactylus chahoua Bavay, 1869:3. Type locality: "Kanala, Lifou" (sic, see Bauer 1985a for a discussion of this locality). Neotype locality: "Vallée d'Amoa, near St. Thérèse, approx. 15 km NW of Poindimié, New Caledonia" (neotype designated by Bauer 1985a).
Rhacodactylus chahoua Boulenger, 1883:125.

Material examined (4 specimens).—Locality 9: 1 Jan. 1986 (CAS 167764), 13 Dec. 1986 (CAS 162177); Locality 13: 6 Apr. 1984 (CAS 156691, 156692 [NEOTYPE]).

Remarks.—Bauer (1985a) designated a neotype to replace the lost type of Bavay (1869), which bore the locality "Kanala, Lifou" (probably a lapsus for Canala, New Caledonia). All specimens were collected at heights of 2–5 m in trees along the Amoa River in eastern New Caledonia. *Rhacodactylus chahoua* appears to be active after dusk on the trunks and branches of trees of moderate size (maximum trunk diameter ca. 2 m).

Rhacodactylus leachianus (Cuvier)

Ascalabotes Leachianus Cuvier, 1829:54. Type locality: not given.
Rhacodactylus Leachianus Bocage, 1873a:201.
Rhacodactylus Aubrianus Bocage, 1873a:202. Type locality: "Nouvelle Calédonie."

Material examined (9 specimens).—Locality 6: July–Aug. 1940 (CAS 80881); Locality 7: Nov. 1985 (CAS 159510); Locality 13: 6 Apr. 1984 (CAS 156690); Locality 15: 28 Aug. 1984 (CAS 165890); Locality 27: 11 Dec. 1986 (CAS 172734); Locality 35: July–Aug. 1940 (CAS 80879–80), 12 Dec. 1986 (CAS 165857, 172735).

Remarks.—This is the largest living species of gecko, attaining 245 mm SVL (CAS 165890). Animals were collected from the trunks and lower branches of trees in humid forests throughout the wetter areas of New Caledonia, most frequently those immediately bordering streams or rivers. Males are much more commonly captured and observed at lower heights on trees, whereas females generally remain in the canopy. In addition to specimens captured, many more *R. leachianus* were observed at heights of 7–30 m in trees where they could not be collected. In the wild this species eats birds, insects, and fruit, and in captivity will also eat mice and other small mammals (Bauer and DeVaney 1987).

Rhacodactylus sarasinorum Roux

Rhacodactylus sarasinorum Roux, 1913:99. Type locality: "Forêt de Prony (env. 100 m. d'altitude)" [New Caledonia].

Material examined (1 specimen).—Locality 32: 18 Oct. 1984 (CAS 157675).

Remarks.—The single specimen was collected at ca. 2000 hr on the branches of a small tree in an area where both *Rhacodactylus auriculatus* and *R. leachianus* are common. The specimen is large (125 mm SVL) and extremely dark, lacking the spots and nuchal collar common in juveniles and smaller adults (Henkel 1987).

Family Scincidae

Caledoniscincus atropunctatus (Roux)

Lygosoma austro-caledonicum atropunctatum Roux, 1913:117. Type locality: "en Nouvelle-Calédonie et aux trois îles Loyalty." Lectotype locality: "Outbatche, Neu-Kaledonien" (restricted by Kramer 1979).
Caledoniscincus atropunctatus Sadlier, 1986:42.

Material examined (16 specimens).—New Caledonia: exchange from NHMB, 1914 (CAS 38828 [PARALECTOTYPE]); Locality 12: 3 Oct. 1984 (CAS 158073), 4 Oct. 1984 (CAS 158080), 1 June 1985 (CAS 158542), 1–2 Jan. 1986 (CAS 159639–40), 15 Dec. 1986 (CAS 162311); Locality 31: 28 Dec. 1985 (CAS 159616), 11 Dec. 1986 (CAS 162273–4); Locality 40: 4 Jan. 1986 (CAS 159643–5), 19–20 Dec. 1986 (CAS 162332, 162347, 162363).

Remarks.—Museum specimens of species of this genus are often difficult to distinguish from one another, as the primary diagnostic features relate to coloration, which is extremely variable. The specimens listed above include all those that are unambiguously assignable to *Caledoniscincus atropunctatus.* Although this small species (max. SVL 51 mm, CAS 162274) is broadly sympatric and syntopic with *C. austrocaledonicus,* and to a lesser extent *C. festivus,* it is more often associated with forests than is *C. austrocaledonicus* (Sadlier 1986). All CAS specimens come from dense forest or forest-edge habitats. In Vanuatu this species is primarily insectivorous and similar to *C. austrocaledonicus* in the breadth of prey categories taken (Medway and Marshall 1975).

Caledoniscincus austrocaledonicus (Bavay)

Lygosoma Austro-Caledonica Bavay, 1869:21. Type locality: "partout en Calédonie et dans les îles Loyalty." Neotype locality: "4 km from summit of Mt. Aoupinie by road, New Caledonia, 21°11′S, 165°16′E" (designated by Sadlier 1986).

Euprepes haplorhinus Günther, 1872:419. Type locality: "New Caledonia."

Lygosoma austro-caledonicum dorsovittatum Roux, 1913:118. Type locality: "du nord au sud de la Calédonie et sur les 3 îles Loyalty." Lectotype locality: "Hienghiene (sic) Neu-Kaledonien" (restricted by Kramer 1979).

Leiolopisma dorsovittatum bodei Börner, 1980:8. Type locality: "unter einerm Baumstamm auf einer trockenen Wiese bei Kutio auf der Ile des Pins südlich von Neu Kaledonien."

Caledoniscincus austrocaledonicus Sadlier, 1986:37.

Material examined (727 specimens).—New Caledonia: exchange from NHMB, 1914 (CAS 38829 [PARALECTOTYPE of *Lygosoma austrocaledonicum dorsovittatum* Roux, 1913], 38830); Locality 1: 2 Oct. 1984 (CAS 158072); Locality 2: 9 Oct. 1984 (CAS 158081); Locality 3: 10–11 Jan. 1986 (CAS 159648-55); Locality 4: 13 Oct. 1984 (CAS 158048–59, 158084); Locality 5: 6–7 Oct. 1984 (CAS 157984–8013); Locality 6: July–Aug. 1940 (CAS 80793–5); Loclaity 7: 10 Oct. 1984 (CAS 158014–34); Locality 10: 12 Oct. 1984 (CAS 158045–7, 158082–3); Locality 11: 12 Oct. 1984 (CAS 158035–44), 2 Jun. 1985 (CAS 158875); Locality 12: 3 Oct. 1984 (CAS 158079), 6 June 1985 (CAS 158546–7), 8 Jan. 1986 (CAS 159646); Locality 14: 1 Oct. 1984 (CAS 157983); Locality 16: 29 Mar. 1984 (CAS 169524); Locality 18: 17 Oct. 1984 (CAS 158064–8, 158096–7); Locality 19: 21 Oct. 1984 (CAS 158086–7); Locality 22: 13–14 Jan. 1986 (CAS 159656–85); Locality 23: 26 May 1985 (CAS 158895–918); Locality 24: 20 Oct. 1984 (CAS 158060); Locality 25: 10 June 1985 (CAS 158867–70); Locality 26: 10 June 1985 (CAS 158866); Locality 28: 18 Dec. 1986 (CAS 162316); Locality 31: 25 May 1985 (CAS 158384–5), 28-29 Dec. 1985 (CAS 159611–5, 159618–37), 10–12 Dec. 1986 (CAS 162244–5, 162271–2, 162275–90); Locality 32: 30 Sept. 1984 (CAS 157974–82, 158069–71, 158077–8), 3 Oct. 1984 (CAS 158074–6), 18 Oct. 1984 (CAS 158061–3, 158088–95); Locality 35: July–Aug. 1940 (CAS 80770, 80772–4, 80776, 80778–82, 80784, 80786–92); Locality 37: 18–20 May 1985 (CAS 158291–3), 28 Dec. 1985 (CAS 159610), 10 Dec. 1986 (CAS 162262); Locality 38: June 1985 (CAS 172743–46); Locality 40: 18–19 Oct. 1984 (CAS 158085, 158098), 18–23 May 1985 (CAS 158557–673), 11–14 June 1985 (CAS 158674–863), 4 Jan. 1986 (CAS 159641–2), 18–22 Dec. 1986 (CAS 162318–21, 1620323–31, 162333–51, 162354–62, 162364–461); Locality 41: 30 May 1985 (CAS 158393–8); Locality 42: 24 Oct. 1940 (CAS 80887–8). CAS 80785, 80796–7 missing from collection.

Remarks.—As mentioned above, the current means of distinguishing species of *Caledoniscincus* from one another is not satisfactory. Some specimens of *C. austrocaledonicus* approach the coloration patterns of each of its congeners, as well as exhibiting a wide array of intermediate patterns. The intermediate size of this species (max. SVL 55 mm, CAS 158561) places individuals well within the range of at least some individuals of each of the other *Caledoniscincus* species. The ventral coloration in life of a series of *C. austrocaledonicus* collected on 12 June 1985 at Locality 40 exemplifies the intrapopulational variability (salmon, orange, yellow, bronze, cream, grey, white, and brown venters were recorded). In other populations, such as that of Plage de Poé, dorsal and ventral coloration are more or less uniform. The chevron marks on the tail employed in the accompanying key are occasionally absent from specimens with original tails, and frequently lacking on regenerated tails. An electrophoretic analysis of variation within and between putative *C. austrocaledonicus* populations may clarify systematic relationships in this group. At least two species are presently included under this name (R. A. Sadlier, pers. comm.).

Caledoniscincus austrocaledonicus is the most common lizard in New Caledonia. It appears to be excluded from dense forest but is common in clearings, forest margins, grassy fields, roadbanks, and nearshore and beach habitats from Boat Pass to the Ile des Pins as well as on the Loyalty Islands.

Bauer and DeVaney (1987) reported a wide range of prey items in the diet of *C. austrocaledonicus* (as *Leiolopisma austrocaledonicum*), including large numbers of crickets and caterpillars. They found some evidence for the preferential feeding of juveniles on collembolans and other very small prey. Beach-wrack-dwelling specimens feed to a great extent on amphipods living in the sand in the splash zone. The species, in turn, is prey to a wide variety of saurian and avian predators, as well as *Litoria aurea* and probably predaceous insects.

Caledoniscincus festivus (Roux)

Lygosoma austrocaledonicum intermedium Roux, 1913:119. Type locality: "Nouvelle-Calédonie: Canala et environs (altit. 300 m), Coindé, Vallée de la Ngoï." Lectotype locality: "Ciu oberhalb Canala, Neu-Kaledonien (restricted by Kramer 1979).

Lygosoma austro-caledonicum festivum Roux, 1913:120. Type locality: "Nouvelle-Calédonie: Coné, environs de Canala, La Foa, Vallée de la Ngoï, Yaté." Lectotype locality: "Canala, Neu-Kanedonien" (restricted by Kramer 1979).

Caledoniscincus festivus Sadlier, 1986:45.

Material examined (8 specimens).—Locality 5: 6 Oct. 1984 (CAS 157971–3); Locality 12: 9 Jan. 1986 (CAS 159647); Locality 26: 10 June 1985 (CAS 158864–5); Locality 31: 28–29 Dec. 1985 (CAS 159617, 159638).

Remarks.—This large species of *Caledoniscincus* (max. SVL 68 mm, CAS 157972) was encountered in open grassy habitat (Locality 26) and in clearings and grassy patches at medium (Locality 12) to high elevations (Locality 5). Campement Vanhalle is a northern record for the species and is very close to Mt. Panié, the only known locality of the very similar *C. orestes*. These skinks appear to be generalist carnivores; CAS 158864 (recorded by Bauer and DeVaney 1987 as *Leiolopisma austrocaledonicum*) had a 2.0 g *Caledoniscincus austrocaledonicus* in its stomach.

Cryptoblepharus novocaledonicus (Mertens)

Cryptoblepharus boutonii novo-caledonicus Mertens, 1928:88. Type locality: "Hienghiène [=Hiénghène] Neukaledonien."

Cryptoblepharus novocaledonicus Sadlier, 1986:53.

Material examined (5 specimens).—Locality 6: 1911 (exchanged from NMBA, 1921) (CAS 53991); Locality 24: 20 Oct. 1984 (CAS 157725–6); Locality 32: 29 Sept. 1984 (CAS 157724); Locality 35: July–Aug. 1940 (CAS 80783).

Remarks.—Despite the high densities and widespread occurrence in nearshore habitats of its congener, *Cryptoblepharus poecilopleurus,* on the islands to the north and east of New Caledonia (Loveridge 1945), *C. novocaledonicus* appears to be greatly outnumbered by members of the genus *Caledoniscincus* over most of its range. CAS 157725–6 from the Baie des Tortues on the central west coast confirm Sadlier's (1986) assumption that the absence of *C. novacaledonicus* from the west of the island was a collecting artifact. The largest CAS specimen (157725), 42 mm SVL, is an adult female carrying one oviductal egg.

Graciliscincus shonae Sadlier

Graciliscincus shonae Sadlier, 1986:12. Type locality: "4 km along the Mt Gouemba road from turnoff 3 km south of La Fause Yaté Bridge, New Caledonia, 22°09′S, 166°54′E."

Material examined (1 specimen).—Locality 31: 28 Dec. 1985 (CAS 159576 [PARATYPE]).

Remarks.—CAS 159576 is one of two known in this monotypic genus. It was collected under a large stone in warm rainy weather.

Leiolopisma nigrofasciolatum (Peters)

Lygosoma (*Mocoa*) *nigrofasciolatum* Peters, 1870:435. Type locality: "Neu Kaledonien."

Lygosoma arborum Bavay, 1869:19. Type locality: Nouvelle-Calédonie by implication. Neotype locality: "Mouac Island off Poum, New Caledonia, 20°13′S, 164°00′E" (designated by Sadlier 1986).

Lygosoma Deplanchei Bocage, 1873b:229 (non *Lygosoma Deplanchei* Bavay, 1869). Type locality: "Nouvelle Calédonie." Neotype locality: "Outbache, New Caledonia, 20°26′S, 164°38′E" (designated by Sadlier 1986).

Leiolopisma nigrofasciolatum Greer, 1974:17.

Material examined (21 specimens).—New Caledonia, July–Aug. 1940 (CAS 80890); Locality 6: July–Aug. 1940 (CAS 80801); Locality 14: 29 Mar. 1984 (CAS 156757); Locality 32: 29–30 Sept. 1984 (CAS 157719–21); Locality 35: July–Aug. 1940 (CAS 80809–11); Locality 40: 18 Oct. 1984 (CAS 157722–3), 23 May 1985 (CAS 158344), 11 June 1985 (CAS 158345), 14 June 1985 (CAS 158346), 4–5 Jan. 1986 (CAS 159573–5), 21 Dec. 1986 (CAS 162463–5); Locality 44: exchanged from NMBH, 1914 (CAS 38825).

Remarks.—Bavay's (1869) name *Lygosoma arborum* has priority over *L. nigrofasciolatum* Peters, 1870. However, the former name has not been used by subsequent authors and we regard it as a nomen oblitum.

Although generally regarded as arboreal (Meier 1979; Sadlier 1986), *Leiolopisma nigrofasciolatum* has been collected in a wide variety of open habitats. Many of the specimens from Goro were collected in vertical crevices in boulders, including several in the splash zone. One *L. nigrofasciolatum* (CAS 158344) was found sharing the same crevice with a *Laticauda colubrina* (CAS 158309). The Goro and Touaourou records are the first published for the southeastern coast of the New Caledonian mainland. The species preys upon cockroaches and other large insects (Bauer and DeVaney 1987), as well as smaller skinks

FIGURE 3. *Marmorosphax euryotis* (CAS 80889) from the Ile des Pins showing dorsal color pattern.

(Roux 1913). The largest specimen is CAS 38825 (112 mm SVL), containing 10 oviductal eggs, presumably collected in December, 1911 (Roux 1913). This is the only CAS specimen lacking a solid dark brown median stripe on the nape and shoulders.

Leiolopisma novaecaledoniae (Parker)

Lygosoma (*Leiolopisma*) *novae-caledoniae* Parker, 1926:493. Type locality: "Upper Houailou River, New Caledonia."
Leiolopisma novaecaledoniae Sadlier, 1986:21.

MATERIAL EXAMINED (1 specimen).—Locality 6: July–Aug. 1940 (CAS 80799).

REMARKS.—*Leiolopisma novaecaledoniae* is known from only a few specimens and localities in New Caledonia. CAS 80799 (SVL 44 mm) fills in part of the gap between the eastern coastal records of Oue Camme and Houailou (Sadlier 1986). It closely matches the squamation and coloration of specimens in previously published accounts.

Leiolopisma steindachnerii (Bocage)

Lioscincus Steindachnerii Bocage, 1873b:228. Type locality: "Nouvelle Calédonie." Neotype locality: "Mt Panie (500 m), New Caledonia, 20°36′S, 164°46′E" (designated by Sadlier 1986).
Lygosoma (*Liolepisma*) *steindachneri* Roux, 1913:129.
Leiolopisma steindachneri Greer, 1974:17.

MATERIAL EXAMINED (1 specimen).—Locality 17: 13 Dec. 1978 (CAS 162121).

REMARKS.—Received in exchange from Australian Museum, original number AMS 77723.

Marmorosphax euryotis (Werner)

Lygosoma euryotis Werner, 1909:271. Type locality: "Ile des Pins, Nouvelle-Calédonie."
Marmorosphax euryotis Sadlier, 1986:36.

MATERIAL EXAMINED (1 specimen).—Locality 41: 24 Oct. 1940 (CAS 80889).

REMARKS.—This species is evidently quite rare, and Sadlier (1986) examined only two specimens. CAS 80889 comes from the type locality and matches the holotype in squamation and approximate size (SVL 36 mm). The coloration of this specimen differs in some respects from that described by Sadlier (1986) and exhibits some features not reported for either of the two known specimens, particularly a distinct, dark nuchal band (see Fig. 3).

Marmorosphax tricolor Bavay

Lygosoma tricolor Bavay, 1869:17. Type locality: Nouvelle-Calédonie by implication. Neotype locality: "summit of Mt Aoupinie (1,086 m), New Caledonia, 21°11′S, 165°16′E" (designated by Sadlier 1986).
Marmorosphax tricolor Sadlier, 1986:32.

MATERIAL EXAMINED (95 specimens).—Locality 6: July–Aug. 1940 (CAS 80800); Locality 9: 11 Oct. 1984 (CAS 157756); Locality 12: 3–10 Oct. 1984 (CAS 157747–55), 12 Oct. 1984 (CAS 157757), 1–9 June 1985 (CAS 158399–429, 158544–5), 29 Dec. 1985–1 Jan. 1986 (CAS 159590–8), 8 Jan. 1986 (CAS 159600–5), 15 Dec. 1986 (CAS 162306–10); Locality 21: 1913 (exchanged from NHMB, 1921) (CAS 53988); Locality 31: 25 May 1985 (CAS 158367–71), 15–16 June 1985 (CAS 158372–7), 28 Dec. 1985 (CAS 159586, 159588), 10–11 Dec. 1986 (CAS 162258–61, 162263–4); Locality 35: July–Aug. 1940 (CAS 80802–8); Locality 40: 5 Jan. 1986 (CAS 159599), 18 Dec. 1986 (CAS 162317), 19 Dec. 1986 (CAS 162322).

REMARKS.—This is the most common skink in heavily forested areas of the wetter regions of New Caledonia. These moderately large skinks (max. SVL 66 mm, CAS 162264) were often found under large stones, where they feed on ants, scorpions, and terrestrial arthropods (Bauer and DeVaney 1987). Juveniles of this viviparous species were collected only during December and January 1985/86 and measured 22–25 mm SVL, confirming Sadlier's (1986) observations.

Nannoscincus gracilis (Bavay)

Lygosoma gracilis Bavay, 1869:24. Type locality: Nouvelle-Calédonie by implication.

Mocoa micropus Günther, 1872:420. Type locality: "Feejee Islands" (amended to New Caledonia in British Museum [Natural History] catalogue).

Nannoscinicus gracilis Sadlier, 1986:58.

MATERIAL EXAMINED (26 specimens).—Locality 12: 4–5 Oct. 1984 (CAS 157685–9), 1–9 June 1985 (CAS 158522–3, 158527–41), 1 Jan. 1986 (CAS 159608–9), 13 Dec. 1986 (CAS 162305) 15 Dec. 1986 (CAS 162313).

REMARKS.—This is the largest (max. SVL 41 m, CAS 162305) and most widespead member of the genus. All material was obtained in very moist conditions under logs and stones (Bauer and DeVaney 1987). The species appears particularly prone to dehydration. Like all members of the genus, *Nannoscincus gracilis* appears to be at least partially fossorial, and it frequently attempts to escape by burrowing rapidly into the substrate. The largest individual, collected in mid-December, contained two very large eggs filling most of the body cavity. This confirms Sadlier's (1986) report and suggests that the rainy December–January period and the periods immediately bracketing it are the periods of breeding and/or birth/hatching for many New Caledonian lizard species.

Nannoscincus greeri Sadlier

Nannoscincus greeri Sadlier, 1986:63. Type locality: "lower east slope of Mt Koyaboa, Poindimié, ca. 20°56′S, 165°20′E" [New Caledonia].

MATERIAL EXAMINED (12 specimens).—Locality 12: 12 Oct. 1984 (CAS 157692–3), 2 June 1985 (CAS 15825–6 [PARATYPES]), 29 Dec. 1985 (CAS 159606 [HOLOTYPE]), 1 Jan. 1986 (CAS 159607 [PARATYPE]), 15 Dec. 1986 (CAS 162312, 162314–5); Locality 35: July–Aug. 1940 (CAS 80819–21), CAS 158524 [PARATYPE] exchanged to Australian Museum, registered as AMS R-123000.

REMARKS.—This smallest of *Nannoscincus* species (max. SVL 34 mm, CAS 162312) has been reported only from central eastern and southwestern New Caledonia. Its microhabitat is identical to that of the sympatric *N. gracilis.* The smallest individual (CAS 162315, 22 mm SVL) was collected in December and differs from larger individuals (as reported by Sadlier 1986) in possessing a prominent light spot on the nape and a broken, pale midvertebral stripe.

The date of collection of the holotype was incorrectly reported as January 1, 1986, by Sadlier (1986).

Nannoscincus mariei (Bavay)

Anotis Mariei Bavay, 1869:29. Type locality: Nouvelle-Calédonie by implication.

Nannoscincus fuscus Günther, 1872:421. Type locality: "Feejee Islands" (amended to New Caledonia in British Museum [Natural History] catalogue).

Nannoscincus mariei Sadlier, 1986:56.

MATERIAL EXAMINED (35 specimens).—Locality 27: 11–12 Dec. 1986 (CAS 162297–304); Locality 31: 25 May 1985 (CAS 158358–9), 15–16 June 1985 (CAS 158360–66), 28–29 Dec. 1985 (CAS 159583–5), 10 Dec. 1986 (CAS 162254–7), 11–12 Dec. 1986 (CAS 162291–5); Locality 35: July–Aug. 1940 (CAS 80813–8). CAS 80812 exchanged to Museum of Comparative Zoology.

REMARKS.—This is another southern New Caledonian endemic and was collected only in extremely moist microhabitats, under rocks and logs, and among the roots of trees. All females of this small skink (max. SVL 39 mm, CAS 158363) collected in December 1986 contained one or two large, elongate eggs.

Nannoscincus slevini (Loveridge)

Lygosoma slevini Loveridge, 1941:193. Type locality: "Mont Canala, New Caledonia."

Nanoscincus slevini Sadlier, 1986:61.

MATERIAL EXAMINED (1 specimen).—Locality 35: July–Aug. 1940 (CAS 80822).

REMARKS.—This species had not been previously recorded from southwestern New Caledonia. Other specimens are from the region of Canala. The Yahoué locality is unique in supporting three species of *Nannoscincus*—*N. greeri, N. mariei,* and *N. slevini.*

Phoboscincus bocourti (Brocchi)

Eumeces Bocourti Brocchi, 1876:95. Type locality "Nouvelle-Calédonie."
Phoboscincus bocourti Greer, 1974:15.

MATERIAL EXAMINED: No CAS specimens.

REMARKS.—This species is known only from the holotype (SVL 275 mm). The senior author observed what was apparently an individual of this species at ca. 2030 hr on 21 December 1986 just south of the Kuébini River. The sighting may have been of a *Phoboscincus garnieri* or an unknown species, but the estimated size of the animal (ca. 400 mm total length) is consistent with *P. bocourti.*

According to Greer's (1974) hypothesis of lygosomine relationships, the separation of *Phoboscincus* and *Tachygia* from *Eugongylis* leaves the last genus paraphyletic. Böhme (1976) considered the generic distinctions proposed by Greer (1974) to be continuously variable in a morphocline of constituent taxa and relegated *Phoboscincus* spp. as well as a new species, *Eugongylus haraldmeieri* (*Geoscincus haraldmeieri* of Sadlier 1986), to the single genus *Eugongylus.* Present evidence tends to favor Böhme's treatment of the group, but in the absence of strictly cladistic analysis, we retain the genera *Phoboscincus* and *Geoscincus* as lineages putatively independent of *Eugongylus.*

Sigaloseps deplanchei (Bavay)

Lygosoma Deplanchei Bavay, 1869:23 (non *Lygosoma Deplanchei* Bocage, 1873). Type locality: Nouvelle-Calédonie by implication.
Hinulia tetragonurus Günther, 1872:420. Type locality: "Feejee Islands" (amended to New Caledonia in British Museum [Natural History] catalogue).
Sigaloseps deplanchei Sadlier, 1986:50.

MATERIAL EXAMINED (65 specimens).—Locality 31: 25 May 1985 (CAS 158871–4, 158876), 15–16 June 1985 (CAS 158877–94), 28 Dec. 1985 (CAS 159577–82, 159587, 159589), 10–12 Dec. 1986 (CAS 162246–53, 162265–70, 162296); Locality 35: July–Aug. 1940 (CAS 80768–69, 80771, 80775, 80777); Locality 40: 19 Oct. 1984 (CAS 157690–1), 19 May 1985 (CAS 158336–8), 14 June 1985 (CAS 158339–43), 20 Dec. 1986 (CAS 162352–3); Locality 41: 30 May 1985 (CAS 158391–2).

REMARKS.—This small (max. SVL 46 mm, CAS 162246) skink is a southern New Caledonian endemic. Specimens were collected from underneath rocks and debris in shaded areas of forest floor in humid montane forest (Localities 31 and 41) and in coastal forest belt (Locality 40). It is intermediate in habitat between *Marmorosphax tricolor* and *Nannoscincus* spp. and eats a variety of small terrestrial prey (Bauer and DeVaney 1987).

Tropidoscincus roehssii (Andersson)

Lygosoma röhssii Andersson, 1908:4. Type locality: "New Caledonia."
Tropidoscincus rohssii Sadlier, 1986:30.

MATERIAL EXAMINED (15 specimens).—Locality 38: June 1985 (CAS 172741–42); Locality 40: 22 May 1985 (158349–50), 11–14 June 1985 (CAS 158347–8, 158351–7), 4 Jan. 1986 (CAS 159572), 21 Dec. 1986 (CAS 162462).

REMARKS.—Like all members of this genus, juveniles of *Tropidoscincus roehssii* have distinctive yellowish dorsolateral and midlateral stripes on the forebody, and a generally reddish-brown tail. Adults are greyish to olive-brown and lack stripes. The venter of adult males is orange-red, fading somewhat on the limbs and tail; the chin and anterior part of the throat are white. Juveniles were most frequently encountered during May–June 1985 (nine of 11 specimens collected during this period). The largest adult specimen measured (CAS 158348) was 75 mm SVL. Comments about the ecology of *Leiolopisma variabile* in Bauer and DeVaney (1987) refer to this taxon.

Tropidoscincus variabilis (Bavay)

Tropidolopisma variabilis Bavay, 1869:26. Type locality: Nouvelle-Calédonie by implication. Neotype locality: "Mt. Panie (750 m), New Caledonia, 20°33′S, 164°45′E" (designated by Sadlier 1986).
Tropidoscincus variabilis Sadlier, 1986:24.

MATERIAL EXAMINED (2 specimens).—New Caledonia: exchanged from NMBA, 1914 (CAS 38827); Locality 6: July–Aug. 1940 (CAS 80798).

REMARKS.—The larger of the two specimens (CAS 38827) measures 67 mm SVL.

Family TYPHLOPIDAE

Ramphotyphlops braminus (Daudin)

Eryx braminus Daudin, 1803:279. Type locality: "Vizagatapam, Bengale, Inde."
Ramphotyphlops braminus Robb, 1966:676.

MATERIAL EXAMINED (7 specimens).—Locality 37: Nov. 1986 (CAS 162092–4), 12 Dec. 1986 (CAS 162095–6), 18 Dec. (CAS 162097), 22 Dec. 1986 (CAS 162098).

REMARKS.—These are the first collected specimens (Bauer 1987) of this widespread, parthenogenetic species and range in size from 66 to 161 mm SVL. The only other typhlopid reported

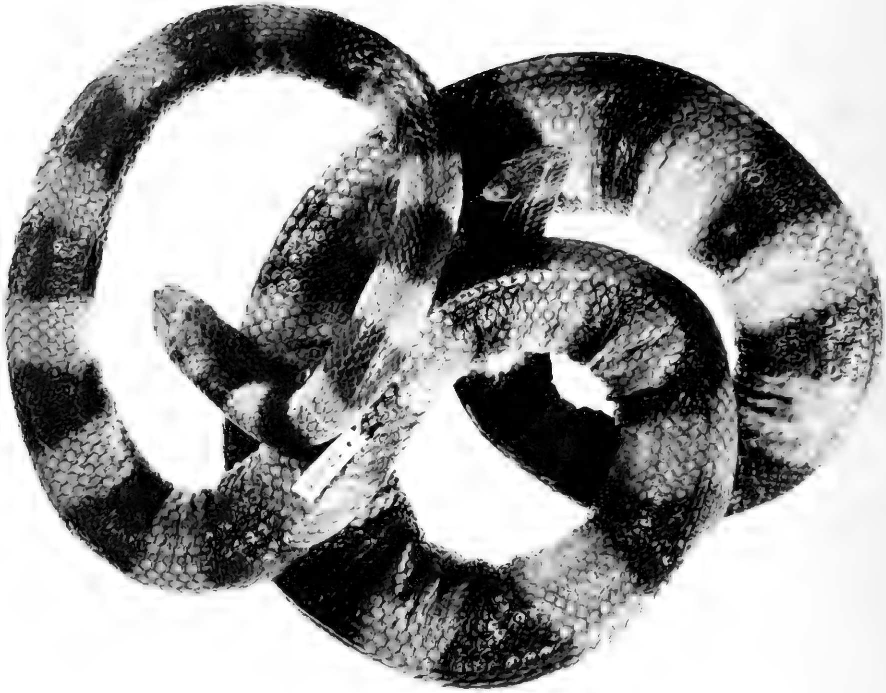

FIGURE 4. *Hydrophis coggeri* (CAS-SU 12430). First record from New Caledonian waters.

from the New Caledonian mainland is *Ramphotyphlops angusticeps,* and only the type of this species, otherwise distributed in the Solomons, bears this locality. It is probable, however, that Peters's (1877) holotype locality of "Neu Kaledonien" is an error (Roux 1913; McDowell 1974), most likely a lapsus for Neu Pommeranien or Neu Brittanien, as this taxon is otherwise known only from the Solomon Islands. Discussion with natives in New Caledonia suggests that typhlopids probably became established within the last decade and that they are now present in most disturbed areas of both the east and west coasts of the island.

Family HYDROPHIIDAE

Hydrophis coggeri (Kharin)

Leioselasma coggeri Kharin, 1984:1538. Type locality: "Fiji, Port Suva" [translated from original Russian].
Hydrophis coggeri Cogger, 1986:658.

MATERIAL EXAMINED (1 specimen).—Locality 43: Apr. 1945 (CAS-SU 12430).

REMARKS.—This specimen (SVL 1,024 mm) (Fig. 4) represents the first confirmed New Caledonian record for the species. It is similar to sea snakes from the Coral Sea and the vicinity of Fiji first reported by McDowell (1972) and Cogger (1975) as *Hydrophis melanocephalus* and later used by Kharin (1984) in his revision of *Leioselasma.* Minton and Dunson (1985) collected specimens probably also referable to this species at the Chesterfield Reefs. We here retain the more familiar generic designation *Hydrophis* for this species.

Laticauda colubrina (Schneider)

Hydrus colubrinus Schneider, 1799:238 (Linnaeus 1758 based his *Coluber laticaudatus* partly on this species and partly on the following species, fide Andersson 1899). Type locality: unknown.

Laticauda colubrinus Stejneger, 1907:406.

Material examined (8 specimens).—Locality 39: 19–23 May 1985 (CAS 158304–10); Locality 43: Apr. 1945 (CAS-SU 12438).

Remarks.—This species is by far the most common nearshore sea snake in New Caledonia. Hundreds of individuals may come ashore, particularly during the period of egglaying (Saint Girons 1964). Most individuals collected were resting in rock crevices at water's edge during daylight hours. The largest specimen examined is CAS 158306, SVL 860 mm.

Laticauda laticaudata (Linnaeus)

Coluber laticaudatus (part) Linnaeus, 1758:222. Type locality: "Indiis."

Laticauda laticaudata Stejneger, 1907:402.

Material examined (3 specimens).—Locality 40: 2 Jan. 1986 (CAS 159568); Locality 43: Apr. 1945 (CAS-SU 12441–2).

Remarks.—This species occurs with *Laticauda colubrina* in most New Caledonia nearshore habitats. The specimen collected in 1986 was obtained in 0.5 m of water at ca. 2100 hr and was one of several specimens that were swimming towards shore. CAS-SU 12441 (SVL 1,088 mm) is the largest specimen.

Biogeography of the New Caledonian Herpetofauna

Roux (1913) first analyzed New Caledonian herpetofaunal characteristics and identified four faunal elements: strictly New Caledonian endemics, regional endemics (New Caledonia and the Loyalty Islands), Melanesian-Polynesian elements, and cosmopolitan elements. Sternfeld (1920), Sarasin (1925), Burt and Burt (1932), Mertens (1934), Brown (1956), Virot (1956), Gibbons (1985), and Bauer (1986, 1988a), among others have since discussed the biogeographic affinities of the herpetofauna of the region. Most of these authors stressed the high levels of endemism and the contrast provided by New Caledonia to the trend of Papuan diminution that typifies many of the islands of the central and eastern Pacific, and have focused on the potential faunal ties of New Caledonia to Australia and New Zealand. With an increased knowledge of the historical geology of the region and the phylogeny of its herpetofauna, it is now possible to begin to redefine the faunal elements of the region.

The marine taxa of New Caledonian waters show little tendency towards endemism, although *Hydrophis coggeri* appears to be restricted to a relatively small area between the Coral Sea and Fiji (Kharin 1984). Most of the sea snakes are primarily inhabitants of the waters of the Australian continental shelf and reach their easternmost limits in New Caledonia, or like *Hydrophis ornatus* and *Laticauda* spp., are distributed broadly from western Asia to the western Pacific (Cogger 1975). These taxa favor shallow waters, and their occurrence around New Caledonia is not surprising given that the Chesterfield Reefs and the northern tip of the Lord Howe Rise provide a shallow-water corridor from the Queensland coast, with only two narrow deeper basins intervening (O.R.S.T.O.M. 1981). The remaining New Caledonian sea snakes, *Emydocephalus annulatus* and *Pelamis platurus,* are both more widely distributed in the Pacific, the latter to the coast of the Americas. All of the New Caledonian sea turtles range widely in the tropical and subtropical Pacific (Iverson 1986). Although turtle populations are conspicuous and easily monitored during nesting periods, the same is not true of the hydrophiids. Some of the sea snake records for New Caledonia are doubtful (see checklist), and more sampling is needed to complete the species list accurately for the region.

Among terrestrial species, *Litoria aurea* and *Hemidactylus frenatus,* and almost certainly *Ramphotyphlops braminus,* have been introduced by man into New Caledonia during historical times. Their arrival in New Caledonia is easily explained by human transport from adjacent, or even distant, regions. *Litoria aurea* presumably arrived from Australia, although the species was already established in parts of New Zealand by the late 1860s (Bell 1982), and the North Island could conceivably have been the source of at least some of the New Caledonian populations. The advent of rapid and frequent shipping contact in the South Pacific during and after World War II makes the determination of the origin of the other two species more problematic. Although this European-era faunal element is of little interest to historical biogeography, it is of prime ecological concern since, at least in the case of *H. frenatus,* native forms appear to be adversely affected by recent migrants (see *Hemidactylus* species accounts).

A second element includes *Lepidodactylus lugubris, Nactus pelagicus, Hemidactylus garnotii,* and *Hemiphyllodactylus typus*—species that are widespread in Oceania or the Pacific and South-East Asia. These are "weedy" species (Bauer 1988a), which by virtue of small size, the calcareous gekkonine eggshell (Werner 1972; Dunson 1982), and parthenogenesis (at least in the first three species and possibly the fourth [Kluge and Eckardt 1969; Cuellar and Kluge 1972; Moritz 1987; Ineich 1988]) have been able to colonize successfully over water.

McCann (1953), Brown (1956), Kluge (1969) and Ineich (1987) outlined suites of biological characteristics conducive to over-water dispersal and colonization. All of the taxa in the first and second faunal-element categories possess most of these features. However, the additional features of human-aided dispersers as outlined by Kluge (1969) are: (1) undifferentiated from probable parent stock; (2) distributed primarily in areas of human settlement; (3) primarily coastal (associated with ports); and (4) dates of introduction established do not necessarily hold true for the second faunal element.

Little work has been done on the variability of the wide-ranging taxa of oceanic lizards. Morphological differentiation among Polynesian populations of *Lepidodactylus lugubris* is low (Blanc and Ineich 1985), and there is high histocompatibility between Hawaiian and French Polynesian populations (Cuellar 1984), but genetic studies have demonstrated that there are at least two bisexual populations and five clonal races in the central South Pacific (Ineich 1987, 1988). In contrast, only a single genetic clone was found by Moritz (1987) among several widely distributed populations of *Nactus pelagicus* from the western Pacific (including New Caledonia). Genetic homogeneity may be an indication of recent establishment or fragmentation of populations, as suggested for the skink *Lipinia noctua* (Zweifel 1979), or it may be a reflection of intrinsically limited genetic variability, as in clonal lineages such as the parthenogenetic New Caledonian taxa *Lepidodactylus lugubris, Nactus pelagicus, Hemidactylus garnotii,* and probably *Hemiphyllodactylus typus* (Cuellar and Kluge 1972; Cuellar 1984; Pasteur et al. 1987). Thus, for parthenogens, Kluge's (1969) first criterion does not distinguish between human-aided and naturally occurring dispersal.

The distribution of *Hemiphyllodactylus, Nactus, Lepidodactylus,* and *Hemidactylus garnotii* is not limited to human habitations or to coastal localities in New Caledonia, and at least the former two taxa are restricted to more undisturbed habitats there. Finally, all of these taxa were recorded by Bavay in 1869, during the earliest stages of French colonization of the island. Their presence in undisturbed areas at this early date argues strongly against dispersal by Europeans, although the transport of some taxa by ship is so easy that it cannot be ruled out entirely (Schnee 1901).

Transportation to New Caledonia via human aid in pre-European times remains a strong possibility, and this means of dispersal has been argued for many lizard species in the central and eastern Pacific (Garman 1908; Zweifel 1979; Gibbons 1985; Crombie and Steadman 1988). Crombie and Steadman (1988) dismissed natural rafting as statistically unlikely between the tiny islands of the central Pacific and suggested that *Lepidodactylus lugubris* arrived in the Cook Islands with the Polynesians, while *Hemidactylus garnotii,* which is spottily distributed and frequents edificarian habitats in Polynesia, may have been an import of the post-Polynesia era. Ineich (1982), however, believed that *L. lugubris,* at least, may have antedated man in Oceania. While lowered sea levels in the Pleistocene (and earlier) (Gibbons 1985) may have had only a minor effect on the small, isolated islands of the central and eastern Pacific, their effect in the New Caledonian region was marked. More "stepping stones" would have been emergent on routes from Australia and New Guinea (Gibbons 1985:135, fig. 3).

Although the navigational prowess and frequent travels of the Polynesians are well established (see Crombie and Steadman 1988), the pre-European movements of Melanesians to and from New Caledonia are less well understood. Nonetheless, data obtained from Lapita pottery

(White et al. 1988) and largely untapped ethnobotanical sources (see O.R.S.T.O.M. 1981) clearly indicate a strong cultural link at least 6,000 years old to northern Melanesia, in particular the Solomons and Bismarks, as well as more recent connections via Fiji into Polynesia. Clearly the possibility exists for the human transport of at least some of the second-element taxa. By the same token, however, other seemingly easily transported taxa such as *Gehyra mutilata* and *Emoia cyanura,* which occur both southeast and northwest of New Caledonia along the probable routes of prehistoric contact, are absent from New Caledonia. For the present, the origin of the four species of second-element lizards remains problematic, although a reasonably recent (post-Pliocene) but pre-European introduction, whether human-aided or not, appears likely.

All species in the first two categories are present in the Loyalty Group as well as on the New Caledonian mainland. Only one species, *Caledoniscincus atropunctatus,* occurs in New Caledonia, the Loyalty Islands, and parts of neighboring Vanuatu, and it is part of a primarily New Caledonian radiation of skinks (Sadlier 1986). It is likely that this species has only recently established itself in Vanuatu (Bauer 1988b), as the paleoposition of Vanuatu would have precluded easy dispersal prior to 6–8 mybp (Chase 1971).

Native regional endemics (occurring both in New Caledonia and the Loyalty Islands) include the geckos *Bavayia crassicollis, B. cyclura, B. sauvagii,* and the skinks *Caledoniscincus austrocaledonicus, Cryptoblepharis novocaledonicus, Leiolopisma nigrofasciolatum,* and *Phoboscincus garnieri.* All but *C. novocaledonicus* and *P. garnieri* are representatives of New Caledonian radiations, probably of great age (Sadlier 1986; Bauer 1986, in press). Colonization of the Loyalty Islands from New Caledonia probably took place recently, perhaps during the Pleistocene period of low sea levels. Most of the Loyalty Islands have probably only been emergent since this time (Bauer 1988a), and being low-lying, have only been able to support those species occurring in coastal forest or marginal strand habitats. Interestingly, *Bavayia sauvagii* is restricted to Maré, the only island with substantial non-coralline areas. This is consistent with this gecko's preference for rocky substrates (Bauer and DeVaney 1987), otherwise lacking in the Loyalties.

Cryptoblepharis novocaledonicus is a member of a pan-Pacific genus of 36 morphologically similar skinks formerly considered as subspecies of a single variable species (Mertens 1934; Greer 1974). Distinct morphological differentiation within the genus supports the pre-human occurrence of *Cryptoblepharis* in the region (Mertens 1931), but its age in the region is uncertain. Like *Bavayia sauvagii, C. novocaledonicus* favors rocky habitats and has been recorded only from Maré in the Loyalties. *Phoboscincus garnieri* (with *P. bocourti* restricted to the New Caledonian mainland) is an offshoot of the genus *Eugongylus* (Greer 1974), a Papuan lineage. Its ancestors may well have arrived via over-water dispersal, and like the previous taxon, it represents an unambiguous pre-human arrival. This is supported by the known dispersal abilities of *Eugongylus* sensu stricto, but too little is known of the biology of the endemic Caledonian taxa to shed light on the issue.

A few species occur only in the Loyalty Islands or in the Loyalties and Oceania at large, excluding New Caledonia (*Emoia cyanura*), or in the Loyalties and the Solomon Islands and other Melanesian Outer Arc (Holloway 1979) islands (*Candoia bibroni, Gehyra vorax*). It appears likely that these taxa reached the Loyalties quite recently via over-water dispersal from northern and/or eastern source areas, and that there has been insufficient time for speciation to occur in the region. The presence of *Candoia* in the Loyalty Islands remains puzzling. The genus shows the typical diminution of species expected for a group of Papuan origin (Gibbons 1985; Bauer 1988b), but if they are correctly identified as boas, their occurrence in the Pacific at all is difficult to understand. Phylogenetic analysis being undertaken by Kluge (1988) may shed light on the problem. Only *Emoia loyaltiensis,* which shares great affinity with the *Emoia samoensis* group, has apparently speciated in the Loyalties (Brown in press). *Rhamphotyphlops willeyi,* described from Lifou in the Loyalties, has also been recorded from the Solomon Islands (McCoy 1980). However, snakes in these two areas may be specifically distinct from one another (McDowell 1974), although they are certainly closely related.

The absence of these Loyalty taxa from New Caledonia has long been recognized (Roux 1913), but its basis is by no means well established. The recent movement of Vanuatu to its present position (Chase 1971) and the emergence of the Loyalty Islands may reduce the problem to one that is analyzable under the equilibrium model of island biogeography (MacArthur and Wilson 1967). The prevailing southern tropical counter current (O.R.S.T.O.M. 1981) would tend to bring propagules to the Loyalties from New Caledonia, while other currents lead from Fiji and Vanuatu toward the Loyalties (Gibbons 1985). Apparently the preference of *Gehyra vorax* and *Emoia* spp. for vegetated over edificarian habitats has prevented accidental transportation and establishment of these taxa on the mainland, in spite of daily boat and air crossings of cargo and passengers.

Among the remaining taxa, 29 species belonging to 8 genera occur only on the New Caledonian mainland or adjacent islands, such as the Ile de Pins, Ile Ouen, and the Iles Belep, which were connected to the mainland during the Pleistocene (Gibbons 1985, fig. 3). These species are limited in vagility by saltwater-permeable eggs (all), specific habitat requirements (such as rainforest; e.g., some *Rhacodactylus*), and low resistance to desiccation (e.g., *Nannoscincus*).

The carphodactyline geckos *Rhacodactylus, Eurydactylodes,* and *Bavayia* represent a natural group that has invaded Australia (Bauer 1986, in press). King (1987) has proposed a Gondwanan origin for geckos as a whole and subsequent phylogenesis associated with the breakup of the supercontinent. We believe that evidence supports the origin of the subfamily Diplodactylinae as a result of the isolation (both geographical and climatical) of eastern Gondwanaland from its neighbors. Immunological investigations in the context of molecular clock dating suggest that the New Caledonian carphodactylines last shared a common ancestor with Australian members of the group at least 66 mybp (King 1987; Bauer and Rainey in prep.). This is compatible with the accepted age of the opening of the Tasman and Coral seas some 80 mypb (see Bauer 1986 for complete discussion).

The origin of the endemic skinks of New Caledonia is less easily explained. *Phoboscincus bocourti* and *Geoscincus haraldmeieri,* following the reasoning outlined above, probably arrived as a result of over-water rafting of a *Eugongylus*-like ancestor. Most of the remaining taxa fall into Greer's (1974) *Leiolopisma* group and were arranged by Sadlier (1986) into the genera *Leiolopisma* sensu stricto, *Caledoniscincus, Tropidoscincus, Marmorosphax,* and *Sigaloseps.* The first genus is apparently paraphyletic, but Sadlier (1986) grouped its New Caledonian members and the following three genera as each other's closest relatives, with *Sigaloseps, Graciliscincus,* and *Nannoscincus* (including the Australian *N. maccoyi*) as separate lineages. Even after the reshuffling of *Leiolopisma,* the biogeography of the group makes no more sense than it did following Greer's generic concepts (see Zug 1985b), and neither vicariance nor dispersal hypotheses alone adequately account for the observed distribution patterns.

The minor radiation of some taxa such as *Tropidoscincus* and *Nannoscincus* in New Caledonia demonstrates that the New Caledonian land mass is large enough and diverse enough ecologically to have supported "continental" speciation (sensu Diamond 1984) in reptiles. The occurrence of the purportedly monophyletic *Leiolopisma* group skinks certainly suggests a long period of evolution in isolation in New Caledonia. Unfortunately, the absence of a broader, explicit phylogenetic hypothesis for the Lygosominae does not permit an application of narrative historical biogeographical methods (sensu Humphries and Parenti 1986), nor are the phylogenies of other biotic components of the region well established enough to effectively utilize the analytical approach of cladistic biogeography. The scincids thus represent the most glaring gap in our general understanding of the zoogeography of the New Caledonian herpetofauna.

Within New Caledonia, some ecogeographic trends are seen. Most noticeably there is a faunal element which, via the vegetation, is tied to the regions of lateritic soils that cover about one third of the land area of the mainland (O.R.S.T.O.M. 1981; Morat et al. 1986; Jaffré et al. 1987). This group includes *Graciliscincus shonae, Tropidoscincus roehssii, Sigaloseps deplanchei, Nannoscincus mariei, Rhacodactylus auriculatus,* and *R. sarasinorum.* All of these taxa occur only in the southern third of the island, the largest single region of lateritic soils. Unfortunately, the exact nature of the relationship between the soil type and these lizards is unclear, although the effect of soil on the peculiar "New Caledonian growth form" of much of the flora is well known (Jaffré 1980).

Other components of the endemic fauna appear to have ranges associated with pluviometric features of the island. The greatest diversity of species occurs on the more humid east coast, where the winter wet season is most pronounced. This is especially true of geckos (Bauer 1986) and

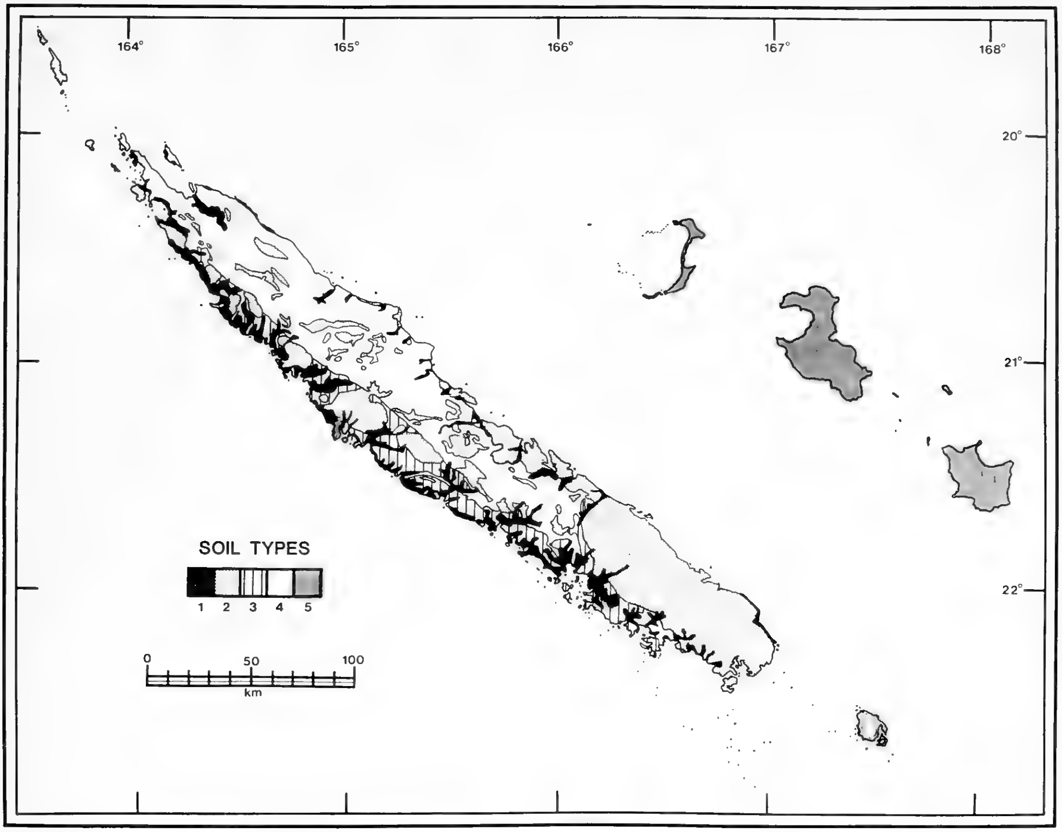

FIGURE 5. Soil types of New Caledonia; 1, alluvial soils; 2, feralitic soils on ultramafic rocks; 3, brown soils over basic rocks; 4, other non-carbonate soils; 5, carbonate soils. Many patterns of intra-island endemism are associated with the lateritic soil types (2 in legend), especially in the large continuous region in southern New Caledonia. (Map modified from Atlas de la Nouvelle-Calédonie et Depéndences, 1981, O.R.S.T.O.M., Paris.)

the sub-fossorial skink species (Sadlier 1986). Elevation appears to play less of a role in New Caledonia than on other high islands, and there are no known high-elevation endemics, although herpetological investigations of the many peaks over 1,000 m has been limited and should have high priority for future research.

Perhaps one of the most intriguing features of the zoogeography of New Caledonia concerns the taxa now extinct, including meiolaniid turtles (Gaffney et al. 1984), mekosuchian crocodiles (Buffetaut 1983; Balouet and Buffetaut 1987), and varanids (Gaffney et al. 1984). All of these animals were probably contemporaneous with man. The occurrence of these fossil forms is somewhat unsettling, as they disrupt the established picture of reptile distribution in the Pacific and may weaken existing hypotheses if applied in the context of cladistic biogeography. Their presence again raises the question of the role of man in shaping the present herpetofauna, not only by means of introductions, but by extinction as well (Cassels 1984; Steadman 1985). For example, *Varanus* may have been a native form that was exterminated by early settlers, or, as in Palau and the Caroline islands, it may have been brought to New Caledonia as food and subsequently died out. Fossil geckos and skinks (perhaps including new taxa) have also recently been discovered, but probably predate the arrival of man in New Caledonia (Balouet and Olson 1989).

The addition of both phylogenetic and geologic hypotheses that are well corroborated has added much to the progress in interpretation of the herpetofauna of New Caledonia. Perhaps the most significant insights since the work of Roux (1913) are that (1) some faunal elements, such as the carphodactyline geckos and some of the skinks, are probably present as the result of vicariant events associated with the breakup of Gondwanaland (Bauer 1986, in press), and (2) the recognition that the fauna of the region, like that of other Pacific high islands (Gibbons 1985; Bauer 1988a, b), is a mosaic of elements derived from a variety of sources.

Among the priorities for establishing a firmer understanding of the biogeography of the new Caledonian herpetofauna are: (1) the erection of an explicit hypothesis of lygosomine relationships; (2) the genetic analysis of Pacific populations of widespread taxa in order to trace potential migration or transport routes (this work has already begun, e.g., Ineich 1988; Moritz 1987); and (3) the study of additional fossil material that may indicate a once broader faunal diversity. Perhaps most basically, more locality data and careful field work in neglected regions of New Caledonia, particularly fossorial and montane habitats, are needed in order to establish the patterns of ecogeographic variation and complete the herpetofaunal list for the region.

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DEEP-WATER OCTOPODS (MOLLUSCA; CEPHALOPODA) OF THE NORTHEASTERN PACIFIC

By

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Abstract: Descriptions and illustrations are given of nine species of Octopoda from depths of 1,000 m to 4,000 m off the coast of Oregon. Eight are new: *Grimpoteuthis bathynectes, G. tuftsi, Benthoctopus robustus, B. canthylus, B. oregonensis. B. yaquinae, B. macrophallus,* and *Graneledone pacifica.* Four genera are treated: *Cirroteuthis* and *Grimpoteuthis* of the Cirrata and *Benthoctopus* and *Graneledone* of the Incirrata. *Cirroteuthis muelleri* is first recorded from the Pacific Ocean and is redescribed. The genus *Benthoctopus* in the North Pacific is discussed and a provisional key for the nine recognized species is provided. The variability and form of the radula of *Graneledone* are considered to be due to degeneracy and not primitiveness, and to lack of selective feeding pressure.

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INTRODUCTION

The deep-water octopod fauna of the northeastern Pacific below 2,000 m is poorly known. Little research on the systematics of deep-sea octopods has been completed since Robson's (1932) monograph, with the exception of Voss's (1976) partial revision of *Graneledone.* Two recent papers, however, provide important reviews of the evolution, phylogeny, and biogeography of deep-sea octopods and relevant background for this paper (see Voss 1988a, b).

The present paper is based on a unique collection of about 90 specimens of deep-water octopods, all from the continental slope and two abyssal plains off the Oregon coast. The specimens were collected by the ships CAYUSE, ACONA and YAQUINA of Oregon State University (OSU) in depths from 1,000 to nearly 4,000 m, with most of the material from depths in excess of 2,500 m. Most of the specimens belong to new species in the genera *Grimpoteuthis* and *Benthoctopus,* with the largest series of specimens in the genus *Graneledone.* All three of these poorly known genera consist of a large number of species, most of which were inade-

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[1] Deceased January 23, 1989.

quately described and illustrated; thus, reference to type material was necessary.

All of the type specimens of deep-water octopods from the northern Pacific in the collections of the United States National Museum of Natural History (USNM) were borrowed, but their poor condition prevented direct comparison of many features. There was little non-type material at the USNM, although some fine specimens of *Graneledone verrucosa* were borrowed for comparison with the Pacific specimens.

In 1975 Voss traveled to Europe to examine the extensive collections at the British Museum (Natural History), the Muséum National d'Histoire Naturelle in Paris, and the Institut Océanographique in Monaco. Much of the type material was in poor condition and its examination failed to assist in the comparisons except in a few cases which bore indirectly upon the problems of the Oregon material. Specimens of *Benthoctopus* were borrowed from Takashi Okutani, Tokai Regional Fisheries Research Laboratory (currently Tokyo University of Fisheries). Examination of these specimens confirmed the separate identity of *B. canthylus,* but left the others in doubt.

Characters previously used to identify deep-water octopods were not sufficient for species recognition. Therefore the specimens were carefully dissected, and when possible, detailed observations were made for each species of the beaks, radulae, digestive tracts, genitalia, spermatophores, and stellate ganglia, as well as the more traditional counts and measurements. All these features were illustrated.

We hope that the details given here will permit positive identification of new material from the northeastern Pacific without necessitating the onerous, frustrating, and detailed examination of every specimen, as encountered in this study. The deep-sea benthic octopods are, however, in need of monographic revision.

CLASSIFICATION OF NORTHEASTERN PACIFIC DEEP-WATER OCTOPODS

- Suborder Cirrata Grimpe, 1916
  - Family Cirroteuthidae Keferstein, 1866
    - Genus *Cirroteuthis* Eschricht, 1836
      - *Cirroteuthis muelleri* Eschricht, 1836
  - Family Opisthoteuthidae Verrill, 1896
    - Genus *Grimpoteuthis* Robson, 1932
      - *Grimpoteuthis bathynectes* new species
      - *Grimpoteuthis tuftsi* new species
- Suborder Incirrata Grimpe, 1916
  - Family Octopodidae Orbigny, 1845
    - Subfamily Bathypolypodinae Robson, 1928
      - Genus *Benthoctopus* Grimpe, 1921
        - *Benthoctopus robustus* new species
        - *Benthoctopus canthylus* new species
        - *Benthoctopus oregonensis* new species
        - *Benthoctopus yaquinae* new species
        - *Benthoctopus macrophallus* new species
    - Subfamily Graneledoninae Voss, 1988a
      - Genus *Graneledone* Joubin, 1918
        - *Graneledone pacifica* new species

MATERIALS AND METHODS

Collections were made with 2.7 to 3.0 m wide beam trawls with 13 mm (stretch) mesh and with otter trawls having a 7 m foot rope and 38 mm mesh with a 13 mm mesh liner in the cod end. Both nets were towed at two knots (3.7 km hr^{-1}) (see Carey and Heyamoto 1972 for descriptions of nets and sampling methods). Over 600 tows were taken on the continental slope and abyssal plains in the northeastern Pacific from depths of 400 to 5,180 m, 32 to 2,225 km offshore, between 1961 and 1974 (Fig. 1, see Pearcy et al. 1982 for details). Of these, 164 tows were from 2,500 to 3,045 m on the Cascadia Abyssal Plain, about 400 tows from 400 to 2,780 m on the continental slope off Oregon, and 35 tows from 2,780 to 5,182 m on the Tufts Abyssal Plain. Octopods from this study were captured at depths from 1,000 m on the continental slope to 3,932 m on Tufts Abyssal Plain from the research vessels ACONA, CAYUSE and YAQUINA. One specimen was caught in a trap at 3,660 m on the Aleutian Abyssal Plain.

Collections, including octopods, were preserved in 10% formalin and seawater at sea. Octopods were moribund or dead after capture, so they were not relaxed or killed prior to preservation.

After the cruises, the muscular, firm-bodied specimens were transferred to 70% ethanol, while the soft-bodied forms were stored in 40% isopropyl alcohol. The delicate cirroteuthids were stored in 10% formalin. Most of the material was transferred to 70% ethanol in Miami. Material stored in formalin, especially cirroteuthids, showed signs of deterioration. Storage in ethanol results in some shrinkage but is preferrable to loss of the specimens.

All descriptions of color are based upon spec-

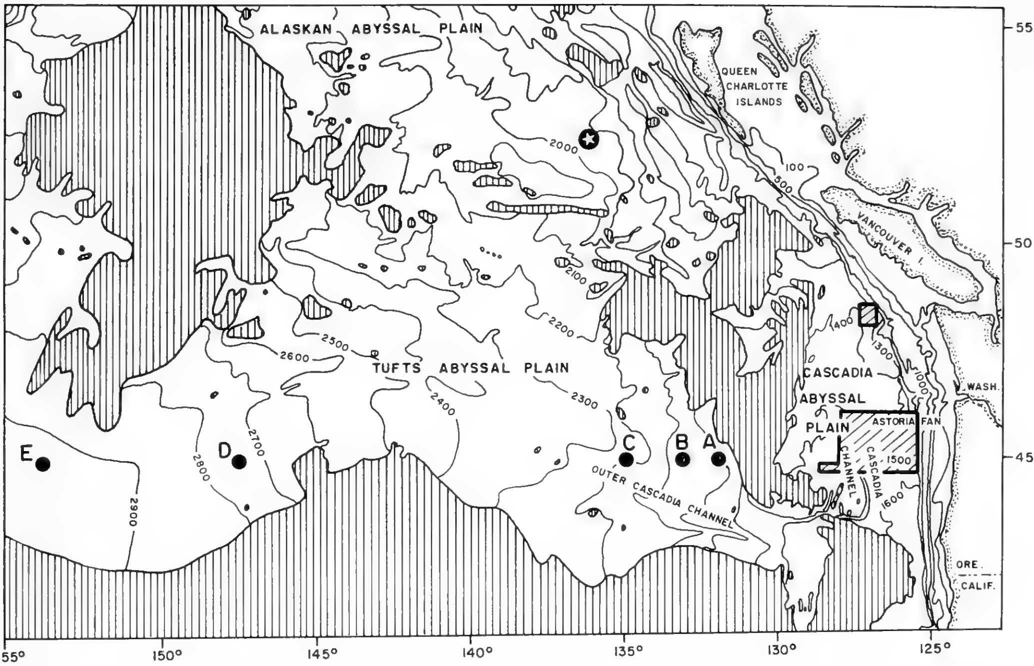

FIGURE 1. Location of trawl collection areas on the continental slope, Cascadia Abyssal Plain, and Tufts Abyssal Plain. Obliquely hatched areas denote general sampling areas on Cascadia Plain, solid dots specific sampling stations on Tufts Plain and the slope. The station on the Alaskan Abyssal Plain shows the location of capture for one *Benthoctopus robustus* in a trap. Vertical hatched areas indicate ridges and hilly topography.

imens preserved in ethanol. No color notes were made of living specimens.

All specimens were carefully examined, and measurements, body proportions, and counts were obtained from the whole animals as described by Voss (1963). The mantle of all specimens was opened to permit examination of the internal anatomy and to count gill lamellae. The digestive tract and genitalia were dissected to permit detailed descriptions and illustrations for each species. Because of the paucity of good specific characters in these octopods, the buccal mass was removed from nearly all specimens and the beaks and radulae extracted, cleaned, and illustrated. The buccal mass was typically immersed in tap water with one or two pellets of potassium hydroxide and gently heated. Beaks and radular ribbons were cleaned in household bleach solution (Chlorox). The beaks were illustrated lying free in a Petri dish, while the radulae were mounted in either Euparol or CMC 10 and drawn with the aid of a camera lucida. The radular ribbon of *Grimpoteuthis tuftsi* was destroyed if the buccal mass was treated as described above; even quick cleaning in bleach caused some radular ribbon deterioration.

Spermatophores were obtained only from *Benthoctopus*. They were so large that mounting was impractical; they were described and illustrated lying free in a Petri dish.

Special attention has been given to the stellate ganglion, particularly in the cirroteuthids, as this structure appears to be of systematic value. The ganglion and its associated nerve fibers were dissected from the mantle wall, mounted on a slide, and drawn with the aid of a camera lucida.

The indices used are those defined by Voss (1963) with the exception of those for fin length (FLI) and width (FWI) of cirroteuthids and the hectocotylized arm index (HcAI), which is expressed as a percentage of the length of its fellow arm on the opposite side. The range and mean of ratios and measurements is given as follows: 60–*80*–100, in which the italicized number is the mean. All measurements are in mm unless otherwise stated.

The cirroteuthids present certain problems not encountered in other octopods, e.g., the method of taking measurements of the cirri, the fins, and the mantle length. Some writers have considered that the cirri can contract differentially depending on the type and strength of the preservative. However, cirri lengths do not vary appreciably within a species and average cirri lengths for conspecific animals are the same whether preserved in formalin, isopropyl alcohol, or ethanol. The cirrus length was taken from the longest cirrus on the arms and measured intact from the base to the tip. In some very flaccid specimens the cirrus was removed, stretched out on a glass slide, and measured.

Fin measurements entailed a reconsideration of terms applied both to squid and cirroteuthids. In squid, fin width is the greatest width across the fins measured from outer angle to outer angle, while length is measured from the anterior lobe to the posterior insertion or the tip of the mantle in fins united posteriorly. This measurement is misleading, however, when applied to the paddle-like fins of cirroteuthids, where fin length was measured from the midpoint of a line drawn across the fin base to the outer angle of the fin. There is considerable difference in measurements made along the posterior and anterior margins, particularly if the fins are directed somewhat anteriorly. Fin width is measured across the individual fin at the widest point when the fin is flattened to include the delicate thin anterior border. Fin-width index is expressed as a percentage of fin length. Fin-length index is expressed as a percentage of the interocular width for reasons given below.

Standard length in octopods has conventionally been considered to be the dorsal mantle length (ML) or the length of the body measured from mantle apex to a line drawn across the head from pupil to pupil. In cirroteuthids this measurement is fraught with difficulties. In some species of *Grimpoteuthis* the posterior end of the mantle coincides with the posterior surface of the shell vestige. In others, particularly *Cirroteuthis* and *Stauroteuthis* but also in some *Grimpoteuthis,* in life or in freshly preserved material, the mantle extends well beyond the shell vestige as a gelatinous, often fluid-filled sac, projecting posteriorly equal to the length of the mantle from the interocular line to the shell vestige. In preservation, this mantle extension is often completely contracted against the shell vestige. As a result, discretion must be used, and as Robson (1932) and others have often given fin length as a ratio of the interocular width, the fin-length index used here is expressed similarly.

Holotypes of the new species described are deposited in the United States National Museum of Natural History (USNM). Other material examined, including the paratypes, are in the collections of the California Academy of Science (CAS), the Santa Barbara Museum of Natural History (SBMNH), the invertebrate collections of the Rosenstiel School of Marine and Atmospheric Science, University of Miami (UMML), and USNM.

The Study Area

The area of sampling has been described by Pearcy et al. (1982). Briefly, the steep and topographically complex continental slope off Oregon adjoins Cascadia Abyssal Plain, a basin bordered by submarine ridges on the west and south (Fig. 1). Its floor slopes gradually to the south and west. The Astoria and Nitinat fans, two large Pleistocene fans associated with the Columbia and Fraser rivers, are dominant features of the basin, producing a gradual slope from depths of 2,100 m on the fans adjacent to the slope to over 3,000 m in the southern portion of the basin.

Tufts Abyssal Plain is farther offshore and much less influenced by terrigenous sedimentation than is Cascadia Plain. It is bordered by the East Pacific Rise on the east and hilly seamounts on the south; it is connected with the Alaskan and Aleutian Abyssal plains on the north and west. Depth of the Tufts Plain increases gradually to the west. Cascadia Channel, which originates in Cascadia Plain and penetrates the East Pacific Rise, is the only deepwater connection between Tufts and Cascadia plains.

The sediments of these plains are mainly fine muds and clays. In general the rate of sedimentation and organic carbon content of the sediments decrease from east to west across both plains (Griggs et al. 1969). The biomass of benthic megafauna, both invertebrates and fishes, also decreases from east to west (Carey 1965; Pereyra and Alton 1972; Pearcy et al. 1982).

Systematics

Order Octopoda

Suborder Cirrata Grimpe, 1916

Deep-sea octopods that live on or just above bottom. Body gelatinous to subgelatinous, with lateral paddle-shaped fins, uniserial suckers, and cirri alternating with suckers; shell vestige cartilaginous U-, V-, or saddle-shaped, well developed, serving mainly as fin support; radula may be present. Representatives have been reported from throughout the world ocean.

Family Cirroteuthidae Keferstein, 1866

As currently recognized, this family contains two monotypic genera—*Cirroteuthis* and *Cirrothauma* (see Voss 1988b:296). Body elongate, gelatinous, fragile, colorless to only lightly pigmented except on oral surface of arms and web; cirri long, conspicuous; fins large and wide; simple crop present; radula absent; gills "sepioid"; median pallial adductor vestigial; "secondary" web present; shell vestige saddle-shaped.

Cirroteuthis Eschricht, 1836

With the characters of the family.

Type Species: *Cirroteuthis muelleri* Eschricht, 1836, by monotypy.

Cirroteuthis muelleri Eschricht, 1836

(Fig. 2, 3)

Cirroteuthis muelleri Eschricht, 1836:627, pls. 46–48. Mörch 1857:440. Hoyle 1886:60. Lönnberg 1891:6. Appellöf 1893: 1. Posselt 1898:269. Appellöf 1899:7–8, pl. 1, figs. 6–7. Friele and Grieg 1901:123. Pfeffer 1908:23, fig. 13. Robson 1926: Passim; 1932:130, fig. 18. Grieg, 1933:9.

Sciadephorus muelleri Reinhardt and Prosch, 1846:187, pls. 1–5.

Material Examined (12 specimens all collected by R/V YAQUINA).—2 males, ML 74–79 mm, Cr. Y7102B haul 262, 45°38.3′N, 126°43.8′W in 2,721 m, 17 Feb. 1971, USNM 817580.—1 female, ML 66 mm, Cr. Y7105B haul 276, 45°56.7′N, 127°38.6′W in 2,761 m, 17 May 1971, SBMNH 35142.—1 female, ML 67 mm, Cr. Y7102B haul 263, 45°36.4′N, 126°44.9′W in 2,730 m, 17 Feb. 1971, UMML 31.1935.—1 male ML 72 mm, 1 female ML 21 mm, Cr. Y7105B haul 278, 45°24.0′N, 127°39.0′W in 2,811 m, 18 May 1971, UMML 31.1936.—1 female, ML 64 mm, Cr. Y7102B haul 265, 45°18.6′N, 126°31.5′W in 2,750 m, 18 Feb. 1971, CAS 067786.—1 female, ML 63 mm, Cr. Y7102B haul 270, 44°38.4′N, 126°42.0′W in 2,830 m, 20 Feb. 1971, SBMNH 35143.—2 females, ML 47–63 mm, Cr. Y7102B haul 268, 44°58.8′N, 126°37.4′W in 2,770 m, 19 Feb. 1971, USNM 817581.—1 male, ML 53 mm, Cr. Y7005C haul 230, 44°27.0′N, 132°14.0′W in 3,655 m, 1 June 1970, CAS 067787.—1 female, ML 40 mm, Cr. Y7301F haul 317, 44°44.5′N, 127°29.0′W in 2,810 m, 3 Feb. 1973, CAS 067788.

Description.—Moderately large species with soft, almost gelatinous consistency; body covered by thin, tough, outer layer except on arms and web where easily torn; all of animal very fragile except for parts of internal anatomy.

Mantle elongate, somewhat tubular but gently rounded posteriorly (Fig. 2a), about half as wide as long (Tables 1–4); head width slightly greater than mantle width with no discernible constriction between head and mantle; mantle aperture narrow, mantle fits snugly around funnel; eyes small, fully formed, with large lenses; eyelid absent but skin transparent over orbit.

Funnel long, conical, narrow, free for about half of its length; funnel organ thin, flat, Λ-shaped, with sharp median point and truncate lower limbs; small cup-shaped olfactory organ located about midway on either side of funnel on an edge of shallow funnel groove.

Fins approximately median, located slightly nearer apex of mantle than eyes (Fig. 2a); each fin paddle-shaped, about twice as long as wide (Tables 1–4); posterior edge nearly straight, curves anteriorly just past midpoint; anterior margin strongly rounded and proximally turns posteriorly to form narrower base; heavy muscular portion of fins well developed, usually occupies most of fin width near base, extends at least halfway to fin end; outer lobe of fin nearly forms semicircle; fins do not project at 90° angle from body axis but are directed slightly anteriorly.

Arms translucent, not muscular, appear filled with fluids in life but usually collapsed, wrinkled when preserved. Arm lengths difficult to obtain due to contractions of arms and distortion by contraction of web; measurements therefore approximate. Arms (Fig. 3a) subequal with perhaps lateral arms slightly longest; single row of arm suckers as far as distal attachment of primary web, beyond which arms slender, smooth, devoid of suckers, whip-like; inner oral surface of arms broad and bear suckers, aborally arms narrower, triangular in cross-section, outer edge of arm located inside secondary or intermediate web extends as lamella to outer or primary web.

Primary web with thin tough outer layer that keeps web intact in preserved specimens; primary web usually torn from arms during capture, attached only to arm near tip on dorsal side at point where suckers terminate; arms along rest of their length attached to primary web by dorsal and ventral intermediate webs (Fig. 3a); interior spaces appear to be filled with fluids; dorsal intermediate web begins at base of arms, widest at about midpoint, and tapers to terminate near primary web-attachment point; ventral inter-

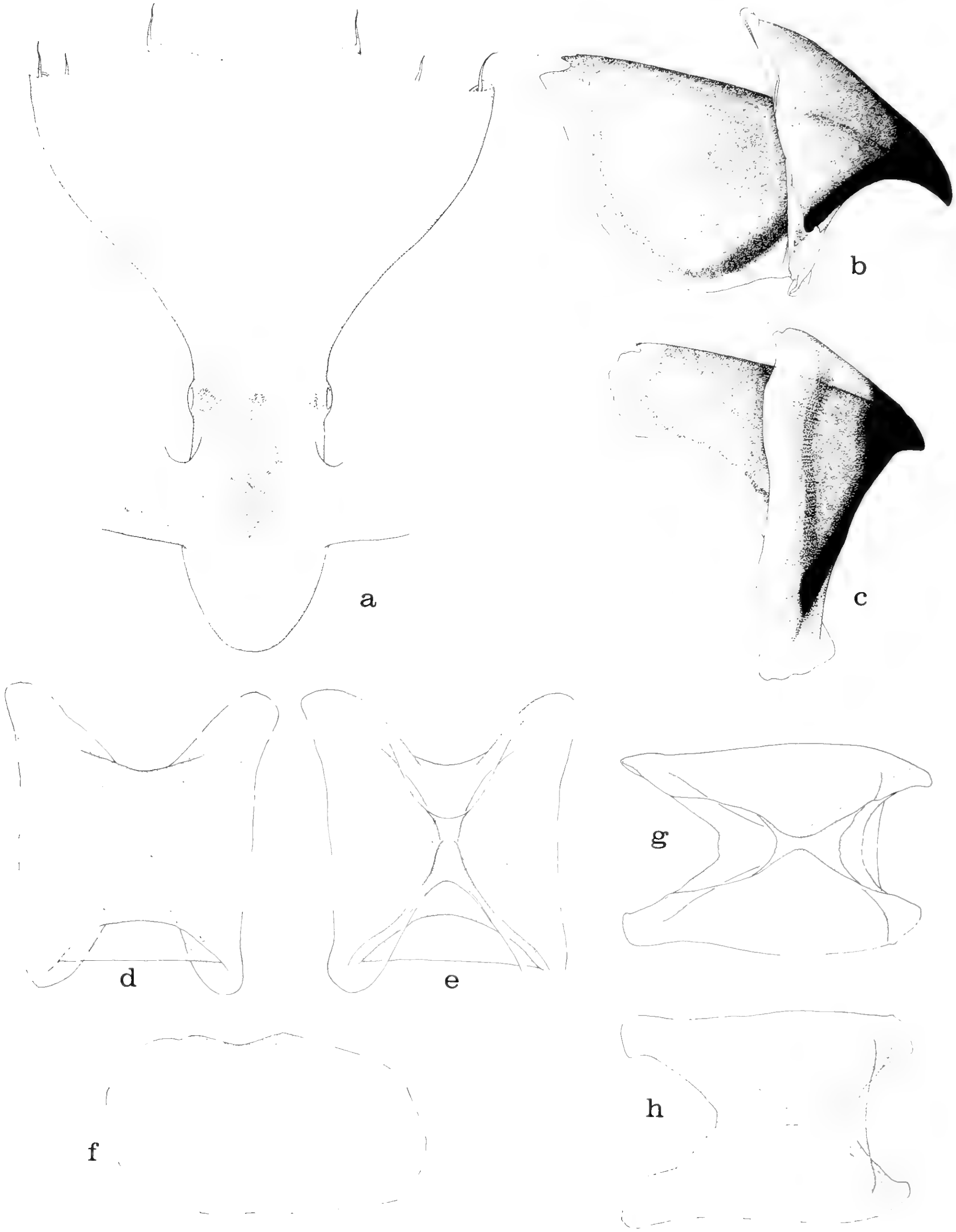

FIGURE 2. *Cirroteuthis muelleri* Eschricht. (a) Dorsal view of male; ML 79 mm. (b–c) Upper and lower beaks. (d–f) Ventral, dorsal, and lateral views of shell vestige of male, 74 mm ML. (g–h) Dorsal and ventral views of shell vestige of male, 53 mm ML.

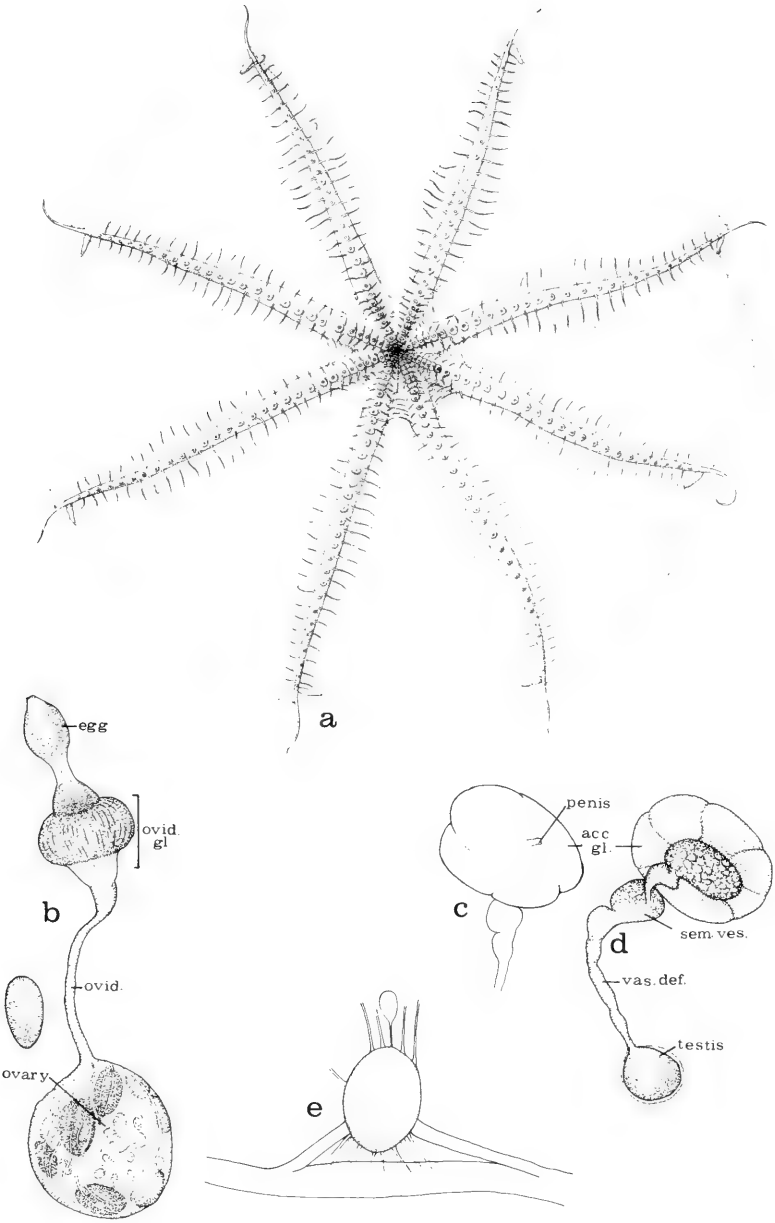

FIGURE 3. *Cirroteuthis muelleri* Eschricht. (a) Oral view of arms and web of male (dorsal side up), 79 mm ML. (b) Genitalia and egg of female, 67 mm ML. (c–d) Genitalia of male, 72 mm ML. (e) Left stellate ganglion.

mediate web originates same as dorsal, is wider, and terminates as moderately wide membrane along inner edge of large, fleshy, thinly tapered process on ventral side of arm a few millimeters proximal to attachment of primary web. This whip-like process (nodule) also the fusion point of primary web, which unites on aboral surface, intermediate web on its oral surface; no indication of unions of webs when viewing primary web aborally.

Suckers small (Tables 1–4); first suckers surrounding mouth small, 2nd and 3rd succeeding suckers usually largest, then size gradually decreases to about 7th or 8th sucker (Fig. 3a). Seven

TABLE 1. Measurements and counts of four males of *Cirroteuthis muelleri* Eschricht, 1836.

	Specimen			
	USNM 817580	USNM 817580	UMML 31.1936	CAS 067787
Mantle length	79.0	74.0	72.0	53.0
Mantle width	47.0	26.0	40.0	27.0
Head width	52.0	34.0	37.0	32.0
Arm length I	170.0	—	145.0	—
Arm length II	178.0	140.0	—	—
Arm length III	170.0	—	—	—
Arm length IV	170.0	—	—	—
Total length	277.0	210.0	222.0	178.0
Fin length	50.0	47.0	47.0	53.0
Fin width	30.0	21.0	30.0	23.0
Sucker diameter	—	1.3	2.1	1.0
Cirrus length	19.2	16.0	18.4	11.0
Gill lamellae	8	9	8	7
Arm formula	21=3=4	—	—	—

TABLE 2. Indices of bodily proportions and counts of four males of *Cirroteuthis muelleri* Eschricht, 1836.

	Specimen				
	USNM 817580	USNM 817580	UMML 31.1936	CAS 067787	$\bar{x}$
ML	79.0	74.0	72.0	53.0	—
MWI	58.7	35.1	55.5	50.4	49.9
HWI	65.0	45.9	51.3	60.3	55.6
MAI	47.0	52.8	49.6	46.9	49.1
ALI	64.2	66.6	65.3	63.4	64.9
SIn	—	1.7	2.9	1.8	2.1
CiI	24.0	21.6	25.6	20.8	23.0
FLI	96.2	138.2	127.0	165.0	131.6
FWI	60.0	44.7	63.8	43.4	52.9

or eight basal suckers cup-shaped, usually raised on broad, heavy pads; suckers smaller distal to 8th sucker, often less than half size of basal suckers, delicate, thin-lipped, often with no apparent suction cup, and formed of two, almost parallel, elements. Sucker bases in undamaged specimens widely spaced, formed of large, delicate, mammilar, fluid-filled structures, surmounted by minute, apparently non-functional sucker cups. When fluid-filled bases collapse, suckers lie flat on arm or appear to be mounted on thin delicate pedicels, according to condition of collapsed bases. Distal to small suckers, at about 28th sucker, normal appearance regained. Ventral web nodule joins at about 3rd or 4th enlarged sucker; suckers gradually become smaller, terminate at union of primary web with arm on dorsal surface; largest of terminal suckers about same diameter as basal suckers.

Cirri small, occur in pairs between either suckers 1 and 2, or 2 and 3, one on each side of sucker slightly proximal to base, appear to alternate with suckers, extend distally to terminal sucker; largest in midportion of arm, attain length of over 19 mm, or 9 to 13 times diameter of largest sucker. (Cirri difficult to measure unless removed from arm and placed on glass slide.)

Gills small, little modified, with 7–8–9 lamellae per outer demibranch, including large, partially divided terminal lamella. Thin, transparent, distinct median pallial adductor muscle, 10–16% ML, unites mantle to viscera; inner attachment on membrane overlaying male or female genitalia in median position.

Posterior third of mantle cavity devoid of structures but filled with tough, viscous, gel-like material that gives body its shape posterior to skeletal structure; may be reservoir for ammonium ions for buoyancy. Area is easily damaged, collapses with too much handling, difficult to measure.

Shell vestige saddle-shaped; originates as flat sheet that curves dorsally on anterior and posterior borders, curls in toward itself, thickens to form supports for large basal fin muscle (Fig. 2d–h).

Beaks thin, weak, and indistinctive (Fig. 2b, c); radula absent, surface normally covered by radula thickened, slightly ridged transversely, bears series of longitudinal folds that resemble lines of various sizes of teeth; cuticular lining not apparent.

Esophagus slender at connection with buccal mass, passes posteriorly between two anterior salivary glands (posterior salivary glands absent); widens into croplike area without diverticulum, but expanded to two to three times diameter of anterior section; posterior to "crop" esophagus narrows, enters distinctly two-parted stomach; spiral caecum nearly as large as both elements of stomach; two large ducts lead into digestive gland through digestive duct appendage; digestive gland round but slightly flattened; intestine large, nearly straight, not divided into parts. Longitudinal folds run full length of intestine, seen clearly through its transparent wall. Ink sac absent; anus without flaps.

Male genitalia unusual (Fig. 3c, d), difficult to compare with those of other octopods: duct from testis large, leads into folded mass with thin-walled out-folding that may correspond to Need-

TABLE 3. Measurements (in mm) of seven females of *Cirroteuthis muelleri* Eschricht, 1836.

	Specimen						
	CAS 067788	USNM 817581	USNM 817581	SBMNH 35143	CAS 067786	SBMNH 35142	UMML 31.1935
Mantle length	40	47	63	63	64	66	67
Mantle width	19	22	32	—	46	43	40
Head width	21	23	35	—	42	42	47
Arm length I	—	—	—	—	114	96	—
Arm length II	—	—	—	—	—	96	—
Arm length III	—	—	—	—	—	94	—
Arm length IV	67	95	108	—	—	91	124
Total length	113	157	190	—	180	172	203
Fin length	41	52	61	52	50.5	46.5	49.5
Fin width	18	24	25	38.0	35.0	36.0	30.0
Sucker diameter	0.6	1.0	1.0	2.1	1.6	1.4	2.4
Cirrus length	8.0	9.0	13.0	16.0	19.2	19.2	13.0
Gill lamellae	7	7	8	8	8	8	7
Arm formula	—	—	—	—	—	1=234	—

ham's sac; distal portion of folded mass smooth with small slender duct (penis?) that protrudes from its center; Needham's sac contains about 10 small ovoid structures, apparently spermatophores (similar to structures found in *Grimpoteuthis*); they do not resemble typical octopodon spermatophore and probably consist only of sperm reservoir.

Female genitalia (Fig. 3b) unpaired, nearly round ovary contains about 12 large, apparently ripe, ovoid, flesh-colored eggs with light wavy linear markings; 10.4 × 9.3 mm; numerous small to minute eggs also present; proximal oviduct single, about 4–5 times length of distal oviduct, rather inflated, swollen at distal end at junction with oviducal gland; oviducal gland large, dark colored, forms ring around oviduct; distal oviduct short, strongly flared at distal opening. Mature egg at end of oviduct, with another lodged in oviducal gland (Fig. 3b) exactly as figured by Reinhardt and Prosch (1846, pl. 4).

Optic ganglia distinct, globular, darkly pigmented, almost same diameter as orbit of eye. The stellate ganglion shown in Figure 3e.

Color in ethanol varies from pale white to purple; inner surfaces of arms and web invariably darkest, purple or purplish-brown.

MEASUREMENTS AND COUNTS.—Males: mantle length 53–*69.5*–79; mantle width 26–*35.0*–47; head width 32–*38.8*–52; arm length I 145–170, II 140–178, III 170, IV 170; total length 178–*221.8*–277; fin length 47–*49.3*–53; fin width 21–*26*–30; sucker diameter 1–*1.5*–2.1; cirrus length 11.0–*16.2*–19.2; number of gill lamellae 7–*8*–9.

Females: mantle length 40-*58.6*–67; mantle width 19–*33.3*–46; head width 21–*35.0*–47; arm length I 96–114, II 96, III 94, IV 67–*97*–124; total length 113–*169.2*–203; fin length 41–*50.4*–61; fin width 18–*29.4*–38; sucker diameter 0.6–*1.4*–2.4; cirrus length 8.0–*13.9*–19.2; number of gill lamellae 7–*7.6*–8.

TYPE.—Zoological Museum, Copenhagen. Robson (1932: 130) erroneously stated that it was in Naturhistorischen Verein of Breslau and Bonn. In a letter to Robson from Sparck dated 8 February 1932, Sparck stated that Robson had made a mistranslation and that the holotype is in the Zoological Museum of Copenhagen (see Kristensen and Knudsen 1983).

TYPE-LOCALITY.—Jakobshavn, West Greenland (Eschricht 1836:627).

DISCUSSION.—A careful examination of the 12 specimens available has revealed no important differences between our material and the descriptions of *Cirroteuthis muelleri* given in the literature (Eschricht 1836; Reinhardt and Prosch 1846; Robson 1932). Some minor differences occur.

Robson (1932:131) drew attention to a peculiar modification of the small suckers on the arms of the British Museum specimen—they were flat. If he referred to the sucker only and not its total base, this condition is also found in our specimens. Eschricht's fig. 1 indicates that the median suckers were smaller in the type, and the coloration seems to indicate that they were on large mammilar bases, just as in our specimens.

The differences in the origin of the cirri (often

TABLE 4. Indices of bodily proportions and counts of seven females of *Cirroteuthis muelleri* Eschricht, 1836.

	Specimen						
	CAS 067788	USNM 817581	SBMNH 35143	USNM 817581	CAS 067786	SBMNH 35142	UMML 31.1935
ML	40	47	63	63	64	66	67
MWI	47.5	46.8	—	50.8	71.9	65.2	59.7
HWI	52.5	48.9	—	55.6	65.6	63.6	70.2
MAI	59.7	49.5	—	58.3	56.1	68.8	54.0
ALI	59.3	60.5	—	56.8	63.3	55.8	61.1
SIn	1.5	2.1	3.3	1.6	2.5	2.1	3.6
CiI	20.0	19.2	25.4	20.6	30.0	29.1	19.4
FLI	195.2	226.0	—	174.0	120.0	110.7	105.3
FWI	44.0	46.2	73.1	40.9	69.3	77.4	60.6

between the 1st and 2nd suckers in our specimens, only between the 2nd and 3rd in the others) seems to be a matter of individual variation. In our specimens cirri may first appear between suckers 1 and 2 in some arms and between 2 and 3 on other arms. Often only one cirrus is present between 1 and 2, both cirri between 2 and 3.

Robson (1929:26) pointed out the possible systematic value of the size of the mantle aperture, and in *C. muelleri* indicated that while Eschricht's original description showed a wide aperture (Robson's 'C'), the British Museum specimen has a small aperture (at least 'B'). We believe the original illustration is of a very flaccid and perhaps stretched specimen. Our specimens all show at least the B condition and often A.

The shape of the fins also is different. Both Eschricht (1836) and Reinhardt and Prosch (1846) show broad flabellate fins with a very unnatural appearance. We believe that this is artistic treatment; our specimens show a remarkable homogeneity of appearance and closely correspond to the more detailed structure shown in pl. 5, fig. 1 of Reinhardt and Prosch (1846).

A more basic difference is the presence or absence of a median pallial adductor muscle. This is discussed by Robson (1932:119–120), who stated that there was no median adductor in the British Museum specimens. A thin but distinct median adductor is present in our specimens; it is easily overlooked because it is small and transparent. Robson was not noted for the delicacy of his dissections and it is possible that, being familiar with the thick, muscular adductors of the Incirrata, he overlooked the pallial adductor in his specimen. Voss examined two fine USNM specimens of *C. muelleri* obtained by the R/V WALTHER HERWIG in the North Atlantic. Both had the narrow, transparent, easily overlooked median pallial adductor muscle.

DISTRIBUTION.–*Cirroteuthis muelleri* was previously known only from the northern part of the North Atlantic (see Robson 1932:130; Voss 1988b). Its presence in the northeastern Pacific indicates either a very broad distribution or a discontinuous circumboreal pattern (Ekman 1953:161). While the shallow waters of the Arctic Ocean may be a barrier, vertical distribution there is not limited by temperature, as shown by the capture of *Cirrothauma murrayi* in an ice hole off Point Barrow (Voss 1967:527). Furthermore, cirromorphs resembling *Cirroteuthis* have been photographed in the Arctic Ocean in 2,360 to

3,786 m (Pearcy and Beal 1973), suggesting a continuous distribution through the Arctic Ocean.

Family OPISTHOTEUTHIDAE Verrill, 1896

Body gelatinous to semigelatinous; bell-shaped or disc-like; fins long to small, and lateral to superior (dorsal); simple crop present or absent; radula present or absent; gills "half orange" type; median pallial adductor present; web single; shell vestige U- or V-shaped. This family contains two genera: *Opisthoteuthis* and *Grimpoteuthis* (Voss 1988b).

Grimpoteuthis Robson, 1932

TYPE SPECIES: *Cirroteuthis umbellata* Fischer, 1883:404. By original designation, Robson (1932: 136).

Grimpoteuthis bathynectes new species

(Figs. 4, 5)

MATERIAL EXAMINED (15 specimens all collected by R/V YAQUINA).—Holotype: male, ML 50 mm, Cr. Y7210A haul 308, 45°01.1′N, 135°12.0′W in 3,932 m, USNM 730715. Paratypes: 2 males ML 46.5–48 mm, 1 female ML 31 mm, Cr. Y7210A haul 300, 44°58.1′N, 132°14.7′W in 3,585 m, 10 June 1972, CAS 067789.—1 male, ML 42 mm, Cr. Y7105B haul 281, 44°38.5′N, 127°39.5′W in 2,816 m, 19 May 1971, SBMNH 35144.—1 male ML 30 mm, 1 female ML 85 mm, Cr. Y7210A haul 303, 45°05.1′N, 133°10.9′W in 3,700 m, 10 July 1972, UMML 31.1938.—1 female, ML 57 mm, Cr. Y7005C haul 232, 44°40.2′N, 133°35.7′W in 3,742 m, 3 June 1970, SBMNH 35145.—2 males, ML 17.5–53 mm, Cr. Y7210A haul 299, 44°56.8′N, 132°11.5′W in 3,580 m, 10 June 1972, UMML 31.1937.—1 male, ML 17 mm, Cr. Y7210A haul 307, 45°03.5′N, 134°45.0′W in 3,900 m, 10 Oct. 1972, CAS 067790.—2 males ML 30–36 mm, 1 female ML 29 mm, Cr. Y7210A haul 305, 45°05.2′N, 134°43.4′W in 3,900 m, 9 Oct. 1972, USNM 817582.—1 male, ML 28 mm, Cr. Y7206B haul 288, 44°06.2′N, 125°22.7′W in 2,940 m, 14 June 1972, CAS 067791.

DIAGNOSIS.—A *Grimpotheuthis* with long fins; short cirri; suckers largest proximally, suckers of males larger than those of females; gills compact with 7–9 lamellae; radula absent.

DESCRIPTION.—Mantle saccular (Fig. 4a), little more than half as wide as long, rounded posteriorly; aperture narrow, of type B; head wider than mantle, not set off by neck region; eyes large, somewhat protruding.

Funnel large, projects far beyond mantle margin, distal quarter or less free; funnel organ broad, thick-limbed, ∧-shaped pad with all angles rounded.

Fins long, moderately wide, situated about halfway between apex of mantle and eyes; posterior margin nearly straight, tips rounded with slight point, anterior margin convex, turning slightly posteriorly at line of mantle to form minor constriction; fins with narrow muscular base, muscular area extends about three-quarters of length of fins.

Arms gelatinous, moderately long, subequal, stout, deeply set into thick web. Arm formula generally I.II.III.IV.

Web single (secondary web absent), thick, fleshy, soft; web formula variable, usually ABCDE; in most large males sector C on left side noticeably larger than C on right; web depth about half arm length, extensive along arms but unequally distributed; large fleshy nodule or finger-like process located on ventral side of arms (Fig. 4b), about one-half to two-thirds of arm length from base, unites web to ventral side of arms, beyond which web may extend only very short distance; nodules on dorsal side of arms absent, web extends to, or nearly to, tip of each arm. Consequently, sector A lacks processes, so web extends to tip of arm on both sides to make this sector deepest; conversely, web sector E is the shallowest with nodules on each side of arms.

Suckers in single row extend from mouth to tips of arms. Dorsal arms with 47 to 58 suckers set into oral surface, their apertures projecting freely; first four to five suckers small to minute, followed by abruptly larger suckers that gradually increase in size for about one-third arm length, after which they gradually decrease in size to arm tip. Suckers over proximal half of arms largest, abruptly enlarged suckers absent indicating lack of hectocotylization; considerable sexual dimorphism in size and shape of suckers (Tables 5–8); in males, suckers (Fig. 4d) larger (SIn 4.3–6.7), more globular, with short, narrow apertural rims that rise from free globular bases where web usually joins suckers; suckers in females and small males (Fig. 4c) smaller (SIn 2.6–3.5), globular base missing or nearly so, and whole sucker smaller, tubular, more erect than those of large males, without webbing between suckers.

Cirri short, about two-thirds to 1.5 sucker diameter in length; located on sides of arms between bases of suckers (Fig. 4c, d), they first appear between suckers 3 and 4 and extend to tips of arms.

Median pallial adductor thin, narrow, length 2.8–9.2% ML. Gills compact, spherical, of "half orange" or *Opisthoteuthis* type (Robson 1932: 124), 7–9 lamellae per gill, closely packed, slightly rugose in appearance.

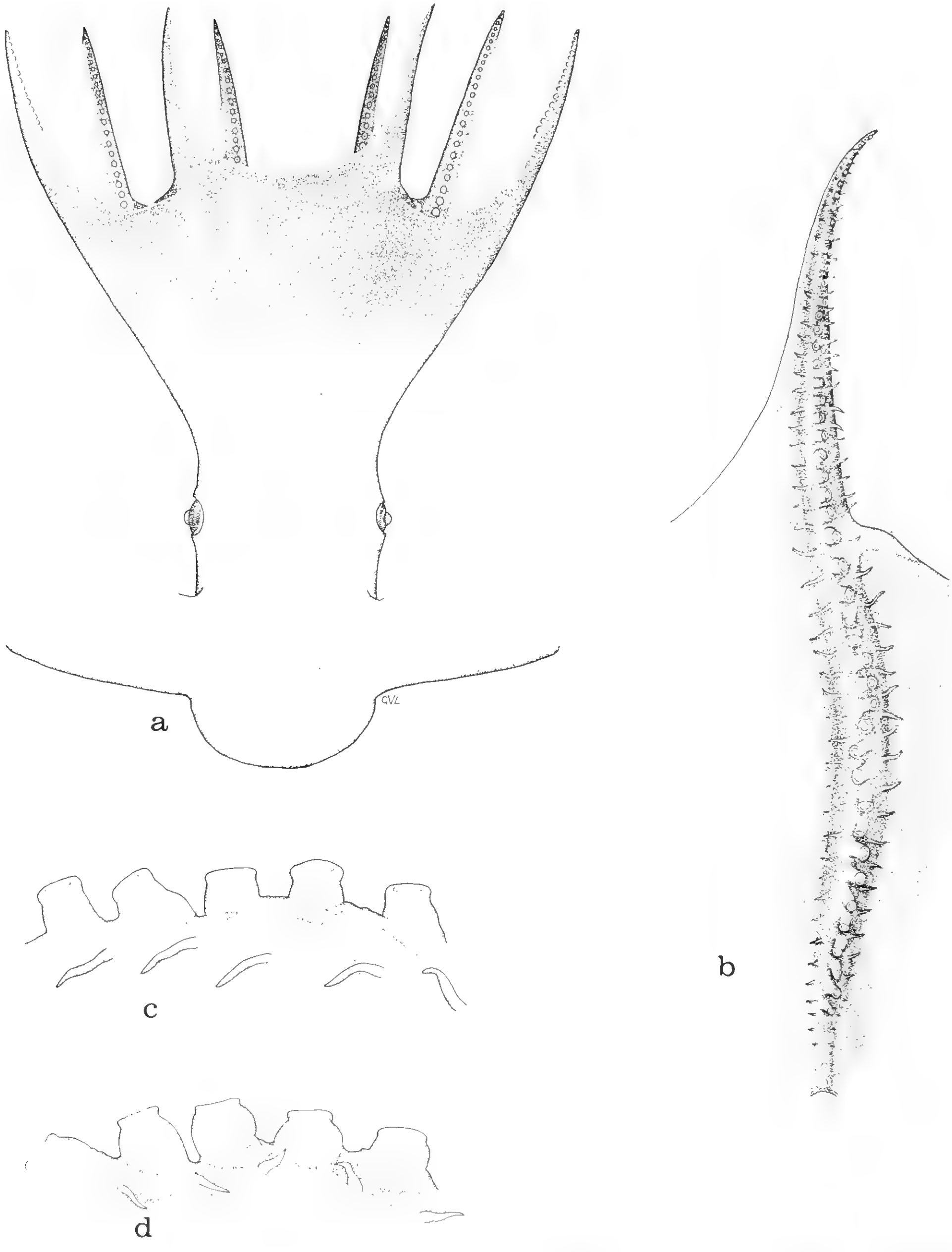

FIGURE 4. *Grimpoteuthis bathynectes* new species. (a) Dorsal view of holotype, USNM 730715, male, 50 mm ML. (b) Oral view of left dorsal arm of male, 50 mm ML. (c) Suckers and cirri of female, 58 mm ML. (d) Suckers and cirri of male, 42 mm ML.

Digestive tract of male shown in Figure 5a; beaks shown in Figure 5d, e. Radula absent; anterior salivary gland apparently absent, two small oval white bodies immediately adjacent and ventral to buccal mass may represent posterior salivary glands; esophagus widens gently posterior to buccal mass but does not form crop; stomach slightly two-parted; buccal mass, esophagus, and stomach densely covered with deep reddish-purple gelatinous tissue, obscuring details until removed; caecum large with strong, almost complete turn; digestive ducts stout, lead from

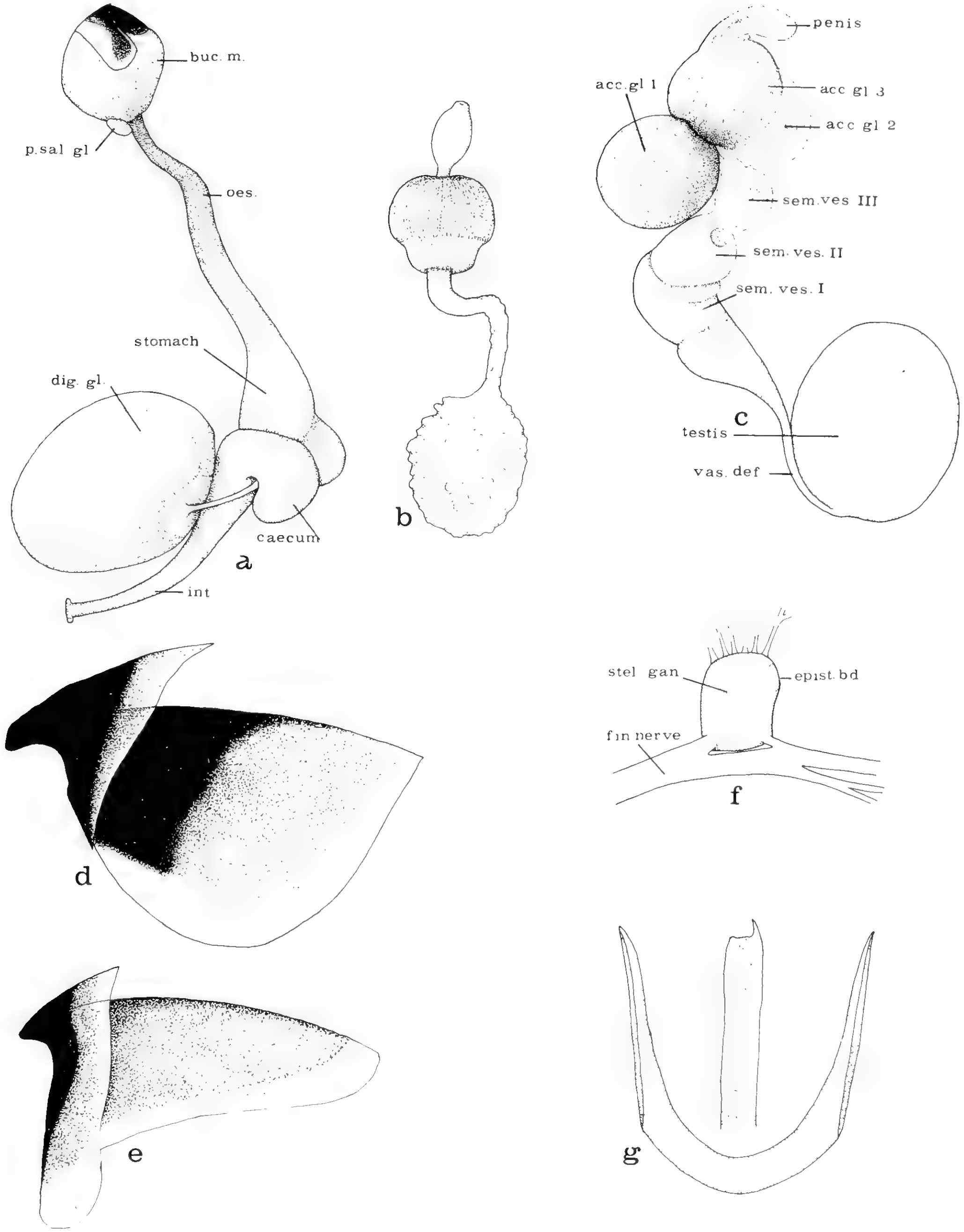

FIGURE 5. *Grimpoteuthis bathynectes* new species. (a) Digestive tract of male, 53 mm ML. (b) Genitalia of female, 85 mm ML. (c) Genitalia of male, 53 mm ML. (d–e) Upper and lower beaks of male, 53 mm ML. (f) Left stellate ganglion of male, 53 mm ML. (g) Dorsal view of shell vestige and lateral view of end, male, 53 mm ML.

caecum-stomach to digestive gland, pass through small but distinct digestive duct appendage area; digestive gland small, globular; intestine small, stout, straight; anal flaps and ink sac absent.

Male genitalia complicated (Fig. 5c). Spermatophores present, similar to those in *Cirroteuthis.*

Female genitalia (Fig. 5b) simple, unpaired;

TABLE 5. Measurements (in mm) of 11 males of *Grimpoteuthis bathynectes* new species.

	Specimen										
	CAS 067790	UMML 31.1937	CAS 067791	USNM 817582	UMML 31.1938	USNM 817582	SBMNH 35144	CAS 067789	CAS 067789	USNM 730715	UMML 31.1937
Mantle length	17	17.5	28	30	30	36	42	46.5	48	50	53
Mantle width	11	14	25	23	16	29	28	34	30	36	38
Head width	17	17	28	31	26	35	32	42	44	41	51
Arm length I	47	45	73	81	58	116	151	116	141	132	135
Arm length II	46	43	67	76	59	103	146	112	147	124	131
Arm length III	43	43	63	73	49	100	134	116	146	115	125
Arm length IV	39	40	59	70	49	103	129	100	137	106	119
Total length	76	70	94	106	85	151	200	156	195	170	190
Fin length	—	19	28	24	35	31	40	39	41	42	43
Fin width	6	10	12	14	13	16	21	19	20	21	22
Sucker diameter	0.6	0.7	1.0	1.2	1.0	2.0	2.8	2.0	3.0	3.0	2.7
Cirrus length	1.0	0.7	1.0	1.0	1.0	2.0	2.5	2.0	2.5	2.2	3.0
Gill lamellae	7	8	8	9	7	7	7	7	7	9	9
Suckers on I	47	48	47	52	48	52	49	53	52	57	50
Arm formula	1234	1234	1234	1234	2134	1234	1234	1324	2134	1234	1234

TABLE 6. Indices of bodily proportions and counts of 11 males of *Grimpoteuthis bathynectes* n. sp.

	Specimen										
	CAS 067790	UMML 31.1937	CAS 067791	USNM 817582	UMML 31.1938	USNM 817582	SBMNH 35144	CAS 067789	CAS 067789	USNM 730715	UMML 31.1937
ML	17	17.5	28	30	30	36	42	46.5	48	50	53
MWI	64.7	80.0	89.3	76.7	53.3	80.6	66.7	73.1	62.5	72.0	71.7
HWI	100.0	97.1	100.0	103.3	86.7	97.2	76.2	90.3	91.7	82.0	96.2
MAI	34.0	38.0	37.8	36.6	50.0	30.5	27.1	39.7	32.2	37.3	38.7
ALI	65.8	65.7	78.7	77.4	70.6	78.2	77.5	75.0	76.0	78.8	72.1
SIn	3.5	4.0	3.6	4.0	3.3	5.6	6.7	4.3	6.3	6.0	5.1
CiL	5.9	4.0	3.6	3.3	3.3	5.6	6.0	4.3	5.2	4.4	5.7
FLI	—	111.8	100.0	77.4	134.6	88.6	125.0	92.9	93.2	102.4	84.3
FWI	—	52.6	42.9	58.3	37.1	51.6	52.5	48.7	48.9	50	51.2
Arm formula	1234	1234	1234	1234	2134	1234	1234	1324	2134	1234	1234

Table 7. Measurements (in mm) of four females of *Grimpoteuthis bathynectes* new species.

	Specimen			
	USNM 817582	CAS 067789	SBMNH 35145	UMML 31.1938
Mantle length	29	31	57	85
Mantle width	16	18	32	67
Head width	24	19	39	59
Arm length I	72	65	124	143
Arm length II	78	72	104	150
Arm length III	73	60	101	143
Arm length IV	67	56	99	141
Total length	95	110	185	240
Fin length	26	28	33	39
Fin width	10	14	21	24
Sucker diameter	1.0	1.0	1.5	3.0
Cirrus length	1.5	1.5	1.5	3.0
Gill lamellae	7	7	8	7
Suckers on I	51	51	58	58
Arm formula	2314	2134	1234	2134

Table 8. Indices of bodily proportions and counts of four females of *Grimpoteuthis bathynectes* new species.

	Specimen			
	USNM 817582	CAS 067789	SBMNH 35145	UMML 31.1938
Mantle length	29	31	57	85
MWI	55	58	56	79
HWI	83	62	69	70
MAI	36	42	46	56
ALI	84	66	67	63
SIn	3.5	3.2	2.6	3.5
CiI	5.2	4.8	2.6	3.3
FLI	108.3	147.4	84.6	66.1
FWI	38.5	50.0	63.6	61.5
Arm formula	2314	2134	1234	2134

ovary of largest female small with no mature eggs; proximal oviduct long, slender; oviducal gland two-parted, proximal third white, distal two-thirds very dark brown to almost black, both parts strongly and finely plicate; distal oviduct about one-third length of proximal oviduct, slender proximally but broadens distally, appears bulbous.

Shell vestige in male (Fig. 5g) deep, U-shaped, formed of rounded-edged flat strip that tapers to thin flat point distally; fin insertions long and form slight angle near base with rounded apex.

Stellate ganglion of male illustrated in Figure 5f.

Color of mantle and head grayish, tinged with purplish brown; posterior edges of fins lined with dark reddish brown; aboral surface of arms and web dark purple or reddish brown; oral surface of arms and web deep purplish brown or chocolate, often with light brown or flesh-colored suckers.

Measurements and Counts.—Holotype: mantle length 50; mantle width 36, head width 41; arm length I 132, II 124, III 115, IV 106; total length 170; fin length 42; fin width 21; sucker diameter 3.0; cirrus length 2.2; number of gill lamellae 9; number of suckers on arm I 57.

Males: mantle length 17–*36.2*–53; mantle width 11–*25.8*–38; head width 17–*33.0*–51; arm length I 45–*99.5*–141, II 43–*95.8*–147, III 43–*91.5*–146, IV 39–*86.5*–137; total length 70–*135.8*–200; fin length 19–*34.2*–43; fin width 6–*15.8*–22; sucker diameter 0.6–*1.8*–3.0; cirrus length 0.7–*1.7*–3.0; number of lamellae 7–*7.7*–9; number of suckers on arm I 47–*50.5*–57.

Females: mantle length 29–*50.5*–85; mantle width 16–*33.3*–67; head width 19–*35.3*–59; arm length I 72–*101.0*–143, II 78–*101.0*–150, III 60–*94.3*–143, IV 56–*90.8*–141; total length 95–*157.5*–240; fin length 26–*31.5*–39; fin width 10–*17.3*–24; sucker diameter 1–*1.6*–3; cirrus length 1.5–*1.9*–3.0; number of gill lamellae 7–*7.3*–8; number of suckers on arm I 51–*54.5*–58.

Type.—Holotype, male, 50 mm ML, USNM 730715 (fixed in formalin and preserved in 50% isopropyl alcohol).

Type-locality.—Off Oregon, Tufts Abyssal Plain, 45°01.1′N, 135°12.0′W, 3,932 m.

Discussion.—Only two species of *Grimpoteuthis*, *G. hippocrepium* (Hoyle, 1904) and *G. albatrossi* (Sasaki, 1920) have been reported from the North Pacific Ocean (Voss 1988b). *Grimpoteuthis hippocrepium* was poorly described from a mutilated specimen and is unrecognizable as far as many important characters are concerned. The type (USNM 382467) is in very poor condition and little can be learned from it. *Grimpoteuthis albatrossi* is well described (Sasaki 1929: 7) but the type (USNM 332949) dried up, and although it has been realcoholed, it is nearly worthless for comparative studies. As Robson remarked (1932:150), *G. albatrossi* resembles the Atlantic *G. grimaldi* (Joubin, 1903) in having small fins and large suckers near the tips of arms. Neither of these species resembles *G. bathynectes*. It appears closely related to *G. umbellata* (Fischer, 1883), but differs from that species in the shape of the shell vestige, particularly in the muscle insertion, the digestive tract, the male

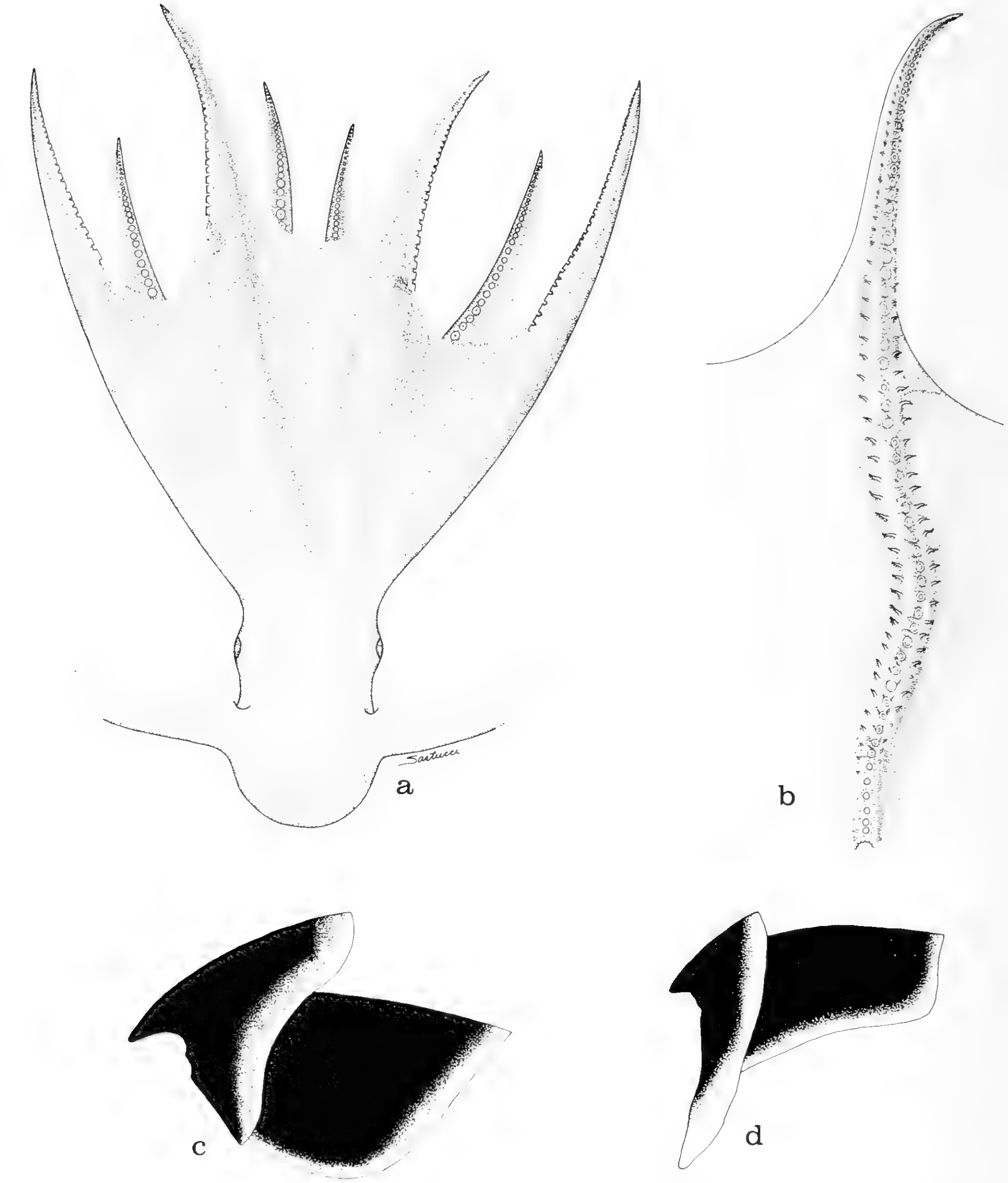

FIGURE 6. *Grimpoteuthis tuftsi* new species. (a) Dorsal view of male, 93 mm ML. (b) Oral view of left dorsal arm of same. (c–d) Upper and lower beaks of male, 72 mm ML.

genitalia, and the shape of the stellate ganglion. Examination of the syntypes in Museum National d'Histoire Naturelle, Paris, did not aid in clarifying the picture; the larger syntype had a different sucker arrangement but the shell vestige was missing; the syntype specimen may be a different species.

While many problems exist in the genus, present material is sufficiently distinct to warrant description as a new species. The specific name *bathynectes* is from the Greek and means deep swimmer.

Thirteen specimens of *G. bathynectes* were collected from Tufts Abyssal Plain and two were from Cascadia Plain. Sampling effort was greater on the Cascadia Plain, hence this species inhabits

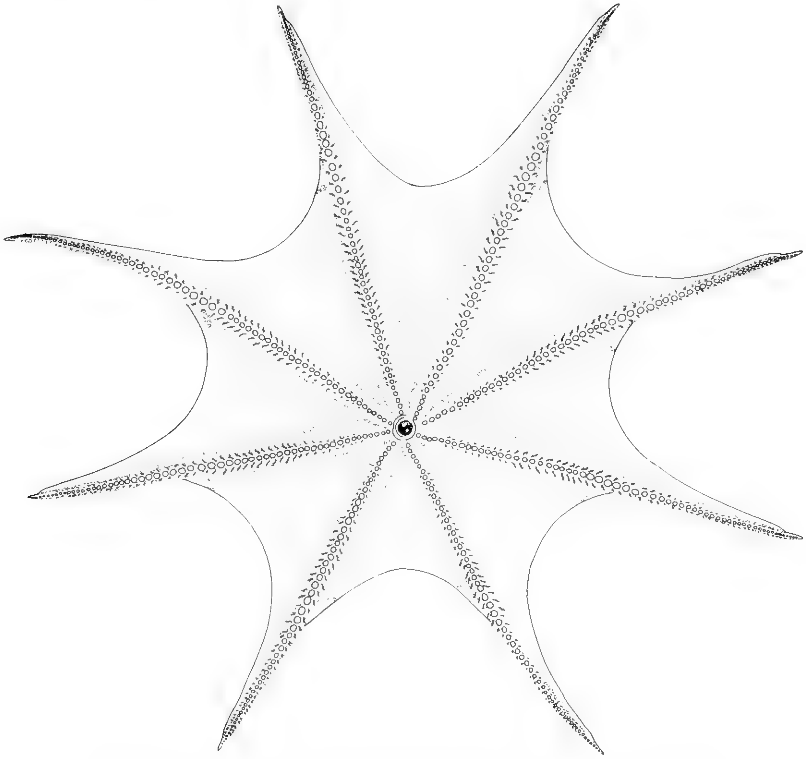

FIGURE 7. *Grimpoteuthis tuftsi* new species. View of web, arms and suckers.

deeper offshore waters and may be found in other abyssal waters of the North Pacific.

Grimpoteuthis tuftsi new species

(Figs. 6–8)

MATERIAL EXAMINED (7 specimens, all collected by R/V YAQUINA):—Holotype: male, ML 101 mm, Cr. Y7210A haul 305, 45°05.2′N, 134°43.4′W in 3,900 m, 9 Oct. 1972, USNM 730714. Paratypes: 1 male, ML 72 mm, Cr. Y7210A haul 300, 44°58.1′N, 132°14.7′W in 3,585 m, 6 Oct. 1972, UMML 31.1939.—1 male, ML 93 mm, Cr. Y7210A haul 302, 44°58.0′N, 133°14.5′W in 3,700 m, 7 Oct. 1972, CAS 067792.—1 male, ML 100 mm, Cr. Y7210A haul 306, 45°02.0′N, 134°42.2′W in 3,900 m, 9 Oct. 1972, SBMNH 35146.—1 female, ML 65 mm, Cr. Y7210A haul 307, 45°03.5′N, 134°45.0′W in 3,900 m, 10 Oct. 1972, UMML 31.1940.—2 females, ML 74–102 mm, Cr. Y7210A haul 305, 45°05.2′N, 134°43.4′W in 3,900 m, 9 Oct. 1972, USNM 817583.

DIAGNOSIS.—A *Grimpoteuthis* with long fins; long cirri; suckers largest distally at web border, suckers of males and females of equal size; gills loosely arranged, with 7–8 lamellae; radula present.

DESCRIPTION.—Mantle (Fig. 6a) saccular, flaccid, width nearly three-quarters length, rounded posteriorly; aperture moderately narrow (27–39% ML); head wider than mantle, not set off by neck region; eyes large, protrude slightly.

Funnel large, broad, projects well beyond mantle margin, distal third or quarter free; funnel organ thick; ʌ-shaped pad covers most of funnel; olfactory organ distinct round tubercle on each side of funnel at corners of aperture.

Fins long, moderately wide, united to mantle about halfway from apex; posterior margin nearly straight for about three-quarters of its length, then turns forward; anterior margin rounded, tip somewhat pointed, base narrow, stout; muscular portion of fins extend for more than half fin length.

Arms somewhat gelatinous, moderately long, stout, deeply set in web. Arm formula generally I.II.III.IV. but varies.

Web (Fig. 7) simple, thick, fleshy; secondary web absent; web formula variable, generally ABCDE; web depth about half arm length; web unequal on two sides of arms (Fig. 6b): on dorsal side web extends nearly to tip of arm, on ventral side nodule or lappet present at about midpoint of arm, apparently strengthener for web attachment; web ends slightly distal to nodule.

Suckers (Fig. 8a) extend in single row from

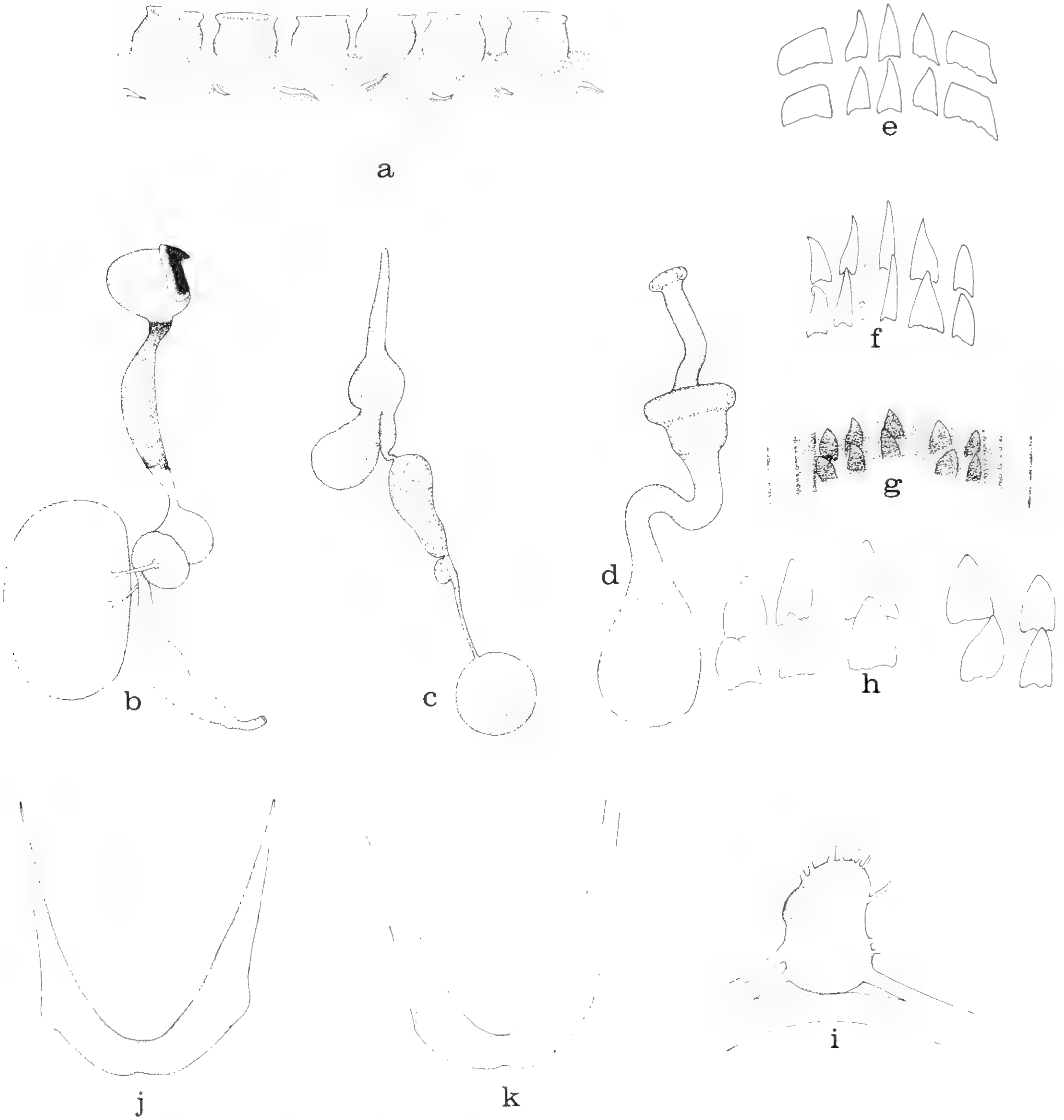

FIGURE 8. *Grimpoteuthis tuftsi* new species. (a) Lateral view of suckers and cirri of male, 93 mm ML. (b) Digestive tract of male, 72 mm ML. (c) Genitalia of male, 72 mm ML. (d) Genitalia of female, 65 mm ML. (e) Radula of male, 72 mm ML. (f) Radula of female, 65 mm ML. (g–h) Radula of male, 93 mm ML; g is uncleaned, h cleaned with ribbon transparent. (i) Stellate ganglion from right side of male, 100 mm ML. (j–k) Ventral and dorsal view of shell vestige of male, 72 mm ML.

mouth to tip of arms; dorsal arms with about 63 to 75 small suckers (SIn 2.5–5.3) set into oral surface of arms with raised apertures; suckers cylindrical or tubular with small apertures, set about two to three sucker diameters apart in some sections but crowded together in others, united by thin transparent web or membrane along oral surface of arms (Fig. 8a). First 6–7 suckers small, then a gradual increase in size to their maximum diameter at or just beyond level of ventral nodule. No sexual dimorphism (Tables 9, 10).

Cirri moderately long, longest 1.5 to 3.5 times longer than diameter of largest suckers; first appear between suckers 5 and 6, or 6 and 7 and extend to arm tip; difficult to distinguish near tip.

Median pallial adductor thin, narrow, length 5.4–11.8% mantle length. Gills nearly spherical

TABLE 9. Measurements (in mm) of four males and three females of *Grimpoteuthis tuftsi* new species.

	Specimen						
	UMML 31.1939	CAS 067792	SBMNH 35146	USNM 730714	UMML 31.1940	USNM 817583	USNM 817583
Sex	M	M	M	M	F	F	F
Mantle length	72	93	100	101	65	74	102
Mantle width	49	75	69	63	50	52	64
Head width	60	101	98	73	60	67	78
Arm length I	289	309	322	312	207	224	285
Arm length II	275	288	320	295	186	222	238
Arm length III	260	270	283	258	170	210	250
Arm length IV	217	261	261	239	—	208	253
Total length	346	457	475	460	285	322	460
Fin length	65	90	95	85	59	60	81
Fin width	30	38	40	31	27	29	35
Sucker diameter	3.8	4.0	4.5	2.5	2.5	2.5	3.0
Cirrus length	6.0	9.0	8.0	9.0	9.0	6.0	5.0
Gill lamellae	8	8	8	7	8	8	7
Suckers on I	71	67	73	63+	69	74	75
Arm formula	1234	1234	1234	1234	1234	1234	1432

("half orange" type), 7 to 8 lamellae per gill, not tightly compacted as in *G. bathynectes,* lamellae rather loose and somewhat elongate in overall appearance; filaments branch off each lamella distinctly separated, to form overlapping leaflike layers.

Digestive tract of 72 mm ML male (Fig. 8b). Beaks (Fig. 6c, d) lack specifically distinct characters. When beaks removed from buccal mass, dark brown radular ribbon discovered. Radulae removed from three animals, cleaned in KOH, and mounted in CMC10. Ribbon delicate, all of dark brown pigment lost and ribbon partly eaten away in four or five seconds. Radulae show great variation (Fig. 8e–h). Female of 65 mm with five homodont teeth, rachidian tall, slender (Fig. 8f); second and third laterals broad to slender triangular, both narrow on one side of band, wide on other; traces of small first laterals in some rows on one side but not on other; no trace of marginal teeth or plates. Radula from 72 mm male (Fig. 8e) with five teeth in a row, three median ones (rachidian and second laterals?) elongate triangular; third laterals broad, flat-topped teeth, those on one side sharply truncate. Teeth from 101 mm male (Fig. 8g, h) all broadly triangular.

Posterior salivary glands absent; esophagus widens in mid-part to form simple crop, entire length covered by dark purple tissue. Esophagus narrows abruptly before entering small round stomach; spiral caecum equal in size to stomach,

TABLE 10. Indices of bodily proportions of four males and three females of *Grimpoteuthis tuftsi* new species.

	Specimen						
	UMML 31.1939	CAS 067792	SBMNH 35146	USNM 730714	UMML 31.1940	USNM 817583	USNM 817583
Sex	M	M	M	M	F	F	F
Mantle length	72	93	100	101	65	74	102
MWI	68.1	80.7	69.0	62.4	76.9	70.3	62.8
HWI	83.3	108.0	98.0	72.3	92.3	90.5	76.5
MAI	24.2	30.0	29.4	31.9	30.7	31.5	34.0
ALI	85.8	67.8	71.6	69.6	64.4	73.0	65.2
SIn	5.3	4.3	4.5	2.5	3.9	3.4	2.9
CiI	8.3	9.7	8.0	8.9	13.9	8.1	4.9
FLI	108	89	97	116	98	90	104
FWI	46	42	42	37	46	48	43
Arm formula	1234	1234	1234	1234	1234	1234	1432

two ducts lead to large round digestive gland; digestive duct appendage prominent; intestine short, inflated; anal flaps and ink sac absent.

Male genitalia complex (Fig. 8c), differ from those of *G. bathynectes*; various glands and their numbering not yet determined; both genitalia similar, spermatophores absent.

Female genitalia (Fig. 8d) simple (immature); large, deflated, thin-walled ovary, eggs absent; proximal oviduct thick, comparatively short; oviducal gland large, two-parted, finely plicate; distal oviduct long, comparatively slender, aperture with flared, incised, or plicate collar.

Shell vestige (Fig. 8j, k) U- or rounded V-shape; stout, strong, somewhat constricted at posterior end; limbs angle slightly at outer posterior inception of fin insertion area, taper to thin, flat, straplike, truncated tips.

Stellate ganglion of male shown in Figure 8i.

Mantle and head pigmented light brownish purple, posterior borders of fins dark purple; web, arms darkish purple aborally, dark purple orally with lighter colored suckers and cirri.

MEASUREMENTS AND COUNTS.—Holotype: mantle length 101; mantle width 63; head width 73; arm length I 312, II 295, III 258, IV 239; total length 460; fin length 85; fin width 31; sucker diameter 2.5; cirrus length 9.0; number of gill lamellae 7; number of suckers on arm 63+.

Males: mantle length 72–*91.5*–101; mantle width 49–*64*–75; head width 60–*83*–101; arm length I 289–*308*–322, II 275–*294.5*–320, III 258–*267.8*–283, IV 217–*244.5*–261; total length 346–*434.5*–475; fin length 65–*83.8*–95; fin width 30–*34.8*–40; sucker diameter 2.5–*3.7*–4.5; cirrus length 6–*8.0*–9; number of gill lamellae 7–*7.8*–8; number of suckers on arm I 67–*70.3*–73.

Females: mantle length 65–*80.3*–102; mantle width 50–*55.3*–64; head width 60–*68.3*–78; arm length I 207–*238.7*–285; II 186–*215.3*–238; III 170–*210*–250, IV 208–253; total length 285–*355*–460; fin length 59–*66.7*–81; fin width 27–*30.3*–35; sucker diameter 2.5–*2.7*–3.0; cirrus length 5–*6.7*–9; number of gill lamellae 7–*7.7*–8; number of suckers on arm I 69–*72.7*–75.

TYPE.—Holotype, male, 101 mm ML, USNM 730714 (fixed in formalin and preserved in 50 percent isopropyl alcohol).

TYPE-LOCALITY.—Off Oregon on the Tufts Abyssal Plain, 45°05.2′N, 134°43.4′W, 3,900 m.

DISCUSSION.—*Grimpoteuthis tuftsi* is somewhat similar to *G. bathynectes* but many characters differentiate them. *Grimpoteuthis tuftsi* has: lack of sexual dimorphism in sucker shape, longer cirri, different genitalia, more elongate gills with separate lamellae, enlarged suckers near nodules, larger funnel organ, and a radula.

The discovery of a radula in this species, unknown elsewhere in the cirrate octopods, requires a careful reexamination of all species, as its absence has been taken for granted by some earlier students of the group and may have been overlooked. It is obviously degenerate and in its simplicity, variability, and loss of teeth resembles the radula of *Graneledone pacifica* (described in this work) and *G. antarctica* (Voss, 1976). Similarly, the radulae of *Thaumeledone* and *Vosseledone* show degeneration in the near loss of all teeth except the rachidian. We hypothesize that in these genera the radula is degenerate and in the process of being lost because of diet and loss of selective pressure.

All specimens of *G. tuftsi* were caught in bottom trawls on Tufts Abyssal Plain, none in Cascadia Basin nearer the North American continent.

Suborder INCIRRATA Grimpe, 1916

Deep-sea, shallow-water, and pelagic octopods with gelatinous to muscular bodies; fins and cirri absent; shell, when present, reduced to pair of slender cartilaginous or calcareous stylets; radula present in all known species; suckers uniserial or biserial; representatives known from throughout world oceans.

Family OCTOPODIDAE Orbigny, 1845

Benthic octopods with semigelatinous to muscular bodies.

Subfamily BATHYPOLYPODINAE Robson, 1928

Restricted to benthic octopods with biserial suckers; hectocotylus well developed; crop large with diverticulum reduced or absent; ink sac absent; radula *Octopus*-like to degenerate.

Benthoctopus Grimpe, 1921

Deepwater octopods of normal *Octopus*-like appearance with short to long arms; suckers biserial; hectocotylus *Octopus*-like, ligula slightly to moderately excavated with indistinct midrib, smooth or bearing low, often indistinct rugae, never laminate; crop present, usually with diverticulum; ink sac absent; radula usually with strongly, seldom weakly, multicuspid rachidian; body entirely smooth, papillae or ocular cirri absent.

Type Species: *Octopus piscatorum* Verrill, 1879:470. By original designation, Grimpe 1921:299.

Discussion.—Examination of Verrill's type specimen (USNM 574641) has shown that it probably is not a *Benthoctopus* but more likely belongs to *Bathypolypus* (personal observation by Voss). If this proves correct, the name *Benthoctopus* should be preserved to maintain nomenclatural stability in this group.

Benthoctopus robustus new species

(Figs. 9, 10)

Material Examined (2 specimens).—Holotype: male, ML 137 mm, R/V ACONA Sta. NAD22, 44°38.5′N, 126°03.8′W in 2,800 m, 1 June 1963, USNM 729994. Paratype: 1 male, ML 114 mm, 140 nautical miles off Tasu Sound, Queen Charlotte Island, B.C., Canada, 52°27′42″N, 135°34′36″W in 3,660 m, 16 Oct. 1978, in sablefish trap, E. Houde, USNM 730895.

Diagnosis.—A *Benthoctopus* with large, strong, transversely ridged lingula; long, sharp calamus; radula with simple rachidian with cusps.

Description.—Body (Fig. 9a) compact, robust, muscular; mantle nearly round, about as wide as long (MWI 80.3), no distinct neck region; head small, narrow (HWI 51.8); eyes and eyelids small; mantle aperture wide.

Funnel large, free for about half of its length, aperture small; funnel organ (Fig. 9f) large, W-shaped, with long, pointed lateral limbs that project slightly anterior to large, round median limb.

Arms (Table 11) moderately long (MAI 64.3; ALI 56.7), stout at base (AWI 12.4), taper to stout, sharp tips, arm formula IV.I.II.III, subequal; web heavy, deep (WDI 34.7), extending along ventral side of arms for about two-thirds their length; web formula DBCAE; suckers biserial, erect on stout bases, well separated, rather small (SIn 5.1) for size of animal; enlarged suckers absent; dorsal arms with about 38–40 suckers.

Third right arm hectocotylized, shorter than its fellow (HcAI 85.1), stout, bordered ventrally by heavy, thickened, in-rolled web that forms incomplete spermatophoral groove, ligula (Fig. 9b) large (LLI 12.4), with deep groove and thickened margins crossed by 14–16 grooves and membranous ridges or folds; calamus large, long, slender, sharply pointed (CLI 45.4).

Gills large with 11 lamellae per outer demibranch.

Upper beak with very small, sharp, curved rostrum (Fig. 9g); rostrum of lower beak forms right angle at jaw angle (Fig. 9h). Radulae with rachidian somewhat different from other Pacific *Benthoctopus* (Fig. 10d, e), rachidian simple, narrow, with smooth-sided, slender darkened portion bordered by narrow clear portion that bears small, irregular cusps, one on each side; admedians with tall sharp ectocone; inner edges of second laterals strongly, smoothly rounded in holotype, nearly straight in paratype; third laterals slender, sabre-like, curved.

Esophagus slender, leads into distinct crop with anterior diverticulum (Fig. 9d, e); crop of holotype unexpanded, without food; posterior esophagus expanded leading into large muscular stomach; spiral caecum small; digestive gland nearly spherical; intestine three-parted, middle section more inflated and larger than others; anal flaps and ink sac absent.

Male genitalia (Fig. 10a): penis very large (PLI 58.4) with long diverticulum; Needham's sac long, filled with incomplete spermatophores (spermatophore partially reconstructed in Fig. 10b); horn end with three tight turns at oral end (Fig. 10c).

Mantle, head, and arms smooth, cirri and papillae absent. Color in ethanol pale tan with light reddish-brown pigmentation on ventral side of head, around and on funnel, around eyes, and on web, which is darkish purple near margins; no color notes made at time of capture.

Measurements and Counts.—Holotype: mantle length 137; mantle width 110; head width 71; length of longest arm (IV) 213; total length 375; length of hectocotylized arm 116.6; ligula length 14.5; calamus length 6.6; number of suckers on arm I 38–40; sucker diameter 7.0; depth of web sector D 73.9; penis length 80; number of gill lamellae in outer demibranch 11.

Type.—Holotype, male, 137 mm ML, USNM 729994 (fixed in formalin and preserved in 50% isopropyl alcohol).

Type-locality.—Oregon, off Newport, eastern portion of Cascadia Abyssal Plain, 44°38.5′N, 126°03.8′W, 2,800 m.

Discussion.—This species seems distinct from all other known species on the basis of the simple rachidian and the ligula. Elucidation of its rela-

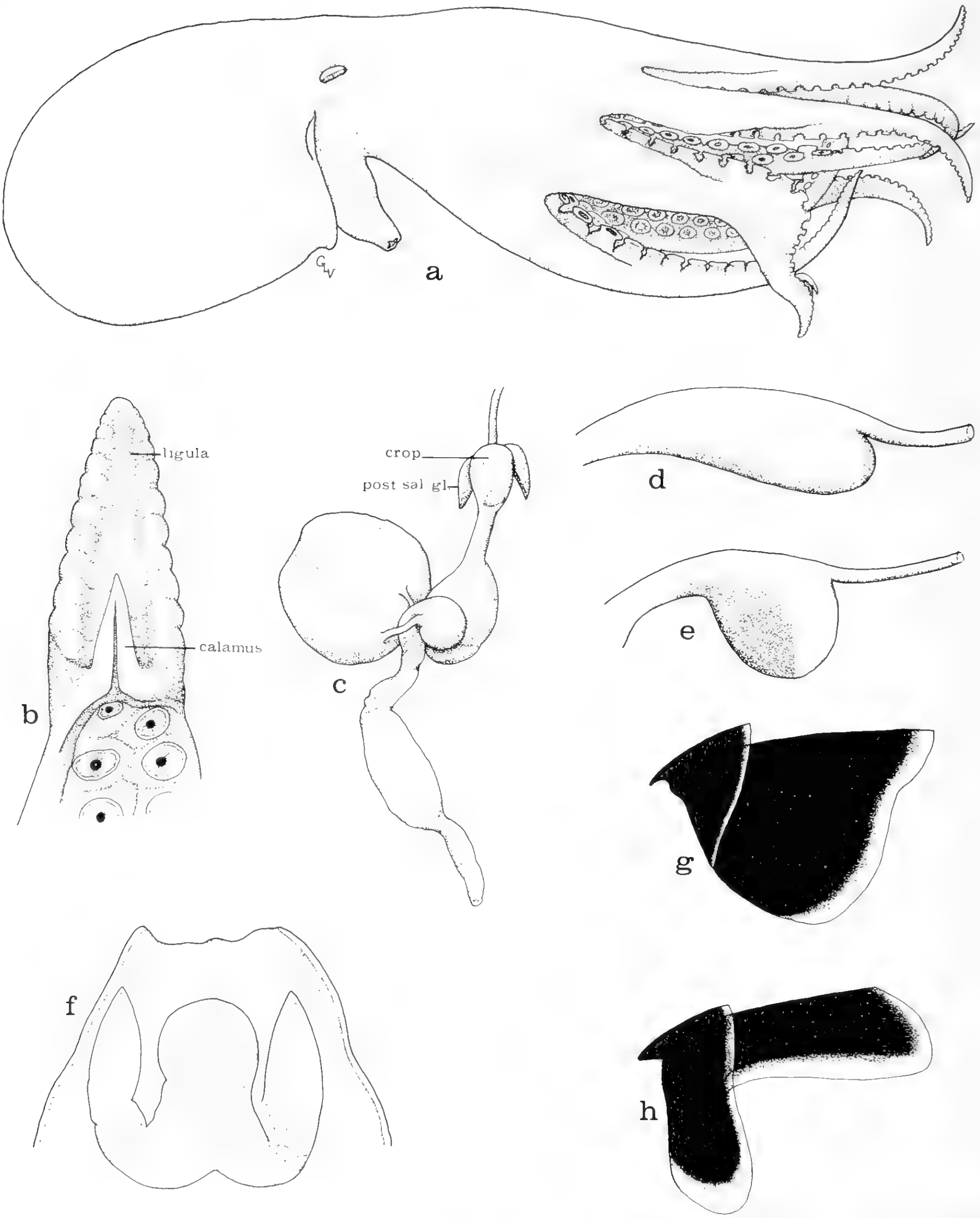

FIGURE 9. *Benthoctopus robustus* new species. (a) Lateral view of holotype, USNM 729994, male, 137 mm ML. (b) Ligula. (c) Digestive tract of paratype, USNM 730895, male, 49 mm ML. (d) Crop of holotype. (e) Crop of paratype. (f) Funnel organ of holotype. (g–h) Upper and lower beaks of holotype.

tionship within the genus must await more material and a full revision of the genus.

The specimen designated as the paratype was found in the collections of the USNM. It was examined to supplement the information on this new species. Although taken somewhat farther north and in deeper water than the holotype, it corresponds very closely in the meristic counts and morphology of ligula, calamus, and funnel organ. The upper beak, however, has a smooth

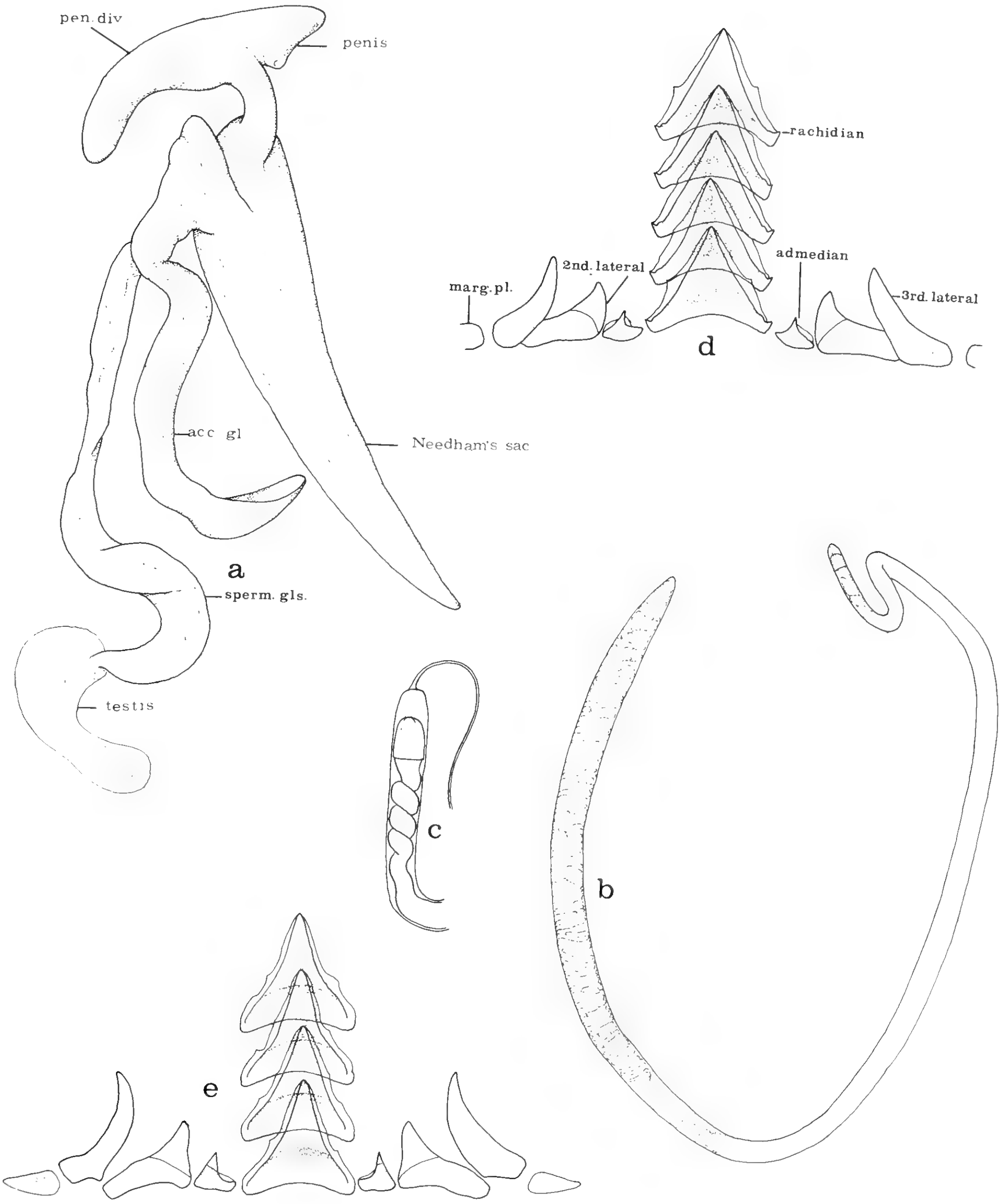

FIGURE 10. *Benthoctopus robustus* new species. (a) Genitalia of holotype. (b–c) Spermatophore of holotype. (d) Radula of holotype. (e) Radula of paratype.

jaw below the rostrum without the rounded tooth. The crest of the lower beak is a little shorter than in the holotype, and the hood wing is a little narrower. These differences probably represent individual variation.

Benthoctopus canthylus new species

(Figs. 11, 12)

MATERIAL EXAMINED.—Holotype: female, ML 54 mm, R/V YAQUINA Cr. Y7102B haul 267, 44°58.1′N, 126°35.8′W in 2,795 m, 19 Feb. 1971, USNM 729993.

TABLE 11. Indices of bodily proportions, counts, and formulae of two male *Benthoctopus robustus*, new species.

	Holotype	Paratype
Mantle length	137	114
MWI	80.3	77
HWI	51.8	48
ALI	56.7	68
MAI	64.3	56
AWI	12.4	15.8
HcAI	85.1	80
LLI	12.4	12.9
CLI	45.4	38.0
WDI	34.7	35.0
SIn	5.1	5.7
PLI	58.4	57.9
Gills	11	11
Web order	DBCAE	CBDAE
Arm formula	4·1=2=3	3214

DIAGNOSIS.—A *Benthoctopus* with thick expansion of midportion of arms I, with greatly enlarged suckers, their diameter 16.3% of mantle length; lower beak with distinct ridge on lateral wall.

DESCRIPTION.—The following description is based upon the holotype and only known specimen. Body (Fig. 11a) (Table 12) firm, overlain by thin semigelatinous layer; mantle broadly elliptical, narrower than long (MWI 77.8); mantle opening wide; head noticeably narrower than mantle (HWI 64.8), no apparent neck region; eyes medium sized with small apertures; funnel moderate sized, free for about half its length, with small aperture; funnel-mantle locking mechanism weakly developed; funnel organ (Fig. 11c) W-shaped with lateral limbs equal in length to median section.

Arms long (MAI 25.1: ALI 74.7), slender (AWI 20.4), taper to fine tips; arms formula I.II.III.IV.; suckers biserial, about 60 pairs on dorsal arms; normal suckers distinct, well separated and small (SIn 6.3).

Dorsal arms (Fig. 11b) normal at base, taper gradually for about 40% of length; arm abruptly swollen for about 25% of length at level of 17th sucker pair; swollen area very muscular, elongate elliptical, with eight pairs of widely spaced, enlarged suckers (SIe 16.3), of which median two to seven pairs greatly enlarged with widely flared apertures; at 26th sucker pair, arm regains normal size and appearance, tapers distally to slender tip; both arms identically modified; other arms normal in all respects.

Web formula BCADE, web moderately deep (WDI 23.7), extends along ventral side of each arm for little more than half arm length; forms rather strong membrane aborally on modified part of dorsal arms and, through contraction, curls modified area aborally.

Gills with 8 lamellae per outer demibranch, including terminal leaflet.

Digestive tract (Fig. 12a) with buccal mass of normal size; upper beak narrow, with sharp rostrum (Fig. 12b); lower beak with distinct groove on lateral wall (Fig. 12c); radula (Fig. 12d) with multicuspid rachidian with asymmetrically arranged cusps in B_{5-6} formula, cusps on upper part of tooth formed of transparent lamina on each side, lower ones darkened, total arrangement of cusps difficult to determine (usually two cusps on each side of rachidian); admedians with tall sharp ectocone; second laterals with inner heel; third laterals with no distinctive features.

Crop distinct, anteriorly lobed; posterior salivary glands paired on each side (Fig. 12a); stomach and spiral caecum approximately equal in size; digestive gland large, somewhat flattened dorsoventrally, nearly round, slightly bilobed posteriorly; large, inflated intestine strongly reflexed in mid portion; ink sac and anal flaps absent.

Female genitalia (Fig. 12e) with round ovary containing immature eggs, proximal oviducts short; oviducal glands enlarged and only slightly striated; distal oviducts approximately four times length of proximal portion.

Surface in preservation somewhat wrinkled, but no trace of sculpture on any part of body. Color of specimen in ethanol pale liver, slightly darker dorsally and on oral surface of web and arms.

MEASUREMENTS AND COUNTS.—Holotype: 54 mm ML, mantle width 42; head width 35; length of longest arm (I) 215; total length 288; depth of web sector B 51; sucker diameter (normal) 3.4 (enlarged) 8.8; gill lamellae in outer demibranch 8.

TYPE.—Holotype, female, 54 mm ML, USNM 729993 (fixed in formalin and preserved in 50% isopropyl alcohol).

TYPE-LOCALITY.—Off Oregon, eastern portion of Cascadia Abyssal Plain, 44°58.1′N, 126°35.8′W, 2,795 m.

DISCUSSION.—When first examined, this specimen was tentatively identified as *Benthoctopus abruptus* (Sasaki, 1920). Examination of the type specimen (USNM 332935) did not entirely solve

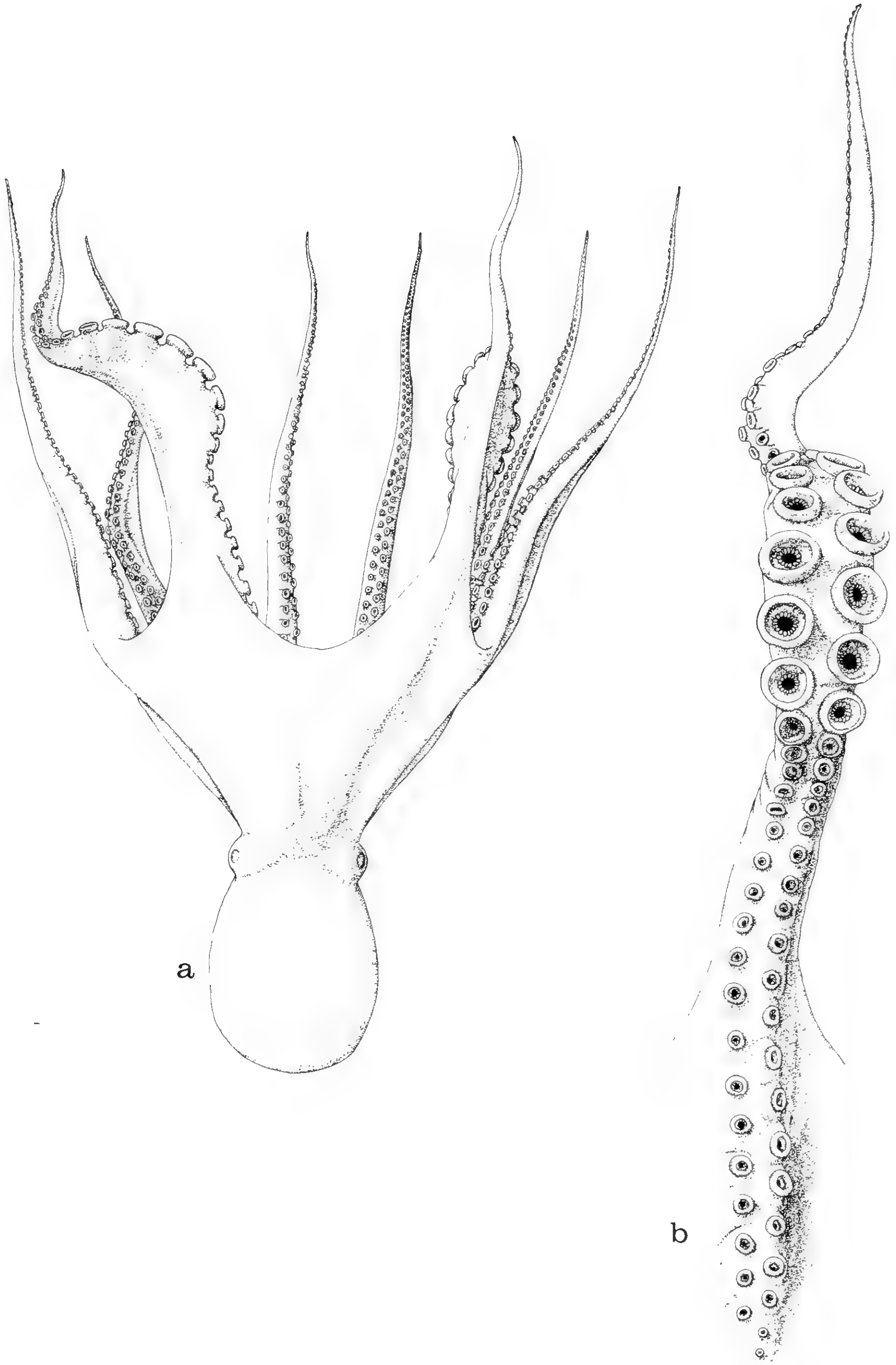

FIGURE 11. *Benthoctopus canthylus* new species. Holotype, USNM 729993, female, 54 mm ML. (a) Dorsal view. (b) Oral view of left dorsal arm.

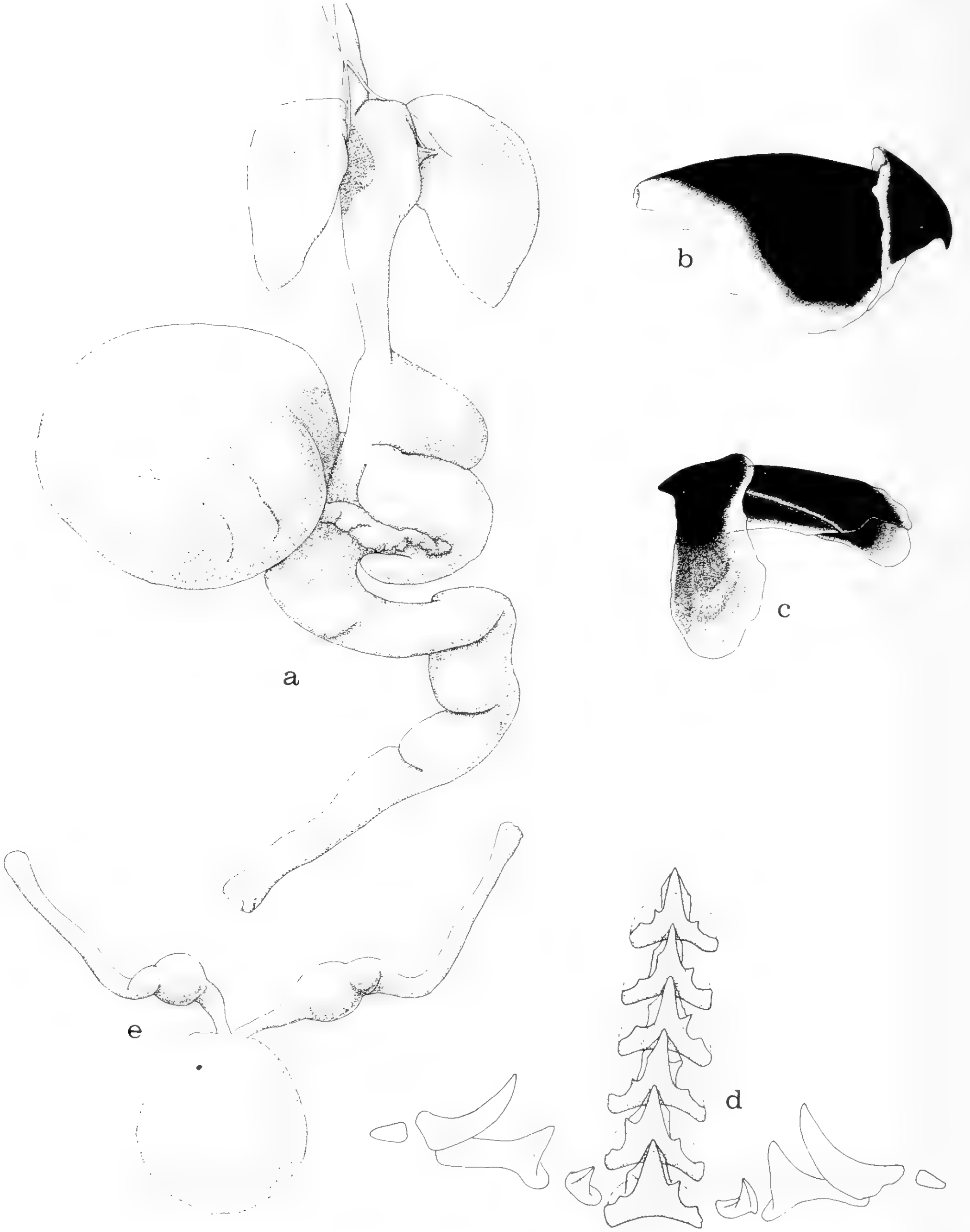

FIGURE 12. *Benthoctopus canthylus* new species. Holotype. (a) Digestive tract. (b–c) Upper and lower beaks. (d) Radula. (e) Genitalia.

the problem because of its poor condition. Dr. Takashi Okutani kindly placed at our disposal a fine series of *B. abruptus* from which it was possible to distinguish the present specimen. In males of *B. abruptus,* the enlargement of the suckers is by no means as abrupt as in *B. canthylus* and the suckers are expanded differently, with wide, thin, almost leaflike rims. There is also no arm swell-

Table 12. Measurements (in mm), counts, and indices of the holotype (female) of *Benthoctopus canthylus* new species.

Mantle length		54		Web depth	
Mantle width		42		Sector A	43
Head width		35		Sector B	51
Arm length	L		R	Sector C	48
Arm length I	210		215	Sector D	38
Arm length II	205		210	Sector E	36
Arm length III	184		184		
Arm length IV	175		184	Sucker diameter	
Arm width		11		normal	3.4
Total length		288		enlarged	8.8
Mantle width index		77.8			
Head width index		64.8		Arm width index	20.4
Mantle arm index		25.1		Web depth index	23.7
Arm length index		74.7			
Arm formula		1234			
Web formula		BCADE		Sucker index	
Number of gills		8		normal	6.3
				enlarged	16.3

ing. The arm suckers in females are unmodified. The funnel organ is W-shaped but the outer limbs are only about half the length of the median portion. *Benthoctopus abruptus* has from 10 to 12 lamellae per outer demibranch, while there are 8 in *B. canthylus.*

Benthoctopus canthylus resembles no other known species of *Benthoctopus.* Unfortunately no males are present in the collection.

The specific name *canthylus* is derived from the Greek *kanthyle,* "swelling," and refers to the peculiar modification of the dorsal arms.

Benthoctopus oregonensis new species

(Figs. 13, 14)

Material Examined (5 specimens).—Holotype: male, ML 93 mm, R/V YAQUINA Cr. 6606, 44°37.0′N, 125°01.0′W in 1,260 m, 6 Aug. 1966, USNM 729991. Paratypes: 1 female, ML 99 mm, R/V ACONA, 44°24.2′N, 125°10.3′W in 1,000 m, 14 Aug. 1964, CAS 061430.—1 female, ML 115 mm, R/V ACONA, 44°31.3′N, 125°05.4′W in 1,250 m, 15 Jan. 1965. Other material (2 specimens in very poor condition, one partly eaten and both mauled in the net): 1 male, ML 62 mm, R/V ACONA, 44°36′N, 126°06.9′W in 3,000 m, 30 Dec. 1963, UMML 31.1943. —1 male, ML 56 mm, R/V ACONA, 44°36′N, 126°06.9′W in 3,000 m, 30 Dec. 1963.

Diagnosis.—A *Benthoctopus* with stout, transversely ridged ligula; short, blunt calamus; thick, stout funnel organ; 11 gill lamellae in outer demibranch; radula with rachidian with asymmetrical B_5 seriation.

Description.—Body large; mantle globose (Fig. 13a), little narrower than long; head small with prominent, non-projecting eyes; head width considerably narrower than mantle width. Funnel large, stout, free for one-third of its length; funnel organ (Fig. 13b, c) √\/-shaped, small, compact, rounded, lateral limbs shorter than level of mid-portion of organ (nearly level in some specimens).

Arms (Tables 13 and 14) long (ALI males 81.0–*82.3*–83.3; females 78.6–*82.8*–87.1; MAI males 19.3–*20.7*–22.0; females 22.5–*24.3*–26.1); arms stout, somewhat rounded in cross-section; soft consistency; arm formula I.II.III.IV. Suckers small (SIn males 5.4–*7.4*–8.6; females 6.1–*6.7*–7.6), deeply set into oral surface of arms, protrude somewhat toward ends of arms.

Hectocotylized arm much shorter than its fellow (HcAI 66.7–*73.0*–81.8); ligula (Fig. 14b, c) short, pointed (LLI 5.0–*5.8*–6.7), with swollen, inturned margin; oral surface crossed by numerous fine ridges or folds; calamus short (CLI 41.7–*42.1*–43.0), with short, blunt spout; spermatophoral groove well developed, formed by deep, strong membrane that in preserved specimens curls hectocotylized arm strongly inward.

Upper beak (Fig. 13d) with pronounced terminal hook of rostrum; lower beak (Fig. 13e) with jaw angle of 90°. Radula (Fig. 14a) with prominent rachidian with two sharp cusps on either side, arranged asymmetrically in B_5 seriation; first laterals small, with poorly developed ectocone and endocone; second laterals with sharp prominent endocone and long base; third laterals sharply pointed, sabre-shaped; marginal plates well developed but small, somewhat rectangular.

Esophagus exits buccal mass between large circular anterior salivary glands (Fig. 13f), leads

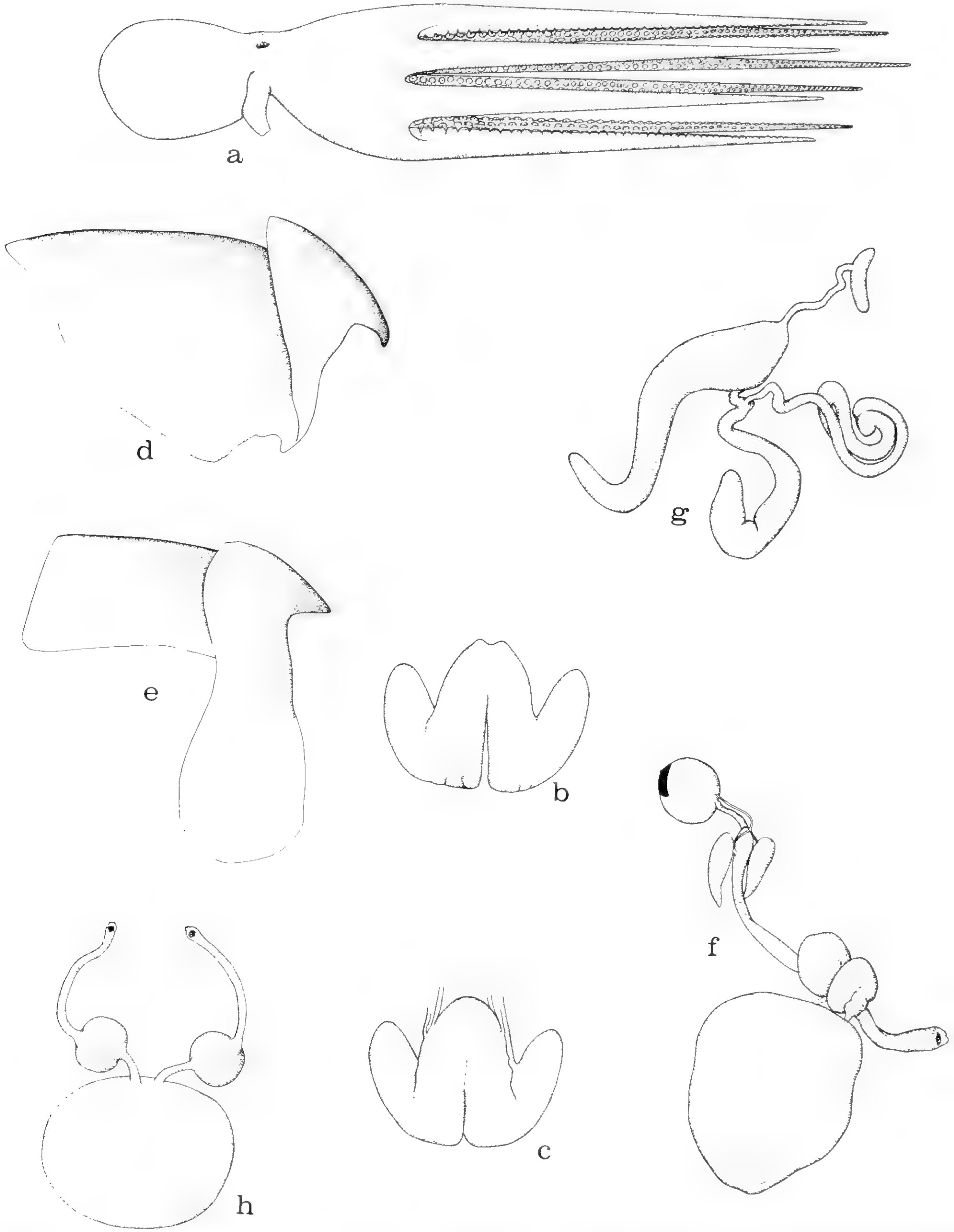

FIGURE 13. *Benthoctopus oregonensis* new species. (a) Lateral view of female, 99 mm ML. (b) Funnel organ of holotype, USNM 729991, male, 93 mm ML. (c) Funnel organ of male, 99 mm ML. (d–e) Upper and lower beaks of holotype. (f) Digestive tract of male, 62 mm ML. (g) Genitalia of holotype, male. (h) Genitalia of female, 99 mm ML.

posteriorly to well-developed crop with anterior diverticulum; posterior salivary glands large, triangular; stomach stout, about one-third larger than spiral caecum; digestive gland very large, rounded; intestine large, inflated; anal flaps and ink sac absent.

Penis (Fig. 13g) remarkably small in mature animal (PLI 18.3), nearly straight with divertic-

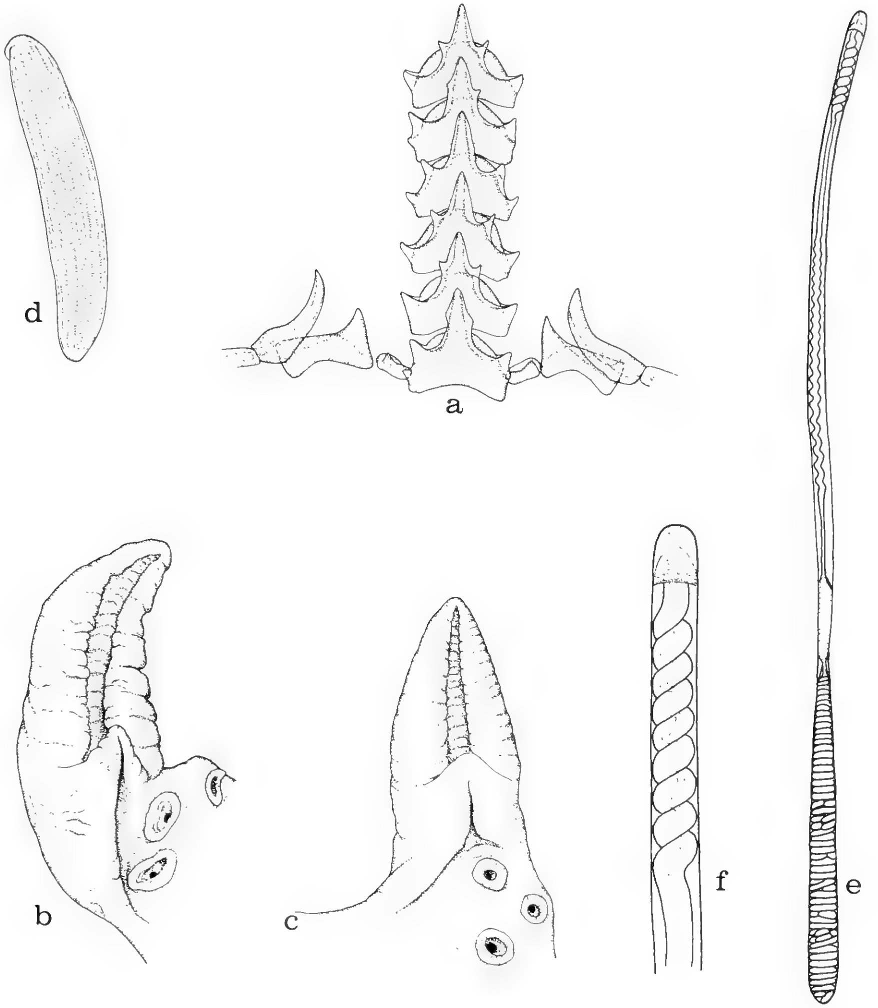

Figure 14. *Benthoctopus oregonensis* new species. (a) Radula of holotype. (b) Ligula of same. (c) Ligula of male, 56 mm ML. (d) Egg of female, 99 mm ML. (e–f) Spermatophore of male, 62 mm ML.

ulum about two-thirds of total length. Spermatophores (Fig. 14e, f) long, slender (SpLI 79.6; SpWI 1.6; SpR 32.4); anterior half of horn composed of tightly wound tube of multiple whorls, posterior half of horn straight; about eight tight coils at oral end; sperm mass heavily wound, reservoir slender.

Eggs in females ripe or near-ripe, dark vinous red, lightly striated (Fig. 14d), maximum size 26 × 6 mm, slender, pointed with clear short stalk; short (Fig. 13h) proximal oviducts lead to comparatively enormous round, dark oviducal glands; distal oviducts slender, three to four times longer than proximal oviducts.

Color in ethanol deep reddish brown to vinous red over most of body, including arms; lighter under head and around funnel; dorsal surface of mantle and head slightly lighter than ventrum, but not distinctly countershaded.

Measurements and Counts.—Holotype: mantle length 93, mantle width 70.7; head width 63.3; length of longest arm (I) 421; total length 525; sucker diameter 5.0; depth of deepest web sector (B) 88.4; number of gill lamellae in outer demibranch 11.

Type.—Holotype, male, 93 mm ML, USNM 729991 (fixed in formalin and preserved in 50% isopropyl alcohol).

TABLE 13. Indices of bodily proportions and counts of three males of *Benthoctopus oregonensis* new species.

	Specimen			
	—	UMML 31.1943	USNM 729991	
ML	56+	62	93	56.0–*70.3*–93.0
MWI	98.2	95.2	76.0	76.0–*89.8*–98.2
HWI	83.9	82.3	68.0	68.0–*78.1*–83.9
MAI	19.3	20.7	22.0	19.3–*20.7*–22.0
ALI	82.6	83.3	81.0	81.0–*82.3*–83.3
AWI	26.8	22.6	20.0	20.0–*23.1*–26.5
WDI	22.8	25.3	21.0	21.0–*23.0*–25.3
SIn	8.6	8.2	5.4	5.4–*7.4*–8.6
HcAI	81.8	66.7	70.6	66.7–*73.0*–81.8
MHI	31.1	34.4	38.8	31.1–*34.8*–38.8
LLI	5.6	6.7	5.0	5.0–*5.8*–6.7
CLI	43.0	41.7	41.7	41.7–*42.1*–43.0
PLI	—	—	18.3	
SpLI	—	—	79.6	
SpWI	—	—	1.6	
SpRI	—	—	32.4	
AF	1234	1234	1234	
WF	ACDBE	CDABE	BACDE	
Gills	11	11	11	

TYPE-LOCALITY.—On the continental slope off Yaquina Bay, Oregon, 44°37.0′N, 125°01.1′W, 1,260 m.

DISCUSSION.—*Benthoctopus oregonensis* is represented by five specimens, all of which show remarkable homogeneity and very little variation in any of their characters. Their identity, however, offered considerable difficulty because of the confusing descriptions of the possibly closely related taxa *B. profundorum* (Robson, 1932) and *B. hokkaidensis* (Berry, 1921).

Benthoctopus oregonensis can be distinguished from *profundorum* by the former's larger number of gill lamellae (11 vs. 6), and a √\ -shaped funnel organ against a W for *profundorum*. *B. oregonensis* can be distinguished from *hokkaidensis* by its short penis, PLI 18.3 vs. PLI 35; its thick, compact, funnel organ vs. a thin loose one; and by the details of the radula. Neither Sasaki (1929) nor Robson (1932) described the radula of *hokkaidensis,* of which few specimens have been recorded. The radula was extracted from the type of *hokkaidensis* (=*Polypus glaber* Sasaki, 1920: 172) (USNM 332981). The slender rachidian has two cusps on each side of the mesocone in an A_5 seriation. The first lateral has a high narrow ectocone. The second lateral is nearly triangular with a short base, while the third lateral is long and very slender. Marginals are present.

TABLE 14. Indices of bodily proportions and counts of two females of *Benthoctopus oregonensis* new species.

	Specimen		
	CAS 061430	—	
ML	99	115	99–*107*–115
MWI	89.0	80.0	80.0–*84.5*–89.0
HWI	65.0	57.4	57.4–*61.2*–65.0
MAI	22.5	26.1	22.5–*24.3*–26.1
ALI	87.1	78.6	78.6–*82.8*–87.1
AWI	19.2	18.3	18.3–*18.8*–19.2
WDI	24.3	22.7	22.7–*23.5*–24.3
SIn	7.6	6.1	6.1–*6.7*–7.6
AF	2134	1234	
WF	BACDE	BCADE	
Gills	11	11	

The specific name *oregonensis* is given in recognition of the species' occurrence off the state of Oregon, as well as in honor of the Oregon State University research ships that captured the specimens.

This species occurs on both the continental slope (1,000–1,260 m) off Oregon and the Cascadia Abyssal Plain, 85 nautical miles off the Oregon coast.

Benthoctopus yaquinae new species

(Figs. 15, 16)

MATERIAL EXAMINED (15 specimens).—Holotype: male, ML 90 mm, R/V ACONA Cr. 6501 haul 49, 44°48.8′N, 125°59.5′W in 2,800 m, 12 Jan. 1965, USNM 729992. Paratypes: 1 male, ML 67 mm, R/V YAQUINA, 45°21.6′N, 127°35.7′W in 2,800

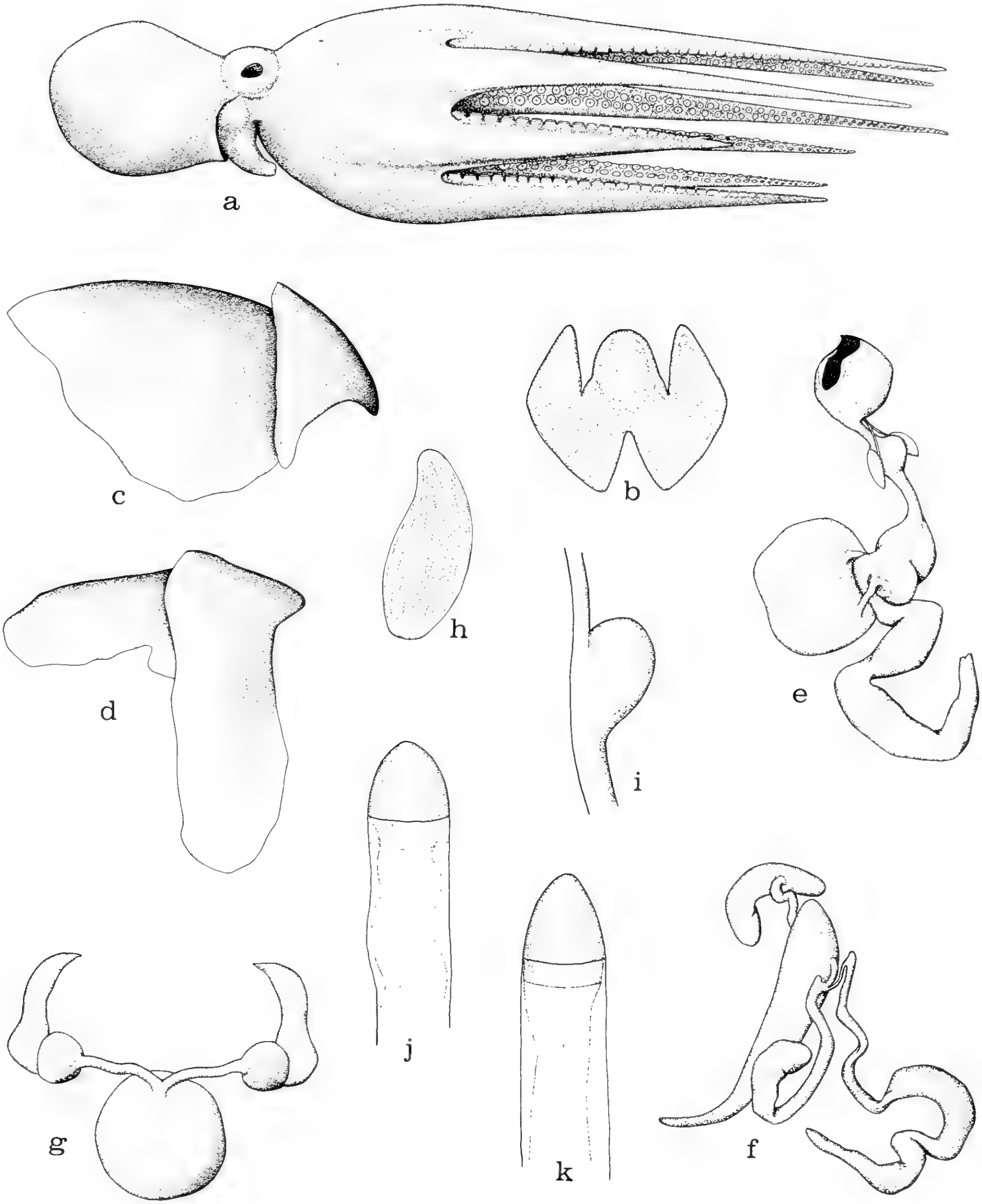

FIGURE 15. *Benthoctopus yaquinae* new species. (a) Lateral view of male, 78 mm ML. (b) Funnel organ of same. (c–d) Upper and lower beaks of male, 78 mm ML. (e) Digestive tract of male, 58 mm ML. (f) Genitalia of same. (g) Genitalia of female, 80 mm ML. (h) Egg of same. (i) Crop of male, 58 mm ML. (j–k) Distal ends of spermatophores.

m, 18 June 1967.—1 male, ML 81 mm, R/V YAQUINA, 45°21.6′N, 127°35.7′W in 2,800 m, 15 May 1971, CAS 061432.—1 male, ML 81 mm, R/V YAQUINA, 44°58.7′N, 124°42.3′W in 2,970 m, 19 Mar. 1970.—1 male, ML 83 mm, R/V YAQUINA Cr. Y72206B haul 294, 43°45.6′N, 125°26.0′W in 3,000 m, 17 June 1972, UMML 31.1945.—1 male, ML 89 mm, R/V YAQUINA Cr. Y7105B haul 278, 45°24.0′N, 127°39.0′W in 2,811 m, 18 May 1971, UMML 31.2544.—1 male ML 82 mm, 1 female ML 23 mm, R/V YAQUINA, 44°06.4′N, 125°24.5′W, in 2,938 m, 15 June 1972.—1 male ML 78 mm, 1 female ML 38 mm, R/V YAQUINA Cr. Y7206B haul 288, 44°06.2′N, 125°22.7′W in 2,940 m, 14 June 1972,

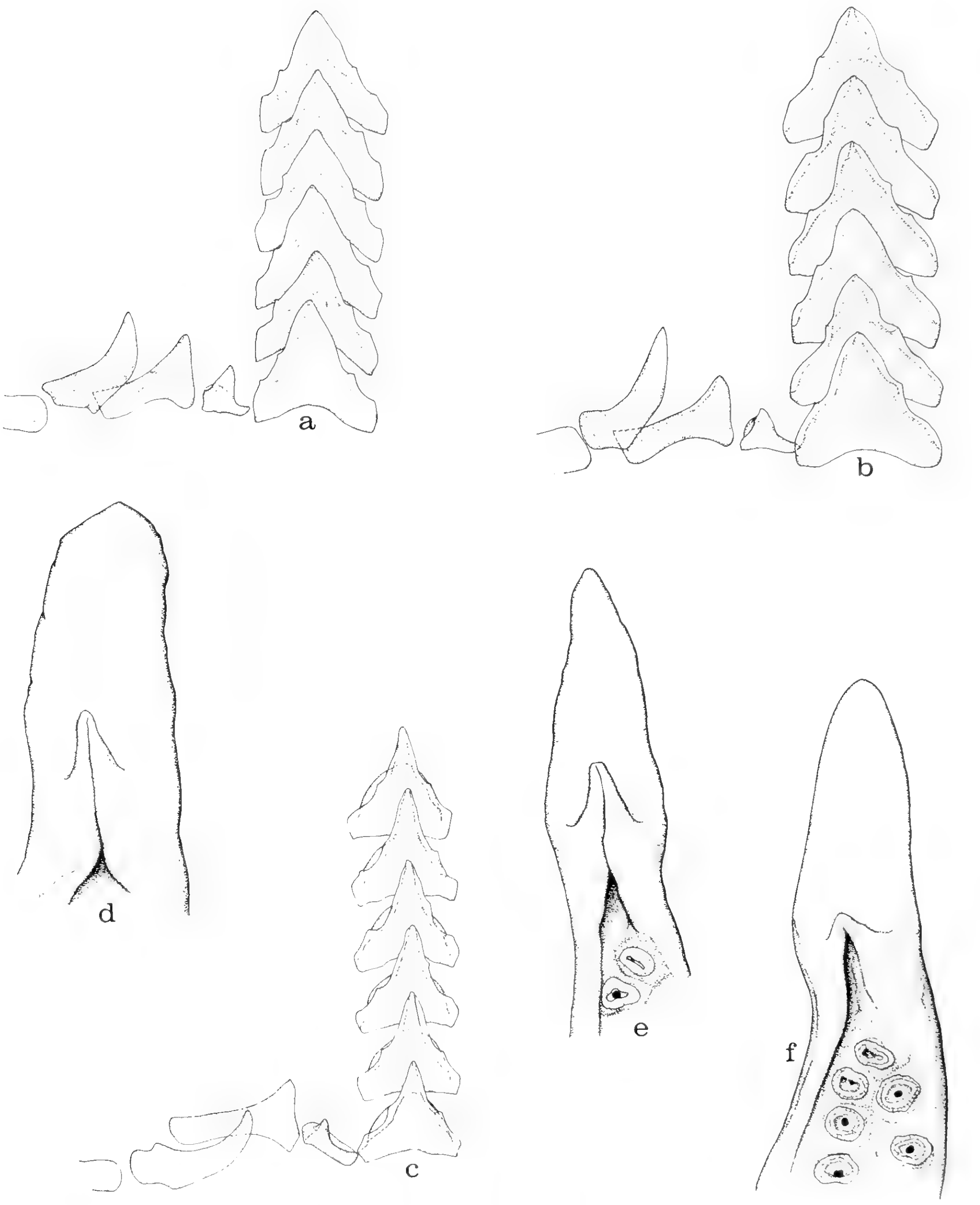

FIGURE 16. *Benthoctopus yaquinae* new species. (a) Radula of male, 78 mm ML. (b) Radula of male, 81 mm ML. (c) Radula of male, 83 mm ML. (d) Ligula of male, 81 mm ML. (e) Ligula of male, 67 mm ML. (f) Ligula of male, 78 mm ML.

UMML 31.2543.—1 female, ML 40 mm, R/V YAQUINA, 44°04.0′N, 125°23.8′W in 2,992 m, 15 June 1972, CAS 061432.—1 female, ML 110 mm, R/V ACONA, 44°39.2′N, 127°27.6′W in 2,800 m, 9 Feb. 1965.—1 female, ML 80 mm, R/V YAQUINA Cr. Y7105B haul 281, 44°38.5′N, 127°39.0′W in 2,816 m, 19 May 1971, UMML 31.1944. Other material: 2 males, ML 30–35 mm, R/V ACONA, 44°24.2′N, 125°10.3′W in 1,000 m, 14 Aug. 1964.

DIAGNOSIS.—A *Benthoctopus* with long, smooth ligula with no transverse ridges and short calamus; rachidian of radula broad with low cusps in irregular asymmetrical seriation; gills with 7–9 lamellae per outer demibranch.

DESCRIPTION (all indices for males are for 11

TABLE 15. Indices of bodily proportions of eight males of *Benthoctopus yaquinae* new species, and other data.

	Specimen							
	—	—	—	UMML 31.2543	—	—	—	UMML 31.1945
ML	30	35	67	78	81	81	82	83
MWI	76.7	68.6	85.1	71.8	85.2	85.2	77.0	74.7
HWI	83.3	74.3	73.1	53.9	65.4	64.2	60.0	62.7
MAI	32.3	33.7	23.9	32.5	27.0	25.3	31.5	28.6
ALI	77.5	68.9	79.6	75.0	77.7	78.8	75.0	76.7
AWI	20.0	19.4	20.9	23.1	19.8	18.5	24.4	15.7
WDI	30.0	31.7	24.3	25.4	24.0	28.8	26.0	28.3
SIn	6.3	4.9	7.5	6.4	5.2	7.2	6.1	6.0
HcAI	73.6	—	72.0	73.9	76.4	73.7	69.0	76.9
MHI	46.9	41.7	37.2	45.9	38.6	38.6	46.1	41.5
LLI	11.1	9.2	11.1	11.8	10.5	9.1	8.4	9.0
CLI	32.1	44.2	50.0	35.0	31.8	47.4	46.7	36.1
PLI	31.6	33.1	64.2	43.6	49.4	61.7	36.6	51.8
SpLI	—	—	—	106.4	—	—	—	136.1
SpWI	—	—	—	3.6	—	—	—	3.5
SpRI	—	—	—	45.8	—	—	—	31.0
AF	—	—	—	2134	1234	1234	1234	1234
WF	—	—	—	CDBA=E	ABCDE	CBADE	B=C=DAE	CDABE
Gills	7	7	9	8	8	9	9	8

TABLE 16. Ranges and means of indices of eight males of *Benthoctopus yaquinae* new species, grouped by sizes (ML) of animals.

	N		
	2	2	4
ML	30.0–*32.5*–35.0	67.0–*72.5*–78.0	81.0–*81.8*–83.0
MWI	68.6–*72.7*–76.7	71.8–*78.5*–85.1	74.7–*80.5*–85.2
HWI	74.3–*78.8*–83.3	53.9–*63.5*–73.1	60.0–*63.1*–65.4
MAI	32.3–*33.0*–33.7	23.9–*28.2*–32.5	25.3–*28.1*–31.5
ALI	68.9–*73.2*–77.5	75.0–*77.3*–79.6	75.0–*77.1*–78.8
AWI	19.4–*19.7*–20.0	20.9–*22.0*–23.1	15.7–*19.6*–24.4
WDI	30.0–*30.9*–31.7	24.3–*24.9*–25.4	24.0–*26.8*–28.8
SIn	4.9–*5.6*–6.3	6.4–*7.0*–7.5	5.2–*6.1*–7.6
HcAI	–	72.0–*73.0*–73.9	69.0–*74.0*–76.9
MHI	41.7–*44.3*–46.9	37.2–*41.6*–45.9	38.6–*41.2*–46.1
LLI	9.2–*10.2*–11.1	11.1–*11.5*–11.8	8.4–*9.3*–10.5
CLI	32.1–*38.2*–44.2	35.0–*42.5*–50.0	31.8–*40.5*–47.4
PLI	31.6–*32.4*–33.1	43.6–*53.9*–64.2	36.6–*49.9*–61.7

specimens, including the eight in Table 15, the holotype, and two additional specimens of 83 and 89 mm ML).—Body medium to large (Tables 15 and 16) with soft, somewhat flabby consistency (some specimens firmer); mantle (Fig. 15a) globose, wide (MWI males 68.6–*80.3*–89.2; females 65.2–*76.9*–88.5); head small (HWI males 53.9–*66.0*–83.3; females 51.8–*63.7*–87.5) with prominent, somewhat protruding eyes and distinct neck section. Funnel large, stout, about distal one-quarter free; funnel organ (Fig. 15b) large, W-shaped, with slender pointed lateral limbs level with, or slightly larger than, anteriorly rounded inner limbs. In some specimens limbs narrow, sharp, with flat organ, but in most organ raised; central and outer limbs padlike with raised rims.

Arm of moderate length (MAI males 25.3–*29.6*–33.7; females 29.6–*34.5*–40.0; ALI males 68.9–*75.6*–79.6; females 68.8–*76.1*–77.9), soft to muscular, squarish in cross-section (AWI males 13.9–*19.1*–24.4; females 17.4–*19.8*–22.5). Arm formula I.II.III.IV. with only two exceptions. Suckers small (SIn males 4.8–*5.9*–7.5; females 3.6–*5.8*–7.9), erect, and protrude over most of arm length.

Web formula variable, commonly BCDAE, with B or C usually longest and E always shortest; web shallow (WDI males 24.0–*27.1*–31.7; females 26.7–*28.5*–33.4) but extends along ventral side of arms I–III nearly to their tips, inconspicuous on IV.

Hectocotylized arm shorter than its fellow (HcAI 64.1–*72.6*–76.9; MHcAI 37.2–*43.8*–55.3); ligula (Fig. 16d–f) large LLI (8.4–*10.2*–11.8), pointed, flattened, with low median ridge; no transverse rugae (although some light lines present); calamus small (CLI 31.8–*40.5*–50.0), well developed, sharply pointed; spermatophoral groove distinct, membrane narrow near midpoint of arm.

Buccal mass exceptionally large; upper beak (Fig. 15c) not distinctive; lower beak (Fig. 15d) with obtuse jaw angle, some with only a shallow smooth curve, low ridge on lower edge of lateral wall.

Radula large, teeth strongly pigmented (Fig. 16a–c). Main modification occurs on rachidian tooth: base broad, stout, darkly pigmented, with somewhat smooth-sided outline; sides of rachidian with supplementary clear rim wholly or partially toothed; dentition variable, usually with two cusps on each side; rachidians with irregular asymmetrical seriation; first laterals with high, very prominent ectocone; second laterals with broad, curved, bladelike endocones on heavy base; third laterals short, sabrelike, rather sharply pointed; marginals vary from elongate-rectangular plates to short buttons.

Buccal mass large (Fig. 15e); anterior salivary glands prominent at base of buccal mass on each side of esophagus; anterior section of esophagus short, stout, followed by small, distinct, anteriorly-lobed crop (Fig. 15i); posterior salivary glands on each side of crop small, elliptical, slightly pointed at each end; stomach large, thick-walled. Stomach and spiral caecum approximately equal in size, closely joined; two ducts from stomach-caecum lead into digestive gland; digestive gland nearly round in outline, but partially divided into two lobes by shallow median

TABLE 17. Indices of bodily proportions of five females of *Benthoctopus yaquinae* new species, and other data.

	Specimen				
	—	UMML 31.2543	CAS 061432	UMML 31.1944	—
ML	23	38	40	80	110
MWI	65.2	79.0	80.0	88.5	71.8
HWI	52.2	65.8	87.5	61.3	51.8
MAI	37.0	34.9	29.6	31.1	40.0
ALI	74.7	77.9	75.0	73.4	68.8
AWI	17.4	18.4	22.5	22.5	18.2
WDI	32.3	29.4	26.7	30.7	33.4
SIn	6.1	5.3	7.9	6.3	3.6
AF	1234	1234	1234	1234	1234
WF	DC=BA−E	ACBDE	C=DB=AE	BCDAE	DCBAE
Gills	9	7	8	8	8

depression; intestine divided into two large, thin-walled sections followed by somewhat narrower distal section; anal flaps and ink sac absent.

Gills large, with 7–9 lamellae per outer demibranch.

Penis (Fig. 15f) large (PLI 31.6–*48.9*–67.5), blunt anteriorly with long, broad, blunt diverticulum; penis and diverticulum form slight to strongly bowed curve; Needham's sac large, about twice length of large penial apparatus; accessory gland as long as Needham's sac, well developed with small distinct appendix; seminal glands large, distal half divided into two well-developed, separate sections, proximal half slender, unites to accessory gland slightly posterior to appendix.

Spermatophores long (SpLI 106.4–*126.4*–136.1), stout (SpWI 2.5–*3.3*–3.6); sperm reservoir stout, thin-walled, occupies one-third to nearly one-half total length of spermatophore; horn section thick-walled, strong; tube straight with no turns; head (Fig. 15j, k) somewhat pointed with pigmented ring or band around posterior margin.

Proximal oviducts short, narrow, widen perceptibly at junction with small, gray, oviductal glands followed by broad distal oviducts; distal oviducts about three times length of proximal oviducts in largest female, about equal in smaller specimen illustrated (Fig. 15g). Eggs ripe or nearly ripe (Fig. 15h), about 12 × 3.8 mm, bluntly pointed posteriorly, brown with light tan stripes; stalk short, flesh colored.

Surface of body smooth, devoid of sculpture. Color distinctly reverse countershaded; pale slate gray on dorsal arms, head, and mantle; ventral surface and oral surface of arms and web dark bluish red; reverse countershading probably an adaptation to light-colored muds of ocean floor where animal lives and to near-bottom bioluminescence.

MEASUREMENTS AND COUNTS.—Holotype: mantle length 90; mantle width 66; head width 53; length of longest arm (I) 280; total length 365; length of hectocotylized arm 185; ligula length 21.5; calamus length 8.0; sucker diameter 4.5; depth of deepest web sector (A) 88; gill lamellae per outer demibranch 8.

TYPE.—Holotype, male, 90 mm ML, USNM 729992 (fixed in formalin and preserved in 50% isopropyl alcohol).

TYPE-LOCALITY.—Off Oregon, eastern portion of Cascadia Abyssal Plain, 44°44.8′N, 125°59.5′W, 2,800 meters.

DISCUSSION.—The identity of this species, like *oregonensis*, caused a great deal of perplexity. Few of the descriptions of any species of *Benthoctopus* give sufficient detail to permit identification from the literature and often are based on insufficient or poorly preserved material. The present description is based upon 15 specimens, all from nearly the same locality, so they should represent a single population.

Benthoctopus yaquinae can be separated from *hokkaidensis* by the much greater ligula length (8.4–11.8 for *yaquinae*; 4.5 for *hokkaidensis*), its radula, and its differently shaped penial apparatus. From *profundorum* it can be distinguished by the general shape of the ligula, its greater ligula length (vs. 6.9 for *profundorum*), its funnel organ, and other characters. It is distinct from all other known *Benthoctopus*.

The name *yaquinae* is derived from the R/V YAQUINA, previously operated by the College of Oceanography, Oregon State University, from which most of the specimens were captured.

Of the 15 specimens, all but two were captured on the Cascadia Abyssal Plain. These two were taken on the continental slope off the central Oregon coast at 1,000 m.

Benthoctopus macrophallus new species

(Fig. 17)

Material Examined.—Holotype: male, ML 83 mm, R/V YAQUINA Cr. Y7102B haul 267, 44°59′N, 126°31.6′W in 2,795 m, 19 Feb. 1971, USNM 730713.

Diagnosis.—A *Benthoctopus* with long, slender ligula with no transverse ridges and short calamus; long penial apparatus, 67.5% of mantle length; spermatophores very large, 180.7% of mantle length; rachidian of radula tall, slender, somewhat lobulate, without lateral cusps.

Description.—Unique specimen contorted, wrinkled; body and arms muscular; mantle nearly round (MWI 89.2) with slightly narrower neck region; head large (HWI 73.5), eyes large. Funnel large, free for about half its length, stout; funnel organ W-shaped, short, with broad lateral limbs that are longer than round median limb.

Arms long (MAI 26.8; ALI 77.9), stout (AWI 18.1), taper to long slender tips; arm formula I.II.III.IV.; suckers small (SIn 4.8), biserial, erect, raised above arm surface on stout, well-separated pads; about 63–65 sucker pairs on I.

Web shallow (WDI 24.8), order BACDE, extends along sides of arms nearly to tips.

Hectocotylized arm short (HcAI 71.9; FHcAI 39.2), stout; bordered by strong, thick membrane that forms spermatophoral groove; ligula (Fig. 17d) large (LLI 10.9), long, slender, inner surface of ligula shallowly excavated with low central ridge, crossed by numerous very fine lines; calamus short (CLI 34.8) with small sharp spout.

Gills large with 9 lamellae per outer demibranch.

Buccal mass of average size; upper beak (Fig. 17a) stout; rostrum strong with slightly obtuse jaw angle; lower beak (Fig. 17b) with nearly 90° jaw angle with short rostrum.

Radula (Fig. 17c) unique; large, darkly pigmented; rachidian tooth stout; mesocone tall, blunt-tipped with smooth, irregular sides with clear transparent lamina on each side near tip; base comparatively slender with cusp on each outer angle, arrangement symmetrical (A); admedians with tall sharp ectocone and short base; second laterals stout with broad blades; third laterals long, curved, slender; marginal plates poorly formed distinct only on inner ends.

Digestive tract not dissected, mantle laid back to permit examination of esophagus and crop with large anterior diverticulum (Fig. 17e); posterior salivary glands small; anal flaps and ink sac absent.

Penis (Fig. 17i) large with long posterior diverticulum (PLI 67.5); Needham's sac long, slender, contains three spermatophores; accessory gland about as long as Needham's sac. Spermatophores (Fig. 17f) 150 mm long; (SpLI 180.7) with stout horn (SpDI 3.4); sperm reservoir nearly half again as wide; horn little more than half spermatophore length (SpHI 53.3; SpRI 46.7), oral end with brownish cap, with narrow dark-brown band at posterior end (Fig. 17h); horn opaque, no coils visible.

Body sculpture absent. Color in ethanol grayish tan dorsally on mantle, head and base of arms with shades of dark purple on ventral side and on oral and aboral surface of arms and web.

Measurements and Counts.—Holotype: mantle length 83; mantle width 74; head width 61; length of longest arm (I) 310; total length 398; length of hectocotylized arm 222.8; ligula length 24.3; calamus length 8.5; number of suckers on arm I 63–65; sucker diameter 4.0; depth of deepest web sector (B) 76.8; number of gill lamellae per outer demibranch 9.

Type.—Holotype, male, 83 mm ML, USNM 730713 (fixed in formalin, preserved in 50% isopropyl alcohol).

Type-locality.—Off Oregon, eastern Cascadia Plain, 44°59′N, 126°31.6′W, 2,795 m.

Discussion.—This species is distinct from all other *Benthoctopus* by the unusual characters of the radula, the beaks, the very large spermatophores, and the unusually long, separate crop diverticulum.

The whole animal is not figured, as it differs little in general appearance from the other species described and illustrated here.

The name *macrophallus* refers to the exceptionally long penial apparatus of this species.

General Discussion of North Pacific *Benthoctopus*

Approximately 16 species have been described in the genus *Benthoctopus* (Robson 1932; Taki 1964; Voss 1988b), of which few have been well enough described and illustrated to be identifiable. To further confuse the picture, several of the types are in poor condition or essential parts have been removed and are now missing.

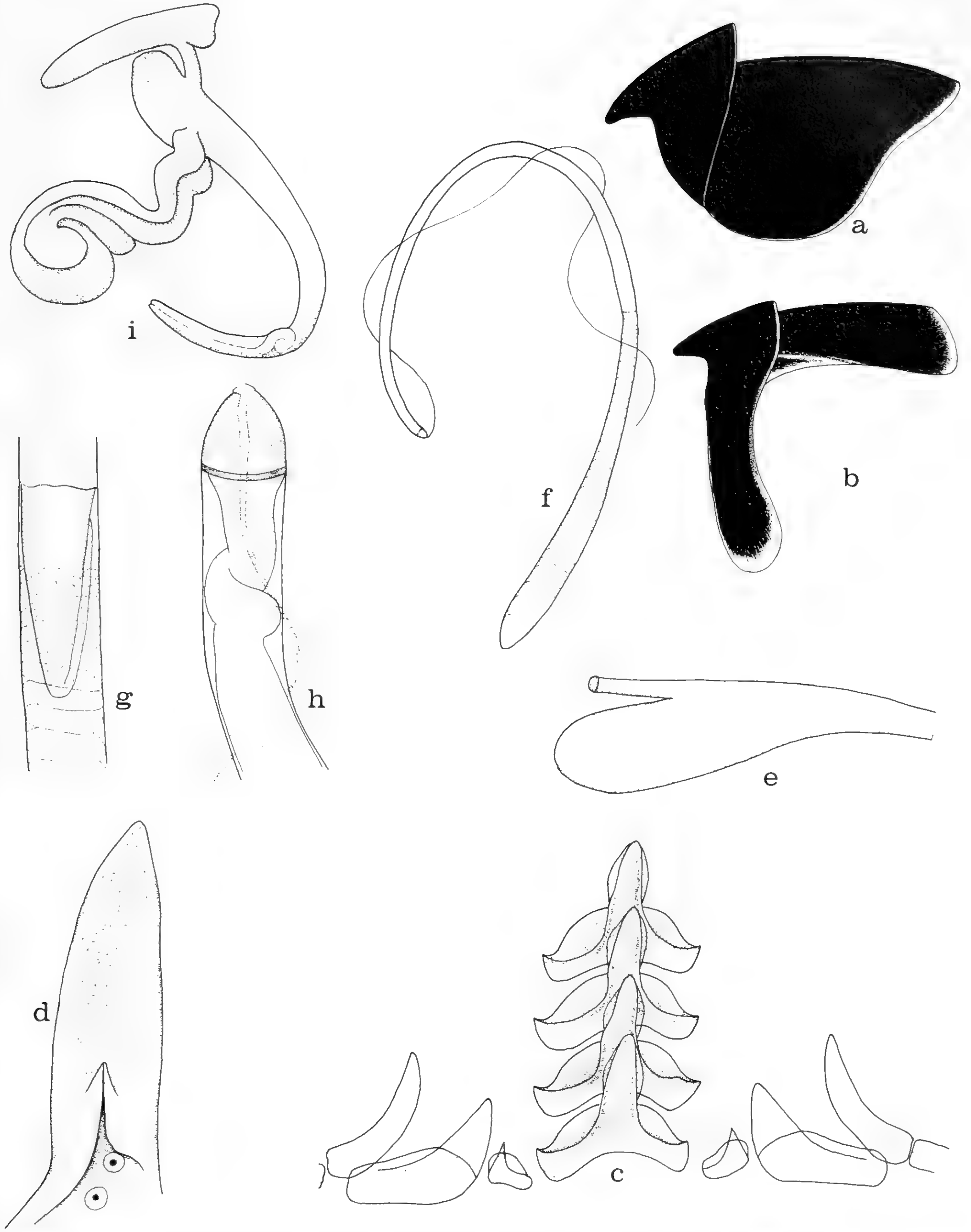

FIGURE 17. *Benthoctopus macrophallus* new species. Holotype, USNM 730713, male, 83 mm ML. (a–b) Upper and lower beaks. (c) Radula. (d) Ligula. (e) Crop. (f) Spermatophore. (g) Cement body. (h) Horn and cap. (i) Genitalia.

Of the 16 species, five are known only from the Atlantic, three from the Southern Ocean, one from the Arctic, and two from the Indian Ocean, for a total of 11. The remaining five species: *abruptus, fuscus, hokkaidensis, profundorum,* and *violescens* are from the North Pacific Ocean. To these are now added *robustus, canthylus, oregonensis, yaquinae,* and *macrophallus,* for a total of 10 North Pacific species. All need to be discussed in evaluating the North Pacific species.

Benthoctopus abruptus was described by Sasaki (1920). It is a well-defined species best characterized by the greatly enlarged, flared suckers on the arms of the males. This character is unique in the genus. *Benthoctopus canthylus,* described here from a single specimen, is the only species with enlarged suckers in females; males are unknown. *Benthoctopus fuscus,* described with a VV-shaped funnel organ (Taki 1964:316), is the only Pacific species with this type of funnel organ.

Benthoctopus hokkaidensis (Berry, 1921) is a replacement name for *Polypus glaber* (Sasaki, 1920). It is known from about four specimens from Japanese waters and was redescribed and illustrated by Sasaki (1929:65). The radula from the type is described here under the discussion of *B. oregonensis,* so the species now is fairly well known. The only discrepancy is the statement by Robson (1932:233) that "the penis has a long diverticle which is bent on itself (?by accident) to confer on the whole structure the shape of S." In the type specimen only the diverticulum is strongly curved inward, not so much as in Sasaki's figure (1929:63; text fig. 25). The funnel organ, also well illustrated, is a wide √V-shape.

No basis exists for separating *B. hokkaidensis* from *violescens* (Taki, 1964). Taki (1964:321) showed that the funnel organ is exactly the same shape as that figured by Sasaki (1929), and both are √V -shaped, not W -shaped as given in his table p. 324–325. The radulae also are the same. Similarly, the penis and its diverticulum have the same curvature, although not as marked in *violescens* as in *hokkaidensis.* In the table, all of the dimensions and indices of *violescens* are within the ranges of *hokkaidensis.* Consequently, *violescens* is placed in the synonymy of *hokkaidensis.*

Throughout this study of *Benthoctopus,* the identity of *B. profundorum* (Robson, 1932) has caused problems. Although Robson (1932:238) stated "this description is largely founded on the type alone," it is a mixture of characters, measurements, and indices of specimens from relatively shallow water and includes specimens from as far away as the Andaman Sea. The type was from off Yokohama in 3,431 m; the other specimens were from depths of 510 to 1,098 m. It is likely that the species as originally described is composed of several species.

The type, BM 1889.4.24.42, was examined by Voss in London in 1975. Robson stated that the ligula index was 6.9; it is now 6.6. According to Robson, "the copulatory groove is very weak," but it is actually deep and well-defined. The calamus is small and pointed but the CLI is 46.7 as measured from the distal sucker. He stated that the funnel organ was √V-shaped, but it is W-shaped with the median section broad and rounded with narrow and pointed lateral limbs. There are six lamellae on the outer demibranch of the gills. The buccal mass has been removed and no trace could be found of either the beaks or the radula. Based upon the type alone, *B. profundorum* must be characterized as having a W-shaped funnel organ, six lamellae on the outer demibranch of the gills, a small ligula (LI 6.6–6.9) with a deep copulatory groove and small pointed calamus, short stout penis with stout diverticulum, ALI 83, SIn 5.9, WDI 34, with beaks and radula unknown.

This leaves *B. robustus, oregonensis, yaquinae* and *macrophallus* to be considered. *Benthoctopus robustus* has a distinctive radula and genitalia. Both *B. oregonensis* and *yaquinae* have been discussed previously. *Benthoctopus macrophallus,* as the name implies, has a very large penis (PLI 67.5), large ligula, a groove on the lamella of the lower mandible, and a nearly smooth, slender rachidian tooth in the radula.

The characters of the nine recognized species of *Benthoctopus* from the North Pacific Ocean are shown in the following key. The first characters given in the couplets refer to distinguishing characters, those following are diagnostic of the species. We emphasize that this key is provisional. Some characters are not known for all species or sexes of a species. It should be used with illustrations and descriptions of species.

KEY TO THE SPECIES OF *BENTHOCTOPUS* OF THE NORTH PACIFIC OCEAN

1. Funnel organ VV; gills 7–11; radula B_5 with high ectocone on 1st lateral; penis small, straight, PLI 12.2; sucker index normal 6.0. Single male known .... *fuscus*
1. Funnel organ W , W , or √V; other characters not as above 2
2. Specially enlarged suckers, SIe 15–16.3, present on some or all arms of males or females 3
2. No specially enlarged suckers on either males or females; SIn 4.8–8.6 4

3. All arms normal; in males suckers of midportion of arms greatly enlarged, SIe 15, SIn 8; females with normal suckers SIn 8; funnel organ W; gills 10–14; radula B_{4-5}; penis moderate, PLI 7.3 .... *abruptus*
3. Middle of dorsal arms of females abruptly swollen and bearing greatly enlarged suckers, SIe 16.3; SIn 6.3; funnel organ W; gills 8; radula B_{5-6}; groove on lamella of lower beak. Single female known .... *canthylus*
4. Groove on lamella of lower beak; funnel organ W ; rachidian with tall, narrow mesocone with undulating margin; 1st laterals with tall, sharp ectocone; gills 9; SIn 4.8; ligula long, slender, LLI 11; calamus short, sharp, CLI 23.3; penis very large, slightly arcuate, PLI 68; spermatophore very long SpLI 180.7. Single male known .... *macrophallus*
4. No groove on lamella of lower beak; funnel organ W or √\; rachidian teeth broad and/or with lateral cusps with B_{4-6} seriation 5
5. Funnel organ W shaped 6
5. Funnel organ √\ shaped 8
6. Arms short, ALI 56, MAI 64; ligula large, deep, rugose, LLI 12.5; calamus long, slender, CLI 45; rachidian broad with nearly smooth margin; gills 11; SIn 5.1; penis large, PLI 58. Single male known .... *robustus*
6. Arms long, ALI greater than 65; MAI less than 40; ligula small, under LLI 8 or if larger, ligula smooth, shallow (LLI 8.4–10.5); rachidian with lateral cusps on mesocone 7
7. Ligula flattened with low median ridge, medium size, LLI 8.4–10.5; rachidian B_5, broad, triangular, with low cusps on mesocone; gills 7–9; strong reverse countershading .... *yaquinae*
7. Ligula deeply excavated, small, LLI 6.6–6.9; gills 6; radula unknown; no reverse countershading; type a male, all other specimens doubtful .... *profundorum*
8. Penis short, nearly straight, with short diverticulum, PLI 18.3; spermatophore small, SpLI 79.6; funnel organ a fat, close √\; ligula short, broad, with deep groove and transverse rugae, LLI 5.0–6.7; gills 11–13 radula B_{4-5} with strong sharp cusps on mesocone; 1st laterals with low ectocone .... *oregonensis*
8. Penis long, with long inwardly curved diverticulum, PLI 35; spermatophore long, SpLI 95.6; funnel organ narrow, widely open √\; ligula short, narrow, with narrow shallow groove, LLI 4.5–5.5; gills about 12; radula B_{5-6} with strong, sharp cusps on mesocone, 1st laterals with tall, slender ectocone .... *hokkaidensis*

Subfamily GRANELEDONINAE Voss, 1988a

Deep-sea octopods with uniserial suckers; large eggs; ink sac absent; crop lacks diverticulum, reduced or absent; reduced number of gill lamellae; reduction or degeneration of homodont radula; funnel organ VV, UU or simple paired pads; spermatophores large and few.

DISCUSSION.—Robson (1932:51–56, 257) discussed the "Eledoninae" and his reasons to consider it a polyphyletic group. Voss (1988a) restricted the Eledoninae to the genera *Pareledone, Eledone, Vosseledone, Velodona,* and *Tetracheledone* and erected the new subfamily for the remaining genera with uniserial suckers, *Graneledone, Thaumeledone,* and *Bentheledone.*

Genus **Graneledone** Joubin, 1918

With characters of family (see above). Body, head, and arms thickly covered with permanent rugose papillae.

TYPE SPECIES: *Eledone verrucosa* Verrill, 1881: 105. By original designation (Joubin 1918:39).

Graneledone pacifica new species

(Figs. 18–20)

?*Graneledone boreopacifica* Nesis, 1982: 322, fig. k, l.

MATERIAL EXAMINED (28 specimens).—Holotype: male, ML 85 mm, R/V YAQUINA Cr. 6907C haul 95, 44°52.0′N, 125°32.8′W in 2,706 m, 16 July 1969, USNM 730716. Paratypes: 1 male, ML 96 mm, R/V ACONA Cr. A6507 haul 78, 45°59.6′N, 125°44.0′W in 2,500 m, 1 Aug. 1965, UMML 31.2539.—1 male, ML 95 mm, R/V YAQUINA, 45°49′N, 125°34′W in 2,121 m, 7 June 1969, CAS 061434.—1 male, ML 90 mm, R/V Yaquina Cr. Y7003B haul 192, 45°37.9′N, 125°46.5′W in 2,450 m, 19 Mar. 1970, UMML 31.1957.—1 male, ML 86 mm, R/V YAQUINA Cr. Y6907C, 44°52′N, 125°32.8′W in 2,706 m, 16 July 1969, UMML 31.1959.—1 male, ML 85 mm, 1 female, ML 45 mm, R/V YAQUINA Cr. Y7003B haul 195, 45°57.6′N, 125°46.2′W in 2,265 m, 20 July 1970, UMML 31.2542.—1 male, ML 62 mm, R/V YAQUINA Cr. Y6910A haul 116, 45°21′N, 125°37.3′W in 2,500 m, 5 Oct. 1969, UMML 31.2541.—1 male, ML 60 mm, R/V YAQUINA, 45°10.5′N, 125°38.0′W in 2,669 m, 15 July 1964.—1 male, ML 49 mm, R/V YAQUINA Cr. Y6910A, 45°21′N, 125°37.3′W in 2,500 m, 5 Oct. 1969.—2 males, ML 58–59 mm, R/V YAQUINA Cr. Y6910A, 45°09.3′N, 125°35.2′W in 2,652 m, 5 Oct. 1969.—1 male, ML 21 mm, R/V CAYUSE, 44°42.1′N, 125°20.2′W in 2,755 m, 2 Oct. 1970.—1 male, ML

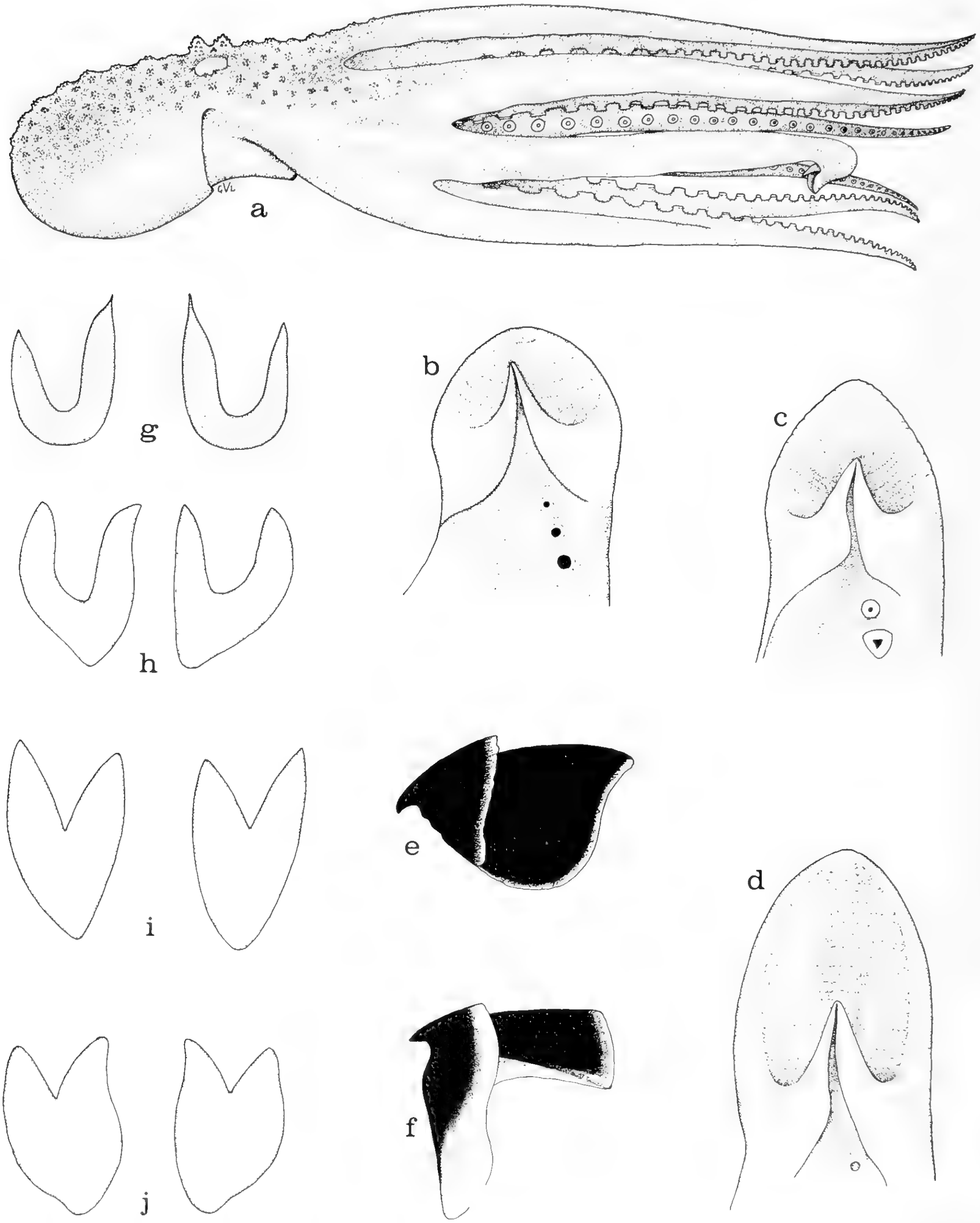

FIGURE 18. *Graneledone pacifica* new species. (a) Lateral view of holotype, USNM 730716, male, 85 mm ML. (b) Ligula of male, 62 mm ML. (c) Ligula of male, 85 mm ML. (d) Ligula of male, 90 mm ML. (e–f) Upper and lower beaks of male, 85 mm ML. (g–j) Funnel organs: g, male, 90 mm ML; h, male, 96 mm ML; i, male, 85 mm ML; j, male, 54 mm ML.

19 mm, R/V YAQUINA Cr. Y6910A, 45°49.2′N, 125°40.1′W in 2,195 m, 4 Oct. 1969.—1 female, ML 105 mm, 1 male, ML 43.5 mm, R/V YAQUINA, 45°59.6′N, 125°44.0′W in 2,500 m, 1 Aug. 1965.—1 female, ML 105 mm, R/V YAQUINA, 45°45.5′N, 125°30.2′W in 2,176 m, 11 Jan. 1967, CAS 061433.—1 female, ML 100 mm, R/V YAQUINA Cr. Y7003B haul 181, 45°17.4′N, 125°49.0′W in 2,605 m, 18 Mar. 1970, UMML 31.1958.—1 female, ML 97 mm, R/V ACONA, in 1,427 m, 10 Dec. 1961.—2 females, ML 13–88 mm, R/V YAQUINA Cr. Y7003B haul 193, 45°39.0′N, 125°52.9′W in 2,425 m, 19 Mar. 1970, UMML 31.2540.—1 female, ML 75 mm, R/V CAYUSE Cr. 6903 haul 72-01, 45°56.1′N,

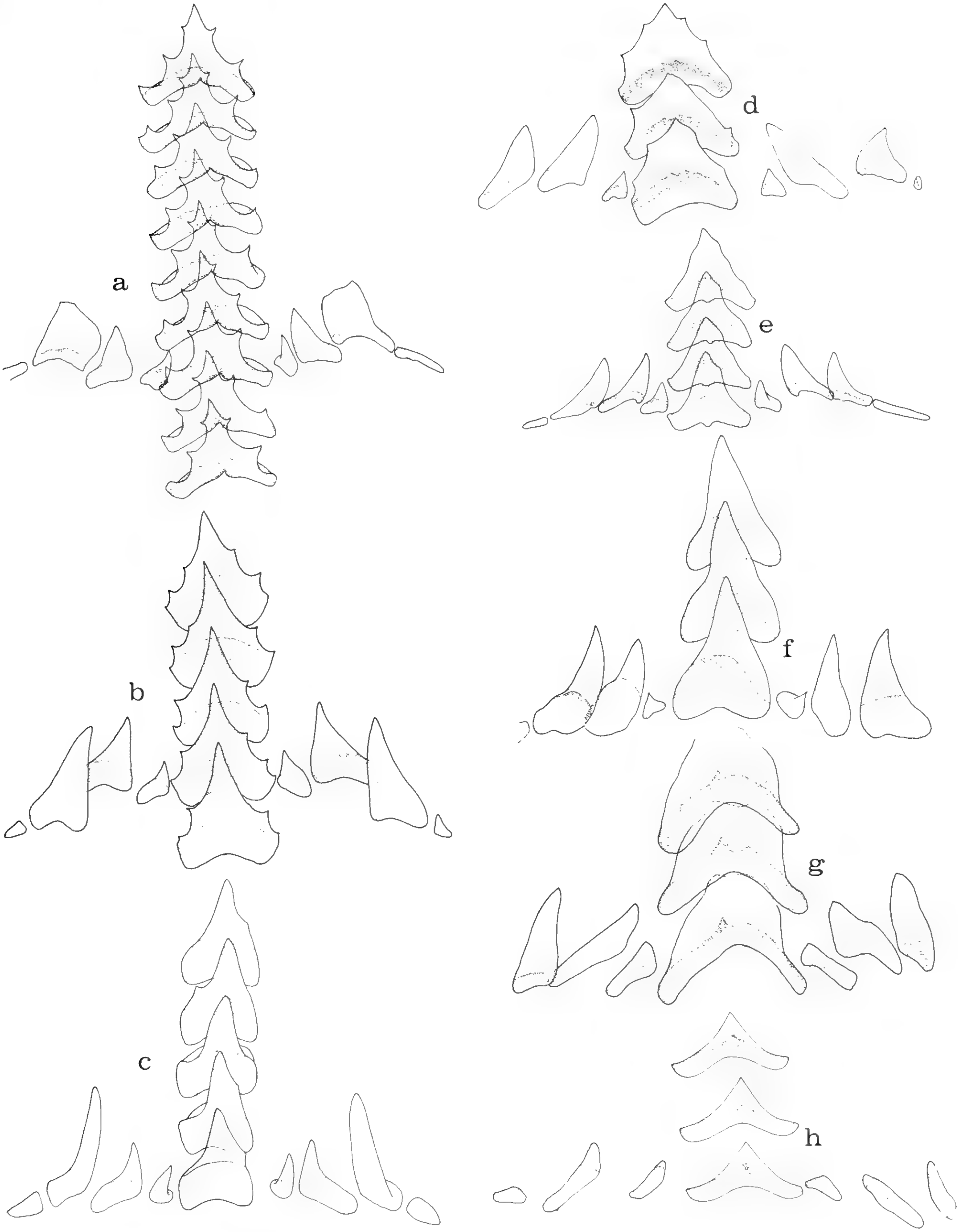

FIGURE 19. *Graneledone pacifica* new species. (a–h) Radulas: a, male, 96 mm ML; b, female, 97 mm ML; c, female, 45 mm ML; d, male, 90 mm ML; e, male, 85 mm ML; f, male, 60 mm ML; g, male, 86 mm ML; h, male, 85 mm ML.

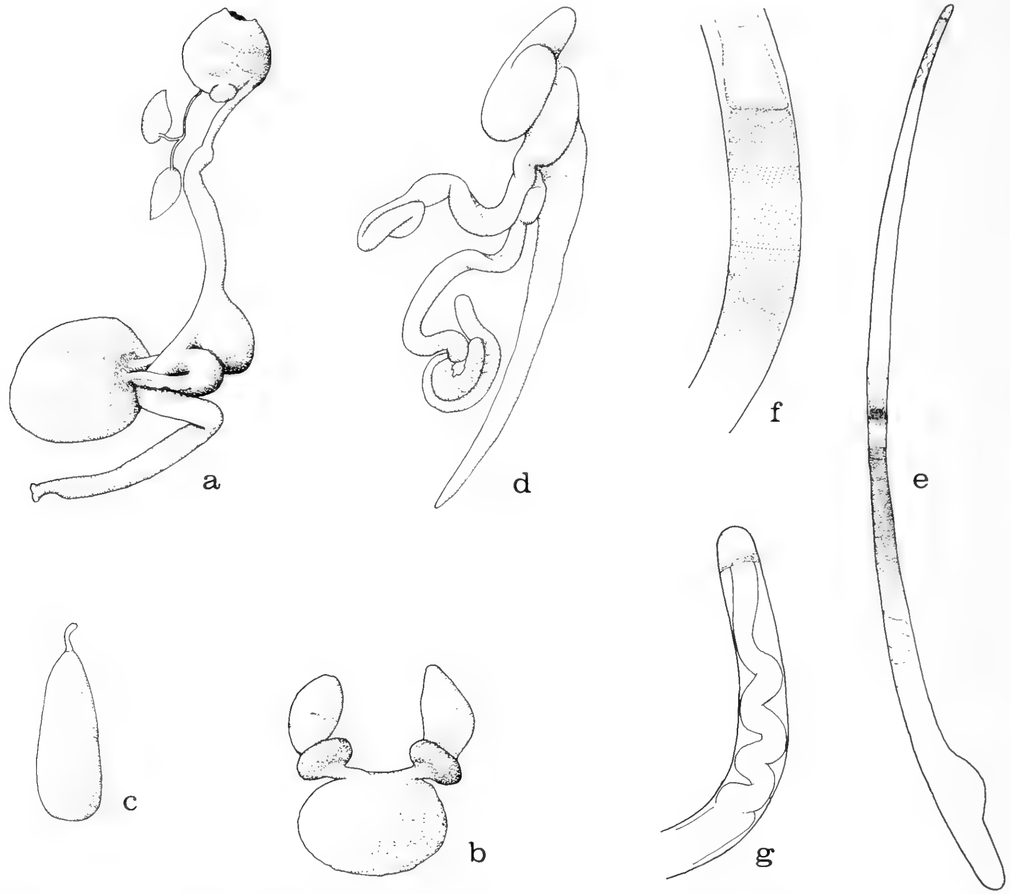

Figure 20. *Graneledone pacifica* new species. (a) Digestive tract from female, 75 mm ML. (b) Genitalia of female, 75 mm ML. (c) Egg of same. (d) Genitalia of male, 96 mm ML. (e) Spermatophore of same. (f) Cement body of same. (g) Horn of same.

125°41.8′W in 2,195 m, 30 Mar. 1969, UMML 31.2538.—1 female, ML 60 mm, R/V CAYUSE, 44°49.6′N, 125°33.0′W in 2,756 m, 8 Mar. 1972.—2 females, ML 41–59 mm, R/V YAQUINA, 45°57.6′N, 125°46.2′W in 2,265 m, 20 July 1970.—1 male, ML 65 mm, 1 female, ML 54 mm, R/V YAQUINA, 45°21′N, 125°37.3′W in 2,500 m, 11 Oct. 1974.—1 female, ML 47 mm, R/V ACONA, 44°25.6′N, 125°13.4′W in 1,530 m, 14 Aug. 1964.—1 female, ML 27 mm, R/V YAQUINA Cr. Y6910A haul 113, 46°04.6′N, 125°34.6′W in 2,156 m, 3 Oct. 1969, UMML 31.2537.

Diagnosis.—A *Graneledone* with VV-shaped funnel organ; short, stout spade-shaped ligula with only faint transverse lines; radula very variable, degenerate, often with various teeth missing; mantle, head and arms with rosettes of papillae, often closely packed, with one or two low, rough, supraocular cirri.

Description.—Body medium to large (Tables 18–19), firm and muscular body; skin loose over most of dorsal surface, bears numerous low to erect wartlike tubercles arranged in small clusters (Fig. 18a). Mantle globose, moderately wide (all indices throughout description from animals in excess of 70 mm ML) (MWI males 87.2–*92.9*–100.0; females 81.0–*92.1*–105.3); head narrower (HWI males 63.2–*72.7*–83.3; females 60.0–*72.0*–93.3), not distinctly set off from mantle; eyes medium to small with small apertures, project only slightly. Funnel large, stout, less than one-quarter of distal end free; inner edge of funnel forms strong flap which inserts into deep pocket in inner mantle wall, that makes an effective locking apparatus; funnel organ VV-shaped, very variable, each pad grading from slender V-shaped to thick pads split anteriorly (Fig. 18g–j); outer limb usually shorter than inner limb but may be equal in length or inner limb may be shorter than outer one, with all intergradations between two extremes.

TABLE 18. Indices of bodily proportions of 14 males of *Graneledone pacifica* new species and other data.

	Specimen													
	—	—	—	—	—	—	UMML 31.2541	—	UMML 31.2542	USNM 730716	UMML 31.1959	UMML 31.1957	CAS 061434	UMML 31.2539
ML	19	21	58	59	49	60	62	65	85	85	86	90	95	96
MWI	111.0	85.7	103.4	86.4	81.6	75.0	77.4	87.7	90.6	100.0	87.2	92.2	89.5	97.9
HWI	105.0	71.4	82.8	66.1	71.4	63.3	72.6	80.0	76.5	64.7	73.3	75.6	63.2	83.3
MAI	30.0	43.8	28.3	31.1	36.6	32.4	37.6	34.0	31.7	25.0	27.7	28.6	27.5	25.3
ALI	77.0	69.6	78.2	75.1	72.4	74.0	71.1	74.3	72.4	79.1	79.5	76.8	80.2	84.4
AWI	24.0	19.1	20.7	18.6	18.4	18.3	19.4	21.5	16.5	20.0	18.6	17.8	15.8	19.8
WDI	25.0	25.0	28.3	27.9	25.9	26.5	29.1	30.9	28.7	26.5	23.6	23.8	17.4	22.1
SIn	7.4	5.7	6.9	5.1	5.1	5.8	4.8	5.4	5.9	5.9	5.8	5.6	6.3	6.3
HcAI	79.7	—	92.5	80.6	92.2	77.0	91.3	90.4	85.1	83.8	85.8	84.2	70.8	84.4
LLI	2.4	—	3.8	4.8	3.7	5.9	4.4	5.3	5.3	5.4	6.5	4.9	6.3	5.0
CLI	16.7	—	58.3	57.1	67.5	40.0	83.3	76.5	66.7	64.3	58.6	63.6	62.1	61.5
PLI	9.0	4.8	27.6	25.4	16.3	20.0	25.8	23.1	36.5	47.1	34.9	36.7	33.7	38.5
SpLI	—	—	—	—	—	—	—	—	145.0	—	169.0	—	—	—
SpWI	—	—	—	—	—	—	—	—	4.0	—	5.0	—	—	—
SpRI	—	—	—	—	—	—	—	—	41.0	—	41.0	—	—	—
AF	1234	2134	1234	1234	1234	1234	1234	2134	1234	1234	2134	2134	2134	1234
WF	CB=DEA	DCBA=E	BC=DAE	BCDAE	BCDAE	DCBEA	CDBAE	CDBAE	C=DEBA	DCA=EB	CDBEA	CDBAE	—	—
Gills	8	7	7	7	7	7	7	7	7	7	8	7	8	7

Arms moderately long (MAI males 25.0–*27.6*–31.7; females 25.3–*29.1*–31.4; ALI males 72.4–*78.7*–84.4; females 74.4–*75.6*–77.1), muscular, round in cross-section, rather stout (AWI males 15.8–*18.1*–20.0; females 18.0–*20.2*–24.0), taper to long slender points; arm formula I.II.III.IV. Suckers in single row, raised on oral surface of arm, somewhat urn-shaped, well-separated; suckers small (SIn males 5.6–*6.0*–6.3; females 5.2–*5.9*–6.7) increase gradually in size from mouth distally, attain greatest size at about margin of web, after which gradually decrease to tips of arms.

Hectocotylized arm shorter than its fellow (HcAI 70.8–*82.4*–85.8); ligula small (LLI 4.9–*5.6*–6.5) broad, somewhat heart shaped, may be very small, broad, deep or more slender, pointed (Fig. 18b–d); shape of ligula variable but consistent in length index, usually deeply excavated with numerous low, transverse laminae, some with low longitudinal median ridges on floor of excavation (Fig. 18d); sides raised, thin, muscular, with considerable variation as shown in figures; calamus large (CLI 58.6–*62.8*–66.7), narrow, sharply pointed, in some smaller specimens calamus length index may exceed 80. Web extends along side of arm, broad, with poorly developed spermatophoral groove but thickened web margin; in preserved specimens contracted web caused end of arm to curl.

Gills large, stout; inner and outer demibranches about equally developed, 7–8 lamellae per outer demibranch.

Buccal mass large; beaks consistent in all features; upper beak (Fig. 18e) with strong deep jaw angle; lower beak (Fig. 18f) with 90° jaw angle, with distinct groove along lower edge of insertion plate.

Eight radulae extracted and examined (Fig. 19a–h); individual radulae very different. Radulae range from multicuspid rachidians with a B_8 seriation to simple rachidians, to almost completely degenerate ones; some with large, well-developed marginal plates, while others with none; one (Fig. 19h) lacks admedians on one side but has them on other side.

Anterior salivary glands small, free from buccal mass (Fig. 20a); posterior salivary glands small, narrowly elliptical; esophagus slender, expanded into a long, thick-walled pseudocrop with no diverticulum; internal walls strongly plicate; anterior half of stomach muscular, posterior thin-walled; spiral caecum comparatively small; digestive gland large, roundish; paired digestive gland ducts large, thin-walled, may be overlooked in some specimens; intestine stout with sharp bend in anterior quarter; anal flaps and ink sac absent. Crop and stomach contents consisted of crustacean remains, primarily copepods and amphipods.

Genitalia of adult female shown in Figure 20b; ovary moderately large, in near-ripe condition; proximal oviducts short, stout; oviductal glands large, round, somewhat flattened, dark blue-gray; distal oviducts large, short, elliptical, very swollen, terminate in small pores. One of distal oviducts contained mass of whitish material that, under microscope, resolved into minute spherical bodies, probably sperm. Genitalia of other females not developed despite long mantle lengths; oviductal glands small; distal oviducts only moderately larger than proximal ducts; stalk short, white; eggs flesh colored with light transverse striations in largest female; eggs large, measuring 16 × 7 mm, widest part at the posterior end (Fig. 20c).

Penis large, stout, somewhat square-tipped (Fig. 20d); duct enters some distance posterior to pore; diverticulum large, stout, strongly turned back upon itself; Needham's sac long and stout anteriorly, long and slender posteriorly; appendix to accessory gland not visible.

Spermatophores (Fig. 20e–g) large (SpLI 145.0–*157.0*–169.0), stout (SpWI 4.0–*4.5*–5.0), with large, flesh-colored sperm reservoir (SpRI 41.0–*41.0*–41.0); main tube semi-transparent or whitish; cement gland portion purplish red, very dark, almost maroon in some, pale bluish in others; tube narrows posteriorly to connective region, then swells out to large, swollen sperm mass. Spermatophore tube straight to near oral end, makes about three to four coils or turns just prior to end; junction of tube with cement gland surface speckled in regular rows; this area formed by hundreds of small tubular bodies packed in series, radiating outward from center; sperm mass formed of large convolutions. All spermatophores appear similar although indices vary somewhat from specimen to specimen.

Color of specimens preserved in ethanol varies considerably: in some large specimens general coloration pinkish gray, liberally covered with small darker-colored spots with tubercles; in others, ground color reddish brown or purple with tubercles standing out as pale spots; in smaller specimens ground color dark slate gray with reddish tinge or dark purple upon which tubercles stand out either lighter or darker, sometimes rather indistinct according to state of contraction. Web and oral surface of arms slightly darker in most specimens. Some specimens show distinct reverse countershading with dorsal surface of mantle, head, and arms lighter than ventral surface; apertures of eyes dark colored in all of lighter-colored specimens.

Surface sculpture distinctive, with little variation other than that from condition of preservation. In well-preserved specimens dorsum of mantle, head, and bases of arms I and II closely covered by small wartlike clusters of tubercles, each cluster raised somewhat from body surface on low fleshy pad; in most specimens pad not discernible, warts set flat on skin; each wart consists of usually six to seven (range 2 to about 11), small blunt tubercles that often, not always, surround somewhat larger central one; warts also surround eyes, but enlarged only dorsally where two, sometimes three, form conspicuous large rough nobs; in life, warts may be erected into tall cirri, but only one specimen exhibits this condition; several specimens, probably preserved in flaccid state, show reverse situation in which warts slightly sunken into general skin surface and even appear as low depressions or pits; examination of these areas under microscope, however, shows similar arrangements of tubercles as found on elevated ones. All stages of conditions between warts and pits present undoubtedly due to flaccidity or contraction at time of fixation, also indicated in that erect warts usually rather close together while flattened ones more widely spaced. Base of lower arms and ventral surface of mantle and head smooth, more darkly colored; two dorsal ocular papillae plainly visible even in smooth or pitted specimens.

MEASUREMENTS AND COUNTS.—Holotype: 85 mm ML; mantle width 85; head width 55; length of longest arm L(I) 346; total length 432; length of hectocotylized arm 290; ligula length 15.6; calamus length 10; sucker diameter 5.0; depth of deepest web sector (D) 91.6; number of gill lamellae in outer demibranch 7.

TYPE.—Holotype, male, 85 mm ML, USNM 730716 (fixed in formalin and preserved in 50% isopropyl alcohol).

TYPE-LOCALITY.—Off Oregon, Cascadia Abyssal Plain near the slope, 44°52.0′N, 125°32.8′W, 2,706 meters.

DISCUSSION.—Six species of *Graneledone* are

TABLE 19. Indices of bodily proportions and other data of 14 females of *Graneledone pacifica* new species.

	Specimen													
	UMML 31.2540	UMML 31.2537	—	UMML 31.2542	—	—	—	—	UMML 31.2538	UMML 31.2540	—	—	—	—
ML	13	27	41	45	47	54	59	60	75	88	97	100	105	105
MWI	111.5	100.0	85.4	66.7	114.9	90.7	106.8	93.3	105.3	85.2	91.8	96.0	93.3	81.0
HWI	115.4	103.7	78.1	66.7	97.9	83.3	98.8	81.7	93.3	68.2	76.3	60.0	67.6	66.8
MAI	30.9	27.0	50.6	39.1	28.7	32.5	39.3	33.7	25.3	28.9	28.5	31.3	31.4	28.9
ALI	70.0	78.1	66.4	71.9	74.5	75.8	76.5	78.8	77.1	74.4	75.1	75.3	75.4	76.4
AWI	23.1	25.9	20.7	15.6	23.4	20.3	23.7	18.3	24.0	20.5	18.6	18.0	20.0	20.0
WDI	30.9	23.0	—	28.7	30.5	27.7	31.3	25.8	26.9	26.2	27.9	25.3	26.4	22.9
SIn	7.7	6.3	4.9	4.4	6.4	5.6	5.1	5.0	6.7	6.3	5.2	6.0	5.7	5.7
AF	1234	1234	2134	1234	1234	1234	2134	1234	1234	1234	1234	1234	1234	1234
WF	CBADE	BCDAE	—	CBDAE	BDCAE	CBDAE	CBDAE	CBDAE	CBDEA	AB=CDE	DCBAE	CDBEA	CBDAE	CDBEA
Gills	7	8	8	8	7	7	8	7	7	7	8	8	7	7

known—*G. verrucosa* (Verrill, 1881) from the North Atlantic (with a possible subspecies *media* Joubin, 1918), *G. challengeri* (Berry, 1916) from the Kermadec Islands, *G. antarctica* (Voss, 1976) from the Ross Sea, Antarctica, *G. macrotyla* (Voss, 1976) from near the Falkland (Malvinas) Islands, and *G. boreopacifica* (Nesis, 1982) from the northwestern Pacific. *G. setebos* (Robson, 1932) from McMurdo Sound, Antarctica, is considered a nomen dubium (Voss 1976:457). Most of the species are very unsatisfactorily known. Knowledge of variation is known only in *G. antarctica.*

The present material, if we are correct in assigning it to a single species, shows great variation in skin sculpture, radula, funnel organ, and hectocotylus, but surprisingly consistent morphometrics and structure of beaks and spermatophores. *G. antarctica* showed similar wide variation in radula dentition but was remarkably consistent in other features.

In view of our incomplete information concerning *G. verrucosa,* it is difficult to compare it with *G. pacifica.* The type of *verrucosa* was borrowed from the USNM, but its condition did not lend itself for comparison. In the USNM, however, there is now a nice series of *verrucosa* taken by the R/V's KNORR, CHAIN, and WALTHER HERWIG. Detailed examination of these specimens has not been done, but preliminary study shows that, in contrast with *pacifica,* these specimens have a consistently formed radula with little variation. These show rachidians with an A_{3-4} seriation, strong admedians, second laterals with elongate bases, and third laterals that are rather short and triangular. The warts on the mantle and head are composed of fewer papillae, 3–4, sometimes 5, and show the same general distribution as in *pacifica* but with a number of large warts all around the eye, some quite large, in addition to the 2–3 large supraocular papillae found in both species.

The description of *G. boreopacifica* (Nesis, 1982) is very brief, contained only in a key to the species of the genus accompanied by two figures. Possibly this species is the same as ours, in which case *boreopacifica* takes precedence. The problem cannot be resolved until a detailed description is published.

On the basis of the differences, *G. pacifica* is considered to represent a new species, but it appears to be closely related to its Atlantic congener.

This species was captured on the continental slope, slope base, and eastern boundary of the Cascadia Abyssal Plain off Oregon. It was not found on the Western Cascadia or Tufts plains and therefore appears to be a bathyal-abyssal species that lives near the continent.

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LAND MOLLUSCA OF BAJA CALIFORNIA, MEXICO

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Abstract: The native land mollusk fauna of Baja California, including the islands of the Pacific coast and the Gulf of California, consists of 117 species and subspecies, distributed among 36 genera of 18 families. All but the amphibious prosobranch *Truncatella* are pulmonates. Three additional species have been introduced through human activity. Two new species, *Rabdotus* (*Plicolumna*) *perhirsutus* (in Bulimulidae) and *Greggelix* (*Matirelix*) *huertai* (in Helminthoglyptidae) are described. Locality lists and synonymic notes are given for all species; distribution maps are provided for most. Three principal land molluscan faunal regions are recognized: Californian, Sonoran, and Cape. The Californian and Sonoran regions are further divided into zones. These biogeographic divisions correspond rather closely to phytogeographic and other zoogeographic subdivisions proposed for Baja California.

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Introduction

The land mollusks of Baja California include a varied, highly endemic group of species that even today are incompletely known. The Baja California peninsula extends approximately 1,300 km from the United States/Mexico border south-southeasterly to Cabo San Lucas. Rugged terrain, extreme aridity in many areas, and problems of inaccessibility have made it unattractive to most malacologists. Particularly in the desert regions and rockslide habitats, land mollusks occur sparsely and are difficult to find in living condition.

The purpose of this paper is to summarize the composition and geographic distribution of the

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land mollusk fauna. Previous published records have been critically reviewed. The bibliography includes all references to Baja California land mollusks that introduce new taxonomic or distributional information. Taxonomic status and distributional records are based on examination of the major collections of Baja California land Mollusca—chiefly those of the U.S. National Museum of Natural History, Academy of Natural Sciences of Philadelphia, California Academy of Sciences, Santa Barbara Museum of Natural History, University of Arizona, and the private collections of authors Miller and Christensen. All newly cited localities have been verified by one or more of the authors, with section responsibility principally as follows: Miller—Succineidae, Helminthoglyptidae; Christensen—Subulinidae, Bulimulidae, Oleacinidae; Miller and Christensen—Valloniidae, Strobilopsidae, Punctidae, Oreohelicidae; Miller, Christensen, and Roth—Truncatellidae, Pupillidae, Haplotrematidae, Helicodiscidae, Arionidae, Zonitidae, Megomphicidae. Two new species are described. Several new synonymies are introduced. Many bulimulid localities here published for the first time were originally cited in a revisionary thesis by Christensen (1978).

This report is the outgrowth of a manuscript begun by Allyn G. Smith in consultation with the other three authors but left unfinished upon his death. The three of us (Miller, Christensen, Roth) acknowledge our profound debt to Allyn for his conviction that a distributional list of Baja California land mollusks was necessary and timely, for his thorough review of the history of investigations in the region, and for making many of the original identifications. Final responsibility for species determinations, however, rests with us, as indicated above.

ACKNOWLEDGMENTS

Thanks are due to the late Joseph C. Bequaert for nourishing the interest of authors Miller and Christensen in minute mollusks, and for commenting on an early draft of the paper. We are grateful to colleagues W. L. Pratt, Richard L. Reeder, F. M. Climo, and the late S. Stillman Berry for discussion of taxonomic aspects of the study; to Judith Terry Smith for specimens collected during her geologic field work in Baja California; to Gene Coan for advice on taxa named by Henry Hemphill; to Peter LaRochelle and C. Clifton Coney for comments on Pupillidae; and to Dick Reeder, Jim Hoffman, Judith Christensen, Betty Sue and William Nixon Miller, Jim Cartwright, Noor Babrakzai, Diana Warr, and H. Lee Fairbanks for valued companionship in the field. Arthur E. Bogan arranged the loan of type material under his care. Stanley C. Williams and Vincent F. Lee kindly provided base maps. Dennis E. Breedlove conscientiously brought us mollusk specimens he collected during his botanical explorations. Peter U. Rodda supported and aided production of the report. The late George Radwin called author Miller's attention to two shells collected by Reid V. Moran in the Cerro de la Mina de San Juan, setting in motion the events that led to the discovery of *Greggelix* (*Martirelix*) *huertai.* Acknowledgment is made to the Secretaría de Agricultura y Ganadería, for issuing permits for scientific collecting. The G Dallas Hanna Fund for Scientific Publication supported publication of this paper.

HISTORY OF INVESTIGATION

The first land snail species described from Baja California was the bulimulid *Naesiotus pallidior* (Sowerby, 1833), originally obtained by the famous British shell collector Hugh Cuming. Additional bulimulid species from Cuming were described by Louis Pfeiffer (1846, 1865). Pfeiffer (1845) also described *Xerarionta levis* and *X. areolata,* collected in 1839 by Richard Brinsley Hinds, surgeon-naturalist on the worldwide exploring voyage of HMS SULPHUR. Gould (1853) described two species of *Rabdotus* and one of *Naesiotus* collected by officers of the United States Army and Navy during the Mexican War (Johnson 1964).

An important early source of Baja California land mollusks was the Hungarian naturalist, János Xántus de Vésey. Xántus operated a United States Coast Survey tidal station at Cabo San Lucas in 1859–1861. He is reported to have collected in the mountains of the Cape region and northward for a distance of 560 km up the east coast, although other evidence implies that he never traveled more than about 120 km from his station (Madden 1949). Some of the land snails that he collected are now in the U.S. National Museum of Natural History (USNM) and the Academy of Natural Sciences, Philadelphia (ANSP).

Bulimulid land snails sent by Xántus led W.

G. Binney to infer a zoogeographic relationship between Baja California and Peru, and for a time the idea took root. Binney (1861) first identified the large Cape region species now known as *Naesiotus montezuma* (Dall, 1893) as a superficially similar Peruvian species, *Bulimus* (now *Scutalus*) *proteus* (Broderip, 1832). Tryon (1867:173) listed *B. proteus* as "a Peruvian species, of which a number of young specimens have been collected in Lower California," illustrated a juvenile shell of the Cape region species, and remarked that it was possibly no more than "an adventitious inhabitant." Binney and Bland (1869) and Fischer and Crosse (1870–1902) listed *B. proteus* from Cabo San Lucas based on material from Xántus. Cooper (1891:101) remarked, "the occurrence of . . . *B. proteus,* also reported from Lower California as well as Peru or Chili [sic], is made more interesting by the similar occurrence of several plants in both regions which are not found anywhere between." Only after visiting the California Academy of Sciences in 1892 and examining over 100 specimens collected in the Sierra Laguna by Gustav Eisen and W. E. Bryant earlier the same year was Willam H. Dall able to conclude that the *Bulimulus proteus* of Peru was not the same as the species from Baja California (Dall 1893a). The concept of biogeographic affinities between the bulimulid snails of Baja California and those of South America has recently been given new life by the demonstration (Hoffman 1988) that several species formerly referred to the North American genus *Rabdotus* are assignable to *Naesiotus,* a widespread South American, Antillean, and Galapagan genus.

John A. Veatch spent the months of June, July, and August 1859 on Isla Cedros prospecting for mineral deposits, especially copper ores. His general report on the topography and resources of the island (Veatch 1869:151) mentions the abundance of "*Helix Veatchiana*" (error for *Arionta veitchii* Tryon, a synonym of *Xerarionta levis canescens*).

The next notable collection of Baja California land snails was made by the geologist, mining engineer, and conchologist, William More Gabb. In the process of investigating mineral resources, Gabb traveled, mostly on horseback, from Cabo San Lucas to San Diego, California, in the period January 5–April 20, 1867, crossing the peninsula several times en route (Gabb 1869). Gabb collected land snails extensively, but his carelessness in recording locality data has limited their usefulness. Some of his land snails are now in the USNM and ANSP.

The interest of the California Academy of Sciences (CAS) in the fauna and flora of Baja California began in the 1880s and developed rapidly. Gustav Eisen's (1895:763–764) review of early Academy expeditions into the area provides an interesting and useful chronology:

1. Expedition in March, 1888. W. E. Bryant. Magdalena Island, San Jorge to Comondu and across the peninsula to La Giganta and Loreto. Back by La Giganta, San Gabriel, San Juan. Back through Comondu.
2. Expedition spring of 1889. W. E. Bryant and Chas. D. Haines. Magdalena Island, Santa Margarita Island, San Jorge, Comondu, from there overland to San Gregorio, San Ignacio, Calmalli, Santa Borgia, El Rosario, San Quintin.
3. Expedition September and October, 1890. W. E. Bryant. San José del Cabo, Agua Caliente, Sierra, Triumfo, La Paz.
4. Expedition March to May, 1892. W. E. Bryant, Gustav Eisen. San José del Cabo, Miraflores, Agua Caliente, Santiago, Gulf shore, Sierra Laguna, San Francisquito, La Paz, Espiritu Santa Island, Guaymas, Sonora, Hermosillo, Durasnillas, San Miguel.
5. Expedition September and October, 1893. Gustav Eisen. San José del Cabo, Sierra El Taste, across to Pescadero and Todos Santos, Cabo San Lucas, and back to San José, Miraflores, San Francisquito, Sierra Laguna, Todos Santos.
6. Expedition September, October, November, 1894. Gustav Eisen, Frank H. Vaslit. San José del Cabo, Miraflores, Santa Anita, La Palma, Sierra San Lazaro, El Taste, Piedra Corral. Overland from San José to La Paz by Santiago, San Bartolo, Triumfo, La Paz. Mazatlan, by steamer to San Blas. Overland to Tepic, by land to Mazatlan, via Santiago Ixtquintla, Squinapa, El Rosario, etc.

Nonmarine mollusks from these Academy expeditions were worked up by James Graham Cooper, who reported a total of 63 land and freshwater species, 17 of them new to science (Eisen 1895:766). From 1891 to 1895, Cooper published six taxonomic and zoogeographic papers on the land mollusks (Cooper 1891, 1892a, b, 1893, 1894, 1895); in these he assembled information on the snails collected by Xántus, Eisen and companions, Lyman Belding, Henry Hemphill, and Charles Russell Orcutt. A total of 47 species and varieties of land mollusks are mentioned by name in these papers, which were among the last malacological works Cooper ever published (Coan 1982).

Dall (1893b) recorded 13 species of *Bulimulus* from Baja California, describing two as new. Robert E. C. Stearns (1894) reviewed the collecting results of many scientists whose specimens are in the USNM, beginning with an expedition in 1876 by W. J. Fisher of San Francisco, and mentioned the contributions made by Capt. Anthony Forrer, Gabb, Henry W. Henshaw, Hemphill, Edward Palmer, and the staff of the U.S. Fish Commission steamer ALBATROSS. Stearns was closely associated with the CAS, serving in various capacities including Vice-President, Curator of Conchology, Director of the Museum, and member of the Committee on Publication. His large personal collection is in the USNM. Stearns (1875, 1904) was the author of the observation, often quoted in molluscan textbooks, that the Baja California snails *Xerarionta levis canescens* and *Naesiotus pallidior* survived six years without food or water in a box in his desk.

Unfortunately, most land snails collected by Eisen, Bryant, Belding, and others that had been deposited in CAS were lost in the San Francisco earthquake and fire of 1906. A small amount of material in private collections escaped destruction and has since been deposited in the CAS collection. Some material from these early investigations survives in the University of California Museum of Paleontology, Berkeley, and in U.S. East Coast museums; that which had been forwarded to Dall is now in the USNM.

The French malacologist Jules Mabille (1895) described, without illustrations, 18 species and subspecies of nonmarine snails collected by Leon M. Diguet on the Baja California peninsula and the Mexican mainland. Most of the species were not localized beyond "La Basse Californie," and as Pilsbry (1895) was quick to point out, not compared or contrasted to other species. Ancey (1905) reviewed the taxa, finding many to be synonyms. In 1966, G Dallas Hanna, then Curator and Chairman of the CAS Department of Geology, photographed as many of Mabille's type specimens as could be found at the Muséum National d'Histoire Naturelle, Paris; Hanna and Smith (1968) illustrated 13 of these specimens, suggesting synonymies and allocations for most. Additional revisions of the Mabille Helminthoglyptidae and Bulimulidae were published following a visit by W. B. Miller to the MNHN in August 1971 (Miller 1972; Christensen and Miller 1976b).

In 1896, A. W. Anthony of San Diego, later Director of the San Diego Museum of Natural History, collected along the west coast, visiting Bahía Santa Rosalillita and the islands of Guadalupe, Cedros, San Martín, Natividad, and the San Benitos (Dall 1900). Charles H. Townsend of the U.S. Fish Commission visited Isla Guadalupe around this time, and "parties from San Diego" collected on Islas Los Coronados, returning with material that was studied by Dall (1900). In 1898–1899, the Hopkins-Stanford Galapagos Expedition, with R. E. Snodgrass and Edmund Heller as participating scientists, landed on Isla Guadalupe and collected land mollusks. A few of these specimens are in the Stanford University collection, now housed at CAS; others, studied by Dall (1900), are in the USNM.

The expedition of CAS to the Galapagos Islands in 1905–1906, aboard the schooner ACADEMY, stopped en route at Ensenada and the islands of San Martín, San Gerónimo, the San Benitos, Cedros, Natividad, and San Benedicto and Socorro of the Revillagigedos group (Slevin 1931). Although Slevin (1931:15) mentions "many dead shells . . . found scattered about in the sheltered gullies" on Isla Natividad, the only land snails from this expedition now in the CAS collection are from the Galapagos.

In the 1920s, CAS sponsored three major expeditions to Baja California, the offshore islands west of the peninsula, and the islands in the Gulf of California. The itineraries have been published in general reports in the Academy Proceedings (Slevin 1923; Hanna 1925, 1926). The first expedition, in 1921, visited several localities on the Sonoran side of the gulf, all of the major gulf islands, and many sites along the eastern shore of the peninsula. The expedition malacologist, Fred Baker of San Diego, concentrated mainly on marine mollusks. Most of the land mollusks, later written up by Hanna (1923), were collected by herpetologist Joseph R. Slevin, botanist Ivan M. Johnston, and entomologists Edward P. Van Duzee and Joseph C. Chamberlin.

The 1922 expedition was sponsored jointly by CAS, the San Diego Society of Natural History, the Scripps Institution for Biological Research, the National Geographic Society, and the government of Mexico. It visited the islands of Guadalupe, San Martín, Cedros, Natividad, the San Benitos, San Roque, Asunción, Magdalena, and Santa Margarita. In addition, landings were made on the west coast of the peninsula at Ensenada, Bahía San Quintín, Bahía San Bartolomé, and Punta Abreojos. Hanna's (1925) general account of this expedition indicates that over 2,000 land shells were collected. Pilsbry (1927) reported on the nonmarine mollusks, describing 12 new species and subspecies. Specimens from this expedition are deposited in CAS and the San Diego Museum of Natural History.

The third CAS expedition, in 1925, visited Isla Guadalupe, the Revillagigedos group, Las Tres Marías, Isla Cedros, and Isla San Martín. Mainland stops were made at San Diego, Mazatlán, Cabo San Lucas, Bahía Magdalena, and Bahía San Quintín. The land mollusks, including many new species, were reported on by Dall (1926); they are deposited in the CAS collection.

A primarily botanical expedition in 1946, organized by Ira L. Wiggins of the Natural History Museum of Stanford University (Anonymous 1947), also brought back land mollusks. Specimens are in the S. S. Berry collection, now at the Santa Barbara Museum of Natural History (SBMNH), and are reported here for the first time.

The next institution-sponsored Baja California expeditions were the Joseph W. Sefton Foundation Expeditions of March–May 1952 and March–April 1953 (Arnaud 1970), using the R/V ORCA. Places visited included many offshore Mexican and Gulf islands and mainland points on both sides of the Baja California peninsula. The many land snails collected were deposited in the CAS and S. S. Berry (now SBMNH) collections; most have not been previously reported.

The 1957 Puritan-American Museum of Natural History Expedition to western Mexico visited numerous localities on the mainland of Baja California and nearby islands (Emerson 1958). Ten species of land mollusks were collected (Jacobson 1958); the materials are in the American Museum of Natural History (AMNH).

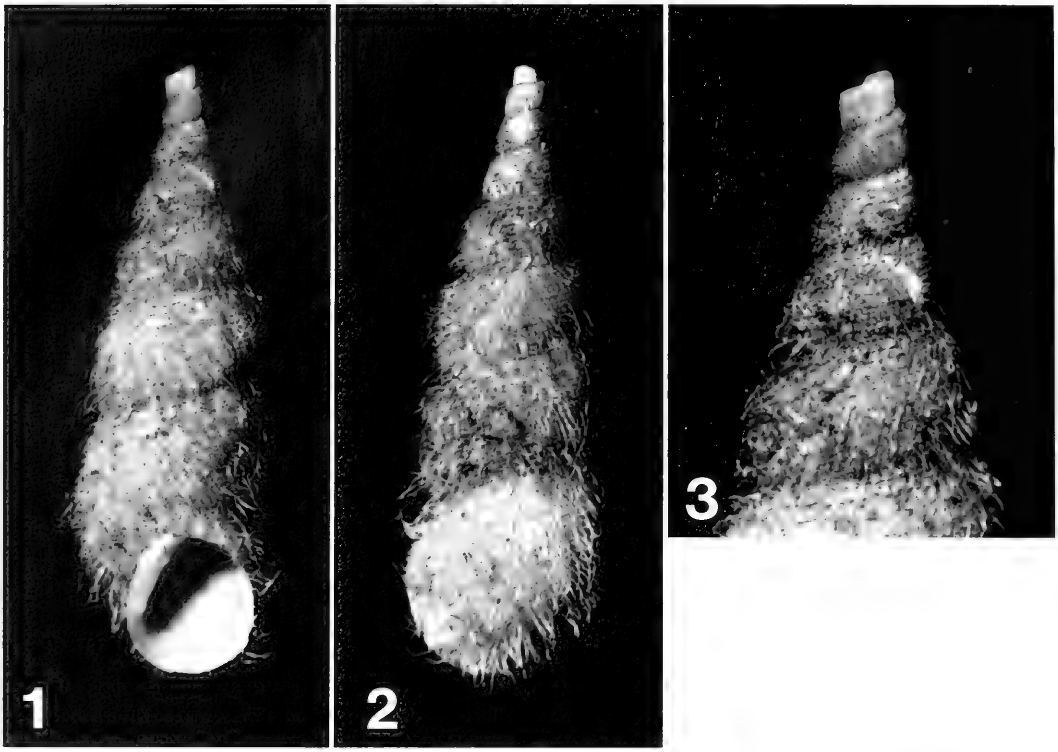
Beginning in 1958, with support from the Belvedere Scientific Fund, CAS organized a number of expeditions and shorter field investigations in Baja California (Smith 1959; Wiggins 1960a). Land mollusks collected during these expeditions were deposited in the CAS collection and are cited in this report for the first time. The first expedition worked in the Cape region in December 1958 and January 1959. Malacologist on the expedition was A. G. Smith; other personnel included botanists Ira L. Wiggins and Reid V. Moran, herpetologist A. E. Leviton, and entomologist Hugh B. Leech. Collections were made in the area south of La Paz generally along the main roads through El Triunfo, Santiago, Boca de la Sierra, Santa Anita, San José del Cabo, Cabo San Lucas, El Pescadero, and Todos Santos. Land snails collected included two species that had not been found since Gustav Eisen's explorations in the 1890s.

A second trip to the Cape region, made in spring 1959, was recounted by Wiggins (1960a). A reconnaissance trip to Bahía de Los Ángeles was made in May of the same year. Land mollusks were collected on both occasions. Again in October 1959, A. G. Smith participated in a CAS-Belvedere Scientific Fund visit to the vicinity of La Paz, adding additional specimens to the CAS collection. In March and April 1961, a CAS party including Smith, Wiggins, and herpetologists Leviton and Benjamin H. Banta explored extensively in the Vizcaino Desert (Wiggins 1969).

In March and April 1962, a Belvedere Scientific Fund-sponsored expedition to the Gulf of California conducted by the San Diego Natural History Museum (SDMNH) visited 32 islands as well as seven stations along the Baja California coast (Lindsay 1962). William K. Emerson and other expedition members collected an extensive series of land shells, later reported on by Emerson and Jacobson (1964). The material was divided between the SDMNH and the AMNH.

Many private collectors have contributed to the knowledge of the land mollusk fauna. Charles Russell Orcutt's collecting extended from the 1880s until 1917, when he spent a month on Isla Magdalena. His field work is mentioned in brief accounts he published as editor of THE WEST AMERICAN SCIENTIST (Orcutt 1886, 1891, 1896, 1900a–c, 1915, 1918) and in a biography by DuShane (1971). Henry Hemphill, preeminent among early west coast shell collectors, made a number of trips across the California border in the 1880s and 1890s, visiting Bahía Todos Santos, Santo Tomás, and Bahía San Quintín. His large personal collection is now in the California Academy of Sciences. Shells that he sold as a dealer have found their way into many other museums. Hemphill's short paper in the JOURNAL DE CONCHYLIOLOGIE (Hemphill 1881), translated into French by H. Crosse, is one of the earliest faunal lists for a specific portion of Baja California.

Herbert N. Lowe of Long Beach, California, collected land snails along the northwest coast of Baja California in 1912 (Lowe 1913). In November 1931, he organized an expedition aboard



Figures 1–3. *Rabdotus* (*Plicolumna*) *perhirsutus* sp. nov., shell. Holotype, SBMNH 35110, apertural and abapertural views and enlargement of apex. Height 19.6 mm.

the yacht PETREL, visiting islands east and west of the peninsula (Lowe 1933), and taking large series of land mollusks. Lowe's main collection is in the SDMNH; some of his specimens have come to the CAS by gift or exchange.

Other specialists who have contributed to museum collections and the knowledge of Baja California land mollusks include S. Stillman Berry (whose large collection is now at the SBMNH), Dennis E. Breedlove, Mr. and Mrs. Emery P. Chace, Robert J. Drake, George Willett, and Stanley C. Williams.

In November 1969, Charlotte Church collected extensively in the middle and southern regions of the peninsula for her father, Munroe Walton, who in turn shared his specimens with Wendell O. Gregg and Walter B. Miller. This stimulated Miller to set out in December 1970 to obtain live specimens of what turned out to be the new genus *Greggelix* Miller. In 1972, Carl C. Christensen undertook to revise the genus *Rabdotus* in Baja California for his doctoral dissertation, and a number of expeditions were conducted throughout the range of that genus. One new species of Bulimulidae, originally diagnosed by Christensen (1978), is described herein. The period from 1970 to date has been devoted to the procurement of live specimens of the species inhabiting the peninsula so that generic and familial relationships can be determined on the basis of anatomical characters. Additional new species and records have continued to come to light as field investigations reach the more inaccessible regions of the peninsula (Christensen 1978, 1983; Christensen and Miller 1975, 1976a, b, 1977; Miller 1972, 1973a, b, 1981a, b, 1982; Miller and Christensen 1980; Roth and Christensen 1984); many of the collection records are reported here for the first time.

Descriptions of New Species

Family Bulimulidae
Genus **Rabdotus** Albers, 1850

Type species: *Bulimulus dealbatus* (Say) (=*Helix dealbata* Say, 1821), by subsequent designation (Kobelt 1880).

Subgenus **Plicolumna** Cooper, 1895

Type species: *Rhodea* var. *ramentosa* Cooper (=*Rhodea californica* Pfeiffer, subsp.? *ramentosa* Cooper, 1891), by monotypy.

Rabdotus (Plicolumna) perhirsutus Miller, Christensen, and Roth, sp. nov.

(Figs. 1–4)

Diagnosis.—A small, acicular *Rabdotus* (*Plicolumna*) with carinate, projecting embryonic whorls, deeply incised suture, granular to cancellate sculpture, and a thick periostracum bearing prominent, coarse hairs that arise from nodes on the spiral cords.

Description of shell of holotype.—Shell (Figs. 1–3) small for the genus, thin, acicular; apical angle 27°. Whorls 7.6, convex, suture deeply impressed. Embryonic whorls 2.0, projecting, flat-sided, strongly carinate at summit, with strong, regular, axial ribs that are straight on the first embryonic whorl but become sinuous and progressively more retractive on the second; interspaces crossed by minute, close, spiral striae. Early teleoconch whorls sculptured with coarse, retractive collabral rugae and (on third and fourth whorls, eight) nodose spiral cords, producing a granular to cancellate appearance. Periostracum thick, yellowish brown, bearing prominent, coarse hairs that arise from the nodes of the spiral cords; periostracal hairs to 1 mm or slightly more in length. From about fifth whorl on, additional spiral cords arising by intercalation, often not reaching the prominence of other cords, and with surmounting periostracal hairs correspondingly reduced in length. Body whorl a little compressed at periphery, base moderately produced, narrowly and obliquely umbilicate. Aperture ovate, peritreme continuous, margins reflected (most strongly so at base), not revolute, columellar margin rolled over umbilical region and continuous across parietal region as a raised callus. Columella without an entering lamella. Shell under periostracum dull white. Height 19.6 mm; diameter 6.8 mm.

Reproductive anatomy (based on paratype SBMNH 35111).—The reproductive system (Fig. 4) exhibits the general characters of the genus. The total length of the terminal male genitalia in the figured preparation is 16.0 mm; penis 6.0 mm long (38% of length of male genitalia), penial sheath 3.5 mm long (58% of length of penis); region of penial diverticula adjacent to penial sheath, its diameter about equal to that of sheath and about twice that of epiphallus; epiphallus 6.0 mm long (38% of length of male genitalia); epiphallic caecum 4.0 mm long (25% of length of male genitalia); spermathecal duct 19 mm long with a 4-mm length of the duct commencing about 4 mm from its anterior end, enlarged to

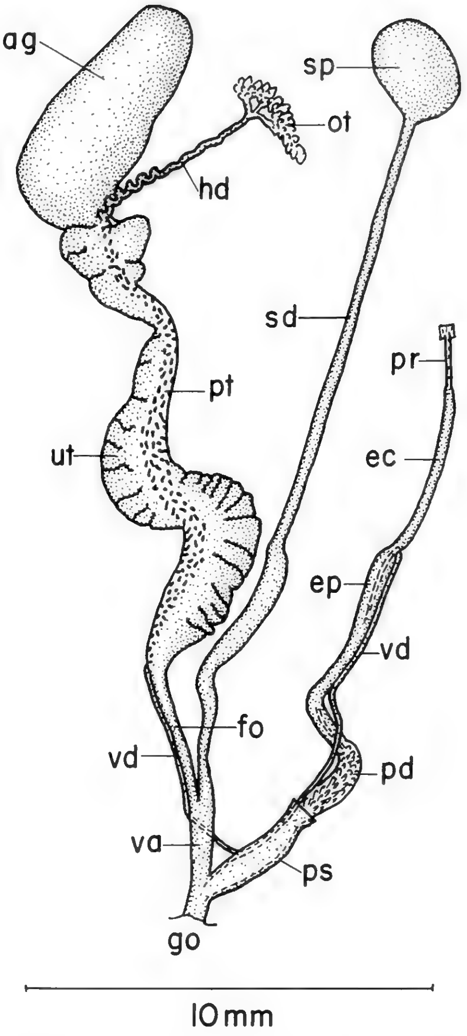
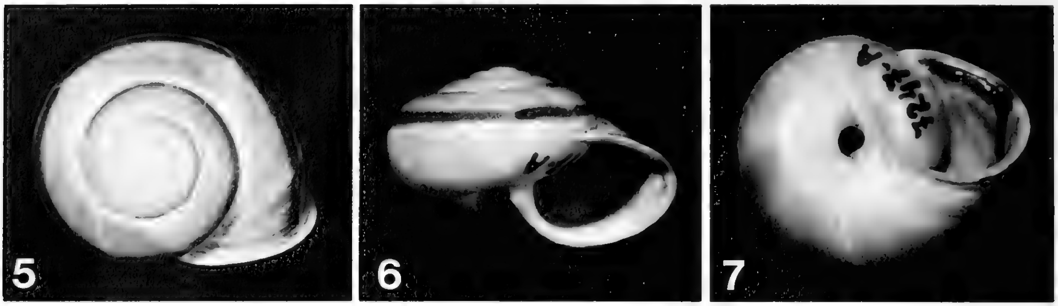


Figure 4. *Rabdotus* (*Plicolumna*) *perhirsutus* sp. nov., dissected reproductive system, drawn from projection of stained whole mount. Paratype, SBMNH 35111. Abbreviations: ag, albumen gland; ec, epiphallic caecum; ep, epiphallus; fo, free oviduct; go, genital orifice; hd, hermaphroditic duct; ot, ovotestis; pd, upper portion of penis, including diverticula; pr, penial retractor; ps, lower portion of penis, including penial sheath; pt, prostate; sd, spermathecal duct; sp, spermatheca; ut, uterus; va, vagina; vd, vas deferens.



FIGURES 5–7. *Greggelix* (*Martirelix*) *huertai* sp. nov., shell. Holotype, SBMNH 35113, top, apertural, and basal views. Diameter 17.8 mm.

almost twice the diameter of the rest of the duct; spermatheca ovate; free oviduct cylindrical, not enlarged.

TYPE MATERIAL.—Holotype, SBMNH 35110 (shell); Mexico, Baja California Sur: along Todos Santos–Cabo San Lucas road 2.2 mi [3.5 km] N of El Saucito, in granite rockpiles at crest of small hill seaward of road, elev. ca. 1,500 ft [460 m]; C. C. Christensen, J. A. Christensen, and W. B. Miller, coll., 22 Dec. 1973. One paratype (shell and whole mount of stained genitalia), SBMNH 35111, from same locality as holotype, W. B. Miller and W. N. Miller, coll., 23 Dec. 1970. Fifteen paratypes, SBMNH 35112, from same locality as holotype. Additional paratypes are deposited in ANSP, CAS, LACM, SDMNH, USNM, and the private collections of authors Christensen and Roth.

REFERRED MATERIAL.—Arroyo Candelaria, 2.3 mi [3.7 km] E of Migriño, elev. 200 ft [60 m], C. C. Christensen, coll., 21 Dec. 1975 (CCC) (one shell).

REMARKS.—In the material examined, shell height ranges from 18.7 to 21.2 mm; diameter, 4.9 to 6.8 mm; height/diameter ratio 2.88 to 4.16. Number of whorls ranges from 7.6 to 8.5.

The extremely long periostracal hairs of *Rabdotus* (*Plicolumna*) *perhirsutus* distinguish it from all other members of the genus. Decorticated shells somewhat resemble *Rabdotus* (*Plicolumna*) *artemisia* (Binney, 1861) but can be distinguished from that species by their more strongly carinate embryonic whorls, stronger sculpture, more convex whorls, and more deeply impressed sutures of the postnuclear shell.

Rabdotus (*Plicolumna*) *perhirsutus* has been collected at only two localities, both near the southern tip of Baja California. The type locality is a relatively arid location, and the vegetation consists of thorn scrub and organpipe cactus. The outcrop in which the shells were found is partly shaded by overhanging trees. Despite repeated efforts to collect living specimens for dissection, only a single living individual was found here. A single broken shell was found a short distance to the north, in a shallow talus slide on the southern slope of Arroyo Candelaria, east of Migriño. The vegetation here is similar to that at the type locality.

ETYMOLOGY.—L., *per,* very, + *hirsutus,* hairy.

Family HELMINTHOGLYPTIDAE
Genus **Greggelix** Miller, 1972

TYPE SPECIES: *Greggelix indigena* (Mabille) (=*Helix indigena* Mabille, 1895), by original designation.

Subgenus **Martirelix** Miller, 1982

TYPE SPECIES: *Greggelix* (*Martirelix*) *babrakzaii* Miller, 1982, by original designation.

Greggelix (Martirelix) huertai Miller and Roth, sp. nov.

(Figs. 5–8)

DIAGNOSIS.—A *Greggelix* (*Martirelix*) with shell similar to *G.* (*M.*) *babrakzaii* but differing in the short, broadly conical verge and tapering summit of the penis; with one vestigial mucus gland inserted on the vagina.

DESCRIPTION OF SHELL OF HOLOTYPE.—Shell (Figs. 5–7) of medium size for the genus, rather solid, depressed-helicoid, umbilicate; umbilicus contained 6.6 times in diameter. Whorls well rounded, slightly shouldered; suture well impressed; spire broadly conic; apical angle 135°.

Embryonic whorls 1.2, with irregular, radiating rugae somewhat broken up into granules (particularly on first half whorl), and a few widely spaced, discrete, dotlike papillae in diagonally descending series. Sculpture of early teleoconch whorls consisting of irregular collabral rugae, strongest below suture, and an overall pattern of minute punctations. Punctations variable in prominence, strongest on shoulder of whorl, generally round but from third whorl on sometimes elongated in direction of spiral growth. Base inflated, crossed by growth rugae, with scattered punctations extending to umbilical region. Last 0.2 of body whorl descending sharply to aperture; growth rugae crowded and somewhat granulose behind lip. Aperture ovate, little interrupted by body whorl, ends of peritreme converging. Peristome at angle of 45° to vertical. Lip broadly expanded and reflected; inner lip encroaching but slightly on umbilicus. Parietal callus very thin, granular, free edge sinuous. Shell with waxy luster, light reddish tan, darker on shoulder and lighter around umbilicus, with a 1-mm-wide russet spiral band prolonging trajectory of suture, with traces of lighter zones above and (more distinctly) below the band. Diameter 17.8 mm; height 11.2 mm; diameter of umbilicus 2.7 mm; 4.7 whorls.

Reproductive anatomy of holotype.—The reproductive system (Fig. 8) exhibits the general characters of the genus, namely exceptionally long spermathecal diverticulum and epiphallic caecum, no dart apparatus, and a small verge in the saccular penis. The verge is short and broadly conical, with a pointed tip. The saccular penis is also conical, being widest at the base of the verge. The summit of the penis tapers rapidly to the slender epiphallus. A single, vestigial mucus gland is inserted near the middle of the vagina.

Type material.—Holotype, SBMNH 35113 (shell and whole mount of stained genitalia); Mexico, Baja California: Cerro de la Mina de San Juan, Sierra La Libertad, in rockpiles on north side of entrance to the mine; 28°42.5′N, 113°34.7′W, elev. ca. 1,300 m; W. B. Miller, C. Huerta, and students of University of Arizona 1981 General Biology 580 class, coll.; 26 Nov. 1981. Ten paratypes (shells), SBMNH 35114, from same locality as holotype. Additional paratypes are deposited in ANSP, CAS, USNM, and the private collection of author Roth.

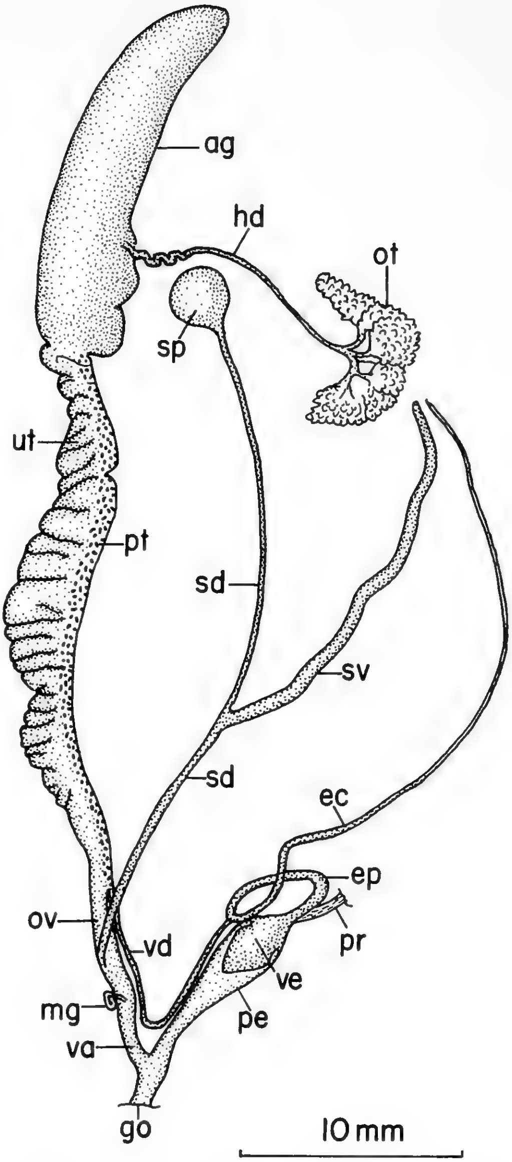


Figure 8. *Greggelix* (*Martirelix*) *huertai* sp. nov., dissected reproductive system, drawn from projection of stained whole mount. Holotype, SBMNH 35113. Abbreviations: ag, albumen gland; ec, epiphallic caecum; ep, epiphallus; go, genital orifice; hd, hermaphroditic duct; mg, mucus gland; ot, ovotestis; ov, oviduct; pe, penis; pr, penial retractor; pt, prostate; sd, spermathecal duct; sp, spermatheca; sv, spermathecal diverticulum; ut, uterus; va, vagina; vd, vas deferens; ve, verge.

Remarks.—The type lot consists of the holotype and 29 adult paratypes. Maximum diameter ranges from 16.7 to 21.5 mm (mean, 18.52 mm); height, 9.7 to 13.1 mm ($\bar{x}$ = 11.27 mm); height/diameter ratio 0.56 to 0.68 ($\bar{x}$ = 0.609).

Only two specimens were found alive—the holotype, which was adult, and an immature individual that died in a terrarium before reaching maturity. Accordingly, no data are available on variation in anatomical characters such as the frequency of the presence of one, two, or (as in *G. babrakzaii*) no vestigial mucus glands.

The reproductive anatomy of *Greggelix* (*Martirelix*) *huertai* resembles that of *G.* (*M.*) *babrakzaii*, which inhabits the lower elevations of the arid eastern canyons of the Sierra San Pedro Mártir some 300 km to the northwest. It differs, however, in the size and shape of the verge, which is short, wide, and conical. The length of the verge is approximately the same (2.5 mm) as in *G. babrakzaii,* but its diameter is more than twice as large at the base (2.2 mm), decreasing rapidly to a sharp conic tip. In *G. babrakzaii* the narrower verge (diameter 1.0 mm) remains cylindrical to the blunt paraboloid tip. Additionally, the penis in *G. babrakzaii* is sharply truncate where it joins the epiphallus, whereas in *G. huertai* it is broadly conic.

The habitat of *Greggelix* (*Martirelix*) *huertai* is within the Vizcaino Desert zone (=sarcophyllous desert, =*Agave-Franseria* region of Shreve [1951]; see section on biogeography, below). The habitat of *G. babrakzaii* is in the Colorado Desert zone (=microphyllous desert, =*Larrea-Franseria* region). Whereas *G. babrakzaii* was found principally under boulders and rockpiles along the riparian lower slopes of canyons such as Cañon el Diablo and Cañon Diablito, *G. huertai* was found only high on the xeric north slope of the Cerro de la Mina de San Juan. It was not found in the lower slopes along Cañada San Juan, which leads west to Rancho San Gregorio, nor in the deep ravines that lead east to El Terminal and Valle Las Flores. The vegetation in the immediate vicinity of the type locality consists mainly of *Idria columnaris, Xylococcus bicolor, Quercus ajoensis, Heteromeles arbutifolia, Rhus laurina, Dodonea viscosa, Simmondsia chinensis, Adenostoma fasciatum,* and *Agave deserti. Greggelix huertai* has not been reported from any locality other than the type locality.

ETYMOLOGY.—The species is named after Dr. Carlos Huerta, author Miller's former biology student and an enthusiastic member of the expedition to the Cerro de la Mina de San Juan, who found the only live adult snail, thereby providing the means to identify the species.

DISTRIBUTIONAL LIST OF LAND MOLLUSCA OF BAJA CALIFORNIA

CONVENTIONS.—The classification at the family level and above is modified slightly from that of Solem (1978), with the addition of the family Thysanophoridae and use of the -oidea suffix for superfamily names as recommended by the International Code of Zoological Nomenclature. Place names are for the most part standardized according to Gerhard and Gulick (1970) except where quoted directly from original sources. The type locality of a taxon is indicated by "TL." To distinguish the state of Baja California (Estado de Baja California) from the peninsula itself, the expression "Baja California Norte" is used for the former. Extralimital distribution of taxa occurring outside of Baja California is given in summary form.

Institutional and private collections are abbreviated as follows: AMNH—American Museum of Natural History; ANSP—Academy of Natural Sciences, Philadelphia; BR—Barry Roth, San Francisco, California; CAS—California Academy of Sciences; CCC—Carl C. Christensen, Honolulu, Hawaii; LACM—Los Angeles County Museum of Natural History; MCZ—Museum of Comparative Zoology, Harvard University; MNHN—Muséum National d'Histoire Naturelle, Paris; RLR—Richard L. Reeder, Tulsa, Oklahoma; SBMNH—Santa Barbara Museum of Natural History; SDMNH—San Diego Museum of Natural History; UA—Department of Ecology and Evolutionary Biology, University of Arizona, Tucson; USNM—United States National Museum of Natural History; WBM—Walter B. Miller, Tucson, Arizona.

Class GASTROPODA
Subclass PROSOBRANCHIA
Superorder MESOGASTROPODA
Superfamily RISSOOIDEA
Family TRUNCATELLIDAE
Genus **Truncatella** Risso, 1826

Truncatella californica Pfeiffer, 1857

SYNONYMS.—*Truncatella gracilenta* 'Gould,' Binney, 1858 (nomen nudum). *Truncatella stimpsoni* Stearns, 1872. *Pseudosubulina ruthae* Pilsbry, 1954.

DISTRIBUTION.—Southern California (Santa Barbara; McLean 1978) to the upper Gulf of California (Taylor *in* Keen 1971). BAJA CALIFORNIA NORTE: Estero S of Ensenada, along road to Punta Banda, under rocks at water's edge, W. B.

Miller, 1 Jan. 1957 (WBM). Isla San Martín, F. Baker, Aug. 1899 (F. Baker 1902; Pilsbry 1927). Isla San Gerónimo (Lowe 1913). Santo Domingo (Orcutt 1900a, 1915).

Snails of this genus are amphibious and live among stones and debris near the high-tide mark. *Truncatella californica* varies in sculpture from strongly ribbed to nearly smooth. McLean (1978) referred to *T. stimpsoni* as the smooth variant, but that name was founded on strongly ribbed individuals. *Pseudosubulina ruthae* (new synonymy herein) was based on the early whorls of *T. californica,* as confirmed by examination of the holotype and paratypes (ANSP 190114).

Truncatella guadalupensis Pilsbry, 1901

Distribution.—BAJA CALIFORNIA NORTE: Isla Guadalupe (TL), R. E. Snodgrass, Nov. 1899 (Pilsbry 1901, 1927; ANSP). Late Pleistocene, Discovery Point Formation, Isla Guadalupe (Lindberg et al. 1980) (SDMNH).

Subclass Pulmonata
Superorder Stylommatophora
Order Orthurethra
Superfamily Pupilloidea
Family Pupillidae
Genus **Gastrocopta** Wollaston, 1878
Subgenus **Gastrocopta** sensu stricto

Gastrocopta (Gastrocopta) pellucida hordeacella (Pilsbry, 1890)

(Fig. 9)

Synonym.—*Bifidaria hordeacella* var. *parvidens* Sterki, 1899.

Distribution.—BAJA CALIFORNIA SUR: Along Transpeninsular Highway 5.0 mi [8.0 km] SE of road to San Ignacio, C. C. Christensen, W. B. Miller, 4 Dec. 1974 (CCC). Gulf slope of Sierra de la Giganta SW of Mulegé, along trail from Pie de la Cueta to Guajademí, in rockslide along trail ca. 1 mi [1.6 km] from Pie de la Cueta, elev. ca. 2,100 ft [640 m], C. C. Christensen, W. B. Miller et al., 22 Oct. 1972 (CCC). Guajademí (Pilsbry 1916–1918, 1948). La. Purísima, W. B. Miller, 1970 (Bequaert and Miller 1973, as *G. procera*; WBM). W of San Miguel Comondú, R. J. Drake, 1953 (UA). San José Comondú, R. J. Drake, 1953 (CAS). San Javier, C. C. Christensen, W. B. Miller, 28 May 1975 (CCC). San Javier, in rockslide across stream from mission, elev. 1,200–1,500 ft [370–460 m], C. C. Christensen, W. B. Miller et al., 25 Oct. 1972 (CCC). In lava rockslide a short distance up arroyo immediately S of San Juánico, C. C. Christensen, W. B. Miller, 28 May 1975 (CCC). Along Transpeninsular Highway at km 69 N of Villa Insurgentes, C. C. Christensen, W. B. Miller, 5 Dec. 1974 (CCC). Juncalito, C. C. Christensen, 30 July 1974 (CCC). Arroyo Candelaria 4.2 mi [6.8 km] E of Migriño and 2.1 mi [3.4 km] W of Candelaria, elev. 300 ft [90 m], C. C. Christensen, J. A. Christensen, 22 Dec. 1975 (CCC). Arroyo Candelaria 2.3 mi [3.7 km] E of Migriño, elev. 200 ft [60 m], C. C. Christensen, J. A. Christensen, 21 Dec. 1975 (CCC). Along Santa Catarina–Los Frailes road 13.5 mi [21.7 km] NE of Santa Catarina, C. C. Christensen, J. A. Christensen, 23 Dec. 1975 (CCC); and 13.5 mi [21.6 km] NE of Santa Catarina, elev. 1,200 ft [370 m], C. C. Christensen, J. A. Christensen, 23 Dec. 1975 (CCC). Boca de la Sierra, C. C. Christensen, W. B. Miller, 7 Dec. 1974 (CCC). Ca. 1–1.5 mi [1.6–2.4 km] W of Boca de la Sierra, C. C. Christensen, W. B. Miller, 7 Dec. 1974 (CCC). Many localities in Cape region from vicinity of La Paz to San José del Cabo, in stream drift, A. E. Leviton, A. G. Smith, I. L. Wiggins, CAS 1958–1959 Exped. (CAS). Along Todos Santos–Cabo San Lucas road 2.1 mi [3.4 km] N of El Saucito, elev. 1,500 ft [460 m], C. C. Christensen, J. A. Christensen, 22 Dec. 1975 (CCC). Isla Coronados, C. C. Christensen, 1 Aug. 1974 (CCC). Isla Carmen, G D. Hanna et al., 1953 ORCA Exped. (CAS). Isla Danzante, P. Turk, Jan. 1978 (CCC). Isla Santa Catalina, G D. Hanna et al., 1953 ORCA Exped. (CAS). Isla Tortuga, CAS 1921 Exped. (Hanna 1923, as *G. p. parvidens*; CAS). SONORA: Isla San Esteban, G D. Hanna et al., 1953 ORCA Exped. (CAS). Isla San Pedro Mártir, G D. Hanna et al., 1953 ORCA Exped. (CAS).

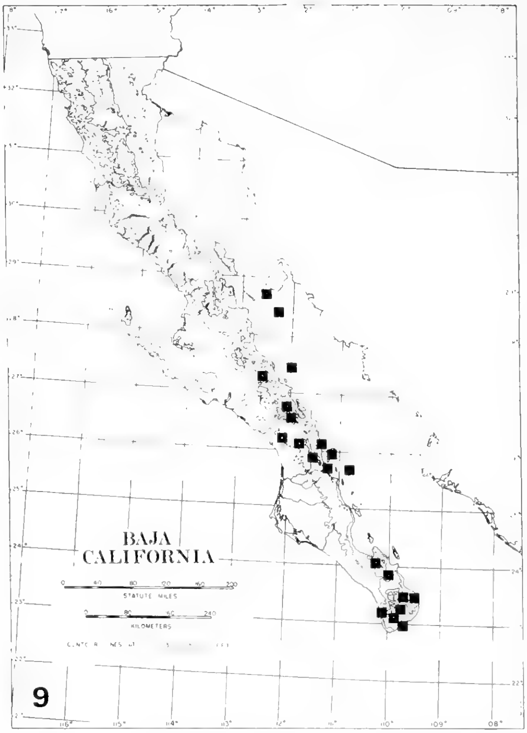


Figure 9. Distribution in Baja California of *Gastrocopta pellucida hordeacella.* In this and subsequent maps, each symbol represents one or more localities.

This species is most commonly found in litter on rocky slopes or beneath vegetation. It will probably be found to occur on other Gulf islands and on the peninsula in the state of Baja California (Norte) when the minute snails of those areas are adequately known. Elsewhere, the range

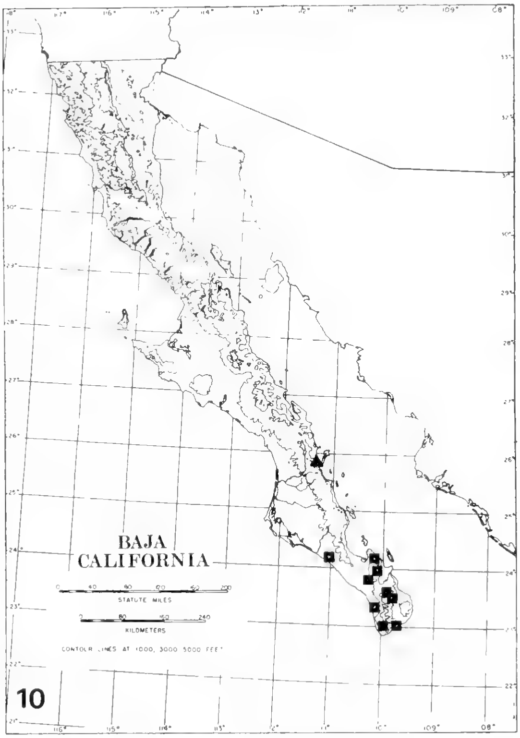


FIGURE 10. Distribution of *Gastrocopta allyni* (squares) and *Gastrocopta* sp., cf. *G. riograndensis* (triangle).

of *G. p. hordeacella* extends from southern California, Arizona, and New Mexico eastward to Florida and, in a narrow strip along the Atlantic coast, north to New Jersey. On the mainland of North and Central America this subspecies occurs as far south as Nicaragua. It occurs on Islas Clarión and Socorro of the Revillagigedos group (Dall 1900). In the West Indies it is replaced by the nominate race of the species (Pilsbry 1948; Bequaert and Miller 1973).

We concur with the opinions of Branson et al. (1966) and Bequaert and Miller (1973) that *Gastrocopta pellucida parvidens* (Sterki) is not separable from other west American representatives of the species. We retain the name *G. p. hordeacella* for mainland populations of this species, but note that comparison with West Indian material may result in its union with the nominate subspecies.

The specimen from La Purísima reported by Bequaert and Miller (1973:171) as *Gastrocopta procera* (Gould) is here redetermined as *G. p. hordeacella.*

Gastrocopta (Gastrocopta) sp., cf. *G.* (*G.*) *riograndensis* (Pilsbry and Vanatta, 1900)

(Fig. 10)

DISTRIBUTION.—BAJA CALIFORNIA SUR: Juncalito, C. C. Christensen, 30 July 1974 (CCC).

Gastrocopta riograndensis occurs from Texas to northeastern Mexico (Pilsbry 1916–1918, 1948; Neck 1980). The apertural teeth of the two specimens from Juncalito are the same as in Texan specimens described by Pilsbry (1948), but the specimens lack a crest behind the aperture.

Subgenus **Immersidens**
Pilsbry and Vanatta, 1900

Gastrocopta (Immersidens) allyni Roth and Christensen, 1984

(Fig. 10)

DISTRIBUTION.—BAJA CALIFORNIA SUR: 0.4 mi [0.6 km] N of km 105 along Transpeninsular Highway N of La Paz, C. C. Christensen, W. B. Miller, 6 Dec. 1974 (CCC). Arroyo de los Pozos, 12.9 mi [20.6 km] E of La Paz, on road to Las Cruces, A. G. Smith, CAS 1958–1959 Exped. (CAS). Sierra Cacachila, 9.8 mi [15.7 km] E of La Paz–Cabo San Lucas highway, elev. 1,400 ft [420 m], C. C. Christensen, J. A. Christensen, 18 Dec. 1975 (CCC). Arroyo ca. 15 mi [24 km] S of La Paz, in drift (TL), A. G. Smith, 2 Nov. 1959 (CAS, CCC). Km 5000.2 S of San Antonio, in leafmold, A. G. Smith, CAS 1958–1959 Exped. (CAS). San Bartolo, W. B. Miller, Dec. 1970 (UA). 5.3 mi [8.5 km] NW of Todos Santos along road to La Pastora, A. G. Smith, CAS 1958–1959 Exped. (CAS). Along road to La Burrera, 7.0 mi [11.2 km] from Cabo San Lucas–Todos Santos road, elev. 1,000 ft [300 m], C. C. Christensen, J. A. Christensen, 20 Dec. 1975 (CCC). Bahía San Pedrito, 3.9 mi [6.2 km] SE of Todos Santos, A. G. Smith, A. E. Leviton, CAS 1958–1959 Exped. (CAS). 0.2 mi [0.3 km] SSE of San José del Cabo on road to La Playa, stream drift, A. G. Smith, A. E. Leviton, CAS 1958–1959 Exped. (CAS). Along road from Cabo San Lucas to Todos Santos, 2.2 mi [3.5 km] N of El Saucito, in granite outcrops W of road, elev. 1,500 ft [450 m], C. C. Christensen, J. A. Christensen, 22 Dec. 1973; C. C. Christensen, 9 Aug. 1974 (CCC). Along road from Cabo San Lucas to Todos Santos, 2.1 mi [3.4 km] N of El Saucito, elev. 1,500 ft [450 m], C. C. Christensen, J. A. Christensen, 22 Dec. 1975 (CCC).

Gastrocopta (Immersidens) rixfordi Hanna, 1923

(Fig. 11)

DISTRIBUTION.—BAJA CALIFORNIA SUR: San Ignacio, elev. 500 ft [150 m], W. B. Miller (Bequaert and Miller 1973, as *Gastrocopta dalliana dalliana*; UA). Along Transpeninsular Highway 5.0 mi [8.0 km] SE of road to San Ignacio, C. C. Christensen, W. B. Miller, 4 Dec. 1974 (CCC). San Javier, in rockslides S of the mission, W. B. Miller, 24 Oct. 1971 (UA, CCC). San José Comondú, elev. 1,500 ft [450 m], W. B. Miller, 20 Dec. 1970 (Bequaert and Miller 1973, as *G. d. dalliana*; UA). Along Transpeninsular Highway at km 69 (42.9 mi) N of Villa Insurgentes, C. C. Christensen, W. B. Miller, 5 Dec. 1974 (CCC). 0.4 mi [0.6 km] N of km 105 along Transpeninsular Highway N of La Paz, C. C. Christensen, W. B. Miller, 6 Dec. 1974 (CCC). Arroyo E of Transpeninsular Highway at km 77 N of La Paz, C. C. Christensen, W. B. Miller, 6 Dec. 1974 (CCC). Sierra Cacachila, along La Paz–Los Planes road, 9.8 mi [15.7 km] E of La Paz–Cabo San Lucas Highway, elev. 1,400 ft [420 m], C. C. Christensen, J. A. Christensen, 18 Dec. 1975 (CCC). San Bartolo, elev. 500 ft [150 m], W. B. Miller, 28 Dec. 1970 (Bequaert and Miller 1973, as *G. d. dalliana*; UA). Along road from Todos Santos to Cabo San Lucas, 0.8 mi [1.3 km] S of Las Barrancas (and 15.8 km S of Las Piedritas), C. C. Christensen, J. A. Christensen, 25 Dec. 1975 (CCC). Arroyo Candelaria at Migriño, C. C. Christensen, J. A. Christensen, 21 Dec. 1975 (CCC). Boca de la Sierra, C. C. Christensen, W. B. Miller, 7 Dec. 1974 (CCC). Isla Monserrate (TL), J. C. Chamberlin, 25 May 1921, CAS 1921 Exped. (Hanna 1923; CAS). Isla Danzante, P. Turk, Jan. 1978 (CCC).

The specimens from the peninsula reported by Bequaert and Miller (1973) as *Gastrocopta dalliana dalliana* (Sterki, 1898) prove on re-examination to be *G. rixfordi,* described from Isla Monserrate. In *G. d. dalliana* the aperture is smaller, the columellar lamella emerges farther on the inner lip, and the angular and parietal lamellae are smaller and closer together than in *G. rixfordi.* Hanna (1923) originally assigned *G. rixfordi* to the subgenus *Albinula* Sterki, 1892, but the apertural dentition is that of *Immersidens.*

Genus **Pupilla** Leach *in* Fleming, 1828

Subgenus **Pupilla** sensu stricto

Pupilla (Pupilla) hebes (Ancey, 1881)

(Fig. 11)

Synonyms.—*Pupilla hebes nefas* Pilsbry and Ferriss, 1910. *Pupilla hebes kaibabensis* Pilsbry and Ferriss, 1911. *Pupilla muscorum idahoensis* Henderson and Daniels, 1917. *Pupilla hebes* mutant *albescens* Ferriss, 1920.

Distribution.—BAJA CALIFORNIA NORTE: Sierra San Pedro Mártir, in rockslide above road 1.4 mi [2.2 km] below astronomical observatory, elev. ca. 8,800–9,000 ft [2,700–2,800 m], C. C. Christensen, 3 Nov. 1973 (CCC). Sierra San Pedro Mártir, in rockslide in ravine above road 0.8 mi [1.3 km] below astronomical observatory, elev. ca. 8,800–9,000 ft [2,700–2,800 m], C. C. Christensen, 3 Nov. 1973 (Miller 1981a; CCC).

Pupilla hebes is widely distributed in the western United States and has also been reported from the state of Chihuahua, Mexico (Pilsbry 1948, 1953). At high elevations in the Sierra San Pedro Mártir, it has been found living in the region of *Pseudotsuga* forest. All specimens found are sinistral.

Subgenus **Striopupilla** Pilsbry, 1921

Pupilla (Striopupilla) sterkiana (Pilsbry, 1890)

(Fig. 11)

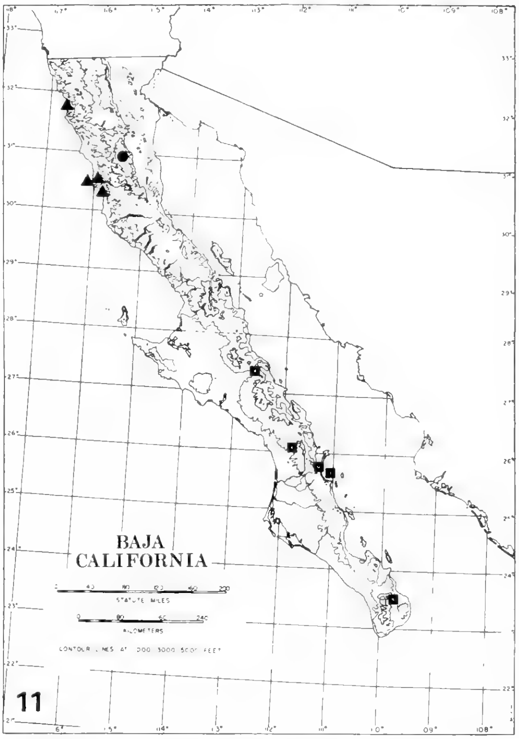


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Figure 11. Distribution of *Gastrocopta rixfordi* (squares), *Pupilla hebes* (circle), and *Pupilla sterkiana* (triangles).

Distribution.—Lower California (TL), C. R. Orcutt (Pilsbry 1890a, b; ANSP). BAJA CALIFORNIA NORTE: On lichen, along the ocean beach N and S of Bahía San Quintín (Orcutt 1886, as *Pupa chordata*; 1891). Under lichen, *Ramalina homalea,* W coast of San Quintín peninsula, W of Winston Hill, S. S. Berry, 25 Mar. 1949 (SBMNH). San Ramón (Pilsbry 1920–1921). Isla San Martín, G D. Hanna, CAS 1922 Exped. (Pilsbry 1927; CAS). Ensenada, under succulents on hillside S of city, W. B. Miller, 16 Oct. 1955 (WBM).

The exact type locality is uncertain. Pilsbry (1920–1921) cited specimens collected at San Ramón (on the Pacific coast near Colonia Guerrero) by C. R. Orcutt, but did not identify them as types.

Pupilla (Striopupilla) goniodon Pilsbry, 1927

Distribution.—BAJA CALIFORNIA NORTE: Isla Guadalupe, Northeast Anchorage, elev. not greater than 100 ft [30 m] in the canyon back of the buildings (TL), G D. Hanna, CAS 1922 Exped. (Pilsbry 1927; CAS, SBMNH). Isla San Benito del Oeste, on dried lower leaves of *Dudleya,* G. E. Lindsay, 5 Feb. 1950 (SBMNH); empty shells in litter from under rocks and agave plants, C. C. Christensen, W. B. Miller, 10 May 1975 (CAS).

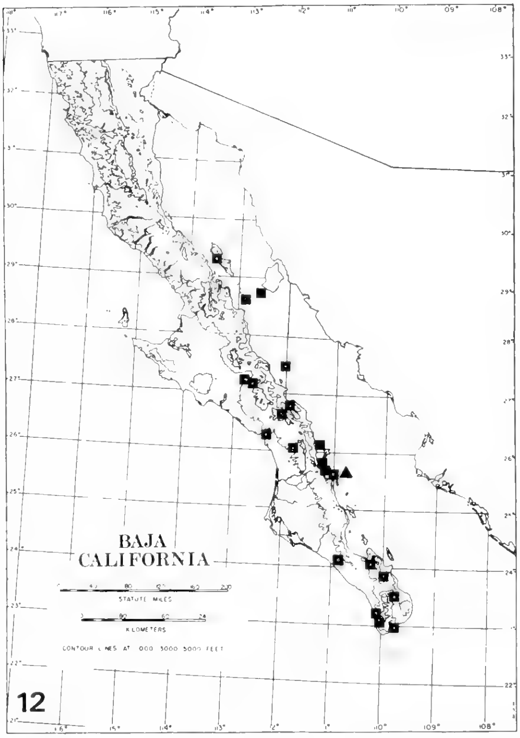

FIGURE 12. Distribution of *Pupoides albilabris* (squares) and *Pupoides catalinensis* (triangle).

The SBMNH collection contains one specimen of *P.* (*S.*) sp., cf. *P.* (*S.*) *goniodon* from a lower human occupation level in an old dune at Punta Baja (C. L. Hubbs coll.); the species has not been found living on the mainland.

Pupilla (Striopupilla) guadalupensis Pilsbry, 1927

DISTRIBUTION.—BAJA CALIFORNIA NORTE: Isla Guadalupe, elev. 1,000 ft [300 m] above Northeast Anchorage (TL); near sea level at Northeast Anchorage; 2 mi [3.2 km] N of S end of island on E side; and crest of Pine Ridge at elev. 3,000 ft [900 m], G D. Hanna, CAS 1922 Exped. (Pilsbry 1927; CAS, SBMNH).

Genus **Pupoides** Pfeiffer, 1854

Pupoides albilabris (C. B. Adams, 1841)

(Fig. 12)

SYNONYMS.—*Cyclostoma marginata* Say, 1821 (non *C. marginatum* G. Fischer, 1807). *Bulimus nitidulus* Pfeiffer, 1839 (non Beck, 1837). *Pupa modica* Gould, 1848. *Pupa* (*Modicella*) *arizonensis* Gabb, 1866.

DISTRIBUTION.—BAJA CALIFORNIA NORTE: Isla Ángel de la Guarda, CAS 1921 Exped. (Hanna 1923, as *P. marginatus*; CAS). Isla San Lorenzo, CAS 1921 Exped. (Hanna 1923, as *P. marginatus*; CAS). BAJA CALIFORNIA SUR: Bahía de la Concepción, G D. Hanna, R. L. Bolin, 1953 ORCA Exped. (CAS). Gulf slope of Sierra de la Giganta, SW of Mulegé; trail from Pie de la Cueta (2.9 mi S of El Potrero) to Guajademí (ca. 1 mi from Pie de la Cueta ranch), W. B. Miller, 22 Oct. 1972 (UA). San José Comondú, elev. 1,500 ft [460 m], W. B. Miller, 20 Dec. 1970 (Bequaert and Miller 1973). San Ignacio, elev. 500 ft [150 m], W. B. Miller, 13 Dec. 1970 (Bequaert and Miller 1973; UA). Along Transpeninsular Highway 5.0 mi [8.0 km] SE of access road to San Ignacio, in rockslide by road, C. C. Christensen, W. B. Miller, 4 Dec. 1974 (CCC). Transpeninsular Highway at km 77 N of La Paz, ca. 0.75 mi [1.2 km] E of road in arroyo, among rocks, C. C. Christensen, W. B. Miller, 6 Dec. 1974 (CCC). Boca de la Sierra, 1.0–1.5 mi [1.6–2.4 km] upstream of village, among granite rocks on S slope, near stream, C. C. Christensen, W. B. Miller, 7 Dec. 1974 (CCC). Arroyo S of San Juánico and Punta Pequeña, in litter of lava rockslide, C. C. Christensen, W. B. Miller, 28 May 1975 (CCC). Many localities in Cape region from vicinity of La Paz to San José del Cabo, in stream drift, A. E. Leviton, A. G. Smith, I. L. Wiggins, CAS 1958–1959 Exped. (CAS). Along road from Todos Santos to Cabo San Lucas, 3.1 mi [5.0 km] S of Las Piedritas (and ca. 19.8 mi S of Todos Santos), C. C. Christensen, J. A. Christensen, 20 Dec. 1975 (CCC). Along road from Todos Santos to Cabo San Lucas, 0.8 mi [1.3 km] S of Los Barrancos (and 9.3 mi S of Las Piedritas), C. C. Christensen, J. A. Christensen, 21 Dec. 1975 (CCC). Isla Coronados (larger island), in litter, rockslide S of peak, C. C. Christensen, 1 Aug. 1974 (CCC). Isla Carmen, Bahía Marquer, W. K. Emerson, 4–5 Apr. 1962, Belvedere Exped. (Emerson and Jacobson 1964). Isla Danzante, P. Turk, Jan. 1978 (CCC). Isla Tortuga, CAS 1921 Exped. (Hanna 1923, as *P. marginatus*; CAS). Isla Monserrate, CAS 1921 Exped. (Hanna 1923, as *P. marginatus*; CAS). SONORA: Isla San Esteban, CAS 1921 Exped. (Hanna 1923, as *P. marginatus*; CAS).

Pupoides albilabris is widely distributed in North America; subspecies occur in the West Indies and South America (Bequaert and Miller 1973).

Pupoides catalinensis Hanna, 1923

(Fig. 12)

DISTRIBUTION.—BAJA CALIFORNIA SUR: Isla Santa Catalina (TL), J. C. Chamberlin, CAS 1921 Exped. (Hanna 1923; CAS, SBMNH); G D. Hanna, 1953 ORCA Exped. (CAS). E side of Isla Santa Catalina, W. K. Emerson, 10 Apr. 1962, Belvedere Exped. (Emerson and Jacobson 1964).

Genus **Vertigo** Müller, 1774
Subgenus **Vertigo** sensu stricto

Vertigo (Vertigo) berryi Pilsbry, 1919

(Fig. 13)

DISTRIBUTION.—BAJA CALIFORNIA NORTE: Valle Trinidad, C. R. Orcutt, 1901 (Pilsbry 1948). Cañon Cantiles, C. R. Orcutt, 2 Aug. 1883 (SBMNH).

This species also occurs in the San Bernardino Mountains of southern California (Pilsbry 1948), the Spring Range, Nevada (Pratt 1976), and Pleistocene deposits in Arizona (Bequaert and

Miller 1973), Nevada (Taylor 1967), and California (Hewett 1956).

Vertigo (Vertigo) ovata Say, 1822

(Fig. 13)

Synonyms.—*Zonites upsoni* Calkins, 1880. *Pupa ovata* f. *antiquorum* Cockerell, 1891.

Distribution.—BAJA CALIFORNIA SUR: 0.2 mi [0.3 km] SSE of San José del Cabo, on the road to La Playa, in stream drift, A. G. Smith, A. E. Leviton, CAS 1958–1959 Exped. (CAS). Sierra Laguna, G. Eisen, 1892 (Cooper 1892b).

This species is widely distributed in North America, from Alaska and Washington eastward to Labrador and south to Arizona, Texas, Florida, and the West Indies (Pilsbry 1948). The collection of this species in the Cape region by Smith and Leviton confirms the earlier record of Cooper (1892b). This locality is far from other portions of the recorded range of *V. ovata.* Orcutt's (1886) record from north of 31°N has not been confirmed and probably was based on another pupillid species.

Genus **Nearctula** Sterki, 1892

Nearctula rowelli diegoensis (Sterki, 1890)

(Fig. 13)

Synonyms.—(?) *Pupa californica* var. *meridionalis* 'Sterki,' Hemphill, 1900 (nomen nudum). *Pupa orcutti* 'Pilsbry,' Orcutt, 1891 (nomen nudum).

Distribution.—BAJA CALIFORNIA NORTE: Bahía Todos Santos, C. R. Orcutt (SBMNH). Near Bahía San Quintín, on lichens, C. R. Orcutt, Apr. 1886 (Orcutt 1891, 1896, as *Pupa orcutti*; SBMNH). Bahía San Quintín, W shore, G D. Hanna, CAS 1922 Exped. (Pilsbry 1927; CAS). Hills W of Bahía San Quintín, in litter among rocks, C. C. Christensen, 28 Dec. 1975 (CCC). San Ramón, C. R. Orcutt, 1886 (Pilsbry 1918–1920; SBMNH). Isla San Martín, G D. Hanna, CAS 1922 Exped. (Pilsbry 1927; CAS).

Nearctula, formerly regarded as a subgenus of *Vertigo,* is here ranked as a genus in accordance with the findings of Coney (1988; pers. comm.). Because of a lectotype designation by Clarke (1960), *Nearctula rowelli* (Newcomb, 1860) is a senior synonym of *Pupa californica* Rowell, 1861, the name formerly used for this species (Roth, in prep.).

Various subspecies of *Nearctula rowelli* occur from the region of San Francisco, California, south to Bahía San Quintín and Isla Guadalupe; *N. r. diegoensis* also occurs in the vicinity of San Diego, California.

Nearctula rowelli catalinaria (Sterki, 1890)

(Fig. 13)

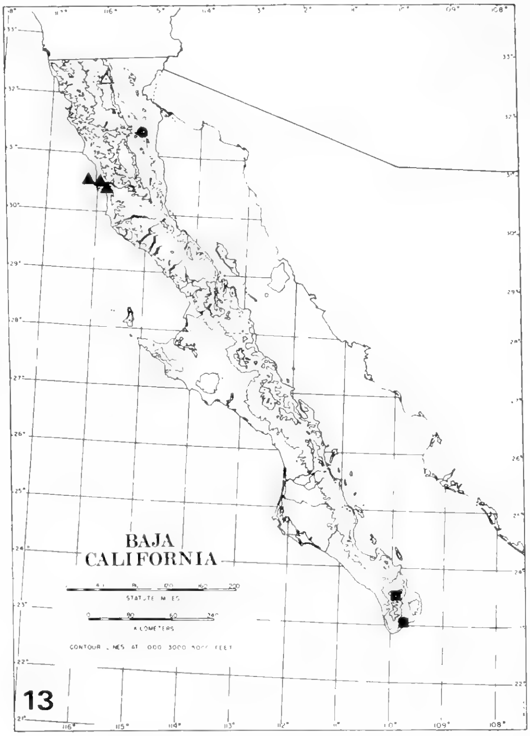

Figure 13. Distribution in Baja California of *Vertigo berryi* (circle), *Vertigo ovata* (squares), *Nearctula rowelli diegoensis* (solid triangles), and *Nearctula rowelli catalinaria* (open triangle).

Distribution.—BAJA CALIFORNIA NORTE: Sierra San Pedro Mártir, along road to astronomical observatory, in rocks in ravine ca. 1.4 road mi [2.2 km] below observatory housing area, elev. ca. 8,800 ft [2,700 m], C. C. Christensen, W. B. Miller, 3 Nov. 1973 (WBM). Isla Guadalupe, Northeast Anchorage and elev. 1,000 ft [300 m] above; and 2 mi [3.2 km] N of S end of island on E side, G D. Hanna, CAS 1922 Exped. (Pilsbry 1927; CAS).

This subspecies also occurs on the southern California Channel Islands—San Clemente, Santa Catalina, San Nicolas, and Santa Barbara.

Nearctula rowelli guadalupensis (Pilsbry, 1927)

Distribution.—BAJA CALIFORNIA NORTE: Isla Guadalupe, elev. 1,000 ft [300 m] above landing at Northeast Anchorage (TL), G D. Hanna, CAS 1922 Exped. (Pilsbry 1927; CAS).

Pilsbry (1927) reported that this subspecies occurred sympatrically with *Nearctula rowelli catalinaria* on Isla Guadalupe. Determination of the name(s) applicable to Isla Guadalupe populations of *Nearctula rowelli* must await a review of variation within the species throughout its range.

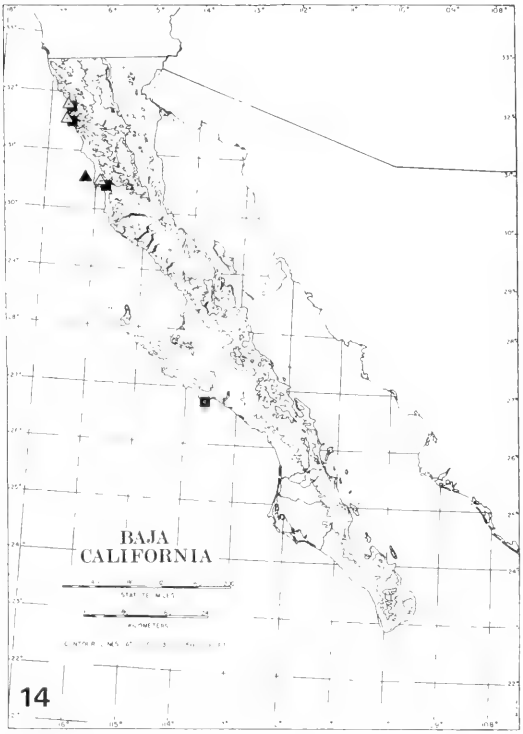

FIGURE 14. Distribution of *Sterkia calamitosa calamitosa* (open triangles), *Sterkia calamitosa martiniana* (solid triangles), and *Sterkia hemphilli* (squares).

Nearctula degeneris (Pilsbry, 1927)

DISTRIBUTION.—BAJA CALIFORNIA NORTE: Isla Guadalupe, elev. ca. 1,000 ft [300 m] above landing at Northeast Anchorage (TL), G D. Hanna, CAS 1922 Exped. (Pilsbry 1927; CAS).

Genus **Sterkia** Pilsbry, 1898

Subgenus **Sterkia** sensu stricto

Sterkia (Sterkia) calamitosa calamitosa (Pilsbry, 1889)

(Fig. 14)

DISTRIBUTION.—BAJA CALIFORNIA NORTE: Near the mouth of San [Santo] Tomás River (TL), H. Hemphill (Pilsbry 1889; ANSP, CAS). Ensenada de Todos Santos, under "*Mesembryanthemum aequilaterale*" (=*Carpobrotus aequilaterus*), C. R. Orcutt, 28 Jan. 1889 (Pilsbry 1948; SBMNH). Hills W of Bahía San Quintín, living snails in litter among rocks, C. C. Christensen, 28 Dec. 1975 (CCC).

Typical specimens of *S. c. calamitosa* occur at Santo Tomás and Ensenada de Todos Santos. Specimens from near San Quintín, on the peninsula adjacent to Isla San Martín, are similar to specimens of *S. c. martiniana* in size but lack the suprapalatal tubercle said to distinguish that subspecies.

Sterkia (Sterkia) calamitosa martiniana Pilsbry, 1927

(Fig. 14)

DISTRIBUTION.—BAJA CALIFORNIA NORTE: Isla San Martín (TL), under stones and among plant debris, G D. Hanna, CAS 1922 Exped. (Pilsbry 1927; CAS). Isla San Martín, near Hassler Cove fishing settlement, in litter, C. C. Christensen, W. B. Miller, 12 June 1975 (CCC).

A weakly characterized subspecies, differing from typical *S. calamitosa* in its slightly larger size and the presence in most specimens of a suprapalatal tubercle.

Sterkia (Sterkia) hemphilli (Sterki, 1890)

(Fig. 14)

DISTRIBUTION.—BAJA CALIFORNIA NORTE: Banks of St. Thomas [Santo Tomás] River (TL), H. Hemphill (Sterki 1890; ANSP). Ensenada de Todos Santos, under decaying "*Mesembryanthemum aequilaterale*" (=*Carpobrotus aequilaterus*), C. R. Orcutt (Pilsbry 1920–1921, 1948; SBMNH). Bahía San Quintín, W shore, G D. Hanna, CAS 1922 Exped. (Pilsbry 1927; CAS). Punta Abreojos, H. Hemphill (Pilsbry 1920–1921, 1948; USNM).

Sterkia hemphilli also occurs in San Luis Obispo, San Bernardino, and San Diego counties, California (Pilsbry 1948; Roth 1973).

Subgenus **Metasterkia** Pilsbry, 1920

Sterkia (Metasterkia) clementina (Sterki, 1890)

SYNONYM.—*Bifidaria clementina oldroydi* Vanatta, 1910.

DISTRIBUTION.—BAJA CALIFORNIA NORTE: Isla Guadalupe, Northeast Anchorage, G D. Hanna, CAS 1922 Exped. (Pilsbry 1927; CAS).

Sterkia clementina has been reported from San Clemente and Santa Barbara islands, California. We now report its occurrence on San Nicolas Island, California, collected by W. B. Miller, 22 May 1954 and 31 Aug. 1958 (WBM), and by D. R. Lindberg and M. G. Kellogg, 12 June 1980 (BR).

Family VALLONIIDAE

Genus **Vallonia** Risso, 1826

Vallonia cyclophorella Sterki, 1892

(Fig. 15)

DISTRIBUTION.—BAJA CALIFORNIA NORTE: Sierra San Pedro Mártir, elev. 8,800–9,000 ft [2,700–2,800 m], W. B. Miller, C. C. Christensen, Nov. 1973 (Miller 1981a).

Vallonia cyclophorella is widely distributed in the western United States (Pilsbry 1948).

Family Strobilopsidae
Genus **Strobilops** Pilsbry, 1893

Strobilops californica Miller and Christensen, 1980

(Fig. 15)

Distribution.—BAJA CALIFORNIA SUR: La Laguna, Sierra de la Victoria, along slope above creek immediately behind La Laguna shelter, elev. ca. 6,500 ft [1,980 m] (TL), W. B. Miller, C. C. Christensen, 31 Dec. 1973 (Miller and Christensen 1980; USNM).

Known from a single empty shell found high in the mountains of the Cape region.

Order Sigmurethra
Suborder Holopodopes
Superfamily Achatinoidea
Family Subulinidae
Genus **Lamellaxis** Strebel and Pfeffer, 1882

Lamellaxis gracilis (Hutton, 1834)

Synonyms.—*Achatina subula* Pfeiffer, 1839. *Bulimus octonoides* Orbigny, 1841. *Bulimus oparanus* Pfeiffer, 1846.

Distribution.—BAJA CALIFORNIA SUR: Arroyo 15 mi [24 km] S of La Paz, a nuclear tip in stream drift, A. G. Smith, CAS 1958–1959 Exped. (CAS). Bahía San Pedrito, 3.9 mi [6.3 km] SE of Todos Santos, A. G. Smith, CAS 1958–1959 Exped. (CAS). Eastern outskirts of San José del Cabo, along an irrigation ditch, I. L. Wiggins, CAS 1958–1959 Exped. (CAS). In stream drift 0.2 mi [0.3 km] SSE of San José del Cabo, on road to La Playa, A. E. Leviton, A. G. Smith, CAS 1958–1959 Exped. (CAS).

Lamellaxis gracilis has been dispersed by commerce throughout the tropical and warm-temperate regions of the world. Pilsbry (1940) believed it indigenous to tropical America, but its presence on the islands of the southwestern Pacific about 2,900 yr ago (Christensen and Kirch 1981) suggests that an Old World origin is equally plausible. It is doubtlessly an introduction to Baja California.

Genus **Opeas** Albers, 1850

Opeas pumilum (Pfeiffer, 1840)

Synonym.—*Helix goodalli* Miller, 1822 (non Férussac, 1821).

Distribution.—BAJA CALIFORNIA SUR: Bahía San Pedrito, 3.9 mi [6.3 km] SE of Todos Santos, A. G. Smith, CAS 1958–1959 Exped. (CAS).

This introduced species has been widely distributed by commerce in many parts of the world.

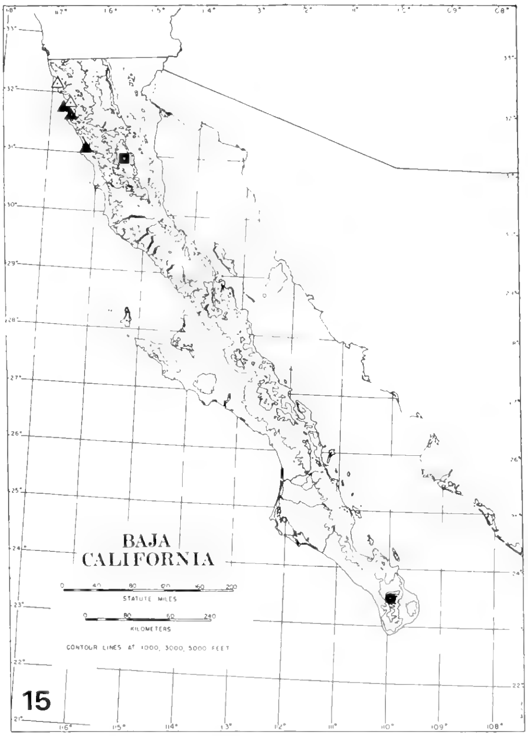

Figure 15. Distribution of *Vallonia cyclophorella* (square), *Strobilops californica* (circle), *Haplotrema caelatum* (solid triangles), and *Haplotrema transfuga* (open triangles).

Superfamily Rhytidoidea
Family Haplotrematidae
Genus **Haplotrema** Ancey, 1881
Subgenus **Haplotrema** sensu stricto

Haplotrema (Haplotrema) guadalupense Pilsbry, 1927

Distribution.—BAJA CALIFORNIA NORTE: Isla Guadalupe, Pine Ridge, elev. ca. 3,000 ft [900 m] (TL), G D. Hanna, CAS 1922 Exped. (Pilsbry 1927; CAS).

Haplotrema (Haplotrema) transufga (Hemphill, 1892)

(Fig. 15)

Distribution.—BAJA CALIFORNIA NORTE: Bahía Todos Santos, H. Hemphill (Binney 1892). Rockslide near San Diego–Ensenada Highway, La Misión Valley, ca. 40 mi [64 km] S of Tijuana, E. P. and E. M. Chace, G. Willett, 1937 (Chace 1937). La Misión Valley, W. O. Gregg, 20 Apr. 1940, 10 Dec. 1947 (H. B. Baker 1941b; LACM). La Misión Valley, along Transpeninsular Highway, in rockslide on S side of valley, seaward side of bridge, W. B. Miller, 14 Feb. 1959 (WBM).

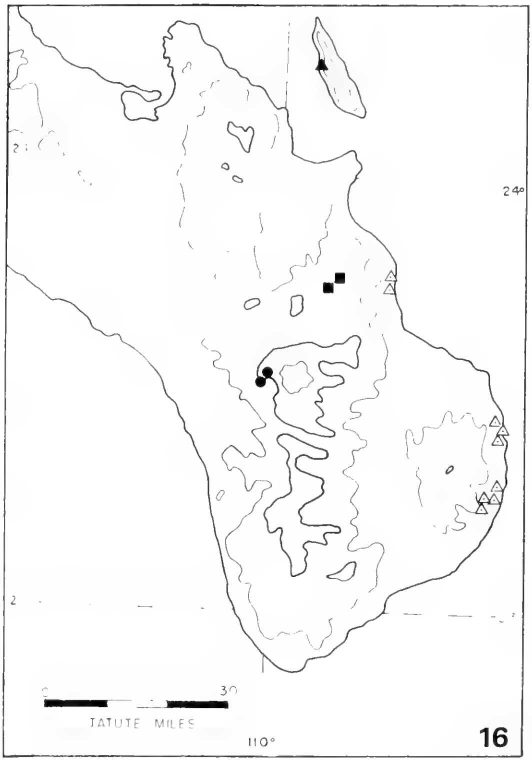

FIGURE 16. Distribution of *Naesiotus altus* (squares), *Naesiotus beldingi* (circles), *Naesiotus harribaueri* (open triangles), and *Naesiotus laevapex* (solid triangle).

"Hills of Lower California near the United States boundary," C. R. Orcutt (Orcutt 1886, as *Macrocyclis sportella*).

This species also occurs in San Diego County, California.

Subgenus **Geomene** Pilsbry, 1927

Haplotrema (Geomene) caelatum (Mazÿck, 1886)

(Fig. 15)

DISTRIBUTION.—BAJA CALIFORNIA NORTE: San [Santo] Tomás, H. Hemphill, L. G. Yates (Cooper 1892a). Punta Banda and banks of San [Santo] Tomás River, H. Hemphill (Binney 1890, as *Selenites duranti* var. *catalinensis*; CAS). Santo Tomás Canyon, 4.1 mi [6.6 km] from Transpeninsular Highway, along road to harbor, under rocks on wooded slope, W. B. Miller, 27 Jan. 1962 (WBM). San Antonio Canyon, about 5 mi [8 km] N of Johnson Ranch, under stones in rockslide on moist east-facing cliff, L. G. Ingles, 18 Dec. 1927 (Berry 1928; SBMNH).

Haplotrema caelatum also occurs in southern California, from Santa Barbara County to San Diego County.

Superfamily BULIMULOIDEA
Family BULIMULIDAE
Genus **Naesiotus** Albers, 1850

Naesiotus(?) altus (Dall, 1893)

(Fig. 16)

SYNONYM.—*Bulimulus* (*Leptobyrsus*) *subspirifer* Mabille, 1895

DISTRIBUTION.—BAJA CALIFORNIA SUR: Sierra Laguna, elev. 3,000 ft [910 m], G. Eisen (USNM; TL, fide Christensen 1978). 1.4 mi [2.3 km] from main highway along access road to microwave station at San Bartolo, among granite boulders in deep ravine above town, elev. ca. 1,400 ft [430 m], W. B. Miller, 19 Dec. 1973 (CCC, WBM); C. C. Christensen, W. B. Miller, 8 Dec. 1974 (CCC, WBM). Ca. 0.6 mi [1.0 km] SE of San Bartolo, among large granite boulders along S side of arroyo, elev. ca. 800 ft [240 m], W. B. Miller, 28 Dec. 1970 (WBM). 1.3 mi [2.1 km] SE of San Bartolo in San Bartolo Arroyo, A. G. Smith, 20 Jan. 1959 (CAS). Ca. 1.8 mi [2.9 km] SE of San Bartolo, among granite boulders along S side of arroyo, elev. ca. 800 ft [240 m], W. B. Miller, 28 Dec. 1970 (WBM).

This species was formerly assigned to *Rabdotus,* sensu stricto. Hoffman (1988) referred it "probably" to *Naesiotus,* although he had examined neither shells nor anatomy.

Naesiotus beldingi (Cooper, 1892)

(Fig. 16)

SYNONYM.—*Bulimulus* (*Leptobyrsus*) *dismenicus* Mabille, 1895

DISTRIBUTION.—BAJA CALIFORNIA SUR: Near San José del Cabo; Punta Arena; Sierra Laguna (Cooper 1892b). "Sierra de la Puna, vers 1.800 mètres d'altitude," L. Diguet (Mabille 1895; TL of *Bulimulus* (*Leptobyrsus*) *dismenicus*). Sierra Laguna, elev. 3,000 ft [910 m], G. Eisen (USNM). "Laguna Valley," elev. 5,000 ft [1,520 m], H. E. Gates, 21 Mar. 1931 (SBMNH). El Sauz, Sierra Laguna, elev. 5,000 ft [1,520 m], E. W. Nelson, E. A. Goldman, 23 Jan. 1906 (USNM). La Laguna, Sierra Laguna, E. W. Nelson, E. A. Goldman, 27 Jan. 1906 (USNM). La Laguna, Sierra Laguna, among rocks on steep slope along creek near cabin, elev. ca. 6,500 ft [1,980 m], C. C. Christensen, W. B. Miller, 31 Dec. 1973 (CCC, WBM). Crest of trail from La Burrera to La Laguna, elev. ca. 6,800 ft [2,070 m], C. C. Christensen, W. B. Miller, 1 Jan. 1974 (CCC, WBM). La Laguna, along trail from cabin to crest of trail at beginning of descent to La Burrera, elev. ca. 6,500–6,800 ft [1,980–2,070 m], C. C. Christensen, 1 Jan. 1974 (CCC). Sierra San Lázaro, elev. 2,000 ft [610 m], G. Eisen (USNM). "San José del Cabo, Cape St. Lucas," L. Belding (USNM).

Published records of the occurrence of this species at San José del Cabo (Cooper 1892b; USNM), Punta Arena (Cooper 1892b), and El Taste Mountains (Cooper 1894) have not been confirmed by recent collections and may, at least in part, have been based upon misidentified material or, in the case of the first of these localities,

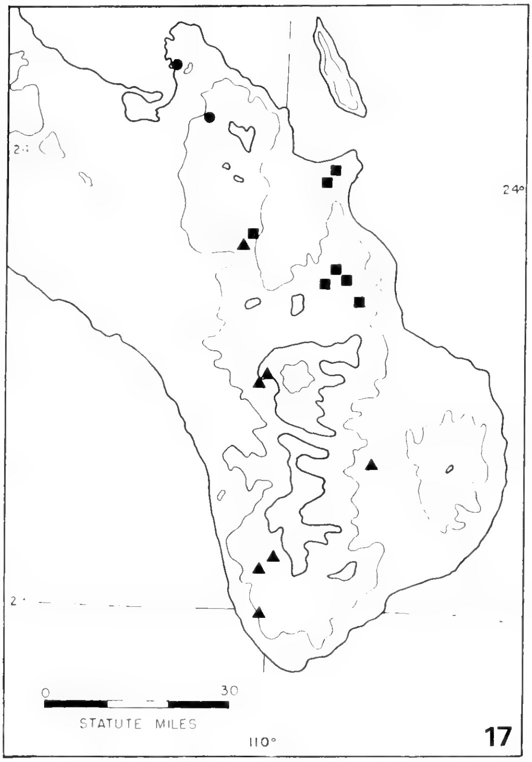

FIGURE 17. Distribution of *Naesiotus cosmicus* (squares), *Naesiotus excelsus* (circles), and *Naesiotus montezuma* (triangles).

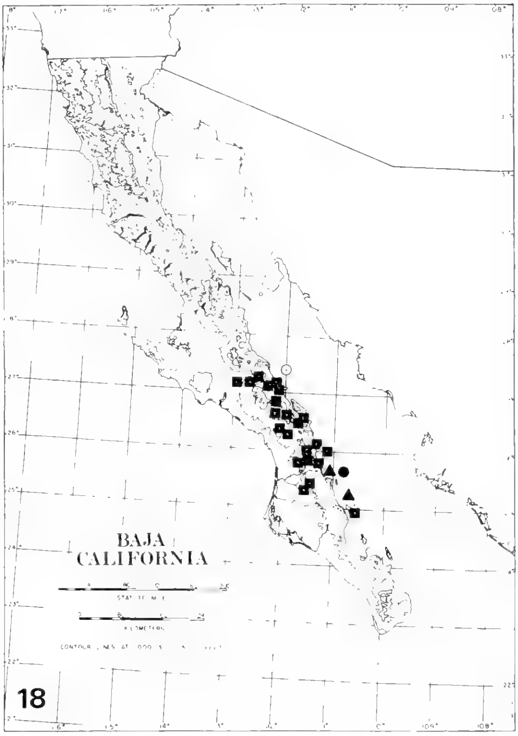

FIGURE 18. Distribution of *Naesiotus dentifer dentifer* (open circle), *Naesiotus dentifer johnstoni* (solid circle), *Naesiotus dentifer lamellifer* (squares), and *Naesiotus dentifer slevini* (triangles).

may represent a very generalized use of the place name.

Naesiotus cosmicus (Mabille, 1895)

(Fig. 17)

DISTRIBUTION.—BAJA CALIFORNIA SUR: "Les Sierras du Sud de la presqu'île" (TL), L. Diguet (Mabille 1895). Canyon in mountains E of old Punta Arena de la Ventana–San Antonio road, 2.0 mi [3.2 km] N of its junction with road leading 3.5 mi [5.6 km] W to Los Planes, C. Church, 30 Dec. 1970 (WBM). Same, but 0.8 mi [1.3 km] N of junction, elev. 500 ft [150 m], C. C. Christensen, 19 Dec. 1975 (CCC). 3 mi [4.8 km] SE of San Antonio, M. D. Robinson, 12 July 1970 (UA). 1.4 mi [2.3 km] from main highway along access road to microwave station at San Bartolo, among granite boulders in deep ravine above town, elev. ca. 1,400 ft [430 m], W. B. Miller, 19 Dec. 1973 (CCC, WBM); C. C. Christensen, W. B. Miller, 8 Dec. 1974 (CCC, WBM). Ca. 0.6 mi [1.0 km] SE of San Bartolo, among large granite boulders along S side of arroyo, elev. ca. 800 ft [240 m], W. B. Miller, 28 Dec. 1970 (WBM). Ca. 1.8 mi [2.9 km] SE of San Bartolo, among granite boulders along S side of arroyo, elev. ca. 800 ft [240 m], W. B. Miller, 28 Dec. 1970 (WBM). 5.7 mi [9.2 km] SE of San Bartolo, elev. ca. 1,100 ft [340 m], C. C. Christensen, 25 Dec. 1975 (CCC). Ca. 0.5 mi [0.8 km] beyond El Coro (near Rancho Buena Vista) along trail leading up canyon into mountains, elev. ca. 2,000 ft [610 m], W. B. Miller, W. B. Miller III, 18 Dec. 1973 (CCC).

Naesiotus dentifer dentifer (Mabille, 1895)

(Fig. 18)

DISTRIBUTION.—BAJA CALIFORNIA SUR: Isla Tortuga (TL), L. Diguet (Mabille 1895); CAS 1921 Exped. (Hanna 1923; CAS, ANSP); H. N. Lowe, 1932 (Lowe 1933; ANSP, SDMNH); J. P. Figg-Hoblyn, 24 Mar. 1952 (SBMNH); 1962 Belvedere Exped. (Emerson and Jacobson 1964); R. V. Moran (WBM).

We regard *Naesiotus dentifer* as a polytypic species with the following included subspecies: *N. d. dentifer* (Isla Tortuga), *N. d. johnstoni* (Isla Santa Catalina), *N. d. lamellifer* (northern peninsular Baja California Sur and Islas San Marcos, Carmen, Danzante, Coronados, and San José), and *N. d. slevini* (Islas Santa Cruz and Monserrate). In our opinion, these allopatric taxa do not differ from each other in shell or anatomical characters to a degree sufficient to justify species-level separation.

Naesiotus dentifer johnstoni (Hanna, 1923)

(Fig. 18)

DISTRIBUTION.—BAJA CALIFORNIA SUR: Isla Santa Catalina (TL), CAS 1921 Exped. (Hanna 1923; CAS, SBMNH); H. N. Lowe, 1932 (Lowe 1933, as *Bulimulus johnsoni* [sic]; ANSP); J. P. Figg-Hoblyn, 14 Apr. 1952 (SBMNH); 1953 ORCA Exped. (Arnaud 1970); 1962 Belvedere Exped. (Emerson and Jacobson 1964); M. D. Robinson, June 1970 (CCC, WBM); L. T. Findley, 13–16 Apr. 1972 (WBM).

Specimens recorded as having been collected on Isla San Benito (ANSP) and Isla Monserrate (I. L. Wiggins, 24 June 1964; CAS) are almost certainly mislabeled.

Naesiotus dentifer lamellifer (Pilsbry, 1896)

(Fig. 18)

SYNONYMS.—*Bulimulus spirifer* var. *orthelasmus* Pilsbry, 1898. *Bulimulus ximenez* Hanna, 1923. *Bulimulus bakeri* Hanna, 1923. *Bulimulus sanmarcosensis* Pilsbry and Lowe, 1932. *Bulimulus carmen* Pilsbry and Lowe, 1932.

DISTRIBUTION.—BAJA CALIFORNIA SUR: "Les montagnes de la Basse Californie vers 800 mètres d'altitude, surtout du volcan de las Virgenes," (Mabille 1895, as *Bulimulus spirifer*). Back of Bahía Agua Verde (Hanna 1923). Mulegé estuary, S entrance at elev. 165–330 ft [50–100 m] 13 mi [21 km] W of San Ignacio, A. G. Smith, 1961 (CAS). Along main road to El Arco ca. 7.5 mi [12.1 km] W of San Ignacio, elev. ca. 600 ft [180 m], W. B. Miller, W. N. Miller, 18 Dec. 1970 (WBM). Along San Ignacio–Santa Rosalía road 23.0 mi [37.0 km] W of Rancho Las Vírgenes and 4.0 mi [6.4 km] E of San Ignacio, C. Church, 16 Jan. 1971 (WBM). Along Transpeninsular Highway ca. 5 mi [8 km] E of San Ignacio, C. C. Christensen, W. B. Miller, 4 Dec. 1974 (CCC, WBM). Along Transpeninsular Highway 39.9 mi [64.2 km] NE of Santa Rosalía, C. C. Christensen, J. A. Christensen, 19 Dec. 1973 (CCC). Along road to Santa Agueda ca. 17.6 mi [28.3 km] from Santa Rosalía–Mulegé road, C. Church, 17 Nov. 1970 (WBM). Along Transpeninsular Highway 20 mi [32 km] N of Mulegé, C. C. Christensen, J. A. Christensen, 20 Dec. 1973 (CCC). Along road to San José de Magdalena ca. 6.0 mi [9.7 km] from Santa Rosalía–Mulegé road, C. Church, 22 Nov. 1970 (WBM). Along road to San José de Magdalena ca. 16.7 mi [26.9 km] from Santa Rosalía–Mulegé road, C. Church, 23 Nov. 1970 (WBM). Along road to San José de Magdalena ca. 20.8 mi [33.5 km] from Santa Rosalía–Mulegé road, C. Church, 24 Nov. 1970 (WBM); W. B. Miller, 4 Jan. 1974 (WBM). Along road to San José de Magdalena ca. 26.9 mi [43.3 km] from Santa Rosalía–Mulegé road, C. Church, 24 Nov. 1970 (WBM). Puerto Escondido, under stones and on hillside, T. Craig, 9 Mar. 1928 (SBMNH). Ca. 6 mi [9.7 km] inland of Mulegé, elev. ca. 250 ft [80 m], C. C. Christensen, 22 Oct. 1972 (CCC). Along road to El Potrero 15.0 mi [24.1 km] W of Mulegé bridge, C. Church, 2 Dec. 1970 (WBM). El Potrero Ranch, SW of Mulegé, H. E. Gates, 31 Mar. 1931 (SBMNH). E slope of Sierra de la Giganta SW of Mulegé, along trail from Pie de la Cueta (2.9 mi [4.7 km] S of El Potrero) to Guajademí, elev. 2,100 ft [640 m], W. B. Miller, D. B. Richman, 22 Oct. 1972 (WBM). Pacific slope of Sierra de la Giganta SW of Mulegé, along trail from Pie de la Cueta to Guajademí, elev. 2,300 ft [700 m], W. B. Miller, 23 Oct. 1972 (WBM). Sierra de la Giganta above Bahía San Carlos, J. P. Figg-Hoblyn, 11 Apr. 1952 (SBMNH). Bahía de la Concepción, along highway 23 mi [37 km] S of Mulegé, W. B. Miller, W. N. Miller, 19 Dec. 1970 (WBM). Hill above Bahía de la Concepción, L. B. Mousley, 6 Jan. 1955 (SBMNH). Bahía de la Concepción, 3 mi [4.8 km] S of El Coyote, C. Church, 3 Dec. 1970 (WBM). Coyote Bay, Bahía de la Concepción (Hanna 1923). El Requesón, Bahía de la Concepción, ca. 27 mi [43 km] S of Mulegé, W. B. Miller, W. N. Miller, 19 Dec. 1970 (WBM); W. B. Miller, 24 Oct. 1972. Bahía de la Concepción, 16 and 20 mi [26 and 32 km] S of Mulegé, I. L. Wiggins, A. M. Vollmer, H. M. Hill, 12 Nov. 1946 (SBMNH). Puerto Santispaquis, Bahía de la Concepción (TL, desig. by Emerson and Jacobson 1964; ANSP). Punta San Antonio, S end of Bahía San Nicolás, CAS 1921 Exped. (Hanna 1923; TL of *Bulimulus bakeri*; CAS, SDMNH). Bahía San Nicolás, just N of ranch at San Nicolás, C. C. Christensen, W. B. Miller, 5 Dec. 1974 (CCC, WBM). Along El Rosarito–San Nicolás road 1.0 mi [1.6 km] inland of San Nicolás, C. C. Christensen, W. B. Miller, 5 Dec. 1974 (CCC, WBM). Same, 5.3 mi [8.5 km] inland of San Nicolás, elev. ca. 100 ft [30 m], C. C. Christensen, W. B. Miller, 5 Dec. 1974 (CCC, WBM). Same, 6.5 mi [10.5 km] from Mulegé–Loreto road, C. Church, 5 Dec. 1970 (WBM). Along Canipolé–San José Comondú road 10 mi [16 km] from Canipolé, elev. ca. 1,000 ft [300 m], W. B. Miller, W. N. Miller, 20 Dec. 1970. Along Canipolé–La Purísima road 9.5 mi [15.3 km] E of La Purísima, C. Church, 8 Jan. 1971 (WBM). 6.5 mi [10.5 km] N of San Isidro, C. Church, Nov. 1969 (UA, WBM). Arroyo Mezquital, SE of Punta Pequeña, J. T. Smith, 1985 (SBMNH). Arroyo de la Purísima, along Canipolé–San Isidro road 3.0 mi [4.8 km] N of San Isidro, elev. 600 ft [180 m], W. B. Miller, W. N. Miller, 21 Dec. 1970 (WBM). Upper Arroyo de la Purísima, 13 mi [21 km] SW of Canipolé, I. L. Wiggins, H. M. Hill, T. Work, 17 Nov. 1946 (SBMNH). 6.8 mi [10.9 km] N of San José Comondú, C. Church, Nov. 1969 (UA, WBM). San José Comondú, R. J. Drake, July 1953 (SBMNH). San José Comondú, elev. 1,200 ft [370 m], W. B. Miller, W. N. Miller, 20 Dec. 1970 (WBM). Comondú Viejo, H. E. Gates, 9 Apr. 1930 (SBMNH). Along Transpeninsular Highway 2.7 mi [4.3 km] N of road to Loreto, C. C. Christensen, S. Kessler, 30 July 1974 (CCC). Along Loreto–San Javier road 8.3 mi [13.4 km] from Transpeninsular Highway, elev. 750 ft [230 m], C. C. Christensen, W. B. Miller, 25 Oct. 1972 (CCC, WBM). Along Loreto–San Javier road 0.6 mi [1.0 km] E of San Javier, C. Church, 11 Dec. 1970 (WBM). San Javier, elev. 1,200–1,500 ft [370–460 m], W. B. Miller, 24 Oct. 1971 (WBM); C. C. Christensen, P. N. D'Eliscu, W. B. Miller, R. L. Reeder, D. B. Richman, 25 Oct. 1972 (CCC, WBM). Juncalito, W. B. Miller, 3 Jan. 1974 (CCC); C. C. Christensen, S. Kessler, 30 July 1974 (CCC). 1 mi [1.6 km] S of Chuenque, C. Church, 8 Dec. 1970 (WBM). Puerto Escondido, H. N. Lowe, Dec. 1931 (ANSP, SDMNH). Canyon west of Puerto Escondido (Hanna 1923). Along Transpeninsular Highway at km 69 N of Villa Insurgentes, C. C. Christensen, W. B. Miller, 5 Dec. 1974 (CCC, WBM). Along Transpeninsular Highway 31 mi [50 km] N of Villa Insurgentes, elev. 900 ft [270 m], W. B. Miller, 31 Oct. 1971 (WBM). Isla San Marcos (Pilsbry and Lowe 1932; TL of *Bulimulus sanmarcosensis*; ANSP); J. P. Figg-Hoblyn, 22–23 Apr. 1952 (SBMNH): SW point, G D. Hanna et al., 31 Mar. 1953, ORCA Exped. (CAS); SW side of island, elev. ca. 300 ft [90 m], R. V. Moran, 22 Mar. 1966 (SDMNH); SW side of island near gypsum mine, M. D. Robinson, 9 Sep. 1970 (CCC, WBM). Islas Coronados, CAS 1921 Exped. (Hanna 1923, as *B. ximenez*; CAS); C. C. Christensen, 1 Aug. 1974 (CCC); S end of [large] island, R. V. Moran, 3 Apr. 1962 (SDMNH). Isla Carmen, H. N. Lowe (ANSP, SDMNH); 1953 ORCA Exped. (CAS): several locations (Hanna 1923); Bahía Marquer (Hanna 1923; TL of *Bulimulus ximenez*; Jacobson 1958); Puerto Balandra, J. P. Figg-Hoblyn, 18 Apr. 1952 (SBMNH); C. C. Christensen, 1 Aug. 1974 (CCC); Bahía Salinas (Pilsbry and Lowe 1932; TL of *Bulimulus carmen*; ANSP, SBMNH); S end of island (Pilsbry and Lowe 1932). Isla Danzante, H. N. Lowe (SDMNH); R. V. Moran, 7 Apr. 1962 (SDMNH); I. L. Wiggins, 21–22 June 1964 (CAS); S anchorage, F. Baker, CAS 1921 Exped. (Hanna 1923; CAS, SDMNH). Isla San José, G D. Hanna et al., 1953, ORCA Exped. (CAS).

Naesiotus dentifer slevini (Hanna, 1923)

(Fig. 18)

Synonym.—*Bulimulus santacruzensis* Hanna, 1923

Distribution.—BAJA CALIFORNIA SUR: Isla Monserrate (TL), J. R. Slevin, E. P. Van Duzee, J. C. Chamberlin, V. Owen, I. M. Johnston, CAS 1921 Exped. (Hanna 1932; CAS, SDMNH); H. N. Lowe, 1931 (Pilsbry and Lowe 1932, Lowe 1933; ANSP, SDMNH); W. K. Emerson, C. F. Harbison, R. V. Moran, 1962, Belvedere Exped. (Emerson and Jacobson 1964; SDMNH); R. C. Banks, 11 May 1963 (SDMNH). Isla Santa Cruz, F. Baker, J. C. Chamberlin, I. M. Johnston, V. Owen, J. R. Slevin, E. P. Van Duzee, CAS 1921 Exped. (Hanna 1923; TL of *Bulimulus santacruzensis*; CAS, SDMNH); H. N. Lowe, 1932 (Lowe 1933; ANSP, SDMNH); J. P. Figg-Hoblyn, 13 Apr. 1952 (SBMNH); G D. Hanna et al., 26 Mar. 1953, ORCA Exped. (Arnaud 1970; CAS); Puritan-AMNH 1957 Exped. (Jacobson 1958); W. K. Emerson, R. V. Moran, I. L. Wiggins, 1962, Belvedere Exped. (Emerson and Jacobson 1964; SDMNH).

Naesiotus excelsus (Gould, 1853)

(Fig. 17)

Synonyms.—*Bulimulus elatus* Gould, 1853. *Bulimulus* (*Scutalus*) *cacotycus* Mabille, 1895. *Bulimulus excelsus* var. *sinaloae* Pilsbry, 1897.

Distribution.—BAJA CALIFORNIA SUR: California (TL) (Gould 1853). "Les Sierras du Sud de la presqu'île" (Mabille 1895; TL of *Bulimulus* (*Scutalus*) *cacotycus*). La Paz (Binney 1861); L. Belding (USNM); H. N. Lowe (ANSP, SDMNH); Henderson Collection (USNM). N slope of La Calavera Mt. above Playa Coromuel, W. B. Miller, 18 Apr. 1958 (WBM). Playa Coromuel, R. S. Houston, J. D. Kudenov, W. B. Miller, 28 Dec. 1971 (WBM); C. C. Christensen, 26 Oct. 1972 (CCC). 12.9 mi [20.6 km] E of La Paz on road to Las Cruces, A. G. Smith (CAS). Cliff of decomposing granite near Rancho Viniamos, 9 mi [12.6 km] E of La Paz, H. E. Gates, 4 Mar. 1930 (SBMNH).

Gould's report of this species from "California" reflects a broader definition for that place name than is now in use. The locality "Sinaloa, state of Sinaloa" reported by Pilsbry (1897–1898) for his "*B. e.* var. *sinaloae*" is undoubtedly erroneous. A USNM lot collected by Belding is labeled "Espiritu Santo, off Lower California," but the species has not been found on that island by recent workers and we doubt its occurrence there.

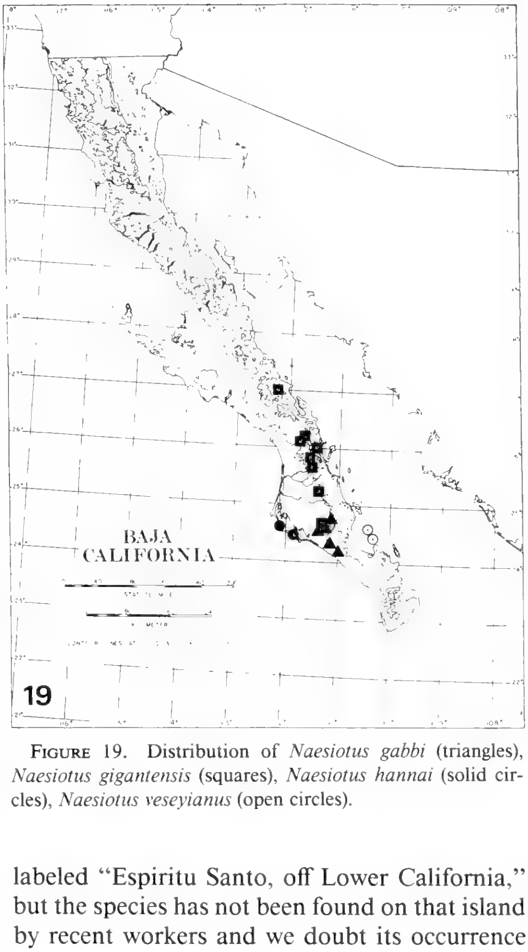

Figure 19. Distribution of *Naesiotus gabbi* (triangles), *Naesiotus gigantensis* (squares), *Naesiotus hannai* (solid circles), *Naesiotus veseyianus* (open circles).

Naesiotus gabbi (Crosse and Fischer, 1872)

(Fig. 19)

Distribution.—BAJA CALIFORNIA SUR: California Mexicana (TL) (Crosse and Fischer 1872; ANSP). Rock outcrop E of road to La Presa, 2.6 mi [4.2 km] NE of junction with road between San Luis Gonzaga and El Obispo, elev. 600 ft [180 m], C. C. Christensen, J. A. Christensen, 16 Dec. 1975 (CCC). Along road between El Obispo and Rancho Tinajitas, I. L. Wiggins, 20 Nov. 1959 (CAS). NE side of Transpeninsular Highway at km 135 N of La Paz, among boulders on south slope of small arroyo near microwave station "El Rifle," elev. ca. 400 ft [120 m], C. C. Christensen, J. A. Christensen, 26 Dec. 1975 (CCC). Rock outcrop NE of Transpeninsular Highway ca. 0.4 mi [0.6 km] NW of km 105 N of La Paz, elev. 400 ft [120 km], C. C. Christensen, W. B. Miller, 6 Dec. 1974 (CCC, WBM). Below caprock on SE slope of large arroyo, 0.6 mi [1.0 km] NE of Transpeninsular Highway at km 77 N of La Paz, R. S. Houston, J. D. Kudenov, W. B. Miller, 23–26 Oct. 1971 (WBM); C. C. Christensen, W. B. Miller, 3 Aug. 1974 and 6 Dec. 1974 (CCC, WBM).

Naesiotus gigantensis (Christensen and Miller, 1977)

(Fig. 19)

Distribution.—BAJA CALIFORNIA SUR: San Javier, in large rockslide immediately S of the mission, elev. 350–450 m (TL), W. B. Miller, 24 Oct. 1971 (Christensen and Miller 1977; WBM); C. C. Christensen, P. N. D'Eliscu, W. B. Miller, R. L. Reeder, D. B. Richman, 25 Oct. 1972 (Christensen and Miller 1977; ANSP, CAS, CCC, DMNH, R. L. Reeder, WBM). Inland of San José de Magdalena on the road to Guadalupe, ca. 26.9 mi [43.3 km] W of Santa Rosalía–Mulegé road, C. Church, 24 Nov. 1970 (Christensen and Miller 1977; WBM). 6.8 mi [10.9 km] N of San José Comondú, C. Church, Nov. 1969 (Christensen and Miller 1977; UA). San José Comondú, R. J. Drake, July 1953 (Christensen and Miller 1977; CAS, UA); V. Roth, 15 Feb. 1966 (Christensen and Miller 1977; UA). Along road from Loreto to San Javier 8.3 mi [13.4 km] W of Transpeninsular Highway, elev. 750 ft [230 m], W. B. Miller, 25 Oct. 1972 (WBM), 25 Oct 1972 (WBM). 0.6 mi [0.8 km] E of San Javier, C. Church, 11 Dec. 1970 (Christensen and Miller 1977; WBM). 9.8 mi [15.8 km] W of San Javier along road to Santo Domingo, C. Church, 12 Dec. 1970 (Christensen and Miller 1977; WBM). Along Transpeninsular Highway 45 mi [72 km] S of Loreto and 31 mi [50 km] NE of Villa Insurgentes, elev. 900 ft [270 m], W. B. Miller, 23 Oct. 1971 (Christensen and Miller 1977; WBM). Along road between El Obispo and Rancho Tinajitas, I. L. Wiggins, 20 Nov. 1970 (Christensen and Miller 1977; CAS).

Naesiotus hannai (Pilsbry, 1927)

(Fig. 19)

Distribution.—BAJA CALIFORNIA SUR: Isla Magdalena: 4 mi [6.4 km] S of village, CAS 1922 Exped. (Pilsbry 1927; CAS); in rocks in ravine below Mt. Isabel, C. C. Christensen, W. B. Miller, 17 May 1975 (CCC, WBM). Isla Margarita, USFCS ALBATROSS (USNM); E. W. Nelson, E. A. Goldman, 30 Nov. 1905 (USNM); P. Bartsch, 19 Mar. 1911 (USNM); H. N. Lowe (ANSP, SDMNH); under stones within one mile, west and south, of the village near the center of the east side of the island (TL), G D. Hanna, CAS 1922 Exped. (Pilsbry 1927; CAS, SBMNH); in rocky outcrops in hills just W of road from Puerto Alcatraz to Puerto Cortez, C. C. Christensen, W. B. Miller, 20 May 1975 (CCC, WBM); ca. 2 mi [3.2 km] NE of Margarita Peak, J. E. Fitch, 28 Nov. 1952 (SBMNH).

Naesiotus harribaueri (Jacobson, 1958)

(Fig. 16)

Distribution.—BAJA CALIFORNIA SUR: Fraile Bay [Bahía de los Frailes], dead on sand dunes and decomposed granite (TL), W. K. Emerson, 19 Apr. 1957 (Jacobson 1958; AMNH). Los Frailes (Arnaud 1970, as *Bulimulus montezuma*). Along road to El Cardonal 0.5 mi [0.8 km] S of Punta Pescadores, elev. ca. 30 ft [10 m], W. B. Miller, 17 Dec. 1973 (WBM). Along road to El Cardonal, near Punta Pescadores, 5.8 mi [9.3 km] N of junction with San Bartolo–Santiago road, W. B. Miller, 20 Dec. 1973 (WBM). Low hills at elevation ca. 100 ft [30 m] behind Cabo Pulmo, D. R. Shasky, Apr. 1965 (SBMNH). Along La Ribera–Los Frailes road 0.8 mi [1.3 km] N of El Pulmo, C. C. Christensen, J. A. Christensen, 24 Dec. 1975 (CCC). Bahía Pulmo, R. C. Brusca, 6 Mar. 1974 (CCC). 0.3 mi [0.5 km] E of Santa Catarina–Los Frailes road 5.3 mi [8.5 km] S of Los Frailes, elev. ca. 50 ft [15 m], C. C. Christensen, J. A. Christensen, 24 Dec. 1975 (CCC). Nine localities along Santa Catarina–Los Frailes road, from 20.2 mi [32.3 km] to 28.4 mi [45.7 km] NE of Santa Catarina, elev. 150–750 ft [45–230 m], C. C. Christensen, J. A. Christensen, W. B. Miller, 26 Dec. 1973 (CCC, WBM). Los Frailes, in midden, J. E. Fitch, 3 Dec. 1952 (SBMNH).

Naesiotus laevapex (Christensen and Miller, 1977)

(Fig. 16)

Distribution.—BAJA CALIFORNIA SUR: W side of Isla Cerralvo, 0.5 km inland of beach at El Limoña anchorage, elev. 50–100 m (TL), C. C. Christensen, 8 Aug. 1974 (Christensen and Miller 1977; CAS, CCC, DMNH, WBM).

Naesiotus montezuma (Dall, 1893)

(Fig. 17)

Synonym.—*Bulimulus* (*Scutalus*) *acholus* Mabille, 1895.

Distribution.—BAJA CALIFORNIA SUR: "Montagnes de la Basse Californie" (Mabille 1895; TL of *Bulimulus* (*Scutalus*) *acholus*). "Lower California, mostly from the mountainous region (3,500 ft alt.)" (TL) (Dall 1893b). Cabo San Lucas, J. Xántus (Binney 1861, as *Bulimulus proteus*; USNM). Sierra Laguna, elev. 3,500 ft, G. Eisen (Cooper 1892b, as *B. proteus*; USNM). Sierra El Taste, G. Eisen (Cooper 1894; USNM). "Toutes les Sierras du Sud de la presqu'île, et, en particulier, auprès du Rancho de San Bartolo" (Mabille 1895). 3 mi [4.8 km] SE of San Antonio, M. D. Robinson, 12 July 1970 (CCC). Foot of Sierra Laguna, elev. 1,000 ft [300 m], 23°40′N, 110°10′W, H. E. Gates, 21 Mar. 1931 (SBMNH). Trail on W face of Sierra Laguna, elev. 1,200–2,500 ft [370–760 m], G. E. Lindsay, 25 July 1951 (SBMNH). W slope of Sierra Laguna, elev. 3,000 ft [910 m], H. E. Gates, 21 Mar. 1931 (SBMNH). La Laguna, along trail from cabin to crest of trail at beginning of descent to La Burrera, elev. 6,500–6,800 ft [1,980–2,070 m], C. C. Christensen, W. B. Miller, 1 Jan. 1974 (CCC, WBM). Along trail from La Burrera to La Laguna, elev. 3,000–6,800 ft [900–2,070 m], C. C. Christensen, W. B. Miller, 1–2 Jan. 1974 (CCC, WBM). Along trail in arroyo W of Boca de la Sierra, elev. 1,000–1,600 ft [300–490 m], W. B. Miller, 7 Dec. 1974 (CCC, WBM). 10 mi [16 km] W of Miraflores, foothills, elev. 1,500 ft [460 m], E. W. Nelson, E. A. Goldman, 20 Jan. 1906 (USNM). Arroyo Candelaria 4.2 mi [6.8 km] E of Migriño and 2.1 mi [3.4 km] W of Candelaria, elev. 300 ft [90 m], C. C. Christensen, J. A. Christensen, 22 Dec. 1975 (CCC). Arroyo Candelaria 2.3 mi [3.7 km] E of Migriño, elev. 200 ft [60 m], C. C. Christensen, J. A. Christensen, 21 Dec. 1970 (CCC). Along Todos Santos–Cabo San Lucas road 6.2 mi [10.0 km] S of Migriño, C. Church, 23 Dec. 1970 (WBM). Along Todos Santos–Cabo San Lucas road 2.2 mi [3.5 km] N of El Saucito, elev. ca. 1,500 ft [460 m], W. B. Miller, W. N. Miller, 23 Dec. 1970 (WBM); C. C. Christensen, J. A. Christensen, W. B. Miller, 22 Dec. 1973 (CCC); C. C. Christensen, 9 Aug. 1974 (CCC). Along Todos Santos–Cabo San Lucas road 2.1 mi [3.4 km] N of El Saucito, elev. ca. 1,500 ft [460 m], C. C. Christensen, J. A. Christensen, W. B. Miller, 22 Dec. 1973 (CCC, WBM); C. C. Christensen, J. A. Christensen, 22 Dec. 1975 (CCC). Granite outcrops, gravelly hills

9 mi [12.6 km] NE of Cabo San Lucas, H. E. Gates, 22 Mar. 1930 (SBMNH).

Naesiotus pallidior (Sowerby, 1833)

(Fig. 20)

Synonyms.—*Bulimulus vegetus* Gould, 1853. *Bulimulus* (*Scutalus*) *pallidior* var. *striatulus* Dall, 1893. *Bulimulus* (*pallidior*?) *vegetus* variety *vegexspiza* Cooper, 1894.

Distribution.—BAJA CALIFORNIA SUR: Along road 31.5 mi [50.7 km] N of La Paz, M. D. Robinson, 24 Jan. 1972 (UA). Todos Santos, M. E. Jones, 1928 (SBMNH). 1.3 mi [2.1 km] S of Todos Santos, elev. ca. 100 ft [30 m], W. B. Miller, W. N. Miller, 23 Dec. 1970 (WBM). Pedricitos Ranch, 23°40′N, 110°10′W, H. E. Gates, 27 Mar. 1931 (SBMNH). Trail on W face of Sierra Laguna, elev. 1,200–2,500 ft [370–760 m], G. E. Lindsay, 25 July 1951 (SBMNH). Along road to La Burrera, 0.6 mi [1.0 km] SW of La Burrera, W. B. Miller, 30 Dec. 1973 (WBM). Along road to La Burrera, 0.8 mi [1.3 km] SW of La Burrera, elev. 1,900 ft [580 m], C. C. Christensen, W. B. Miller, 30 Dec. 1973 (WBM). Along road to La Burrera, ca. 1.5 mi [2.4 km] SW of La Burrera and 12.3 mi [19.8 km] E of Todos Santos–Cabo San Lucas road, elev. 1,600 ft [490 m], C. C. Christensen, J. A. Christensen, 20 Dec. 1975 (CCC). Along road to La Burrera, 2.0 mi [3.2 km] SW of La Burrera and 12.0 mi [19.3 km] E of Todos Santos–Cabo San Lucas road, C. Church, 22 Dec. 1970 (WBM); C. C. Christensen, J. A. Christensen, W. B. Miller, 30 Dec. 1973 (CCC, WBM). Along road to La Burrera, 7.0 mi [11.3 km] E of Todos Santos–Cabo San Lucas road, elev. 1,000 ft [300 m], C. C. Christensen, J. A. Christensen, 20 Dec. 1975 (CCC). Along road to La Burrera, 5.3 mi [8.5 km] E of Todos Santos–Cabo San Lucas road and 1.0 mi [1.6 km] E of junction with road to Los Horconsitos, W. B. Miller, 30 Dec. 1973 (WBM). Along road to La Burrera, 3.0 mi [4.8 km] E of Todos Santos–Cabo San Lucas road, C. Church, 21 Dec. 1970 (WBM); W. B. Miller, 29 Dec. 1973. Ca. 5 mi [8 km] S of Todos Santos, C. C. Christensen, J. A. Christensen, 19 Dec. 1975 (CCC). San Venancio Ranch, E of Pescadero, E. S. Ross, 8 Oct. 1941 (CAS). Rancho Cañada Honda, between Todos Santos and coast road, J. T. Smith, 15 Mar. 1984 (SBMNH). Todos Santos, G. E. Lindsay, 27 July 1951 (SBMNH). Along Todos Santos–Cabo San Lucas road 3.1 mi [5.0 km] S of Las Piedritas and ca. 19.8 mi [31.9 km] S of Todos Santos, C. C. Christensen, J. A. Christensen, 20 Dec. 1975 (CCC). Along Todos Santos–Cabo San Lucas road 2.2 mi [3.5 km] N of Las Barrancas, elev. 500 ft [150 m], C. C. Christensen, 21 Dec. 1975 (CCC). Arroyo Candelaria 2.3 mi [3.7 km] NE of Migriño, elev. 200 ft [60 m], C. C. Christensen, J. A. Christensen, 21 Dec. 1975 (CCC). Along Todos Santos–Cabo San Lucas road 2.2 mi [3.5 km] N of El Saucito, elev. 1,500 ft [460 m], C. C. Christensen, 9 Aug. 1974 (CCC). 20 mi [32 km] S of Todos Santos, M. E. Jones, 18 Sep. 1930 (SBMNH). In wash below mountains immediately behind Cabo San Lucas, ca. 0.25 mi [0.4 km] W of N end of town of San Lucas, C. C. Christensen, J. A. Christensen, W. B. Miller, 24 Dec. 1973 (CCC, WBM). Cape St. Lucas, J. Xántus (USNM). 4.7 mi [7.5 km] SE of San Bartolo, C. C. Christensen, J. A. Christensen, 21 Dec. 1975 (CCC). Along San Bartolo–Santiago road 0.8 mi [1.3 km] S of Rancho Buena Vista monument, C. C. Christensen, J. A. Christensen, W. B. Miller, 27 Dec. 1973 (CCC, WBM). Along San Bartolo–Santiago road at junction with road to El Coro (near Rancho Buena Vista), W. B. Miller, 18 Dec. 1973 (WBM). Santiago, L. B. Mousley, 13 Jan. 1955 (SBMNH). Along coast road from Agua Caliente to Los Frailes 5.2 mi [8.4 km] NW of La Ribera, C. Church, 29 Dec. 1970 (WBM). Along La Ribera–Los Frailes road 5.0 mi [8.0 km] NW of Casa Huéspedes Laguna and ca. 5 mi [8 km] SE of La Ribera, elev. 300 ft [60 m], C. C. Christensen, J. A. Christensen, 24 Dec. 1975 (CCC). Along La Ribera–Los Frailes road 3.1 mi [5.0 km] NW of Casa Huéspedes Laguna and ca. 6.7 mi [10.8 km] SE of La Ribera, C. C. Christensen, J. A. Christensen, 24 Dec. 1975 (CCC). Hills near Punta Arena, H. E. Gates, 5 Mar. 1931 (SBMNH, WBM). Along San Bartolo–Santiago road 9.8 mi [15.8 km] S of Rancho Buena Vista, C. C. Christensen, J. A. Christensen, 21 Dec. 1973 (CCC). 6.8 mi [11.0 km] S of Misión Santiago, or 1 mi [1.6 km] S of Refugio, G D. Hanna, J. W. Durham, 24 Apr. 1965 (CAS). 1.5 mi [2.4 km] SE of Boca de la Sierra, C. C. Christensen, W. B. Miller, 7 Dec. 1974 (CCC, WBM). Miraflores, H. E. Gates, 15 Mar. 1930 (SBMNH). Along Santiago–San José del Cabo road 4.5 mi [7.2 km] S of Caduano, C. C. Christensen, J. A. Christensen, 21 Dec. 1973 (CCC). Along Santa Catarina–Los Frailes road 15.6 mi [25.1 km], 15.9 mi [25.6 km], 17.9 mi [28.8 km], and 19.4 mi [31.2 km] NE of Santa Catarina, C. C. Christensen, J. A. Christensen, W. B. Miller, 26 Dec. 1973 (CCC, WBM). Along Santa Catarina–Los Frailes road 13.5 mi [21.7 km] NE of Santa Catarina, elev. 1,200 ft [370 m], C. C. Christensen, J. A. Christensen, 23 Dec. 1975 (CCC). San José Viejo, C. C. Christensen, J. A. Christensen, 21 Dec. 1973 (CCC). 1.1 mi [1.8 km] S of Rancho Los Dedos (ca. 6.5 mi [10.5 km] SE of Santa Catarina), C. C. Christensen, J. A. Christensen, W. B. Miller, 23 Dec.

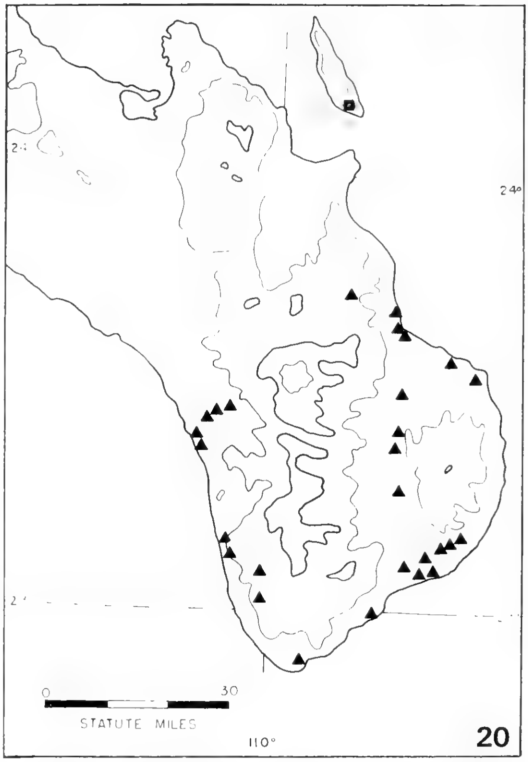

Figure 20. Distribution of *Naesiotus pallidior* (triangles) and *Rabdotus ceralboensis* (square).

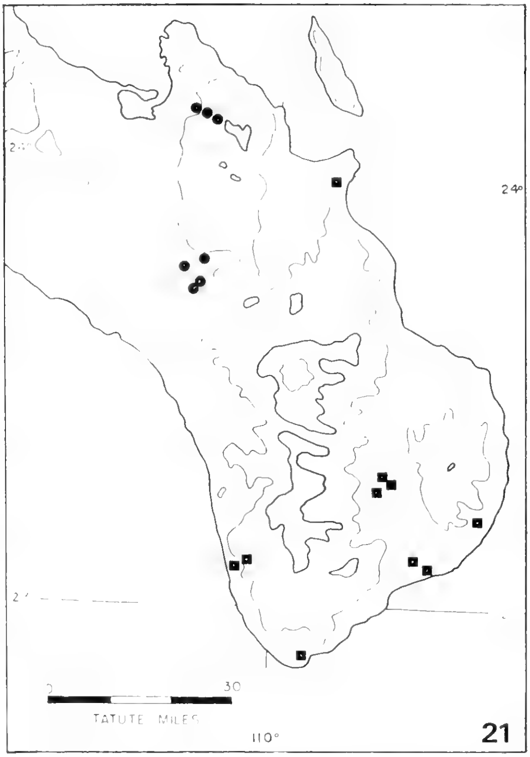

FIGURE 21. Distribution of *Naesiotus rimatus* (squares) and *Naesiotus spirifer* (circles).

1973 (CCC, WBM). Near coast 11.5 mi [18.5 km] NE of Rancho La Laguna and 4.3 mi NE of Campamento La Fortuna, C. C. Christensen, J. A. Christensen, W. B. Miller, 23 Dec. 1973 (CCC, WBM). Rancho La Laguna, H. E. Gates, 3 Mar. 1931 (SBMNH); C. C. Christensen, J. A. Christensen, 23 Dec. 1975 (CCC). East of Arroyo San José, NE of Santa Anita, J. T. Smith, 1985 (SBMNH). Canyon 10 mi [16 km] N of San José del Cabo, H. E. Gates, 18 Mar. 1930 (SBMNH). 1.1 mi [1.8 km] NE of lighthouse NE of San José del Cabo and ca. 4.5 mi [7.2 km] SW of Rancho La Laguna, C. C. Christensen, J. A. Christensen, 23 Dec. 1973 (CCC, WBM). San José, L. Belding (USNM); M. E. Jones, Jan. 1928 (SBMNH); H. N. Lowe, 20 Mar. 1929 (SBMNH). Seaward of Transpeninsular Highway at km 24 (14.9 mi NE of Cabo San Lucas), C. C. Christensen, J. A. Christensen, 21 Dec. 1973 (CCC). Granite outcrops, gravelly hills 9 mi [12.6 km] NE of Cabo San Lucas, H. E. Gates, 22 Mar. 1930 (SBMNH). Cabo San Lucas, J. P. Figg-Hoblyn, 19 May 1952 (SBMNH).

Records of this species from Isla Carmen (Dall 1893b, Stearns 1894; USNM) are based upon mislabeled specimens.

Naesiotus rimatus (Pfeiffer, 1846)

(Fig. 21)

SYNONYMS.—*Bulimulus* (*Mesembrinus*) *inscendens* var. *bryanti* Cooper, 1891. *Bulimulus* (*Leptobyrsus*) *inscendens* var. *monticola* Dall, 1893.

DISTRIBUTION.—BAJA CALIFORNIA SUR: Near San José del Cabo, W. E. Bryant (Cooper 1891; USNM). San José del Cabo to La Paz (Cooper 1892a). Sierra el Taste, G. Eisen (Cooper 1894). Rancho Guamuchil, J. R. Slevin, 7 Aug. 1919 (Hanna 1923; CAS). Elev. 3,000 ft, Sierra Laguna, G. Eisen (USNM). Small canyon in mountains E of old Punta Arena de la Ventana–San Antonio road 0.8 mi [1.3 km] N of its junction with road leading 3.5 mi [5.6 km] W to Los Planes, elev. ca. 500 ft [150 m], C. C. Christensen, 19 Dec. 1975 (CCC; cf. *R. rimatus*). Along trail in arroyo W of Boca de la Sierra, elev. 1,000–1,600 ft [300–490 m], W. B. Miller, 26 Dec. 1970 (WBM). Along trail 1–2 mi [1.6–3.2 km] W of Boca de la Sierra, C. C. Christensen, W. B. Miller, 7 Dec. 1974 (CCC, WBM). Cañon San Pedro, between Cayuco and San Pedro, ca. 5 mi [8 km] W of Caduano, elev. 300–400 ft [90–120 m], R. V. Moran, 12 May 1959 (CAS). Arroyo Candelaria 4.2 mi [6.8 km] E of Migriño and 2.1 mi [3.4 km] W of Candelaria, elev. 300 ft [90 m], C. C. Christensen, J. A. Christensen, 22 Dec. 1975 (CCC). Arroyo Candelaria 2.3 mi [3.7 km] E of Migriño, elev. 200 ft [60 m], C. C. Christensen, J. A. Christensen, 21 Dec. 1975 (CCC). Arroyo Candelaria at Migriño, C. C. Christensen, J. A. Christensen, 21 Dec. 1975 (CCC). Sierra San Lázaro, G. Eisen (USNM). Gravelly hills 9 mi [12.6 km] NE of Cabo San Lucas, H. E. Gates, 22 Mar. 1930 (SBMNH). Mountains immediately behind Cabo San Lucas, ca. 0.25 mi [0.4 km] W of N end of town of San Lucas, C. C. Christensen, J. A. Christensen, W. B. Miller, 24 Dec. 1974 (CCC, WBM). Along Santa Catarina–Los Frailes road 23.4 mi [37.7 km] NE of Santa Catarina, elev. 500 ft [150 m], C. C. Christensen, J. A. Christensen, W. B. Miller, 26 Dec. 1973 (CCC, WBM). Along Santa Catarina–Los Frailes road 3.2 mi [5.1 km] NE of Santa Catarina, C. C. Christensen, J. A. Christensen, W. B. Miller, 23, 26 Dec. 1973 (CCC, WBM). 0.6 mi [1.0 km] SW of Rancho La Laguna and ca. 0.6 mi [1.0 km] NE of San José del Cabo, elev. 300 ft [90 m], C. C. Christensen, J. A. Christensen, 23 Dec. 1975.

No type locality has been designated for *N. rimatus*. Christensen (1978) indicated that the type locality of *Bulimulus* (*Mesembrinus*) *inscendens* var. *bryanti* should be restricted to San José del Cabo and that, pending a lectotype designation, the type locality of *B.* (*Leptobyrsus*) *inscendens* var. *monticola* should be regarded as Sierra Laguna, at 3,000 ft [900 m] elevation.

Naesiotus spirifer (Gabb, 1868)

(Fig. 21)

SYNONYM.—*Bulimulus* (*Leptobyrsus*) *lapidovagus* Mabille, 1895.

DISTRIBUTION.—BAJA CALIFORNIA SUR: "In the mountains, among rocks from San Antonio, below La Paz, to near San Borja, and in the mountains perhaps even farther north" (TL) (Gabb 1868; Baker 1963; Coan and Bogan 1988; ANSP). "Sierra de la Cacachila au Sud de la Paz" (Mabille 1895; TL of *Bulimulus* (*Leptobyrsus*) *lapidovagus*). Sierra Cacachila, along La Paz–Los Planes road 9.3 mi [15.0 km] SE of La Paz–Todos Santos road, elev. ca. 1,450 ft [440 m], R. S. Houston, J. D. Kudenov, W. B. Miller, 27 Oct. 1971 (WBM). Sierra Cacachila, along La Paz–Los Planes road 9.8 mi [15.8 km] E of La Paz–Todos Santos road, elev. 1,400 ft [430 m], C. C. Christensen, J. A. Christensen, 18 Dec. 1975 (CCC). Sierra Cacachila, along

La Paz–Los Planes road 2.1 mi [3.4 km] SE of La Huerta and 14.4 mi [23.2 km] SE of La Paz–Todos Santos road, elev. 2,100–2,200 ft [640–670 m], C. C. Christensen, W. B. Miller, 8 Dec. 1974 (CCC, WBM). Sierra Cacachila, 4.6 mi [7.4 km] SE of La Huerta and 0.5 mi [0.8 km] SW of La Paz–Los Planes road, W. B. Miller, 8 Dec. 1974 (WBM). Sierra Cacachila, along La Paz–Los Planes road 20.2 mi [32.5 km] SE of La Paz–Todos Santos road, elev. ca. 2,250 ft [690 m], R. S. Houston, J. D. Kudenov, W. B. Miller, 27 Oct. 1971 (WBM). Sierra Cacachila, along La Paz–Los Planes road 15.5 mi [24.9 km] W of Los Planes, C. Church, 30 Dec. 1970 (WBM). Along road to El Carrizal 2 mi [3.2 km] W of La Paz–Todos Santos road and 7 mi [11 km] S of San Pedro, C. Church, Dec. 1969 (UA). Mountains E of La Paz–Todos Santos road, near road from Valle Perdido to Las Gallinas, 0.3 mi [0.5 km] SE on side road from point 1.2 mi [1.9 km] from shrine near Las Gallinas, C. Church, 20 Dec. 1970 (WBM); C. C. Christensen, W. B. Miller, 29 Dec. 1973 (CCC, WBM). Along road from Valle Perdido to ranch at Bajada del Molino 2.0 mi [3.2 km] E of Bajada del Molino, elev. ca. 1,400 ft [430 m], C. C. Christensen, W. B. Miller, 28–29 Dec. 1973 (CCC, WBM). 1.3 mi [2.1 km] N of El Triunfo, A. G. Smith, 20–21 Jan. 1959 (CAS).

Naesiotus veseyianus (Dall, 1893)

(Fig. 19)

Distribution.—BAJA CALIFORNIA SUR: Isla Espíritu Santo (TL), L. Belding (Dall 1893; USNM); H. E. Gates, 17 Mar. 1931 (SBMNH): El Candelero, I. M. Johnston, CAS 1921 Exped. (Hanna 1923; CAS); north end section of island, I. M. Johnston, CAS 1921 Exped. (Hanna 1923; CAS); NW end of island, J. P. Figg-Hoblyn, 5 Apr. 1952 (SBMNH); Ballena Cove, elev. ca. 100 ft [30 m], W. K. Emerson et al., 1962, Belvedere Exped. (Emerson and Jacobson 1964; SDMNH); SW side of island, C. C. Christensen, 5 Aug. 1974 (CCC); N talus slope of peak on S end of island, M. W. Williams, 18 Apr. 1937 (SBMNH). "Espíritu Santo Island, North Island" [=Isla Partida], V. Owen, CAS 1921 Exped. (Hanna 1923; CAS). Isla Partida, west side, W. K. Emerson et al., 1962, Belvedere Exped. (Emerson and Jacobson 1964; SDMNH).

Naesiotus xantusi (Binney, 1861)

(Fig. 22)

Distribution.—BAJA CALIFORNIA SUR: Cabo San Lucas (TL), J. Xántus (Binney 1861; USNM). Sierra El Taste (Cooper 1894). Along road from Valle Perdido to ranch at Bajada del Molino 2.0 mi [3.2 km] from Bajada del Molino, elev. ca. 1,400 ft [430 m], C. C. Christensen, W. B. Miller, 28–29 Dec. 1973 (CCC, WBM). Along trail from La Burrera to La Laguna, elev. ca. 3,000 ft [910 m], W. B. Miller, 2 Jan. 1974 (WBM). Sierra Laguna, Animas Ranch, B. Hammerly, E. S. Ross, 12 Oct. 1941 (CAS). Canyon W of Boca de la Sierra, ca. 4 mi [6.4 km] above town, elev. ca. 1,500 ft [460 m], W. B. Miller, 26 Dec. 1970 (WBM). 1–2 mi [1.6–3.2 km] above Boca de la Sierra, W. B. Miller, 7 Dec. 1974 (WBM). Arroyo Candelaria, 2.1 mi [3.4 km] W of Candelaria, elev. ca. 300 ft [90 m], C. C. Christensen, 22 Dec. 1975 (CCC). Arroyo Candelaria, 2.3 mi [3.7 km] E of Migriño, elev. 200 ft [60 m], C. C. Christensen, 21 Dec. 1975 (CCC). Along Todos Santos–Cabo San Lucas road, 2.2 mi [3.5 km] N of El Saucito, elev. ca. 1,500 ft [460 m], W. B. Miller, W. N. Miller, 23 Dec. 1970 (WBM); C. C. Christensen, W. B. Miller, 22 Dec. 1973; C. C. Christensen, 9 Aug. 1974 (CCC). Along Todos Santos–Cabo San Lucas road, 2.1 mi [3.4 km] N of El Saucito, elev. ca. 1,500 ft [460 m], C. C. Christensen, W. B. Miller, 22 Dec. 1973 (CCC, WBM).

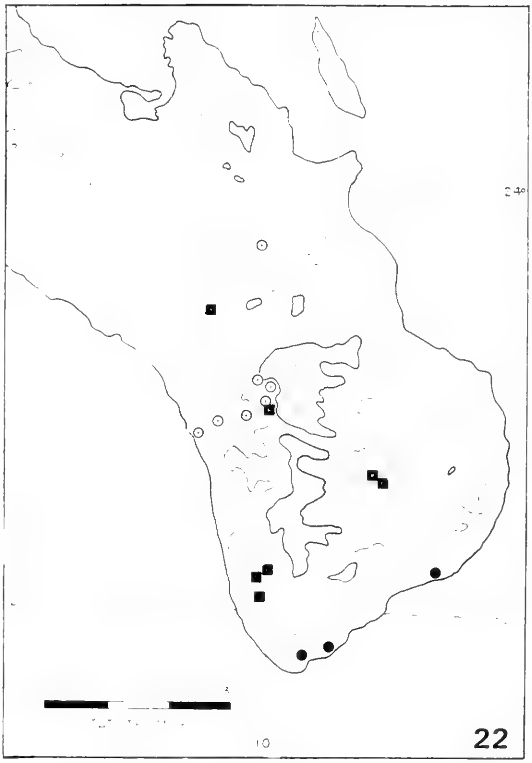

Figure 22. Distribution of *Naesiotus xantusi* (squares), *Rabdotus levis* (open circles), and *Rabdotus pilula* (solid circles).

Naesiotus(?) sp.

Distribution.—BAJA CALIFORNIA SUR: Mountains E of La Paz–Todos Santos road, near road from Valle Perdido to Las Gallinas, 0.3 mi [0.5 km] SE on side road from junction 1.2 mi [2.0 km] from shrine near Las Gallinas, W. B. Miller, 29 Dec. 1973 (WBM). Along road from Valle Perdido to ranch at Bajada del Molino 2.0 mi [3.2 km] E of Bajada del Molino, in rockslides in N-facing slope of large arroyo S of road, elev. ca. 1,400 ft [430 m], C. C. Christensen, W. B. Miller, 28–29 Dec. 1974 (CCC, WBM). 1.4 mi [2.3 km] from main highway along access road to microwave station at San Bartolo, among granite boulders in deep ravine above town, elev. ca. 1,400 ft [430 m], C. C. Christensen, W. B. Miller, 8 Dec. 1974 (CCC, WBM). Ca. 0.6 mi [1.0 km] SE of San Bartolo, among large granite boulders along S side of arroyo, elev. ca. 800 ft [240 m], W. B. Miller, 28 Dec. 1970 (WBM). Ca. 1.8 mi [2.9 km] SE of San Bartolo, on S side of arroyo, elev. ca. 800 ft [240 m], W. B. Miller, 28 Dec. 1970 (WBM). Along road to La Burrera 7.0 mi [11.2 km] E of Todos Santos–Cabo San Lucas road, elev. 1,000 ft [300 m], C. C. Christensen, J. A. Christensen, 20 Dec. 1975 (CCC). Arroyo W of Boca de la Sierra, ca. 4 mi [6.4 km] above town, elev. ca. 1,500 ft [460 m], W. B. Miller, 26 Dec. 1970. Along trail in arroyo 1–2 mi [1.6–3.2 km] above Boca de la Sierra, C. C. Christensen, W. B. Miller,

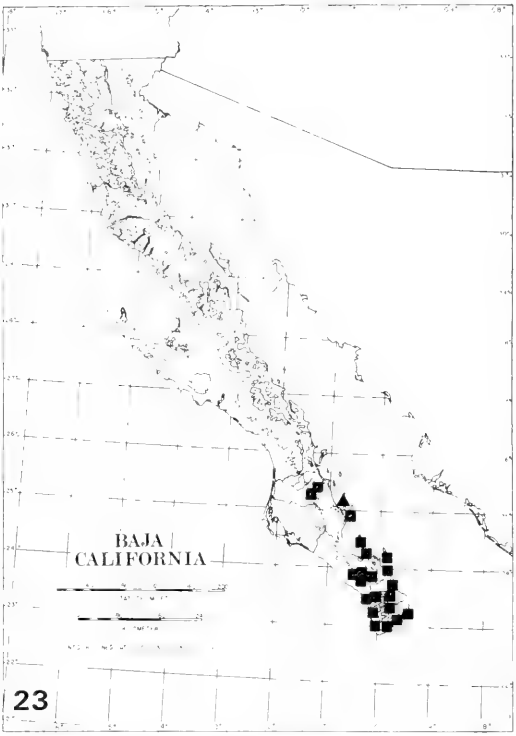

FIGURE 23. Distribution of *Rabdotus chamberlini* (triangle) and *Rabdotus sufflatus* (squares).

7 Dec. 1974 (CCC, WBM). Along Todos Santos–Cabo San Lucas road, 3.1 mi [5.0 km] S of Las Piedritas, C. C. Christensen, J. A. Christensen, 20 Dec. 1975 (CCC). Along Todos Santos–Cabo San Lucas road, 2.2 mi [3.5 km] N of Las Barrancas, elev. 500 ft [150 m], C. C. Christensen, J. A. Christensen, 21 Dec. 1975 (CCC). Arroyo Candelaria, 2.3 mi [3.7 km] E of Migriño, elev. 200 ft [60 m], C. C. Christensen, J. A. Christensen, 21 Dec. 1975 (CCC). 0.6 mi [1.0 km] SW of Rancho La Laguna and 4.7 mi [7.5 km] NE of lighthouse E of San José del Cabo, elev. 300 ft [90 m], C. C. Christensen, J. A. Christensen, 23 Dec. 1975 (CCC).

The above records include the *Rabdotus* new species A and B of Christensen (1978). At least one species, not assignable to any recognized species of *Naesiotus*, occurs at several localities in the Cape region. The anatomy is unknown, and more material will be necessary to clarify its relationships.

Genus **Rabdotus** Albers, 1850
Subgenus **Rabdotus** sensu stricto

Rabdotus (Rabdotus) ceralboensis (Hanna, 1923)

(Fig. 20)

DISTRIBUTION.—BAJA CALIFORNIA SUR: Isla Cerralvo, 1953 ORCA Exped. (CAS); west of Ruffo's ranch house (TL), J. C. Chamberlin, 7 June 1923, CAS 1921 Exped. (Hanna 1923; CAS); El Mostrador, J. C. Chamberlin, CAS 1921 Exped. (Hanna 1923; CAS); El Mostrador, north of Ruffo's ranch, west side of island, elev. 75–150 ft [23–46 m], among boulders (Emerson and Jacobson 1964); Punta Gordas (Arnaud 1970); 1 mi [1.6 km] SE of Piedras Gordas Point, G D. Hanna, 20–21 Mar. 1953 (CAS); SW end of island, in arroyo halfway between sea and divide, W. Farmer, R. Banks, 22 May 1962 (SDMNH); S end of island, J. P. Figg-Hoblyn, 1–2 Apr. 1952 (SBMNH).

A single shell of *Rabdotus ceralboensis* is contained in a mixed lot with *Naesiotus dentifer slevini* from Isla Santa Cruz (WBM *ex* CAS), undoubtedly by error. The species is otherwise recorded only from Isla Cerralvo.

Rabdotus (Rabdotus) chamberlini (Hanna, 1923)

(Fig. 23)

DISTRIBUTION.—BAJA CALIFORNIA SUR: Isla San Diego (TL), J. C. Chamberlin, 27 May 1921, CAS 1921 Exped. (Hanna 1923; CAS); I. L. Wiggins, 19 Apr. 1962 (CAS); elev. 50 ft [15 m] to crest of island, 1962, Belvedere Exped. (Emerson and Jacobson 1964; SDMNH).

Rabdotus (Rabdotus) levis (Dall, 1893)

(Fig. 22)

SYNONYM.—*Bulimulus* (*Thaumastus*) *digueti* Mabille, 1895.

DISTRIBUTION.—BAJA CALIFORNIA SUR: Rancho Lagunas, Punta Arena, W. E. Bryant; Sierra Laguna, mostly near La Chuparosa [sic], elev. 2,000 ft (Cooper 1892b, as *Bulimulus xantusi*; Dall 1893b; USNM). El Taste Mountains, elev. about 4,000 ft; near Cape St. Lucas (Cooper 1894). Sierra de la Victoria (Mabille 1895; TL of *Bulimulus* (*Thaumastus*) *digueti*). Along San Antonio–San Bartolo road 5.9 mi [9.4 km] from San Antonio, C. C. Christensen, 10 Aug. 1974 (CCC). La Aguja, ca. 16 mi [26 km] NE of Todos Santos, elev. 1,900 m, R. V. Moran, 18 May 1959 (CAS). Trail to meadow at La Laguna, elev. 4,500–6,000 ft [1,370–1,830 m], G. E. Lindsay, 25 July 1951 (SBMNH). La Laguna, Sierra Laguna, E. W. Nelson, E. A. Goldman, 27 Jan. 1906 (USNM). La Laguna, Sierra Laguna, elev. ca. 6,500–6,800 ft [1,980–2,070 m], C. C. Christensen, W. B. Miller, 31 Dec. 1973–1 Jan. 1974 (CCC, WBM). "Laguna Valley," elev. 5,000 ft [1,520 m], H. E. Gates, 21 Mar. 1931 (SBMNH). Several localities along trail from La Burrera to La Laguna, elev. 2,000–6,800 ft [610–2,070 m], C. C. Christensen, W. B. Miller, 1–2 Jan. 1974 (CCC, WBM). Sierra Laguna, trail on ridge above Las Animas, E. S. Ross, 13 Oct. 1941 (CAS). Along road to La Burrera 5.6 and 7.0 mi [9.0 and 11.2 km] E of Todos Santos–Cabo San Lucas road, C. C. Christensen, J. A. Christensen, Dec. 1975 (CCC). Along road to La Burrera 5.2–5.3 mi [8.3–8.5 km] E of Todos Santos–Cabo San Lucas road, C. Church, 21 Dec. 1970 (WBM); W. B. Miller, 30 Dec. 1973 (WBM). Along road to Horconsitos 6.7 mi [10.7 km] E of Todos Santos–Cabo San Lucas road, C. Church, 22 Dec. 1970 (WBM). 1.3 mi [2.1 km] S of Todos Santos, elev. ca. 100 ft [30 m], W. B. Miller, W. N. Miller, 23 Dec. 1970 (WBM).

A record of this species near San Javier ("along road from Loreto to San Javier 6 mi [9.6 km] E of San Javier, C. Church, 11 Dec. 1970" [Delaware Museum of Natural History; CCC ex DMNH]) has not been confirmed despite extensive field work in that region by others; we believe the specimens to be mislabeled.

Rabdotus (Rabdotus) pilula (Binney, 1861)

(Fig. 22)

SYNONYMS.—*Bulimulus cooperi* "Dall" Cooper, 1895. *Bulimulus cooperi* Dall, 1896.

DISTRIBUTION.—BAJA CALIFORNIA SUR: "Habitat in paeninsulae Californiae, ad Todos Santos Mission, et in insula Marguerita [Margarita]" (Binney 1861). San José del Cabo (Cooper 1891). Mts. near La Paz, G. Eisen, 1893 (USNM). Laguna Ranch, 8 mi [13 km] E of San José del Cabo, H. E. Gates, 3 Mar. 1931 (SBMNH, CCC, WBM). 2.4 mi [3.8 km] N of Cabo San Lucas, A. G. Smith, CAS 1959 Exped. (CAS). 5.4 mi [8.6 km] ENE of Cabo San Lucas, road to San José del Cabo, A. G. Smith, 17 Jan. 1959 (CAS).

No type locality was designated in the original description of *R. pilula.* Binney and Bland (1869) selected three specimens from "Todos [Santos] Mission" as "types." Binney's (1861) record of this species from Isla Margarita is undoubtedly in error. All recently collected specimens seen by us were collected in the Cabo San Lucas–San José del Cabo region.

Rabdotus (Rabdotus) sufflatus (Gould in Binney, 1859)

(Fig. 23)

SYNONYMS.—*Bulimulus vesicalis* Gould, 1853 (non *B. vesicalis* Pfeiffer, 1853). *Bulimus juarezi* Pfeiffer, 1865. *Bulimulus sufflatus* var. *insularis* Cooper, 1892. *Bulimulus insularis* var. *chinchensis* Cooper, 1894. *Bulimulus* (*Globulus*) *recognitus* Mabille, 1895.

DISTRIBUTION.—BAJA CALIFORNIA SUR: "In provincia pacifica reipublicae Mexicanae" (Pfeiffer 1865; TL of *Bulimus juarezi*). "Basse Californie," L. Diguet (Mabille 1895; TL of *Bulimulus* (*Globulus*) *recognitus*; MNHN). El Chinche Mountains, elev. 2,000 ft (Cooper 1894; TL of *Bulimulus sufflatus* var. *chinchensis*). Along Transpeninsular Highway at km 69 N of Villa Insurgentes, among rocks to S of road, C. C. Christensen, W. B. Miller, 5 Dec. 1974 (CCC, WBM). Along Transpeninsular Highway 31 mi [50 km] N of Villa Insurgentes, in lava rockslides on S side of arroyo, W. B. Miller, 23 Oct. 1971 (WBM). Sandy plain 7 mi [11.2 km] W of La Paz, I. L. Wiggins, H. M. Hill, 25 Nov. 1946 (SBMNH). Dry wash E of La Paz, H. E. Gates, 9 Mar. 1930 (SBMNH). La Paz (TL, desig. by Emerson and Jacobson 1964), Maj. W. Rich (Johnson 1964; MCZ); L. Belding (USNM); M. E. Jones, Mar. 1928 (SBMNH). W shore of Ensenada de La Paz, W. B. Miller, 28 Oct. 1971 (WBM). 0.2–0.5 mi [0.3–0.8 km] E of Punta San Lorenzo, on sandy flats behind beach, C. C. Christensen, 6 Aug. 1974 (subfossil; CCC); C. C. Christensen, J. A. Christensen, 25 Dec. 1975 (subfossil; CCC). Hillside above road at Playa Coromuel, C. C. Christensen, 26 Oct. 1972 (CCC). Along La Paz–Los Planes road 9.3 mi [15.0 km] SE of main highway S of La Paz, elev. ca. 1,450 ft [440 m], J. D. Kudenov, R. S. Houston, W. B. Miller, 27 Oct. 1971 (WBM). Bahía de los Muertos, H. E. Gates, 13 Mar. 1930 (SBMNH). Punta Arena, W. E. Bryant (USNM). Punta Arena, under bushes on sandy hillside near beach, C. Church, 29 Dec. 1970 (WBM). Punta Arena de la Ventana, under bushes in sand behind beach, J. D. Kudenov, R. S. Houston, W. B. Miller, 27 Oct. 1971 (WBM). Ca. 1 mi [1.6 km] inland from lighthouse at Punta Arena de la Ventana, C. C. Christensen, J. A. Christensen, 18 Dec. 1975 (CCC). Ensenada de los Muertos, under agaves, H. N. Lowe, Jan. 1932 (ANSP). Puerto de la Bahía de los Muertos, W. B. Miller, 27 Oct. 1971 (WBM). 7 mi [11 km] S of San Pedro, 2 mi [3.2 km] W of highway on road to El Carrizal, C. Church, Nov. 1969 (UA). 1.9 mi [3.1 km] W of La Paz–Todos Santos road, 7.2 mi [11.6 km] S of junction with La Paz–El Triunfo road, elev. 900 ft [270 m], C. C. Christensen, J. A. Christensen, 19 Dec. 1975 (CCC). Along road from Valle Perdido to ranch at Bajada del Molino, 2.0 mi [3.2 km] E of Bajada del Molino, in large arroyo S of road, elev. 1,400 ft [430 m], C. C. Christensen, W. B. Miller, 28–29 Dec. 1975 (CCC). Pedricitos Ranch, 23°40′N, 110°10′W, H. E. Gates, 27 Mar. 1931 (SBMNH). San Antonio, H. E. Gates, 12 Mar. 1930 (SBMNH). 2.5 mi [4.0 km] from San Antonio on road to Los Planes, C. C. Christensen, W. B. Miller, 8 Dec. 1974 (CCC). Along San Antonio–San Bartolo road 3.9 mi [6.3 km] NE of San Antonio, elev. 1,800 ft [550 m], C. C. Christensen, J. A. Christensen, 19 Dec. 1975 (CCC). Along San Antonio–San Bartolo road 5.9 mi [9.5 km] E of San Antonio, C. C. Christensen, 10 Aug. 1974 (CCC). Along San Antonio–San Bartolo road 12.5 mi [20.1 km] NW of San Bartolo, W. B. Miller, 16 Dec. 1973 (WBM). 1.4 mi [2.3 km] from main highway at San Bartolo along road to microwave station, among granite boulders in steep ravine above the town, elev. ca. 1,400 ft [430 m], C. C. Christensen, W. B. Miller, 8 Dec. 1974 (CCC). Ca. 1.8 mi [2.9 km] SE of San Bartolo, along S side of arroyo, elev. 800 ft [240 m], W. B. Miller, 28 Dec. 1970 (WBM). Along road from Las Palmas to El Cardonal and Punta Pescadores 5.8 mi [9.3 km] from main highway at Las Palmas, W. B. Miller, 20 Dec. 1973 (WBM). Along San Bartolo–Santiago road 9.8 mi [15.8 km] S of Rancho Buena Vista, C. C. Christensen, J. A. Christensen, 21 Dec. 1973 (CCC). Ca. 0.5 mi [0.8 km] beyond El Coro (near Rancho Buena Vista) along trail leading up canyon into mountains, elev. ca. 1,000 ft [300 m], W. B. Miller, W. B. Miller III, 18 Dec. 1973 (WBM). Rancho La Laguna, H. E. Gates, 3 Mar. 1931 (SBMNH). Sierra Laguna, near Cabo San Lucas, G. Eisen (USNM). Las Animas Ranch, Sierra Laguna, E. Hammerly, E. S. Ross, 12 Oct. 1941 (CAS). Along trail from La Burrera to La Laguna, 2,000–3,000 ft [610–910 m], W. B. Miller, 2 Jan. 1974 (WBM). West slope of Sierra La Laguna, elev. 3,000 ft [910 m], H. E. Gates, 21 Mar. 1930 (SBMNH). Along road to La Burrera 0.6 mi [1.0 km] SW of La Burrera, W. B. Miller, 30 Dec. 1970 (WBM). Along road to La Burrera 0.8 mi [1.3 km] SW of La Burrera, elev. 1,900 ft. [580 m], C. C. Christensen, W. B. Miller, 30 Dec. 1973 (CCC, WBM). Along road to La Burrera 2.0 mi [3.2 km] SW of La Burrera, W. B. Miller, 30 Dec. 1973 (WBM). Along road to La Burrera 13.0 mi [20.9 km] E of Todos Santos–Cabo San Lucas road, C. C. Christensen, J. A. Christensen, W. B. Miller, 30 Dec. 1973 (CCC). Along road to La Burrera 7.0 mi [11.3 km] E of Todos Santos–Cabo San Lucas road, elev. 1,000 ft [300 m],

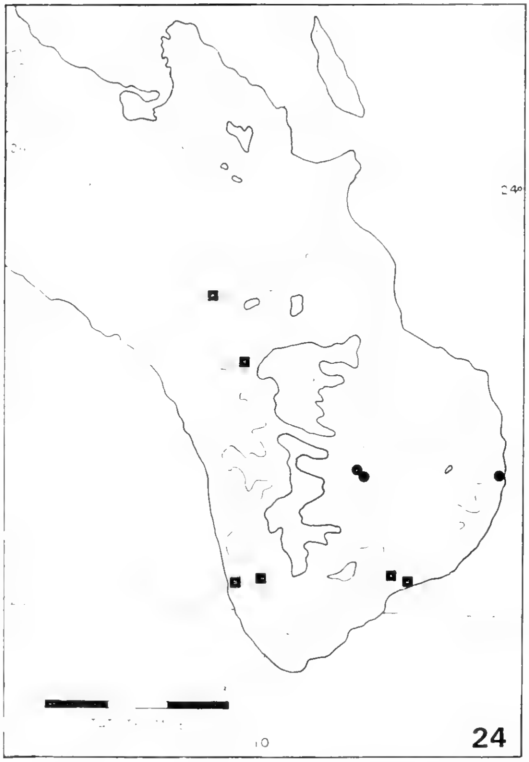

FIGURE 24. Distribution of *Rabdotus abbreviatus* (circles) and *Rabdotus ramentosus* (squares).

C. C. Christensen, J. A. Christensen, 20 Dec. 1975 (CCC). Along road to La Burrera 5.6 mi [9.0 km] E of Todos Santos–Cabo San Lucas road, C. C. Christensen, J. A. Christensen, W. B. Miller, 29–30 Dec. 1973 (CCC). Along road to La Burrera 5.3 mi [8.5 km] E of Todos Santos–Cabo San Lucas road and 1.0 mi [1.6 km] E of junction with road to Los Horconsitos, W. B. Miller, 30 Dec. 1973 (WBM). Along road to La Burrera 8.0 mi [12.9 km] E of Todos Santos–Cabo San Lucas road, C. Church, 22 Dec. 1970 (WBM). Along road to Los Horconsitos 6.7 mi [10.8 km] E of Todos Santos–Cabo San Lucas road, C. Church, 22 Dec. 1970 (WBM). Boca de la Sierra, along trail in arroyo W of village, elev. 1,000–1,600 ft [300–490 m], W. B. Miller, 26 Dec. 1970 (WBM). Boca de la Sierra, 1–2 mi [1.6–3.2 km] above village, C. C. Christensen, W. B. Miller, 7 Dec. 1974 (CCC, WBM). 1.5 mi [2.4 km] E of Boca de la Sierra along road to Miraflores, C. C. Christensen, W. B. Miller, 7 Dec. 1974 (CCC, WBM). Miraflores, H. E. Gates, 15 Mar. 1930 (SBMNH). Along Todos Santos–Cabo San Lucas road 3.1 mi [5.0 km] S of Las Piedritas, C. C. Christensen, J. A. Christensen, 20 Dec. 1975 (CCC). Rancho Cañada Honda, between Todos Santos and coast road, J. T. Smith, 15 Mar. 1984 (SBMNH). Along Todos Santos–Cabo San Lucas road 2.1–2.2 mi [3.4–3.5 km] N of El Saucito, elev. ca. 1,500 ft [460 m], C. C. Christensen, J. A. Christensen, W. B. Miller, 22 Dec. 1973 (CCC, WBM). Sierra El Taste, elev. 3,200 ft [980 m], G. Eisen, F. H. Vaslit (USNM). 0.3 mi [0.5 km] E of Santa Catarina–Los Frailes road at point 5.3 mi [8.5 km] S of Los Frailes, elev. 50 ft [15 m], C. C. Christensen, J. A. Christensen, 24 Dec. 1975 (CCC). Along Santa Catarina–Los Frailes road 20.1 mi [32.3 km] NE of Santa Catarina, C. C. Christensen, J. A. Christensen, W. B. Miller, 26 Dec. 1973 (CCC). 1.1 mi [1.8 km] S of Rancho Los Dedos (ca. 6.5 mi [10.5 km] SE of Santa Catarina), C. C. Christensen, J. A. Christensen, W. B. Miller, 23 Dec. 1973 (CCC, WBM). Along Santa Catarina–Los Frailes road 3.2 mi [5.1 km] E of Santa Catarina, in rock outcrops on NW side of wash, C. C. Christensen, W. B. Miller, 23, 26 Dec. 1973 (CCC). Hills at Cabo San Lucas, H. E. Gates, 28 Feb. 1931 (SBMNH). Isla San José: Bahía Amortajada, G D. Hanna et al., 24 Mar 1953, ORCA Exped. (CAS); W side of island, C. F. Harbison, I. L. Wiggins, 12 Apr. 1962 (SDMNH). Isla Espíritu Santo, W. E. Bryant (Cooper 1892b, TL of *Bulimulus sufflatus* var. *insularis*; USNM); SE end of island, on desert floor, M. W. Williams, 18 Apr. 1937 (probably subfossil; SBMNH). Isla Cerralvo, R. C. Banks, 26 May–1 June 1962 (CAS); S end of island, J. P. Figg-Hoblyn, 1–2 Apr. 1952 (SBMNH).

Subgenus **Plicolumna** Cooper, 1895

Rabdotus (Plicolumna) abbreviatus (Cooper, 1892)

(Fig. 24)

DISTRIBUTION.—BAJA CALIFORNIA SUR: Sierra Laguna (TL) (Cooper 1892b). Sierra El Taste, elev. ca. 4,200 ft [1,300 m], G. Eisen (Cooper 1894). San Lázaro, G. Eisen, F. H. Vaslit (USNM). Along trail above Boca de la Sierra, elev. 1,000–1,600 ft [300–490 m], W. B. Miller, 26 Dec. 1970 (WBM); C. C. Christensen, W. B. Miller, 7 Dec. 1974 (CCC, WBM). 0.3 mi [0.5 km] E of Santa Catarina–Los Frailes road, 5.3 mi [8.5 km] S of Los Frailes, C. C. Christensen, J. A. Christensen, 24 Dec. 1975 (CCC).

Rabdotus (Plicolumna) artemisia (Binney, 1861)

(Fig. 25)

DISTRIBUTION.—BAJA CALIFORNIA SUR: Cabo San Lucas (TL), J. Xántus (Binney 1861; USNM). Sierra Laguna, elev. 3,000 ft [910 m] (Cooper 1892b). Sierra El Taste, elev. 3,400–4,200 ft [1,040–1,280 m], G. Eisen (Cooper 1894; USNM). Sierra San Lázaro, G. Eisen (Cooper 1895; USNM). Mts. E of La Paz, H. N. Lowe, Feb. 1929 (ANSP). Sierra Cacachila, along La Paz–Los Planes road 9.3 mi [15.0 km] SE of La Paz–Todos Santos road, elev. ca. 1,450 ft [440 m], R. S. Houston, J. D. Kudenov, W. B. Miller, 27 Oct. 1971 (WBM). Sierra Cacachila, along La Paz–Los Planes road 2.1 mi [3.4 km] SE of La Huerta and 14.4 mi [23.2 km] SE of La Paz–Todos Santos road, elev. 2,100–2,600 ft [640–670 m], C. C. Christensen, W. B. Miller, 8 Dec. 1974 (CCC, WBM). Sierra Cacachila, along La Paz–Los Planes road 15.5 mi [24.9 km] W of Los Planes, C. Church, 30 Dec. 1970 (WBM). Sierra Cacachila, along La Paz–Los Planes road 20.2 mi [32.5 km] SE of La Paz–Todos Santos road, elev. ca. 2,250 ft [690 m], R. S. Houston, J. D. Kudenov, W. B. Miller, 27 Oct. 1971 (WBM). 12.1 mi [19.5 km] NW of San Bartolo, A. G. Smith, 9 Jan. 1959 (CAS). 1.4 mi [2.3 km] from main highway along access road to microwave station at San Bartolo, among granite boulders in deep ravine above town, elev. ca. 1,400 ft [430 m], W. B. Miller, 19 Dec. 1973 (WBM); C. C. Christensen, W. B. Miller, 8 Dec. 1974. Ca. 0.6 mi [1.0 km] SE of San Bartolo, among large granite boulders

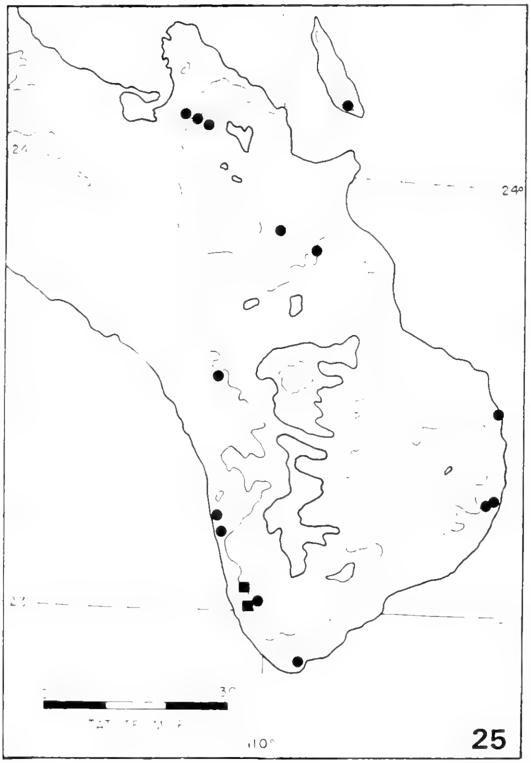

FIGURE 25. Distribution of *Rabdotus artemisia* (except for occurrence on Isla Espiritu Santo) (circles) and *Rabdotus perhirsutus* (squares).

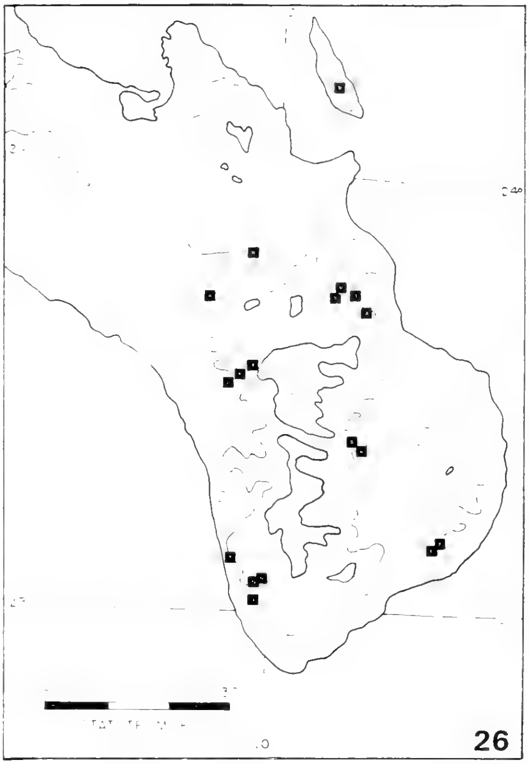

FIGURE 26. Distribution of *Rabdotus inscendens.*

along S side of arroyo, elev. ca. 800 ft [240 m], W. B. Miller, 28 Dec. 1970 (WBM). Along road to La Burrera 0.6 mi [1.0 km] SW of La Burrera, W. B. Miller, 30 Dec. 1973 (WBM). Along Todos Santos–Cabo San Lucas road 3.1 mi [5.0 km] S of Las Piedritas and ca. 19.8 mi [31.9 km] S of Todos Santos, C. C. Christensen, J. A. Christensen, 21 Dec. 1975 (CCC). Along Todos Santos–Cabo San Lucas road 2.2 mi [3.5 km] N of Las Barrancas, elev. 500 ft [150 m], C. C. Christensen, J. A. Christensen, 21 Dec. 1975 (CCC). Along Todos Santos–Cabo San Lucas road 2.2 mi [3.5 km] N of El Saucito, elev. 1,500 ft [460 m], C. C. Christensen, J. A. Christensen, W. B. Miller, 22 Dec. 1973 (CCC). Cabo San Lucas, H. N. Lowe, 1929 (ANSP). Mountains immediately behind Cabo San Lucas, ca. 0.25 mi [0.4 km] W of N end of town of San Lucas, C. C. Christensen, J. A. Christensen, W. B. Miller, 24 Dec. 1974 (CCC, WBM). Northernmost seaward-facing slope of Punta Los Frailes, elev. ca. 300 ft [90 m], C. Church, 27 Dec. 1970 (WBM). Along Santa Catarina–Los Frailes road 25.6 mi [41.2 km] NE of Santa Catarina, C. C. Christensen, J. A. Christensen, W. B. Miller, 26 Dec. 1973 (CCC). Same road, 23.4 mi [37.7 km] NE of Santa Catarina, elev. 550 ft [170 m], C. C. Christensen, J. A. Christensen, W. B. Miller, 26 Dec. 1973 (CCC, WBM). E of Arroyo San José, NE of Santa Anita, J. T. Smith, 1985 (SBMNH). Isla Espíritu Santo: NE end of island, J. Ball, G D. Hanna, 1953 ORCA Exped. (CAS); canyon back of Candelero Bay, A. G. Smith, 30 Aug. 1960 (CAS). Isla Cerralvo, SW anchorage, 1 mi [1.6 km] SE of Piedras Blancas Point, elev. 1,500 ft [460 m], G D. Hanna, 1953 ORCA Exped. (CAS).

Rabdotus (Plicolumna) inscendens (Binney, 1861)

(Fig. 26)

DISTRIBUTION.—BAJA CALIFORNIA SUR: 3 mi [4.8 km] SE of San Antonio, M. D. Robinson, 12 July 1970 (UA). Along road from Valle Perdido to ranch at Bajada del Molino 2.0 mi [3.2 km] by road from Bajada del Molino, in rockslides on N-facing slope of large arroyo S of road, elev. 1,400 ft [430 m], C. C. Christensen, W. B. Miller, 28–29 Dec. 1973 (CCC, WBM). 1.4 mi [2.3 km] from main highway at San Bartolo along road to microwave station, in deep ravine above town, elev. ca. 1,400 ft [430 m], W. B. Miller, 19 Dec. 1973 (WBM); C. C. Christensen, W. B. Miller, 8 Dec. 1974 (CCC, WBM). 0.6 mi [1.0 km] SE of San Bartolo, along S side of arroyo, among large granite boulders, elev. ca. 800 ft [240 m], W. B. Miller, 28 Dec. 1970 (WBM). Ca. 1.8 mi [2.9 km] SE of San Bartolo, along S side of arroyo, among granite boulders, elev. ca. 800 ft [240 m], W. B. Miller, 28 Dec. 1970 (WBM). 3.7 mi [6.0 km] SE of San Bartolo, small arroyo entering San Bartolo arroyo from N, C. C. Christensen, J. A. Christensen, 21 Dec. 1973 (CCC). 5.7 mi [9.2 km] SE of San Bartolo, along S side of arroyo, among granite boulders, C. C. Christensen, 25 Dec. 1975 (CCC). Ca. 0.5 mi [0.8 km] beyond El Coro (near Rancho Buena Vista) along trail leading up canyon into mountains, elev. ca. 2,000 ft [610 m], W. B. Miller, W. B. Miller III, 18 Dec. 1973 (WBM). Along trail from La Burrera to La Laguna, elev. 3,000 ft [910 m], W. B. Miller, 2 Jan. 1974 (WBM). Along trail from La Burrera to La Laguna, elev. 4,500–6,800 ft [1,370–2,070 m], C. C. Christensen, W. B. Miller, 1 Jan. 1974 (CCC, WBM). 0.6 mi [1.0 km] SW of La Burrera, in rocks along wash, W. B. Miller, 30 Dec. 1973 (WBM). Along road from Todos Santos to La Burrera, 8.1 mi [13.0 km] NE of junction with road to Los Horconsitos, in rocks above arroyo, C. Church, 22 Dec. 1970 (WBM). Along trail W of Boca de la Sierra, elev. 1,000–1,600 ft [300–490 m], W. B. Miller, 26 Dec. 1970 (WBM). Along trail 1–2 mi [1.6–3.2 km] W of Boca de la Sierra, C. C. Christensen, W. B. Miller, 7 Dec. 1974 (CCC, WBM). Sierra San Lázaro, elev. 5,000 ft [1,520 m], G. Eisen (USNM). Along Todos Santos–Cabo San Lucas road 2.2 mi [3.5 km] N of Las Barrancas, elev. 500 ft [150 m], C. C. Christensen, J. A. Christensen, 21 Dec. 1975 (CCC). Arroyo Candelaria 2.1 mi [3.4 km] SW of La Candelaria, elev. 300 ft [90 m], C. C. Christensen, J. A. Christensen, 22 Dec. 1975 (CCC). Arroyo Candelaria 2.3 mi [3.7 km] NE of Migriño, elev. 200 ft [60 m], C. C. Christensen, J. A. Christensen, 21 Dec. 1975 (CCC). Arroyo Candelaria at Migriño, C. C. Christensen, J. A. Christensen, 21 Dec. 1975 (CCC). Along Todos Santos–Cabo San Lucas road 2.2 mi [3.5 km] N of El Saucito, granite rockpiles at crest of small hill seaward of road, elev. ca. 1,500 ft [460 m], W. B. Miller, W. N. Miller, 23 Dec. 1970 (WBM); C. C. Christensen, W. B. Miller, 22 Dec. 1973 (CCC, WBM); C. C. Christensen, 9 Aug. 1974 (CCC). Along Todos Santos–Cabo San Lucas road 2.1 mi [3.4 km] N of El Saucito, among granite rocks inland of road, elev. ca. 1,500 ft [460 m], C. C. Christensen, J. A. Christensen, W. B. Miller, 22 Dec. 1973 (CCC); C. C. Christensen, J. A. Christensen, 22 Dec. 1975 (CCC). 0.8 mi [1.3 km] N of Los Pozos, C. Church, Nov. 1969 (WBM). Along Santa Catarina–Los Frailes road 15.6 mi [25.1 km] NE of Santa Catarina, C. C. Christensen, J. A. Christensen, W. B. Miller, 26 Dec. 1973 (CCC, WBM). Along road from San José del Cabo to Los Frailes 4.2 mi [6.8 km] E of La Escopita], C. Church, 26 Dec. 1970 (WBM). Cape St. Lucas, J. Xántus (USNM). Granite outcrops of gravelly hills 9 mi [12.6 km] NE of Cabo San Lucas, H. E. Gates, 22 Mar. 1930 (SBMNH). Isla Cerralvo, CAS 1921 Exped. (CAS).

Rabdotus (Plicolumna) perhirsutus Miller, Christensen, and Roth, sp. nov.

(Fig. 25)

Distribution.—BAJA CALIFORNIA SUR: Arroyo Candelaria, 2.3 mi [3.7 km] E of Migriño, elev. 200 ft [60 m], C. C. Christensen, 21 Dec. 1975 (CCC). Along Todos Santos–Cabo San Lucas road 2.2 mi [3.5 km] N of El Saucito, elev. ca. 1,500 ft [460 m] (TL), W. B. Miller, W. N. Miller, 23 Dec. 1970 (SBMNH); C. C. Christensen, J. A. Christensen, W. B. Miller, 22 Dec. 1973 (SBMNH, ANSP, BR, CAS, CCC, LACM, SDMNH, USNM); C. C. Christensen, 9 Aug. 1984 (CCC).

Rabdotus (Plicolumna) ramentosus (Cooper, 1891)

(Fig. 24)

Distribution.—BAJA CALIFORNIA SUR: Mountains N of San José del Cabo, W. E. Bryant (TL, fide Cooper 1892a). Foothills near San José del Cabo, G. Eisen (Cooper 1893; USNM). Along Santa Catarina–Los Frailes road 3.2 mi [5.1 km] NE of Santa Catarina, C. C. Christensen, W. B. Miller, 23, 26 Dec. 1973 (Christensen and Miller 1975; CCC, WBM). Along road from Valle Perdido to ranch at Bajada del Molino, 2.0 mi [3.2 km] E of Bajada del Molino, elev. ca. 1,400 ft [430 m], C. C. Christensen, W. B. Miller, 28–29 Dec. 1973 (CCC, WBM). Along trail from La Burrera to La Laguna, elev. ca. 3,000 ft [910 m], W. B. Miller, 2 Jan. 1974 (WBM). Arroyo Candelaria, 2.1 mi [3.4 km] W of Candelaria, elev. ca. 300 ft [90 m], C. C. Christensen, 22 Dec. 1975 (CCC). Arroyo Candelaria at Migriño, C. C. Christensen, 21 Dec. 1975 (CCC). Sierra San Lázaro, G. Eisen (ANSP; USNM). 0.6 mi [1.0 km] SW of Rancho La Laguna and ca. 6 mi [9.6 km] NW of San José del Cabo, elev. 300 ft [90 m], C. C. Christensen, J. A. Christensen, 23 Dec. 1975 (CCC).

Subgenus uncertain

Rabdotus(?) sp.

Distribution.—BAJA CALIFORNIA SUR: Isla Carmen, Oto Bay, just E of main arroyo entering bay, Pleistocene (Durham 1950, as *Bulimulus* sp.; Univ. California [Berkeley] Mus. Paleo. 32892).

The single specimen is an external mold in coarse sandstone matrix of the spire of a species of *Rabdotus* or perhaps *Naesiotus,* but not further identifiable.

Genus **Berendtia** Crosse and Fischer, 1869

Berendtia taylori (Pfeiffer, 1861)

(Fig. 27)

Synonym.—*Cylindrella* (*Urocoptis*) *newcombiana* Gabb, 1868.

Distribution.—BAJA CALIFORNIA SUR: "Hidden under loose volcanic rocks in the high table lands of the interior of Lower California, especially about Moleje [Mulegé]," W. M. Gabb, 1867 (Gabb 1868; H. B. Baker 1963; Coan and Bogan 1988; TL of *Cylindrella newcombiana*; ANSP). Canyon back of Puerto Escondido, I. M. Johnston, J. C. Chamberlin, CAS 1921 Exped. (Hanna 1923; CAS, SBMNH). Puerto Escondido, H. N. Lowe, 1931 (Lowe 1933). Rocky slope of side canyon at Comondú Viejo, H. E. Gates, 9 Apr. 1930 (SBMNH). San José Comondú, R. J. Drake, July 1953 (CAS, SBMNH). San José Comondú, elev. 1,200 ft [360 m], W. N. Miller, W. B. Miller, 20 Dec. 1970 (WBM). Pacific slope of Sierra de la Giganta SW of Mulegé, along trail from Pie de la Cueta to Guajademí, in rockslide ca. 0.75 mi [1.2 km] S of trail summit, elev. 2,300 ft [700 m], C. C. Christensen, W. B. Miller, 23 Oct. 1972 (CCC). Along Canipolé–San José Comondú road 10 mi [16 km] SW of Canipolé, elev. ca. 1,000 ft [300 m], W. N. Miller, W. B. Miller, 20 Dec. 1970 (WBM). 12.6 mi [20.2 km] E of La Purísima, along road to Canipolé, C. Church, 10 Jan. 1971 (WBM). Arroyo de la Purísima, 12 mi [19 km] S of Canipolé, I. L. Wiggins, H. M. Hill, 17 Nov. 1946 (SBMNH). Arroyo de la Purísima, in rockslide S of road 3.0 mi [4.8 km] NE of San Isidro, elev. 600 ft [180 m], W. N. Miller, W. B. Miller, 21 Dec. 1970 (Christensen and Miller 1975; WBM). Rockslide W of Transpeninsular Highway 2.7 mi [4.3 km] N of turnoff to Loreto, C. C. Christensen, S. Kessler, 30 July 1974 (CCC). San Javier, in rockslide immediately S of mission, elev.

1,200–1,500 ft [370–460 m], C. C. Christensen, W. B. Miller, 25 Oct. 1972 (Christensen and Miller 1975; CCC). 1.0 mi [1.6 km] S of Chuenque, C. Church, 8 Dec. 1970 (WBM). Along Transpeninsular Highway at km 69 N of Villa Insurgentes, C. C. Christensen, W. B. Miller, 5 Dec. 1974. Along Transpeninsular Highway 31 mi [50 km] N of Villa Insurgentes, elev. 900 ft [270 m], W. B. Miller, 23 Oct. 1971 (WBM).

Berendtia is a monotypic genus restricted to the Sierra de la Giganta. Living snails may be found sealed to the undersides of rocks in the numerous large accumulations of lava talus in this area. Although formerly placed in Urocoptidae and made the type-genus of a new subfamily, Berendtinae, by Fischer and Crosse (1872 [1870–1902]), *Berendtia* is anatomically similar to *Rabdotus* and *Spartocentrum* (Christensen and Miller 1975a). *Berendtia taylori*, described from an unknown locality, was recognized as Baja Californian by Bland (1870). Breure (1978, 1979) described the radula and gave additional anatomical notes.

Genus **Spartocentrum** Dall, 1895

Spartocentrum digueti (Mabille, 1895)

(Fig. 28)

Distribution.—BAJA CALIFORNIA SUR: Plateaus above Arroyo de la Purissima [Purísima] (TL) [type lot labeled "Plateau de San Javier," fide Breure 1978], L. Diguet (Mabille 1895; MNHN).

This species has not been collected since its discovery by Diguet. Breure (1978) redescribed and illustrated specimens from the type lot at the MNHN. *Spartocentrum digueti* is the type species, by designation of Breure (1979), of *Teneritia* Mabille 1897, a junior synonym of *Spartocentrum*.

Spartocentrum eisenianum (Pilsbry, 1900)

Distribution.—"Lower California" (TL), F. L. Button (Pilsbry 1900, 1902–1903; ANSP). BAJA CALIFORNIA SUR: Cabo San Lucas, G. Eisen (Bartsch 1906, as *Coelocentrum* [*Spartocentrum*] *eiseni* Pilsbry).

This species has not been collected recently; it is known only from one specimen. We seriously doubt the occurrence of any species of *Spartocentrum* in the Cape region of Baja California.

Spartocentrum insulare (Hanna, 1923)

(Fig. 28)

Synonym.—*Coelocentrum oweni* Hanna, 1923.

Distribution.—BAJA CALIFORNIA SUR: Isla Carmen, Puerto Bellandra [Balandra] (TL), F. Baker, V. Owen, 21 May 1921, CAS 1921 Exped. (Hanna 1923; CAS, SBMNH); C. C. Christensen, 1 Aug. 1974 (CCC, WBM). Isla Carmen: Bahía Marquer, E. P. Van Duzee, J. C. Chamberlin, CAS 1921 Exped. (Hanna 1923; CAS); W. K. Emerson et al., 1962, Belvedere Exped. (Emerson and Jacobson 1964, as *Coelocentrum oweni*); Agua Grande, V. Owen, 15 June 1921, CAS 1921 Exped. (Hanna 1923; TL of *Coelocentrum oweni*; CAS, SBMNH). Isla Monserrate, J. C. Chamberlin, CAS 1921 Exped. (Hanna 1923; CAS). Isla Danzante, F. Baker, I. M. Johnston, CAS 1921 Exped. (Hanna 1923; CAS); H. N. Lowe, 1931 (Lowe 1933); W. K. Emerson et al., 1962, Belvedere Exped. (Emerson and Jacobson 1964, as *Coelocentrum oweni*); P. Turk, 4–8 Jan. 1978 (CCC, WBM). Isla Santa Catalina, CAS 1921 Exped. (Hanna 1923; CAS).

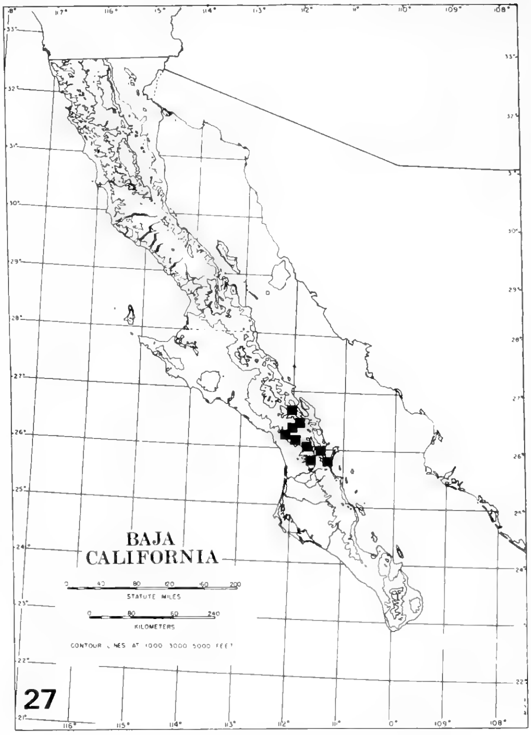

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Figure 27. Distribution of *Berendtia taylori*.

Spartocentrum irregulare (Gabb, 1868)

(Fig. 28)

Synonyms.—*Berendtia minorina* Mabille, 1895. *Coelocentrum minorinum gabbi* Pilsbry, 1900. *Coelocentrum clavigeroi* Hanna, 1923.

Distribution.—BAJA CALIFORNIA SUR: "Table lands in the interior of Lower California, especially about Moleje [Mulegé]" (TL), W. M. Gabb, 1867 (Gabb 1868; Pilsbry 1900; Coan and Bogan 1988; ANSP, CAS, USNM); same data for type lot of *Coelocentrum minorinum gabbi* Pilsbry (1900; ANSP). Along road from Santa Rosalía to San José de Magdalena, at 20.8 mi [33.3 km] from Mexico Highway 1, W. B. Miller, 4 Jan. 1974 (WBM). Along road from Rosarito to Bahía San Nicolás, at 5.3 road mi [8.5 km] from San Nicolás, W. B.

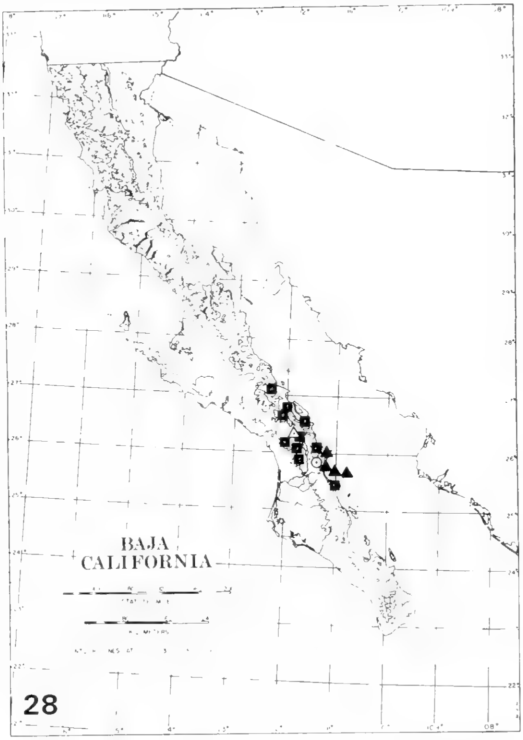

FIGURE 28. Distribution of *Spartocentrum digueti* and *Spartocentrum* sp. (open triangle), *Spartocentrum insulare* (solid triangles), *Spartocentrum irregulare* (squares), and *Spartocentrum vanduzeei* (open circle).

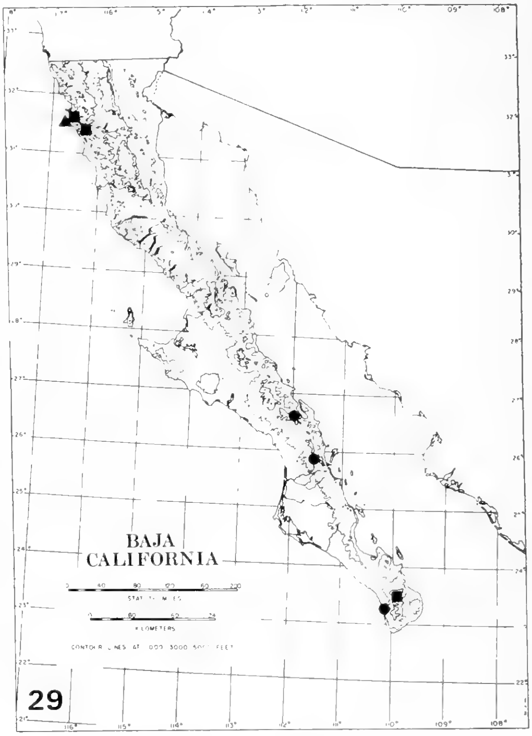

FIGURE 29. Distribution in Baja California of *Paralaoma caputspinulae* (triangle), *Deroceras laeve* (squares), and *Hawaiia* sp. (circles).

Miller, C. C. Christensen, 5 Dec. 1974 (CCC, WBM). El Potrero Ranch, SW of Mulegé, H. E. Gates, 31 Mar. 1931 (SBMNH). E slope of Sierra de la Giganta SW of Mulegé, along trail from Pie de la Cueta (2.9 mi [4.6 km] S of El Potrero) to Guajademí, elev. ca. 2,100 ft [640 m], C. C. Christensen, W. B. Miller, 22–23 Oct. 1972 (CCC, WBM). Guajademí, E. W. Nelson, E. A. Goldman (Bartsch 1906, as *Coelocentrum* [*Spartocentrum*] *minorinum gabbi*). San José Comondú, R. J. Drake, July 1953 (SBMNH); at edge of town, in canyon leading to San Javier, elev. ca. 1,200 ft [360 m], W. N. Miller, W. B. Miller, 20 Dec. 1970 (WBM). Along Canipolé–San José Comondú road, 10 mi [16 km] from Canipolé, elev. ca. 1,000 ft [300 m], W. N. Miller, W. B. Miller, 20 Dec. 1970 (WBM). 6.5 mi [10.4 km] N of San Isidro (0.6 mi [1.0 km] S of Huerto Vieja), C. Church, Nov. 1969 (UA). Near Loreto, C. C. Christensen, S. Kessler, 30 July 1974 (CCC). Bahía Agua Verde, I. M. Johnston, 26 May 1921, CAS 1921 Exped. (Hanna 1923; TL of *Coelocentrum clavigeroi*; CAS). Arroyo de la Purísima, in cracks of shady cliff, I. L. Wiggins, H. M. Hill, 17 Nov. 1946 (SBMNH). Plateaus above Arroyo de la Purissima [Purísima], L. Diguet (Mabille 1895; TL of *Berendtia minorina*; MNHN). Along Mexico Highway 1 at a point 0.4 mi [0.6 km] N of km 105 (measured from La Paz), 6 Dec. 1974, W. B. Miller, C. C. Christensen (CCC, WBM). At km 77 along Mexico Highway 1 between La Paz and Ciudad Constitución, R. Houston, J. Kudenov, W. B. Miller, 23–26 Oct. 1971 (WBM); C. C. Christensen, 3 Aug. 1974 (CCC); W. B. Miller, C. C. Christensen, 6 Dec. 1974 (CCC, WBM).

The type locality of *Spartocentrum irregulare* was never clearly stated; Gabb (1868) only remarked that the species was in similar locations to his *Cylindrella newcombiana* (=*Berendtia taylori*). The holotype is in ANSP (H. B. Baker 1963); original lot or paratypic material is in CAS (Hanna 1923) and USNM (Bartsch 1906). We have compared the holotype of *Coelocentrum clavigeroi* with original lot material of *S. irregulare* in CAS and found them identical; therefore we place *C. clavigeroi* in synonymy.

The type lot of *Coelocentrum minorinum gabbi* was selected out of the original lot of *S. irregulare* by Pilsbry (1900).

Breure (1978) redescribed and illustrated type material of *Berendtia minorina* from the MNHN.

Spartocentrum vanduzeei (Hanna, 1923)
(Fig. 28)

DISTRIBUTION.—BAJA CALIFORNIA SUR: W side of Puerto Escondido (TL), E. P. Van Duzee, 14 June 1921, CAS

1921 Exped. (Hanna 1923; CAS); H. N. Lowe, 1931 (Lowe 1933). Puerto Escondido, R. Moran, M. Soulé, 1962, Belvedere Exped. (Emerson and Jacobson 1964); under stones on arid hillside, T. Craig, 9 Mar. 1928 (SBMNH). Juncalito, W. B. Miller, 3 Jan. 1974 (CCC, WBM); C. C. Christensen, S. Kessler, 30 July 1974 (Christensen and Miller 1975a; CCC). 1 mi [1.6 km] S of Chuenque, C. Church, 8 Dec. 1970 (Christensen and Miller 1975; WBM).

Breure (1978) briefly described the radula and the histology of part of the reproductive system.

Spartocentrum sp.

(Fig. 28)

DISTRIBUTION.—BAJA CALIFORNIA SUR: San Javier, in lava rockslide immediately S of the Mission, elev. 1,200–1,500 ft [370–460 m], W. B. Miller, 24 Oct. 1971 (WBM); W. B. Miller et al., 25 Oct. 1972 (CCC). 0.6 mi [1.0 km] E of San Javier, C. Church, 11 Dec. 1970 (WBM). Along San Javier–Santo Domingo road, 9.8 mi [15.7 km] W of San Javier, C. Church, 12 Dec. 1970 (WBM).

One or more undescribed species occur in the vicinity of San Javier. Their description is postponed until more material is available.

Suborder AULACOPODA
Superfamily ARIONOIDEA
Family PUNCTIDAE
Genus **Paralaoma** Iredale, 1913

Paralaoma caputspinulae (Reeve, 1852)

(Fig. 29)

SYNONYMS.—*Helix conspecta* Bland, 1865. *Punctum conspectum pasadenae* Pilsbry, 1896.

DISTRIBUTION.—BAJA CALIFORNIA NORTE: Along road to Puerto Santo Tomás, 4.0 mi [6.4 km] from Transpeninsular Highway, a single specimen found in leaf litter, W. B. Miller, 27 Jan. 1962 (WBM).

This "weedy" species is very widely distributed, at least in part by human agency (Roth 1986, as *Punctum pusillum,* an invalid name [Roth 1987]). It is known also from Alaska, British Columbia, Idaho, Montana, Washington, Oregon, California, Arizona and New Mexico, and is recorded from Kamchatka (Bequaert and Miller 1973). A subspecies, *P. c. jaliscoense* (Pilsbry), occurs in Jalisco and México, D. F. This is the first record of the genus in Baja California.

Family HELICODISCIDAE
Genus **Helicodiscus** Morse, 1864
Subgenus **Hebetodiscus** Baker, 1929

Helicodiscus (Hebetodiscus) singleyanus (Pilsbry, 1890)

(Fig. 30)

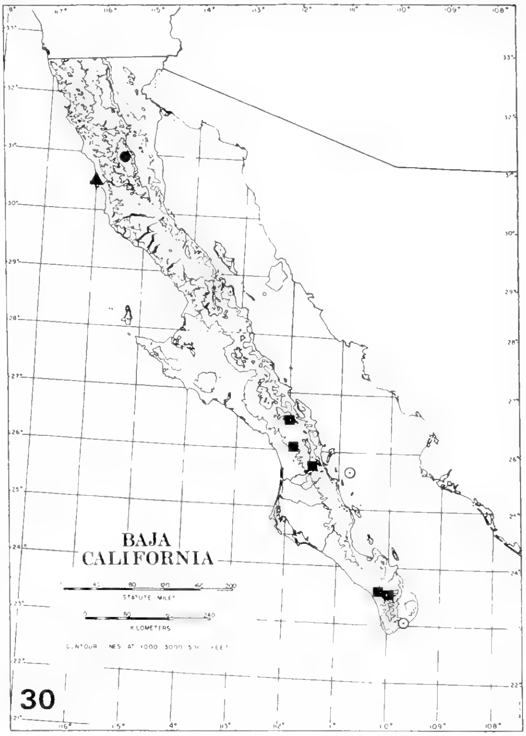

FIGURE 30. Distribution in Baja California of *Helicodiscus singleyanus* (open circles), *Binneya notabilis* (triangle), *Euconulus fulvus* (solid circle), and *Glyphyalinia indentata paucilirata* (squares).

SYNONYMS.—*Hyalinia laeviuscula* Sterki, 1892. *Hyalinia texana* Sterki, 1892 (nomen nudum).

DISTRIBUTION.—BAJA CALIFORNIA SUR: 0.2 mi [0.3 km] SSE of San José del Cabo, on road to La Playa, in stream drift, A. G. Smith, A. E. Leviton, CAS 1958–1959 Exped. (CAS); the large series collected appears to belong to this species. (?) Isla Santa Catalina, G D. Hanna, 1953 (CAS); three broken, worn, immature specimens.

This species also occurs from the southeastern U.S. north to New Jersey and Indiana, west to South Dakota, Colorado, New Mexico, and Arizona, and south to Sonora and Tamaulipas, Mexico; it is adventive in California (Bequaert and Miller 1973). This is the first record of the genus in Baja California.

Family ARIONIDAE
Genus **Binneya** Cooper, 1863
Subgenus **Binneya** sensu stricto

Binneya (Binneya) notabilis Cooper, 1863

(Fig. 30)

DISTRIBUTION.—BAJA CALIFORNIA NORTE: "Four living individuals . . . and one or two dead shells were found

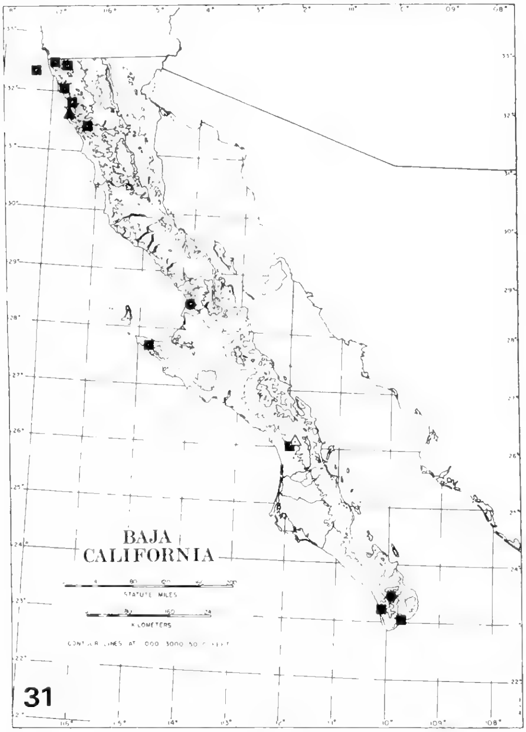

FIGURE 31. Distribution in Baja California of *Succinea californica* (solid triangle), *Succinea rusticana* (circles), *Catinella rehderi* (squares), and *Oxyloma nuttallianum* (open triangle).

under decaying trunks of the maguey (Agave shawii) at an elevation of a few hundred feet among the hills north of San Quentin bay [Bahía San Quintín]," by C. R. Orcutt, Apr. 1885 (Binney 1886b).

Pilsbry (1948) predicted that the form from Bahía San Quintín would turn out to be a species distinct from *B. notabilis* of Santa Barbara and San Nicolas islands, California. Live-collected material from Baja California, which would allow the critical comparisons to be made, has not been obtained recently.

Subgenus **Allothyra** Pilsbry, 1948

Binneya (Allothyra) guadalupensis Pilsbry, 1927

DISTRIBUTION.—BAJA CALIFORNIA NORTE: Isla Guadalupe: G. W. Dunn, prior to 1884 (Anonymous 1884, as *B. notabilis*); W. E. Bryant, E. Palmer (Binney 1879; Cooper 1887, 1892a, as *B. notabilis*); A. W. Anthony, 1896 (Dall 1900, as *B. notabilis*); Templeton Crocker Exped., 16 Mar. 1932 (CAS); 3 mi [5 km] S of Northeast Anchorage (TL); Pine Ridge at elev. 3,000 ft [900 m]; and 2 mi [3.2 km] N of S end of island, G D. Hanna, CAS 1922 Exped. (Pilsbry 1927; CAS); Puerto Norte, under rocks near shore and at elev. ca. 500 ft [150 m], W. L. Lee, 24–29 Dec. 1974 and 15 Feb. 1975 (CAS); West Anchorage, under rocks in arroyo bottoms, G. E. Lindsay, 30 Jan. 1950 (SBMNH).

Superfamily SUCCINEOIDEA
Family SUCCINEIDAE
Genus **Succinea** Draparnaud, 1801

Succinea californica Crosse and Fischer, 1878

(Fig. 31)

DISTRIBUTION.—BAJA CALIFORNIA NORTE: San [Santo] Tomás (TL), H. Hemphill (Crosse and Fischer 1878). Santo Tomás Valley, W. B. Miller, 27 Jan. 1962 (WBM).

Miller collected this species in the vicinity of the type locality and confirmed its generic placement by dissection of living adult specimens.

Succinea guadelupensis Dall, 1900

DISTRIBUTION.—BAJA CALIFORNIA NORTE: Isla Guadalupe (TL): A. W. Anthony, 1896 (Dall 1900); Pine Ridge, at elev. ca. 3,000 ft [900 m], G D. Hanna, CAS 1922 Exped., fragments only (Pilsbry 1927; CAS).

Succinea rusticana Gould, 1846

(Fig. 31)

DISTRIBUTION.—BAJA CALIFORNIA NORTE: South to 31°N, C. R. Orcutt (Cooper 1892b). Ojos Negros, slow stream through meadow, I. L. Wiggins, H. M. Hill, 3 Oct. 1946 (SBMNH). 55 km N of Guerrero Negro, under dead agave, C. C. Christensen, 1973 (CCC). BAJA CALIFORNIA SUR: Common in the Sierra Laguna, G. Eisen (Cooper 1892b).

These records need verification based on anatomical studies of live-collected animals. *Succinea rusticana* is reported also from British Columbia, Washington, Oregon, and California (Pilsbry 1948).

Genus **Catinella** Pease, 1871

Catinella rehderi (Pilsbry, 1948)

(Fig. 31)

DISTRIBUTION.—BAJA CALIFORNIA NORTE: Lower California N of 31°N lat., C. R. Orcutt (Orcutt 1886, as *Succinea oregonensis*). Islas Los Coronados (CAS). Tecate Valley near the U.S. border, H. Hemphill (CAS). 4.5 mi [6.8 km] S of La Misión, elev. 500 ft [150 m], S. C. Williams, 1969 (CAS). Punta Banda, elev. 100 ft [30 m], S. C. Williams, V. F. Lee, 1969 (CAS). Stream bank W of Ensenada road about 9 mi [15 km] N of Santo Tomás, L. G. Ingles, 17 Dec. 1927 (Berry 1928, as *Succinea* sp.). 0.5 mi [0.8 km] N of San Vicente, elev. 300 ft [90 m], S. C. Williams, 1969 (CAS). San Telmo Mesa, under dead agave, I. L. Wiggins, A. M. Vollmer, H. M. Hill, 10 Oct. 1946 (SBMNH). Brush 50 m back from beach, 25 mi [40 km] N of El Rosario, I. L. Wiggins, H. M. Hill, 23 Oct. 1946 (SBMNH). Miller's landing, under dead *Echinocereus mari-*

timus, I. L. Wiggins, H. M. Hill, 29 Oct. 1946 (SBMNH). Arroyo 9 mi [14 km] E of Miller's Landing, I. L. Wiggins, A. M. Vollmer, H. M. Hill, 29 Oct. 1946 (SBMNH). Under dead agaves, 8 mi [13 km] S of Miller's Landing, I. L. Wiggins, A. M. Vollmer, H. M. Hill, 29 Oct. 1946 (SBMNH). Under dead agaves, summit of mesa just S of Rancho Mezquital, I. L. Wiggins, A. M. Vollmer, H. M. Hill, 30 Oct. 1946 (SBMNH). BAJA CALIFORNIA SUR: Bahía San Bartolomé [Bahía Tortugas], H. Hemphill (CAS). 12 mi [19 km] SW of San Miguel Comondú, probably fossil, R. J. Drake, July 1953 (CAS). Bahía San Pedrito, 3.9 mi [6.3 km] SE of Todos Santos, A. G. Smith, CAS 1958–1959 Exped. (CAS). In stream drift 0.2 mi [0.3 km] SSE of San José del Cabo, on road to La Playa, A. E. Leviton, A. G. Smith, CAS 1958–1959 Exped. (CAS).

Allocation of these specimens to *C. rehderi* is provisional. Authoritative identification of Baja California Succineidae, as previously indicated, must be based on anatomical studies. Shells with the general form of *C. rehderi* are known also from Montana and Washington to southern California (Pilsbry 1948).

Genus **Oxyloma** Westerlund, 1885

Oxyloma nuttallianum (Lea, 1841)

(Fig. 31)

DISTRIBUTION.—BAJA CALIFORNIA SUR: 12 mi [19 km] SW of San Miguel Comondú (possibly fossil), R. J. Drake, July 1953 (UA).

Oxyloma nuttallianum is reported to be widespread in western North America, but its range is not well defined. This is the first record of the genus in Baja California.

Superfamily LIMACOIDEA
Family HELICARIONIDAE
Genus **Euconulus** Reinhardt, 1883

Euconulus fulvus (Müller, 1774)

(Fig. 30)

SYNONYMS.—*Helix trochiformis* Montagu, 1803. *Helix egena* Say, 1825. *Helix mortoni* Jeffreys, 1830. *Conulus fulvus alaskensis* Pilsbry, 1899.

DISTRIBUTION.—BAJA CALIFORNIA NORTE: Sierra San Pedro Mártir, elev. 8,800–9,000 ft [2,700–2,800 m], W. B. Miller, C. C. Christensen, Nov. 1973 (Miller 1981a; WBM).

Euconulus fulvus is distributed almost throughout the Holarctic realm.

Family ZONITIDAE
Genus **Glyphyalinia** von Martens, 1892

Glyphyalinia indentata paucilirata (Morelet, 1851)

(Fig. 30)

SYNONYM.—*Zonites indentatus* var. *umbilicatus* Cockerell, 1893.

DISTRIBUTION.—BAJA CALIFORNIA SUR: High on the Sierra Laguna, G. Eisen (Cooper 1892b). Sierra El Taste, G. Eisen, 1892 (Cooper 1894). Eastern slope of Sierra de la Giganta, ca. 1.0 mi [1.6 km] from Pie de la Cueta along trail to Guajademí, elev. 2,100–2,450 ft [640–750 m], C. C. Christensen, W. B. Miller, 22 Oct. 1972 (WBM). Lower arroyo 12 mi [19 km] SW of San Miguel Comondú (probably fossil), R. J. Drake, 1953 (CAS). San Javier, in rockslide immediately N of the mission, W. B. Miller, 24 Oct. 1971 (WBM). Along road from Valle Perdido to ranch at Bajada del Molino, in rockslides on N-facing slope of arroyo S of road, elev. ca. 1,400 ft [430 m], C. C. Christensen, 28, 29 Dec. 1973 (CCC). Summit of trail from La Burrera to La Laguna, in large rockslide, elev. ca. 6,800 ft [2,100 m], W. B. Miller, 1 Jan. 1974 (WBM). La Laguna, in rocks along creek at cabin, elev. ca. 6,500 ft [1,980 m], C. C. Christensen, W. B. Miller, 31 Dec. 1973 (CCC, WBM).

All cited specimens are assigned to this taxon provisionally. The recorded range of *G. i. paucilirata* includes the southeastern U.S., northern Mexico, and states as far west as Arizona and Utah, but western records may pertain to other taxa (W. L. Pratt, pers. comm., 1980).

Genus **Striatura** Morse, 1864
Subgenus **Pseudohyalina** Morse, 1864

Striatura (Pseudohyalina) pugetensis (Dall, 1895)

SYNONYM.—*Radiodiscus hubrichti* Branson, 1975.

DISTRIBUTION.—BAJA CALIFORNIA NORTE: Isla Guadalupe: hills above Northeast Anchorage, elev. ca. 1,000 ft [300 m]; and 2 mi [3.2 km] N of S end of island on E side, G D. Hanna, CAS 1922 Exped. (Pilsbry 1927; CAS).

Striatura pugetensis also ranges from British Columbia through Montana and Washington to southern California. It has been reported from Kauai, Hawaiian Islands (H. B. Baker 1941a, Pilsbry 1946).

Genus **Hawaiia** Gude, 1911

Hawaiia sp.

(Fig. 29)

DISTRIBUTION.—BAJA CALIFORNIA SUR: Eastern slope of Sierra de la Giganta, 1.0 mi [1.6 km] from Pie de la Cueta (located 2.9 mi. S of El Potrero and ca. 20 mi S of Mulegé) along trail to Guajademí, elev. 2,100–2,450 ft [640–750 m], C. C. Christensen, W. B. Miller, 22 Oct. 1972 (WBM). San Javier, in rockslide immediately S of the mission, W. B. Miller, 24 Oct. 1971 (WBM). Bahía San Pedrito, 3.9 mi [6.3 km] SE of Todos Santos, A. G. Smith, CAS 1958–1959 Exped. (CAS).

A few specimens of a *Hawaiia* have been found in the Sierra de la Giganta of Baja California Sur. Bequaert and Miller (1973) referred them to the species *H. minuscula,* but we refrain from assigning the Baja California material to a species pending completion of studies of western North American *Hawaiia* by other workers.

Family Limacidae
Genus **Deroceras** Rafinesque, 1820

Deroceras laeve (Müller, 1774)

(Fig. 29)

Synonyms.—*Limax* (*Eulimax*) *campestris* var. *occidentalis* Cooper, 1872. *Limax montanus* Ingersoll, 1875 (non Leydig, 1871). *Limax castaneus* Ingersoll, 1875. *Agriolimax montanus* forms *typicus, intermedius, tristis* Cockerell, 1888. *Limax hemphilli* Binney, 1890. *Limax hemphilli* var. *pictus* Binney, 1892. *Agriolimax campestris* var. *zonatipes* Cockerell, 1892. *Agriolimax hemphilli ashmuni* Pilsbry and Vanatta, 1910.

Distribution.—BAJA CALIFORNIA NORTE: San [Santo] Tomás, H. Hemphill (Binney 1890, as *Limax hemphilli*). San [Santo] Tomás River, H. Hemphill (Binney 1892, TL of *L. hemphilli* var. *pictus*; Cockerell 1897, as *Agriolimax berendti* var. *pictus*). 0.5 mi [0.8 km] N of San Vicente, elev. 300 ft [90 m], S. C. Williams, V. F. Lee, 1969 (CAS). BAJA CALIFORNIA SUR: La Laguna, Sierra de la Victoria, elev. 6,500 ft [1,980 m], W. B. Miller, C. C. Christensen, 31 Dec. 1973 (WBM).

The synonymy given for this Holarctic, often-named species is not intended to be complete but includes only nominal taxa with type-localities in western North America.

Cooper's (1892b) report of an unidentified *Limax* "from the mountains" may refer to *Deroceras laeve,* as may Orcutt's (1886) citation of a species from north of 31°N. Mabille's (1895) record of *Limax guatemalensis* Crosse and Fischer, 1870, from "dans les herbes au bord des torrents de la Laguna" may refer to *D. laeve,* which Miller and Christensen collected at La Laguna, Sierra de la Victoria.

Genus **Milax** Gray, 1855

Milax gagates (Draparnaud, 1801)

Synonym.—*Limax* (*Amalia*) *hewstoni* Cooper, 1872.

Distribution.—BAJA CALIFORNIA NORTE: Near mouth of San [Santo] Tomás River, H. Hemphill (Hemphill 1881, Binney 1883, as *Limax hewstoni*).

This species is introduced from western Europe.

Suborder Holopoda
Superfamily Polygyroidea
Family Polygyridae
Genus **Polygyra** Say, 1818
Subgenus **Erymodon** Pilsbry, 1956

Polygyra (Erymodon) behri (Gabb, 1865)

Distribution.—BAJA CALIFORNIA SUR: Sandy lowlands 0.2–0.5 mi [0.3–0.8 km] E of Punta San Lorenzo, C. C. Christensen, 6 Aug. 1974 (CCC).

A single empty shell of this mainland Mexican species (TL: near Guaymas, Sonora; Coan and Bogan 1988) was found just inland of the beach near Punta San Lorenzo, on the Baja California peninsula northeast of La Paz. It was found with apparently subfossil shells of *Rabdotus sufflatus* and *Xerarionta areolata,* but is almost certainly a beach drift shell, not an actual inhabitant of Baja California.

Polygyra behri is the type species of the monotypic subgenus *Monophysis* Pilsbry, 1956. Pilsbry (1956) distinguished *Monophysis* from the subgenus *Erymodon,* proposed in the same paper, solely by the absence of an upward collabral extension of the outer lip denticle. In a system as labile as apertural dentition in the Polygyridae, this character is probably of no more than species-level significance; we regard *Monophysis* as a synonym of *Erymodon.*

Family Thysanophoridae
Genus **Thysanophora** Strebel and Pfeffer, 1880

Thysanophora hornii (Gabb, 1866)

(Fig. 32)

Distribution.—BAJA CALIFORNIA SUR: Saltito Pass, elev. 3,200 ft [975 m], G. Eisen, 1893 (Cooper 1894). Bahía Agua Verde, N side of canyon back of landing, CAS 1921 Exped. (Hanna 1923; CAS); G D. Hanna, 1953 ORCA Exped. (CAS). Gulf slope of Sierra de la Giganta SW of Mulegé, along trail from Pie de la Cueta to Guajademí, ca. 1.5 mi [2.4 km] from Pie de la Cueta, C. C. Christensen, 23 Oct. 1972 (CCC); and 1 mi [1.6 km] from Pie de la Cueta, elev. ca. 2,100 ft [640 m], C. C. Christensen, 22 Oct. 1972 (CCC). San José Comondú, elev. 1,500 ft [460 m], W. B. Miller, 20 Dec. 1970 (Bequaert and Miller 1973; WBM). San Javier, in rockslide across stream from mission, elev. 1,300 ft [400 m], C. C. Christensen, 25 Oct. 1972 (CCC). Along main highway from Loreto to Villa Insurgentes at km 69 N of Villa Insurgentes, at crest of Sierra de la Giganta among rocks, C. C. Christensen, W. B. Miller, 5 Dec. 1974 (CCC). Road between El Obispo and Rancho Tinajitas, I. L. Wiggins, 20 Nov. 1959 (CAS). Juncalito, in rockslide, C. C. Christensen, S. Kessler, 20 July 1974 (CCC). Arroyo de los Pozos, 12.9 mi [20.6 km] E of La Paz on road to Las Cruces, A. G. Smith, CAS 1958–1959 Exped. (CAS). 1.3 mi [2.0 km] N of El Triunfo, A. G. Smith, CAS 1958–1959 Exped. (CAS). Arroyo ca. 15 mi [24 km] S of La Paz, in drift, A. G. Smith, CAS 1959 Exped. (CAS). Km 5000.2 S of San Antonio, in leafmold, A. G. Smith, CAS 1958–1959 Exped. (CAS). In granite rocks in deep ravine 1.4 mi [2.2 km] from highway on road to microwave station above San Bartolo, C. C. Christensen, W. B. Miller, 8 Dec. 1974 (CCC). Arroyo by road to Valle Perdido, 2.0 mi [3.2 km] from Bajada del Molino, elev. ca. 1,400 ft [430 m], C. C. Christensen, W. B. Miller, 28, 29 Dec. 1973 (CCC). Along trail from La Burrera to La Laguna, Sierra de la Victoria, elev. 4,500–6,000 ft [1,400–1,800 m], C. C. Christensen, 1 Jan. 1974 (CCC). Boca de la Sierra, A. G. Smith, CAS 1958–1959 Exped. (CAS). Boca de la Sierra, 1–1.5 mi [1.6–2.4 km] upstream of village, among granite rocks

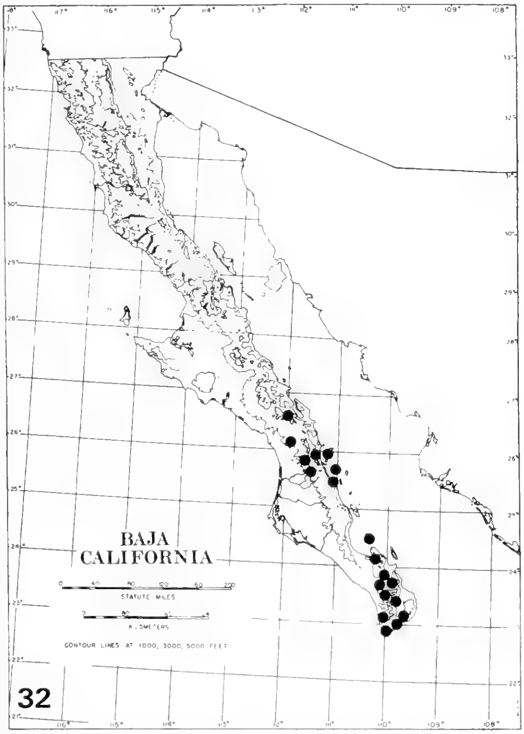

FIGURE 32. Distribution in Baja California of *Thysanophora hornii.*

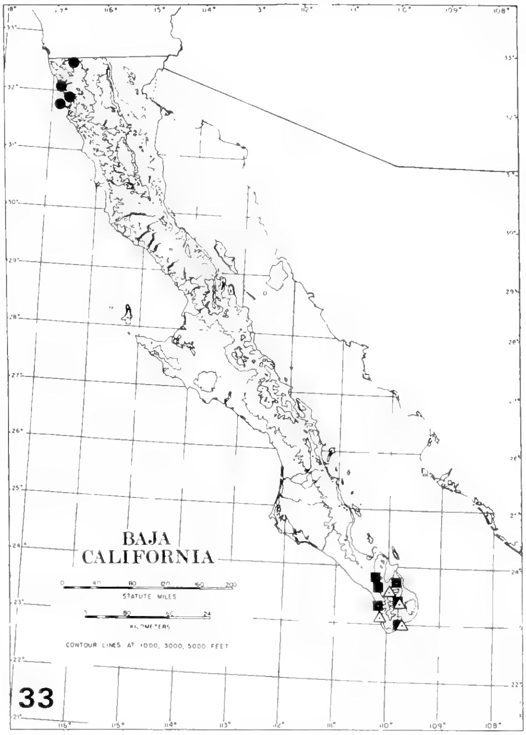

FIGURE 33. Distribution of *Pseudosubulina eiseniana* (open triangles), *Pseudosubulina tastensis* (squares), and *Glyptostoma newberryanum depressum* (circles).

near stream, C. C. Christensen, W. B. Miller, 7 Dec. 1974 (CCC). Boca de la Sierra, ca. 1 mi [1.6 km] above village, from litter, C. C. Christensen, W. B. Miller, 7 Dec. 1974 (CCC). Arroyo Candelaria, 2.3 mi [3.7 km] inland from Migriño, elev. 20 ft [60 m], C. C. Christensen, J. A. Christensen, 21 Dec. 1975 (CCC). 13.5 mi [21.6 km] NE of Santa Catarina on road to Los Frailes, elev. 1,200 ft [360 m], C. C. Christensen, J. A. Christensen, 23 Dec. 1975 (CCC). Sierra Cacachila, 9.8 mi [15.7 km] E of La Paz–Cabo San Lucas Highway, elev. 1,400 ft [430 m], C. C. Christensen, J. A. Christensen, 18 Dec. 1975. 0.2 mi [0.3 km] SSE of San José del Cabo on road to La Playa, stream drift, A. G. Smith, A. E. Leviton, CAS 1958–1959 Exped. (CAS). 5.4 mi [8.6 km] ENE of Cabo San Lucas on road to San José del Cabo, A. G. Smith, CAS 1958–1959 Exped. (CAS). 5.3 mi [8.5 km] NW of Todos Santos along road to La Pastora, A. G. Smith, CAS 1958–1959 Exped. (CAS). Bahía San Pedrito, 3.9 mi [6.2 km] SE of Todos Santos, A. G. Smith, CAS 1958–1959 Exped. (CAS). Along road between Cabo San Lucas and Todos Santos, 2.2 mi [3.5 km] N of El Saucito, in granite outcrops W of road, elev. ca. 1,500 ft [460 m] C. C. Christensen, J. A. Christensen, W. B. Miller, 22 Dec. 1973; C. C. Christensen, 9 Aug. 1974. N slope of highest hill at Cabo San Lucas, elev. ca. 250 ft [80 m], C. C. Christensen, J. A. Christensen, W. B. Miller, 24 Dec. 1973 (CCC). Isla Carmen, CAS 1921 Exped. (Hanna 1923; CAS). Isla Monserrate, CAS 1921 Exped. (Hanna 1923; CAS). Isla Espíritu Santo, C. C. Christensen, 5 Aug. 1974 (CCC).

This species, widespread in the region from Mulegé south and on several of the Gulf islands, also occurs in Arizona, New Mexico, Texas, and the Mexican states of Sonora, Chihuahua, Sinaloa, Jalisco, Nuevo León, Tamaulipas, and San Luis Potosí (Bequaert and Miller 1973).

Superfamily OLEACINOIDEA
Family OLEACINIDAE
Genus **Pseudosubulina** Strebel and Pfeffer, 1882

Pseudosubulina eiseniana (Cooper, 1893)

(Fig. 33)

DISTRIBUTION.—BAJA CALIFORNIA SUR: Cape Region, under stones (TL), G. Eisen, 1892 (Cooper 1893). Boca de la Sierra, near Miraflores, A. G. Smith, CAS 1958–1959 Exped. (CAS). In stream drift, 0.2 mi [0.3 km] SSE of San José del Cabo, on road to La Playa, A. G. Smith, A. E. Leviton, CAS 1958–1959 Exped. (CAS). La Laguna, among rocks along stream near cabin, elev. ca. 6,500 ft [1,980 m], C. C. Christensen, W. B. Miller, 31 Dec. 1973 (WBM). Along trail from La Burrera to La Laguna, in rockslide, elev. ca. 3,000 ft [900 m], W. B. Miller, 2 Jan. 1974 (WBM). Along Todos Santos–Cabo San Lucas road 2.2 mi [3.5 km] N of El Saucito (and ca. 14 mi N of Cabo San Lucas), among granite rocks at crest of hill, elev. ca. 1,200 ft [360 m], W. B. Miller, W. N. Miller, 23 Dec. 1970 (WBM).

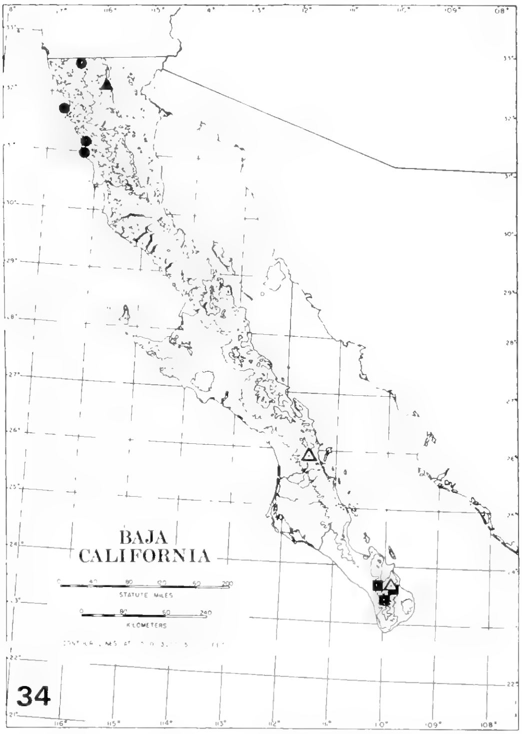

FIGURE 34. Distribution of *Radiocentrum discus* (squares), *Radiocentrum exorbitans* (open triangles), *Helminthoglypta tudiculata* (circles), and *Helminthoglypta* sp. (solid triangle).

Cooper (1893) did not specify an exact type locality for *P. eiseniana,* noting only that Eisen found 14 specimens living under stones; reference throughout the Cooper paper is to material collected by the CAS expedition of March to May 1892.

Pseudosubulina tastensis (Cooper, 1894)

(Fig. 33)

DISTRIBUTION.—BAJA CALIFORNIA SUR: Saltito Pass, just N of Sierra El Taste, elev. 3,200 ft [975 m] (TL), G. Eisen, 1893 (Cooper 1894). 1.3 mi [2.1 km] N of El Triunfo, A. G. Smith, CAS 1958–1959 Exped. (CAS). 5.3 mi [8.5 km] NW of Todos Santos, on road to La Pastora, A. G. Smith, CAS 1958–1959 Exped. (CAS). Boca de la Sierra, near Miraflores, A. G. Smith, CAS 1958–1959 Exped. (CAS). 0.2 mi [0.3 km] SSE of San José del Cabo, in stream drift, A. G. Smith, A. E. Leviton, CAS 1958–1959 Exped. (CAS). About 0.6 mi [1.0 km] SE of San Bartolo, along S side of arroyo, among granite boulders, W. B. Miller, 28 Dec. 1970 (WBM). Along road from Valle Perdido to ranch at Bajada del Molino, in rockslides on N-facing slope of arroyo S of road, elev. ca. 1,400 ft [430 m], C. C. Christensen, W. B. Miller, 28, 29 Dec. 1973 (CCC).

Superfamily CAMAENOIDEA
Family MEGOMPHICIDAE
Genus **Glyptostoma** Bland and Binney, 1873

Glyptostoma newberryanum depressum Bryant, 1902

(Fig. 33)

DISTRIBUTION.—BAJA CALIFORNIA NORTE: "Found alive under dead plants of a species of *Cotyledon* in a canyon near Todos Santos bay," C. R. Orcutt (Orcutt 1886, as *G. newberryanum*). Bluffs N of Ensenada de Todos Santos (TL), F. W. Bryant (Bryant 1902). El Tigre canyon, ca. 9 mi [14 km] N of Ensenada, along highway to Tijuana, W. B. Miller, 15 Feb. 1959 (WBM). Slope of bluff near mouth of Río El Tigre, 6 mi [10 km] N of Ensenada, E. P. Chace, E. M. Chace, 1 Feb. 1939 (SBMNH). Puente San Miguel, Río El Tigre, C. C. Christensen, 9 Nov. 1973 (CCC). Rock slide near S end of highway bridge, El Tigre canyon, S. S. Berry, H. L. Fletcher, 26 Jan. 1948 (SBMNH). Under stones near the San Diego road 2 mi. [3.2 km] N of Ensenada, L. G. Ingles, 15 Dec. 1927 (Berry 1928, as *G. newberryanum*; SBMNH). Isla Todos Santos, H. N. Lowe, 1912 (Lowe 1913); H. Hemphill (Hemphill 1881; CAS). Nachoguero Valley [Cañada Macho Güero] (Dall 1897, as *G. newberryanum*).

Glyptostoma newberryanum depressum is a weakly characterized subspecies of the otherwise southern Californian species *G. newberryanum* (Binney, 1858). Berry (1928) doubted the validity of the subspecies, but Pilsbry (1939) retained it pending an anatomical investigation.

Family OREOHELICIDAE
Genus **Radiocentrum** Pilsbry, 1905

Radiocentrum discus Christensen and Miller, 1976

(Fig. 34)

DISTRIBUTION.—BAJA CALIFORNIA SUR: Along road from Valle Perdido to ranch at Bajada del Molino, 3.2 km by road from Bajada del Molino, in rockslides on N-facing slope of large arroyo S of the road, elev. ca. 425 m (TL), C. C. Christensen, W. B. Miller, 28, 29 Dec. 1973 (Christensen and Miller 1976a; CAS, SBMNH). 1 km SE of San Bartolo, on N-facing slope of arroyo, among granite boulders, elev. ca. 250 m, W. B. Miller, 28 Dec. 1970, 19 Dec. 1973 (WBM). 5 km E of La Burrera, in large rockslide along trail from La Burrera to La Laguna, elev. ca. 1,000 m, W. B. Miller, 2 Jan. 1974 (WBM).

Radiocentrum exorbitans (Miller, 1973)

(Fig. 34)

DISTRIBUTION.—BAJA CALIFORNIA SUR: Sierra de la Giganta at Misión San Javier, in lava rockslides immediately S of the mission, approximately 32 km by road SW of Loreto, elev. 400–450 m (TL), W. B. Miller, Oct. 1971 (Miller 1973; CAS). 1 km SE of San Bartolo, W. B. Miller, 28 Dec. 1970 (Miller 1973; WBM).

Superfamily HELICOIDEA
Family HELMINTHOGLYPTIDAE
Genus **Helminthoglypta** Ancey, 1887
Subgenus **Helminthoglypta** sensu stricto

Helminthoglypta (Helminthoglypta) tudiculata (Binney, 1843)

(Fig. 34)

SYNONYM.—*Helix tudiculata* var. *binneyi* Hemphill, 1890.

DISTRIBUTION.—BAJA CALIFORNIA NORTE: "Among the hills of Lower California near the United States boundary," C. R. Orcutt (Orcutt 1886). Near Bahía de Todos Santos (Hemphill 1881). Nachoguero Valley [Cañada Macho Güero] (Dall 1897). Punta Banda, M. W. Williams, K. W. Kenyon, 1946 (SBMNH). Near the narrowed part of Punta Banda, L. G. Ingles, 17 Dec. 1927 (Berry 1928; SBMNH). San Antonio Canyon, about 5 mi [8 km] N of Johnson Ranch, under stones in rockslide on moist E-facing cliff, L. G. Ingles, 18 Dec. 1927 (Berry 1928; SBMNH). Johnson Ranch, S. Peyton (CAS).

Helminthoglypta tudiculata extends north in southern California to Los Angeles and San Bernardino counties. Berry (1928) found Baja California specimens to be "fairly typical" in morphology and not distinguishable taxonomically from specimens from San Diego, the type locality.

Subgenus **Charodotes** Pilsbry, 1939

Helminthoglypta (Charodotes) hannai hannai Pilsbry, 1927

DISTRIBUTION.—BAJA CALIFORNIA NORTE: Isla Guadalupe: W. E. Bryant (Cooper 1892a, as *Helix traskii* var. *carpenteri*); A. W. Anthony, 1896 (Dall 1900, as *Epiphragmophora* sp. indet.); G. Willett, 8 Apr. 1938 (CAS); Pine Ridge, elev. 3,000 ft [900 m] (TL), under stones beneath moisture-laden pine trees, G D. Hanna, July 1922, CAS 1922 Exped. (Pilsbry 1927; CAS, SBMNH).

Helminthoglypta hannai hannai has a relatively flat, widely umbilicate shell with smooth, olive-green periostracum; it is not closely related to nearby mainland *H. traskii* subsp. populations.

Helminthoglypta (Charodotes) hannai diodon Pilsbry, 1927

DISTRIBUTION.—BAJA CALIFORNIA NORTE: Isla Guadalupe, Northeast Anchorage (TL), and 3 mi [4.8 km] S of Northeast Anchorage, G D. Hanna, July 1922, CAS 1922 Exped. (Pilsbry 1927; CAS, SBMNH).

The two specimens comprising the type material of *H. h. hannai* (CAS 2560, 2561) are thin, fragile, fresh adult shells; they show evidence of incipient callus nodules on the parietal wall. The type material of *H. h. diodon* (four specimens, CAS 2562, 2563–2565) are old, possibly fossil, thicker, worn shells with well-developed callus nodules. We suspect that *H. h. diodon* may not be truly a subspecies but consists, rather, of gerontic individuals of *H. hannai*, perhaps selectively preserved by post-mortem processes.

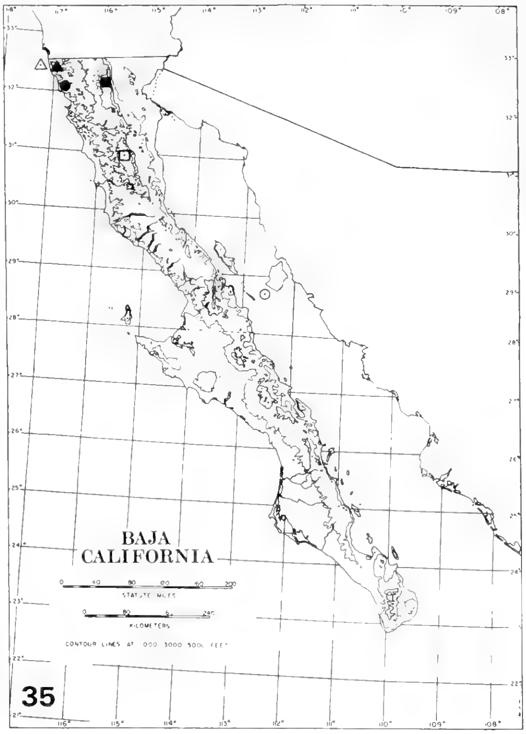

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FIGURE 35. Distribution of *Helminthoglypta coelata* (solid triangle), *Helminthoglypta misiona* (solid circle), *Helminthoglypta reederi* (open square), *Helminthoglypta traskii coronadoensis* (open triangle), *Eremarionta indioensis* (solid square), and *Eremarionta rowelli bechteli* (open circle).

Helminthoglypta (Charodotes) coelata (Bartsch, 1916)

(Fig. 35)

DISTRIBUTION.—BAJA CALIFORNIA NORTE: 7 mi [11 km] S of Tijuana, E. P. and E. M. Chace, Feb. 1939 (CAS).

This species also occurs in California along the coast of San Diego County as far north as La Jolla and Soledad Mountain (CAS).

Helminthoglypta (Charodotes) misiona Chace, 1937

(Fig. 35)

Distribution.—BAJA CALIFORNIA NORTE: La Misión Valley, in rockslide near the San Diego–Ensenada highway, about 40 mi [64 km] S of Tijuana (TL), E. P. and E. M. Chace, G. Willett, 1937 (Chace 1937; LACM; CAS). La Misión Valley, along Tijuana–Ensenada highway, in rockslide on S side of valley, seaward side of bridge, W. B. Miller, 14 Feb. 1959 (WBM). El Progreso, Sandoval Ranch area (ca. 30 mi [48 km] S of Tijuana), E. P. Chace, 8 Dec. 1957 (CAS). 16 mi [26 km] N of Ensenada, G. Willett (CAS).

Helminthoglypta (Charodotes) reederi Miller, 1981

(Fig. 35)

Distribution.—BAJA CALIFORNIA NORTE: Sierra San Pedro Mártir, in rock outcrops in a small canyon which crosses the road to the astronomical observatory, at a distance of about 2.5 road km below the observatory housing area, elev. ca. 2,575 m (TL), W. B. Miller, R. L. Reeder, C. C. Christensen, 3 Nov. 1973 (Miller 1981a; CAS, RLR, USNM, WBM).

Helminthoglypta (Charodotes) traskii coronadoensis (Bartsch, 1916)

(Fig. 35)

Synonym.—*Epiphragmophora traskii chrysoderma* Berry, 1920.

Distribution.—BAJA CALIFORNIA NORTE: Islas Los Coronados (TL), H. Hemphill (Bartsch 1916; USNM; CAS); G. W. Dunn (Cooper 1892a, as *Helix traskii* var. *carpenteri*). South Coronado Island, among loose talus on higher portion of southern end, G. Willett, 13 Dec. 1918 (Berry 1920; TL of *Epiphragmophora traskii chrysoderma*; CAS; SBMNH, ex S. S. Berry).

The form *chrysoderma* was based upon bandless, xanthic specimens, which are evidently numerous in certain colonies.

Helminthoglypta (Charodotes) traskii subsp.

Distribution.—BAJA CALIFORNIA NORTE: Near mouth of Santo Tomás River, H. Hemphill (Hemphill 1881; CAS). Santo Tomás Canyon, 4.1 mi [6.6 km] from Transpeninsular Highway, along road to harbor, under rocks on wooded slope, W. B. Miller, 27 Jan. 1962 (WBM).

The shells found "as far south as Santo Tomas," reported as *Arionta traskii* by Orcutt (1886: 62) represent an unidentified subspecies.

Subgenus uncertain

Helminthoglypta sp.

(Fig. 34)

Distribution.—BAJA CALIFORNIA NORTE: Ca. 35 mi [56 km] SE of Rumorosa, Sierra Juárez, under heavy granite rocks in *Pinus parryana* forest, E. C. Jaeger, R. S. Phair, 23 June 1958 (SBMNH).

This undescribed species is known from shells only. Its description is postponed until more material, including soft parts, is available.

Genus **Micrarionta** Ancey, 1880

Micrarionta guadalupiana (Pilsbry and Vanatta, 1898)

Distribution.—BAJA CALIFORNIA NORTE: Isla Guadalupe (TL): E. Palmer, 1875 (Binney 1879, as *Arionta facta*); G. W. Dunn (Cooper 1887, as *Helix facta*); A. W. Anthony, 1896; R. E. Snodgrass, E. Heller, 1899 (Dall 1900); Northeast Anchorage and 3 mi [4.8 km] to the south; Pine Ridge, NW end of island, elev. ca. 3,000 ft [900 m]; West Anchorage, G. E. Lindsay, 30 Jan. 1950 (SBMNH); near lobster camp, E side of island, E. P. Chace, 18 Dec. 1957 (SBMNH); E side of island 2 mi [3.2 km] N of the South Point, G D. Hanna, CAS 1922 Exped. (Pilsbry 1927; CAS, SBMNH); S end of island, M. W. Williams, Dec. 1946 (SBMNH). Outer islet, 2 mi [3.2 km] off S end of Isla Guadalupe, G. E. Lindsay, 27 Jan. 1950 (SBMNH).

This species dates from the publication of a figure of its reproductive system by Pilsbry and Vanatta (1898), rather than from the description of the shell by Dall (1900).

Pilsbry (1927) noted that in a specimen sent to him by Dall, he found the dart sac absent; in other specimens from near Northeast Anchorage a well-developed dart sac was present. Although he stated, "I incline to the theory that the organs of the paratype . . . which I examined are not mature or were abnormal" (Pilsbry 1927:165), we do not rule out the possibility that two species may actually exist, one with dart apparatus and the other without. The species *Micrarionta opuntia* Roth, 1975, from San Nicolas Island, California, lacks a dart sac.

Genus **Plesarionta** Pilsbry, 1939

Plesarionta orcutti (Dall, 1900)

(Fig. 36)

Synonyms.—*Epiphragmophora traskii* var. *tularensis* 'Hemphill,' Pilsbry, 1895 (nomen nudum) (non *Arionta tudiculata* var. *tularensis* Hemphill in Binney, 1892). *Epiphragmophora traskii tularica* Bartsch, 1916.

Distribution.—BAJA CALIFORNIA NORTE: "Rosario mesas, in northern Lower California" (TL), C. R. Orcutt, May 1886 (Dall 1900; SBMNH). Mesa about 1.5 mi [2.4 km] N of El Rosario, under *Agave shawii*, S. S. Berry, C. L. Hubbs, 13 Apr. 1954 (SBMNH). El Rosario, elev. 100 ft [30 m], S. C. Williams, 1969 (CAS). Rosario Mesa, W. B. Miller, C. C. Christensen, 1973 (WBM).

This species differs from *Plesarionta stearnsiana* in color pattern and in the presence of incised spiral lines in the shell; there are no discernible differences in anatomy. *Plesarionta orcutti* is sympatric with *P. stearnsiana* on Rosario Mesa. We do not exclude the possibility that it is only a local conspecific variant of *P. stearnsiana.* The misallocation of the type material of *Epiphragmophora traskii tularica* to "Frasers Mills, Tulare County, California," was discussed by Roth (1982).

The agave habitat at the type locality of *P. orcutti* has been destroyed by conversion of the land to agriculture.

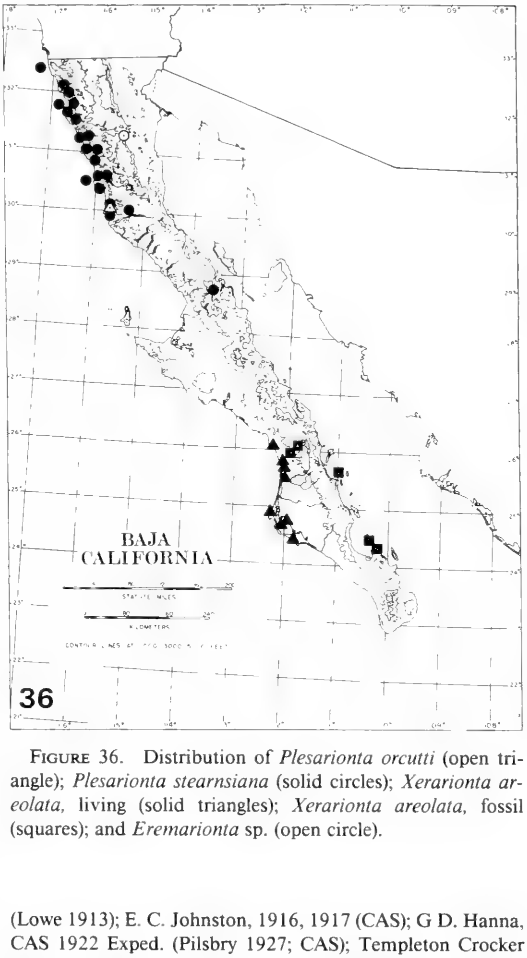

FIGURE 36. Distribution of *Plesarionta orcutti* (open triangle); *Plesarionta stearnsiana* (solid circles); *Xerarionta areolata,* living (solid triangles); *Xerarionta areolata,* fossil (squares); and *Eremarionta* sp. (open circle).

Plesarionta stearnsiana (Gabb, 1868)

(Fig. 36)

DISTRIBUTION.—BAJA CALIFORNIA NORTE: Islas Los Coronados, F. E. Blaisdell, 1881 (CAS); H. Hemphill (Hemphill 1881, 1901; CAS); E. C. Johnston, R. A. Coleman, USFC ALBATROSS, 22 May 1916 (CAS). North Coronado Island, W. G. Craig, L. H. Miller, 6 May 1928 (SBMNH); near boat landing, B. W. Evermann (CAS); rockslides on E slope of island, M. W. Williams, K. W. Kenyon, 2 Mar. 1946 (SBMNH). Middle Coronado Island, K. W. Kenyon, 26 July 1946 (SBMNH). South Coronado Island, A. G. Smith, 21 July 1912, Mar 1919 (Berry 1928; CAS, SBMNH); G. Willett, 13 Dec. 1918 (Berry 1928; SBMNH). Point S of Mesquite Point, near El Descanso, in clumps of *Agave shawii,* S. S. Berry, H. L. Fletcher, 27 Jan. 1948 (SBMNH). Rockslide near San Diego–Ensenada highway, La Mision Valley, ca. 40 mi. Arroyo 9 mi. [64 km] S of Tijuana, E. P. and E. M. Chace, G. Willett, 1937 (Chace 1937). Slope of bluff near mouth of Río El Tigre, E. P. Chace, E. M. Chace, 1 Feb. 1939 (SBMNH). Rockslides near S end of highway bridge, El Tigre, S. S. Berry, H. L. Fletcher, 26 Jan. 1948 (SBMNH). Rockslides on S canyon wall below Misión San Miguel, S. S. Berry, H. L. Fletcher, 27 Jan. 1948 (SBMNH). Canyon 5 mi [8 km] inland from Ensenada, on and under *Opuntia,* V. W. Owen, 1 July 1923 (CAS). Punta Banda, H. N. Lowe, 1912 (CAS); S. S. Berry, H. L. Fletcher, 25 Jan. 1948 (SBMNH); L. G. Ingles, 17 Dec. 1927 (SBMNH). Arbolitos, SW side of Punta Banda, S. S. Berry, 10 Apr. 1954 (SBMNH). Islas de Todos Santos, H. Hemphill (Hemphill 1881), H. N. Lowe, 1912 (Lowe 1913); E. C. Johnston, 12 Feb. 1917 (CAS); J. R. Slevin, May 1923 (CAS); G. Willett (CAS); I. L. Wiggins, J. H. Thomas, 4 Feb. 1949 (SBMNH); Puritan-AMNH Exped., 1957 (Jacobson 1958). "Found under stumps of Maguey from Sto. Tomas to a little beyond Rosario" (TL) (Gabb 1868, Pilsbry 1939, Coan and Bogan' 1988; ANSP). Near mouth of San [Santo] Tomás River (Hemphill 1881; CAS). Santo Tomás, E. C. Johnston, 13 Feb. 1917 (CAS). Punta China, C. L. Hubbs, 18 Sep. 1948 (SBMNH). Punta Cabras, C. L. Hubbs, 15 Aug. 1948 (SBMNH). Near San Isidro, C. R. Orcutt, June 1919 (SBMNH). Coast just N of mouth of Río San Telmo, C. L. Hubbs, 6 Sep. 1948 (SBMNH). San Telmo Mesa, under dead agave, I. L. Wiggins, A. M. Vollmer, H. M. Hill, 10 Oct. 1946 (SBMNH). 5 mi [8 km] S of Colonet, in dead agave stalk, P. H. Arnaud, 24 Apr. 1963 (CAS). 8 mi [13 km] E of San Telmo de Arriba, elev. 500 ft [150 m], S. C. Williams, V. F. Lee, 13 July 1969 (CAS). Vicinity of Colonet, San Telmo, and Colonia Guerrero (Miller 1981a). 10 mi [16 km] S of Camalú, G. Wiggins, 21 June 1971 (CAS). Isla San Martín, A. W. Anthony, 1896 (Dall 1900); F. Baker (1902); H. N. Lowe, 1912 (Lowe 1913); E. C. Johnston, 1916, 1917 (CAS); G D. Hanna, CAS 1922 Exped. (Pilsbry 1927; CAS); Templeton Crocker Exped. of CAS, 19 Aug. 1932 (CAS); Hassler Cove, M. W. Williams, K. W. Kenyon, 3 Apr. 1946 (SBMNH); volcanic peaks, and rockslide at elev. 100 ft [30 m], SW side of island, M. W. Williams, K. W. Kenyon, 7 Apr. 1946. Numerous localities from California border to W shore of Bahía San Quintín, H. Hemphill (1901); G D. Hanna, CAS 1922 Exped. (Pilsbry 1927; CAS); H. N. Lowe, 1912 (Lowe 1913); L. G. Ingles, Dec. 1927 (Berry 1928; SBMNH); C. R. Orcutt, 1 June 1919 (Berry 1928); I. L. Wiggins, H. M. Hill, 23 Oct. 1946 (SBMNH); S. S. Berry, G. Brandt, 23 Mar. 1949 (SBMNH); K. B. Macdonald (1969, as *Micrarionta* sp.; CAS). Canyon on N side of Santa María valley near San Simon, ca. 7–8 mi [11–13 km] from coast, E. P. Chace, 11 Sep. 1955 (SBMNH). "Mt. Ceniza," Bahía San Quintín, E. C. Johnston, 2 Mar. 1917 (CAS). 5 mi [8 km] S of Rancho El Socorro turnoff from main Baja California highway, A. G. Smith, 27 Mar. 1961 (CAS). 9 mi [14 km] N of El Rosario, ca. 1.5 mi [2.4 km] inland, I. L. Wiggins, 14 Oct. 1959 (CAS). Mesa near Rosario, C. R. Orcutt, 1885 (Orcutt 1886; SBMNH). 1.5 mi [2.4 km] E of Meling Ranch, elev. 2,450 ft [750 m], C. C. Christensen, W. B. Miller, 4 Nov. 1973 (CCC, WBM). Rosario Mesa, S. S. Berry, C. L. Hubbs, 13 Apr. 1954 (SBMNH); I. L. Wiggins, A. M. Vollmer, H. M. Hill, 24 Oct. 1946 (SBMNH); W. B. Miller, C. C. Christensen, 1973 (WBM). Coastal terrace, S side of Arroyo del Rosario, S. S. Berry, C. L. Hubbs, 12 Apr. 1954 (SBMNH). El Rosario, elev. 100 ft [30 m], S. C. Williams, 6 Apr. 1969 (CAS). 1 mi [1.6 km] E of El Rosario, elev. 100 ft [30 m], S. C. Williams, 7 Apr. 1969 (CAS). 10 mi [16 km] S of El Rosario, I. L. Wiggins, 20 June 1971 (CAS). 12 mi [19 km] SE of El Rosario, around old agaves, I. L. Wiggins, 14 Oct. 1959 (CAS). 8 mi [13 km] NW of El Progreso, E. S. Ross, D. Q. Cavagnaro, 17 Apr. 1965 (CAS). [14.4 km] E of Millers Landing, I. L. Wiggins, A. M. Vollmer, H. M. Hill, 29 Oct. 1946 (SBMNH). La Zonja, Sierra San Pedro Mártir, J. P. Figg-Hoblyn, 16 June 1953 (CAS). Cerro de la Mina de San Juan, Sierra La Libertad, W. B. Miller, 1981 (WBM).

In California, *Plesarionta stearnsiana* occurs in southwestern San Diego County as far north as the vicinity of La Jolla (Berry 1928, Pilsbry 1939).

Genus **Xerarionta** Pilsbry, 1913

Xerarionta areolata (Pfeiffer, 1845)

(Fig. 36)

Synonyms.—*Helix areolata* var. *albida* Hemphill, 1890 (nomen nudum). *Helix areolata* var. *exanimata* Cooper, 1892. *Micrarionta areolata* var. *arida* Pilsbry, 1913. *Micrarionta areolata* var. *scammoni* Pilsbry, 1913. *Micrarionta areolata* var. *aspersa* Pilsbry, 1913.

Distribution.—BAJA CALIFORNIA SUR: Bahía Santa María, J. P. Figg-Hoblyn, 21 May 1952 (SBMNH); NE shore, T. Craig, 25 Feb. 1928 (SBMNH). Hills near abandoned Rancho Amargosa, central Isla Santa Margarita, J. T. Smith, 18 Mar. 1985 (SBMNH). Isla Margarita, southern division, G D. Hanna, CAS 1922 Exped. (Pilsbry 1927; CAS). E shore, Bahía Almejas, I. L. Wiggins, H. M. Hill, 22 Nov. 1946 (SBMNH). Sandy rolling hills 7 mi [11 km] SE of Estero Salina, Bahía, Almejas, I. L. Wiggins, A. M. Vollmer, H. M. Hill, 2 Nov. 1946 (SBMNH). 2.9 mi [4.6 km] N of San Juánico on W side of road to Candeje, J. T. Smith, 22 Mar. 1984, 1985 (SBMNH). Bahía San Juánico, A. S. Loukashkin, 14 Aug. 1961 (CAS). 16 mi [26 km] S of San Juánico, I. L. Wiggins, CAS 1958–1959 Exped. (CAS). 10 mi [16 km] N of Pozo Grande, E. S. Ross, B. Hammerly, G. E. Bohart, 24 Oct. 1941 (CAS). 4 mi [6.4 km] N of Pozo Grande, I. L. Wiggins, CAS 1958–1959 Exped. (CAS). Magdalena Plain, 25°50′N, 112°00′W, H. E. Gates, 10 Feb. 1931 (SBMNH). 11 mi [18 km] S of Pozo Grande, I. L. Wiggins, H. M. Hill, 29 Nov. 1946 (SBMNH). San Jorge, G. E. Lindsay, 5 Aug. 1951 (SBMNH). 10 mi [16 km] N of Santo Domingo, I. L. Wiggins, H. M. Hill, 20 Nov. 1946 (SBMNH). 5 mi [8 km] N of Santo Domingo, E. S. Ross, B. Hammerly, G. E. Bohart, 23 Oct. 1941 (CAS); I. L. Wiggins, H. M. Hill, 21 Nov. 1946 (SBMNH). San [Santo] Domingo Ranch, sandy mesa 5 mi [8 km] from coast, I. L. Wiggins, H. M. Hill, 19 Nov. 1946 (SBMNH). Bahía Magdalena (TL, designated by Pilsbry 1913:391): R. B. Hinds, 1839; W. M. Gabb, 1867; R. C. Macgregor (Pilsbry 1913); W. J. Fisher, 1876 (Stearns 1894); W. Newcomb (Dall 1900); C. R. Orcutt, Mar 1917, 1919 (SBMNH); ocean beach, G D. Hanna, CAS 1922 Exped. (Pilsbry 1927; CAS); Man-of-War Cove, R. V. Moran (SBMNH). Isla Magdalena, C. R. Orcutt, Mar. 1917 (Orcutt 1918; SBMNH); G D. Hanna, CAS 1922 Exped. (Pilsbry 1927; CAS); H. E. Gates, 15–16 Feb. 1931 (SBMNH); H. N. Lowe, 1931 (CAS); N of village, Puritan-AMNH Exped., 1957 (Jacobson 1958). Salada, near Bahía Magdalena (Gabb 1869). Sand hills, Médano Amarillo, H. E. Gates, 27 Mar. 1932 (SBMNH). Médano Amarillo, J. H. Thomas, 21 May 1959 (CAS). N end of Cabo San Lázaro, Isla Magdalena, J. T. Smith, 1985 (SBMNH). Punta Belcher, H. N. Lowe, 1931 (Lowe 1933; CAS).

Fossil records.—San José Comondú, and lower arroyo 12 mi [19 km] SW of San Miguel Comondú, R. J. Drake, July 1953 (CAS). N end of Cabo San Lázaro, in fluvial-beach-terrace deposit, J. T. Smith, 1985 (SBMNH). Isla Espíritu Santo, W. E. Bryant, 1892 (Cooper 1892b; TL of *Helix areolata* var. *exanimata*; USNM; CAS); desert floor, SE end of island, M. W. Williams, 18 Apr. 1937 (SBMNH). Punta Coyote, N of La Paz, in a post-Pleistocene raised beach, L. B. Mousley, 17 Dec. 1952 (SBMNH); A. G. Smith, CAS 1958–1959 Exped. (CAS). NE end of Isla Monserrate, E. P. Van Duzee, CAS 1921 Exped. (Hanna 1923; CAS).

According to Pilsbry (1913), this and *Xerarionta levis* were collected in Baja California by Hinds during the voyage of HMS SULPHUR; he discussed earlier errors concerning the type locality. The varieties *arida, scammoni,* and *aspersa* (all, Pilsbry 1913) are intrapopulation variants, of less than subspecific rank.

Specimens from Isla Espíritu Santo, Isla Monserrate, and Punta Coyote on the peninsula immediately south of Isla Espíritu Santo, were formerly referred to *Micrarionta exanimata* (Cooper) (e.g., by Hanna 1923). They are not distinguishable from *X. areolata.* The species apparently is extinct at these localities. One lot (CAS 032530) from the W. J. Raymond collection with data "Espiritu Santo I/Near La Paz/Cal. Acad. Sci. 1892" contains two fossil shells along with four fresh shells probably mixed in from another source. Coan (1982:163) regarded the fossil shells of this lot as syntypes of *Helix areolata* var. *exanimata.*

The southern limit of living *X. areolata* is unknown; no field work has been done along the coast between Bahía Magdalena and the vicinity of Todos Santos.

Xerarionta levis levis (Pfeiffer, 1845)

(Fig. 37)

Distribution.—BAJA CALIFORNIA NORTE: Vicinity of Colonet, San Telmo, and Colonia Guerrero (Miller 1981a). Ocean bluff back of Hamilton Ranch, C. L. Cass, 1928 (SBMNH). Sand dunes 6–7 mi [10–11 km] NW of San Quintín, I. L. Wiggins, 8 May 1948 (SBMNH). "Mt. Ceniza," Bahía San Quintín, E. C. Johnston (CAS). Volcanic hills W of Bahía San Quintín, C. C. Christensen, J. A. Christensen, 28 Dec. 1975 (CCC). Along shore road W of Kenton Hill, San Quintín Peninsula, S. S. Berry, 24 Mar. 1949 (SBMNH). Bahía San Quintín, on beach, USFC ALBATROSS, 21 Apr. 1916 (CAS). "Under the trunks and among the leaves of Agave Shawii, on a high mesa near Rosario," C. R. Orcutt (Orcutt 1886; CAS, SBMNH); A. G. Smith, CAS 1958–1959 Exped. (CAS). Rosario Mesa, F. M. Reed, 3 Feb. 1929 (SBMNH); H. E. Gates, 30 May 1930 (CAS); under *Penstemon,* M. W. Williams, K. W. Kenyon, 9 Apr. 1946 (SBMNH); S. S. Berry, C. L. Hubbs, 13 Apr. 1954 (SBMNH); W. B. Miller, C. C. Christensen, 1973 (WBM). On road between El Rosario and Punta Baja, M. W. Williams, K. W. Kenyon, 9 Apr. 1946 (SBMNH). Coastal terrace, N side of Punta Baja, S. S. Berry, C. L. Hubbs, 12 Apr. 1954 (SBMNH). Punta Baja, O. L. Bowen, 26 June 1962 (CAS). Isla San Geronimo, H. N. Lowe (Pilsbry 1913), fossil only. 6 mi [10 km] S of El Marmolito, A. G. Smith, 30 Mar. 1961 (CAS). Between Punta Prieta and Punta Rosarito, I. L. Wiggins, 18 Oct. 1959 (CAS). 12.5 mi [20.0 km] S of Punta Prieta, under dead agaves, I. L. Wiggins, H. M. Hill, 28 Oct. 1946 (SBMNH). 15 mi [24 km] S of Punta Prieta, I. L. Wiggins, H. M. Hill, 28 Oct. 1946 (SBMNH); S. C. Williams, K. B. Blair, 7 July 1973 (CAS). 35 mi [56 km] S of Punta Prieta, under agaves, I. L. Wiggins, A. M. Vollmer, H. M. Hill, 29 Oct. 1946 (SBMNH). NE of Santa Rosalillita, D. E. Breedlove, 21 Mar. 1984 (CAS). "Rosalia Bay" [Bahía Santa Rosalillita], A. W. Anthony, 1896 (Dall 1900). 7 mi [11 km] and 3 mi [4.8 km] NNW of Rosarito, A. G. Smith, Mar.–Apr. 1961 (CAS). Sandy hills N side of estero at mouth of Arroyo del Rosario, 17 Nov. 1967 (CAS). 2.5 mi [4.0 km] S of Rosalillita Beach, I. L. Wiggins, 1959 (CAS). 4 mi [6.4 km] NW of San Javier (N of Millers Landing), S. C. Williams, 15 Apr. 1969 (CAS). Between Rosalillita and Millers Landing, I. L. Wiggins, 18 Oct. 1959 (CAS). 5 mi [8 km] N of Millers Landing, H. E. Gates, 6 Apr. 1931 (SBMNH). Arroyo 9 mi [14 km] E of Millers Landing, I. L. Wiggins, A. M. Vollmer, H. M. Hill, 29 Oct. 1946 (SBMNH). Millers Landing, under dead *Echinocereus maritimus,* I. L. Wiggins, H. M. Hill, 29 Oct. 1946 (SBMNH). 2 mi [3.2 km] S of Millers Landing, I. L. Wiggins, 1959 (CAS). 8 mi [13 km] S of Millers Landing, I. L. Wiggins, A. M. Vollmer, H. M. Hill, 29 Oct. 1946 (SBMNH). 5 mi [8 km] NW of Rancho Mezquital, granite boulder hill, A. G. Smith, 30 Mar. 1961 (CAS). 4 mi [6.4 km] N of Rancho Mezquital, E. S. Ross, B. Hammerly, G. E. Bohart, 29 Oct. 1941 (CAS); A. G. Smith et al., Mar. 1961 (Wiggins 1969). Mesa just S of Rancho Mezquital, under dead agaves, I. L. Wiggins, A. M. Vollmer, H. M. Hill, 30 Oct. 1946 (SBMNH). Laguna Santo Domingo, C. R. Orcutt (CAS, SBMNH). Near Laguna Manuela, H. Hemphill (CAS, SBMNH). Puerto San José, and road to Puerto San José at elev. 250 m, I. L. Wiggins, 9 Feb. 1962 (CAS). 16 mi [26 km] N of Espina, E of Guerrero Negro, I. L. Wiggins, 19 Oct. 1959 (CAS). 5 km E of La Espina, A. G. Smith, A. E. Leviton, I. L. Wiggins, B. H. Banta, 30 Mar. 1961 (Wiggins 1969; CAS). Laguna Guerrero Negro, A. G. Smith, 4 Nov. 1959 (CAS). BAJA CALIFORNIA SUR: Desert flats 4.5 mi [7.2 km] E of Guerrero Negro, I. L. Wiggins, 1959 (CAS). 5 km E of Guerrero Negro, A. G. Smith, 30–31 Mar. 1961 (Wiggins 1969). 4.5 mi [7.2 km] E of El Solito, I. L. Wiggins, 1969 (CAS). Scammons Lagoon [Laguna Ojo de Liebre], W. M. Pierce (CAS); L. M. Huey, 22 May 1926 (SBMNH). S shore of Scammons Lagoon, opposite deepest channel, G. C. Ewing, Feb. 1957 (SBMNH). Port San Bartolomé [Bahía Tortugas] (TL, designated by Pilsbry 1913:388), R. B. Hinds, 1839; H. Hemphill (Pilsbry 1913; CAS, SBMNH); G D. Hanna, CAS 1922 Exped. (Pilsbry 1927; CAS); E. P. Chace, 16 July 1954 (SBMNH); Puritan-AMNH Exped., 1957 (Jacobson 1958). North side, Bahía Tortugas, G D. Hanna, 12 Mar. 1953 (CAS). Cerro de la Banderilla, Sierra de Placeros, on road to Bahía Tortugas, D. E. Breedlove, 24 Mar. 1984 (CAS). Bahía San Roque, E. C. Johnston (CAS). Punta Asunción, J. P. Figg-Hoblyn, 28 Mar. 1952 (SBMNH). Isla Asunción, W. J. Fisher, 1876 (Stearns 1894); G D. Hanna, CAS 1922 Exped. (Pilsbry 1927; CAS).

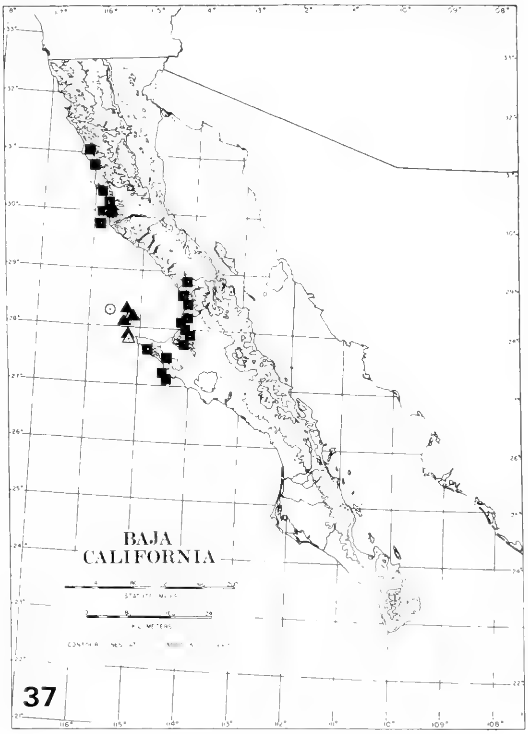

FIGURE 37. Distribution of *Xerarionta levis levis* (squares), *Xerarionta levis canescens* (solid triangles), *Xerarionta levis crassula* (open triangle), and *Xerarionta pandorae* (open circle).

We can find no anatomical differences between specimens of *Xerarionta levis levis* on the mainland and *X. l. canescens* from Islas Cedros and Natividad. There are populations of *X. l. levis* that approach the size and shape of *X. l. canescens.* There is also a lot (CAS 26301) of *X. levis crassula* from Isla Natividad that appears to be fossil. It is our opinion that mainland populations are all *X. l. levis,* with large variations in shell size. We believe that *X. l. canescens* of Islas Cedros and Natividad and the peninsular *X. l. levis* evolved from a recent common ancestor and are only subspecifically distinct.

Baily (1942) reported a sinistral specimen of "*Micrarionta levis*" from salt flats south of Santo Domingo. The locality description is suggestive of Santo Domingo (del Pacífico) in Baja California Sur, within the range of *X. areolata,* and we suspect that the specimen was misidentified.

The apparent disjunction in the mainland range of this species (Fig. 37) is probably an artifact of the inaccessibility of the coastal zone between El Rosario and Millers Landing. The southern limit is not well known, owing to the lack of field investigation in likely habitats south of Bahía San Roque.

Xerarionta levis canescens (Adams and Reeve, 1848)

(Fig. 37)

Synonyms.—*Arionta veitchii* 'Newcomb,' Tryon, 1866. *Helix areolata* var. *cedrosensis* Hemphill, 1890 (nomen nudum). *Epiphragmophora leucanthea* Dall, 1900. *Micrarionta levis globosa* Pilsbry, 1913.

Distribution.—BAJA CALIFORNIA NORTE: Isla Cedros (TL): J. A. Veatch, 1859 (Stearns 1894; SBMNH); A. W. Anthony, 1896 (Dall 1900); H. Hemphill; H. N. Lowe, 1912 (Pilsbry 1913; ANSP, CAS); E. C. Johnston, 13 Jan. 1917 (CAS); F. Baker (1918); M. W. Williams, K. W. Kenyon, 1946 (SBMNH); K. E. Lucas, 17 Mar. 1973 (CAS); elev. 0–300 ft [0–90 m], Hubbs-Flynn "ZACA" Exped., 20 Aug. 1946 (SBMNH); Abalone Cove, N end of island, C. B. Perkins, Feb. 1932 (SBMNH); 1 mi [1.6 km] up canyon back of anchorage, NE end of island, M. W. Williams, 28 Feb. 1941 (SBMNH); NE landing, E. C. Johnston, 29 May 1916 (CAS); E side of island (Dall 1900; TL of *Epiphragmophora leucanthea*; USNM); NE of Cedros Village near spring, C. C. Christensen, W. B. Miller, 12 May 1975 (CCC, WBM); W side near Red Rocks; Bernstein's Spring at elev. 2,000 ft [600 m], on desert plants; N end near old mine; "Grand Canyon" near center of E side of island; Bernstein's Camp; and South Bay, G D. Hanna, CAS 1922 Exped. (Pilsbry 1927; CAS); abalone camp, L. G. Hertlein, 1932 (CAS); S end of island, A. E. Colburn, 15 Nov. 1926 (SBMNH); J. R. Slevin, 1940 (CAS); South Bay, and 1 mi [1.6 km] E and 4 mi [6.4 km] S of North Point, Puritan-AMNH Exped., 1957 (Jacobson 1958). BAJA CALIFORNIA SUR: Isla Natividad: A. W. Anthony, 1896 (Pilsbry 1913); M. W. Williams, K. W. Kenyon, 15 May 1946 (SBMNH); C. C. Christensen, W. B. Miller, 13 May 1975 (CCC, WBM); N side below first giant cactus, G D. Hanna, CAS 1922 Exped. (Pilsbry 1927; CAS).

Pilsbry (1913) discussed the provenance of the type material of *Helix canescens,* originally stated to be from Africa. *Arionta veitchii* (emended to "*veatchii*" by later authors) is not consistently distinguishable from *X. l. canescens,* and we consider it to be a high-spired form that appears in various populations. Dall's (1900) *Epiphragmophora leucanthea* has been treated as an infrasubspecific form by Pilsbry (1927) and Jacobson (1958); we consider it to have no taxonomic standing. Likewise, we consider *Micrarionta levis globosa,* described from Isla Cedros, a synonym of *X. l. canescens.*

Xerarionta levis crassula (Dall, 1900)

(Fig. 37)

Distribution.—BAJA CALIFORNIA SUR: Isla Natividad (TL): A. W. Anthony, 1896 (Dall 1900; USNM); G D. Hanna, CAS 1922 Exped. (Pilsbry 1927; CAS); From soft sandstone near middle of E side of island, M. W. Williams, K. W. Kenyon, 16 May 1946 (SBMNH).

This name is applicable to fossil populations from Isla Natividad consisting of shells consistently smaller than modern snails inhabiting that island. Fossil shells from Isla San Gerónimo are similar to *X. l. crassula* in size and contour (Pilsbry 1913; CAS, SBMNH).

Xerarionta pandorae (Forbes, 1850)

(Fig. 37)

Synonyms.—*Helix damascenus* Gould, 1856. *Epiphragmophora pandorae bonitosensis* Pilsbry and Vanatta, 1898.

Distribution.—BAJA CALIFORNIA NORTE: Islas San Benito (TL), HMS HERALD and PANDORA, 1849 (Pilsbry 1913); A. W. Anthony, 1896 (Dall 1900); H. Hemphill (Pilsbry 1913; ANSP, SBMNH); H. N. Lowe, 1931 (Lowe 1933). Isla San Benito del Oeste: G. E. Lindsay, 5 Jan. 1950 (SBMNH); Puritan-AMNH 1957 Exped. (Jacobson 1958); R. C. Brusca, 6 Jan. 1954 (WBM); W. B. Miller, C. C. Christensen, 1975 (WBM); in rockslides on N side, NE point, and S side, G D. Hanna, CAS 1922 Exped. (Pilsbry 1927; CAS); elev. 0–500 ft [0–150 m], near E end of island, Hubbs-Flynn "ZACA" Exped., 10 Aug. 1946 (SBMNH). Isla San Benito del Este: G D. Hanna, CAS 1922 Exped. (Pilsbry 1927; CAS); J. W. Sefton, 6 Feb. 1950 (SBMNH); in talus just above beach, SW end of island, M. W. Williams, 26 Feb. 1941 (SBMNH).

Pilsbry (1913) discussed the provenance of the type material of *Helix pandorae,* originally stated to be from the vicinity of the Columbia River, Washington-Oregon. Johnson (1964) selected and illustrated a lectotype for *Helix damascenus* Gould.

Genus **Eremarionta** Pilsbry, 1913

Eremarionta indioensis (Yates, 1890)

(Fig. 35)

Distribution.—BAJA CALIFORNIA NORTE: Cañon de Guadalupe, Sierra Juárez, E. P. Chace, 19 May 1957; W. B. Miller, 1 Jan. 1960 (WBM). Unnamed canyon ca. 10 mi [16 km] S of Cañon de Guadalupe, T. Danielson, 1958 (SBMNH). In decomposed granite on N exposure of left fork ca. 0.25 mi. above forks of Cañon Carrizo, E side of Sierra Juárez, R. S. Phair, 29 Nov. 1957 (SBMNH).

The various subspecies of *Eremarionta indioensis* were discussed at length by Pilsbry (1939). Specimens from the Sierra Juárez are not distinguishable from topotypes of *E. i. indioensis* from Indio, Riverside County, California, although these localities are separated by more than 150 km. The presence of *Eremarionta* in Baja California Norte was noted by Bequaert and Miller (1973), based on specimens from Cañon de Guadalupe.

Eremarionta rowelli bechteli (Emerson and Jacobson, 1964)

(Fig. 35)

Distribution.—SONORA: Isla San Esteban (TL), in rockslide, G D. Hanna, 1953 ORCA Exped.; elev. 300 m, R. V. Moran, 22 Mar. 1962, Belvedere Exped. (Emerson and Jacobson 1964; CAS, SDMNH, AMNH).

Although Isla San Esteban is politically a part of Sonora rather than of Baja California, the occurrence there of *Eremarionta* is included in the interest of a comprehensive listing of land snails of the gulf islands.

Other subspecies of *Eremarionta rowelli* (Newcomb, 1865) occur in the desert region of southeastern California and western Arizona and in the region of the Sierra de San Francisco and Puerto Libertad, Sonora (Bequaert and Miller 1973).

Eremarionta sp.

(Fig. 36)

Distribution.—BAJA CALIFORNIA NORTE: S side of Paso San Matías, near N end of Sierra San Pedro Mártir, E. C. Jaeger, 8 Feb. 1955 (SBMNH). Near granite boulders on burned-over, juniper-covered hills 9 mi [14.4 km] W of Alaska, I. L. Wiggins, H. M. Hill, 4 Oct. 1946 (SBMNH).

Genus **Sonorelix** Berry, 1943

Subgenus **Herpeteros** Berry, 1947

Sonorelix (Herpeteros) chacei (Willett, 1940)

(Fig. 38)

Distribution.—BAJA CALIFORNIA NORTE: Lower end of El Tigre Canyon, about 9 mi [14.4 km] N of Ensenada (TL), E. P. and E. M. Chace, W. O. Gregg, G. Willett, 22 Feb. 1937, 21 Apr. 1940 (Willett 1940; LACM, CAS); S. S. Berry, H. L. Fletcher, 26 Jan. 1948 (SBMNH); R. L. Reeder, 8 Nov. 1973 (WBM).

This species is as yet known only from a small number of specimens collected at and near its type locality. It has not been dissected. *Sonorelix chacei* apparently differs from other Baja California forms in its relatively high-spired shell and nearly closed umbilicus, but its status must remain uncertain until more material becomes available for study.

Sonorelix (Herpeteros) inglesiana (Berry, 1928)

(Fig. 38)

Distribution.—BAJA CALIFORNIA NORTE: On moist N slope of the Red Rock [Peña Colorada] under rocks, about 3 mi [4.8 km] from the sea and 0.5 mi [0.8 km] from Hamilton Ranch, W of Santo Domingo (TL), L. G. Ingles, 19 Dec. 1927 (Berry 1928; SBMNH); G. Willett (CAS); I. L. Wiggins, H. M. Hill, 22 Oct. 1946 (Berry 1947; SBMNH). "Red Rock" at Hamilton Ranch, in fissures at top of letters "HR," W. B. Miller, W. N. Miller, 12 Dec. 1970; C. C. Christensen, W. B. Miller, 5 Nov. 1973 (WBM, CCC). Side canyon ca. 1 mi [1.6 km] above Misión Santo Domingo, W. Clune, 22 Mar. 1949 (SBMNH). Near Misión Santo Domingo, C. R. Orcutt, June 1919 (Berry 1928; SBMNH). San Antonio, near junction of Santo Domingo and Sanca streams, brushy hillside, elev. 2,200 ft [670 m], I. L. Wiggins, H. M. Hill, 13 Oct. 1946 (SBMNH).

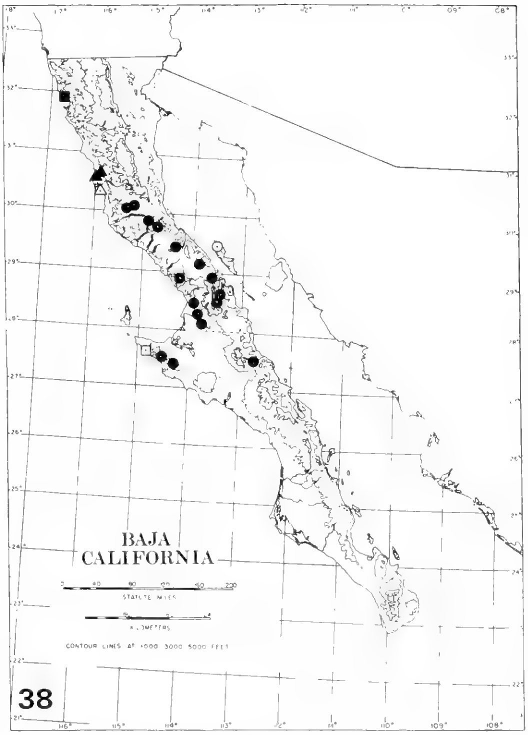

Figure 38. Distribution of *Sonorelix chacei* (solid square), *Sonorelix inglesiana* (solid triangles), *Sonorelix peninsularis* (solid circles), *Sonorelix evermanni* (open square), *Sonorelix merrilli* (open triangle), and *Sonorelix* (*Herpeteros*)(?) sp. (open circle).

Empty shells collected 2 mi [3.3 km] east of El Rosario by A. G. Smith, CAS 1958–1959 Exped. (CAS) and near El Rosario by S. C. Williams, 1969 (CAS) may belong to this species. Apparently, Orcutt collected similar shells in the vicinity of El Rosario prior to 1886 (Orcutt 1886).

The few intact specimens available for study are somewhat smaller than specimens from other locations identified by us as *S. peninsularis,* but do not differ significantly in shell form or umbilical size. The two taxa may be found to be conspecific when larger samples from the vicinity of Hamilton Ranch become available.

Sonorelix (Herpeteros) peninsularis (Pilsbry, 1916)

(Fig. 38)

Distribution.—BAJA CALIFORNIA NORTE: "Trinidad, on the west coast near San Borga [Borja]" (TL), W. M. Gabb, 1867 (Pilsbry 1916). Foothills of the Sierra de Calmalli, about 30 mi [48 km] S of Misión San Borja (Gabb 1868, as *Helix remondi*). Two mi [3.2 km] back of Bahía de Los Ángeles, I. M. Johnston, CAS 1921 Exped. (Hanna 1923; CAS). About 1 mi [1.6 km] E of Misión San Borja, G D. Hanna, I. L. Wiggins, CAS 1959 Exped. (CAS). North end of mountain W of Bahía de Los Ángeles, W. O. Gregg, 12 Oct. 1960 (CAS, SBMNH). 1.6 km S of Sauzalito Mine, C. Church, 23 Jan. 1971 (WBM). 1.6 km E of Rancho Arenoso along Mexico Rte. 1, in rockslides S of road, elev. 650 ft [200 m], W. B. Miller, W. N. Miller, 13 Dec. 1970 (WBM). 8 mi [13 km] N of El Progreso, E. S. Ross, D. Q. Cavagnaro, 1956 (CAS). 5 mi [8 km] W of Rancho Pénjamo, A. G. Smith, CAS 1961 Exped. (CAS). Agua Dulce Spring, in rocks on bluff S of the spring, elev. 2,200 ft [670 m], W. B. Miller, W. N. Miller, 13 Dec. 1970 (WBM). 17.0 mi [27.2 km] E of Desengaño along road to Bahía de Los Ángeles, in rocks, elev. 800 ft [140 m], W. B. Miller, W. N. Miller, 15 Dec. 1970 (WBM). 6.0 mi [9.7 km] S of Marmolito, A. G. Smith, I. L. Wiggins, CAS 1961 Exped. (CAS). 4.5 mi [7.2 km] NW of [Rancho] Mezquital, R. L. Bezey, W. C. Sherbrooke, 28 July 1965 (WBM). 4 mi [6.4 km] N of Rancho Mezquital, E. S. Ross, B. Hammerly, 1941 (SBMNH). 1 mi [1.6 km] and 5 mi [8 km] NW of Rancho Mezquital, A. G. Smith, CAS 1961 Exped. (CAS). Under dead agaves, summit of mesa just S of Rancho Mezquital, I. L. Wiggins, A. M. Vollmer, H. M. Hill, 8 Apr. 1961, CAS 1961 Exped. (Wiggins 1969); under dead agaves on rocky slope, elev. 500 ft [150 m], W. B. Miller, W. N. Miller, 17 Dec. 1970 (WBM). 6 mi [9.7 km] N of Cataviña, A. G. Smith, CAS 1961 Exped. (CAS). Arroyo Calamajué, 5 mi [8 km] S of the mission ruins, A. G. Smith, CAS 1961 Exped. (CAS). 7 mi [11 km] NNW of Rosarito, A. G. Smith, CAS 1961 Exped. (CAS). 15 mi [24 km] S of Punta Prieta, S. C. Williams, K. B. Blair, 7 July 1973 (CAS). BAJA CALIFORNIA SUR: 5.0 mi [8.0 km] E of San Ignacio, A. G. Smith, CAS 1961 Exped. (CAS). Sierra de Placeros, 22 mi [35 km] ESE of Bahía Tortugas, elev. 1,500 ft [460 m], D. E. Breedlove, 26 Mar. 1984 (CAS). Cerro de Banderilla, Sierra de Placeros, D. E. Breedlove, 24 Mar. 1984 (CAS).

For a discussion of the type locality of this species, see Hanna (1923:503–504). Miller (1972) figured the genitalia. Specimens from the Vizcaino Peninsula tend to be smaller than the usual *S. peninsularis* from farther north and more weakly sculptured, but identical shells are also found near Misión San Borja and in the vicinity of Bahía de Los Ángeles.

Sonorelix (Herpeteros) evermanni (Pilsbry, 1927)

(Fig. 38)

Distribution.—BAJA CALIFORNIA SUR: Turtle Bay [Bahía Tortugas], N side (TL), G D. Hanna, E. K. Jordan, June 1925 (Pilsbry 1927; CAS); H. Hemphill (CAS).

All known specimens are fossil. Taxonomic placement is provisional pending dissection of live-collected material.

Sonorelix (Herpeteros) merrilli (Bartsch, 1904)

(Fig. 38)

Distribution.—BAJA CALIFORNIA NORTE: Below San Quintín (TL), G. P. Merrill (Bartsch 1904; USNM).

No specimens besides the type lot have been collected. Taxonomic placement is provisional pending dissection of live-collected material.

Sonorelix (Herpeteros)(?) sp.

(Fig. 38)

Distribution.—BAJA CALIFORNIA NORTE: Puerto Refugio, Isla Ángel de la Guarda, CAS 1921 Exped. (Hanna 1923, as *Micrarionta* sp.; CAS).

An unidentified species of *Sonorelix* or *Eremarionta*. Its presence on Isla Ángel de la Guarda is noteworthy.

Genus **Greggelix** Miller, 1972

Subgenus **Greggelix** sensu stricto

Greggelix (Greggelix) indigena (Mabille, 1895)

(Fig. 39)

Synonyms.—*Helix digueti* Mabille, 1895. *Sonorella lohrii lioderma* Pilsbry, 1904.

Distribution.—BAJA CALIFORNIA SUR: above 800 m on peaks of the Sierra, throughout most of the central part of the Peninsula of California (TL), L. Diguet (Mabille 1895; MNHN). San José Comondú and 12 mi [19 km] SW of San Miguel Comondú (probably fossil), R. J. Drake, July 1953 (CAS, SBMNH). Mesa de San Alejo, NW of San Javier, Sierra de la Giganta, elev. 800 m, A. Carter, 1961 (CAS). Arroyo de La Purísima, in a lava rockslide 3.0 mi [4.8 km] E of San Isidro, along road to Canipolé, W. B. Miller, 21 Dec. 1970 (Miller 1972; WBM). San José Comondú in a rockslide at the edge of town along road to San Javier, W. B. Miller, 20 Dec. 1970 (Miller 1972; WBM). Near Moleje [Mulegé] (Pilsbry 1904; TL of *Sonorella lohrii lioderma*; ANSP).

The type locality of *Greggelix indigena* was not stated precisely and that of *Helix digueti* not specified except as Baja California. The synonymy of these taxa was demonstrated by Miller (1972).

Greggelix (Greggelix) loehrii (Gabb, 1868)

(Fig. 39)

Synonyms.—*Helix steganella* Mabille, 1895. *Helix invecta* Mabille, 1895.

Distribution.—BAJA CALIFORNIA SUR: "Higher table lands near Moleje [Mulegé]," (TL), W. M. Gabb, 1867 (Gabb

1868, H. B. Baker 1963, Coan and Bogan 1988; ANSP). Above 800 m on the peaks of the Sierra, throughout most of the central part of the Peninsula of California, L. Diguet (Mabille 1895; TL of *Helix steganella*; MNHN). San Javier (SBMNH); immediately S of the mission, in immense rockslide, W. B. Miller, 24 Oct. 1971 (Miller 1981b; WBM).

The type locality of *Helix invecta* was not specified except as Baja California. The synonymy follows Miller (1972).

Greggelix (Greggelix) punctata Miller, 1981

(Fig. 39)

Distribution.—BAJA CALIFORNIA SUR: Gulf slope of Sierra de la Giganta SW of Mulegé, along trail from Pie de la Cueta (2.9 mi [4.6 km] S of El Potrero) to Guajademí, in rockslide along trail about 1.5 mi [2.4 km] from Pie de la Cueta (or about 0.75 mi from trail summit), elev. ca. 2,450 ft [750 m] (TL), C. C. Christensen, W. B. Miller, R. L. Reeder, 23 Oct. 1972 (Miller 1981b; CAS). Guajademí, E. W. Nelson, E. A. Goldman, 30 Oct. 1905 (Miller 1981b; USNM).

Subgenus **Martirelix** Miller, 1982

Greggelix (Martirelix) babrakzaii Miller, 1982

(Fig. 39)

Distribution.—BAJA CALIFORNIA NORTE: Cañon Diablito, E slope of Sierra San Pedro Mártir, ca. 1 km up canyon from its mouth, among large granite boulders in decomposing granite, on right bank, elev. ca. 700 m (TL), R. H. Russell, W. B. Miller, 16 May 1970; N. Babrakzai, W. B. Miller, R. L. Reeder, 15 Mar. 1981 (Miller 1982; CAS). Cañon el Diablo, ca. 1.6 km N of Cañon Diablito, N. Babrakzai, W. B. Miller, R. L. Reeder, 15 Mar. 1981 (WBM). Canyon on E side of Sierra San Pedro Mártir, ca. 4 mi [6.4 km] NW of Algodón (rancho SW of San Felipe), E. C. Jaeger, 20 Dec. 1954 (SBMNH). Mouth of Cañon Borrego, ca. 3 mi [5 km] S of Cañon La Providencia, E side of Sierra San Pedro Mártir, E. C. Jaeger, G. A. Becker, 26 Jan. 1957 (SBMNH). Cañon Borrego, among granite rocks, elev. 1,100 ft [340 m], N. Briggs, 18 Dec. 1962 (SBMNH). 3 mi [5 km] and 0.5 mi [0.8 km] N of Colonia Morelia, Sierra San Pedro Mártir, 1 Jan. 1968 (SBMNH).

Greggelix (Martirelix) huertai Miller and Roth, sp. nov.

(Fig. 39)

Distribution.—BAJA CALIFORNIA NORTE: Cerro de la Mina de San Juan, Sierra la Libertad, in rockpiles on north side of entrance to the mine, 28°42.5′N, 113°34.7′W, elev. ca. 1,300 m, W. B. Miller et al., 26 Nov. 1981 (WBM).

Subgenus uncertain

Greggelix sp.

(Fig. 39)

An undescribed fossil species of *Greggelix* has been found at a locality along the Transpeninsular Highway at km 77, north of La Paz (WBM). A shell assignable to *Greggelix* was found in a fluvial-beach-terrace deposit at the north end of Cabo San Lázaro by J. T. Smith, 1985 (SBMNH).

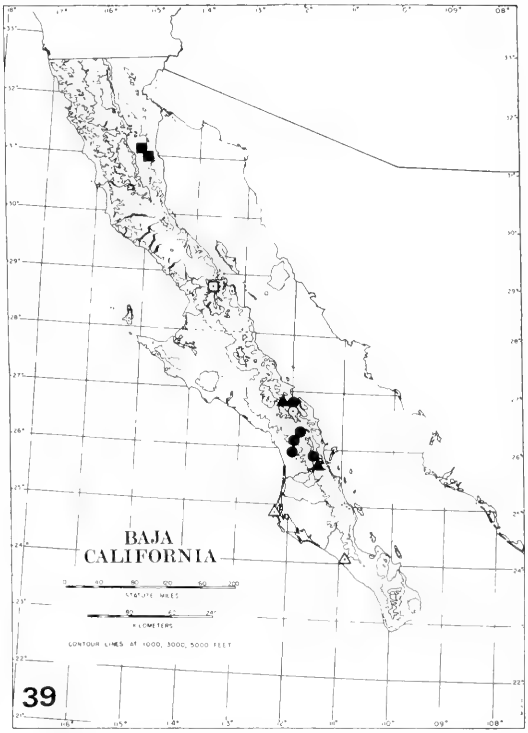

Figure 39. Distribution of *Greggelix indigena* (solid circles), *Greggelix loehrii* (solid triangles), *Greggelix punctata* (open circle), *Greggelix babrakzaii* (solid squares), *Greggelix huertai* (open square), and *Greggelix* sp. (open triangle).

Species Reported from Baja California in Error

The following species have been reported from Baja California but do not actually occur there. The names are given in the form in which the records were originally published.

Arionta rowelli (Newcomb, 1865). Record of fragments from Isla Guadalupe (Binney 1879) probably refers to *Helminthoglypta hannai hannai*.

Bulimulus (*Scutalus*) *baileyi* Dall, 1893. Dall's specimens from "Cape St. Lucas" were undoubtedly mislabeled, as the species has not been found in Baja California by recent workers. We have seen recent material from Sonora and Sinaloa.

Bulimulus proteus (Broderip, 1832). Baja Californian records by Binney (1861), Tryon (1867), Binney and Bland (1869), Fischer and Crosse (1870–1902), and Cooper (1891) refer to *Naesiotus montezuma,* as Dall (1893a) noted.

Epiphragmophora arnheimi Dall, 1896. Reported from Nachoguero Valley [Cañada Macho Güero], Lower California (Dall 1896, 1897); the specimen, USNM 128949, proves to be *Helminthoglypta* sp., cf. *H. traskii isidroensis* (Bartsch, 1918). The specimen label specifies "Nachoguero Valley, San Diego Co." (California), and we therefore exclude the record from Baja California.

Epiphragmophora ellipsostoma Pilsbry, 1894. Type locality stated to be "San Juan del Norte," which Pilsbry (1894) inferred to be on the east coast of Baja California. The label with the holotype, ANSP 10745, states "San Juan del Norte, SE Nicaragua, W. M. Gabb," the "SE Nicaragua" later scratched over in pencil. The specimen is a thin, light tan, strongly malleated shell, possibly belonging to a species of *Tryonigens* or *Leptarionta.* It has the appearance of a forest snail and is definitely not from Baja California. It may have been collected while Gabb was working as a geologist in Costa Rica, 1873–1876; his fossils from Costa Rica were bequeathed to ANSP (Dall 1909).

Gastrocopta dalliana dalliana (Sterki, 1898). Reported from Baja California by Bequaert and Miller (1973); here redetermined as *G. rixfordi.*

Gastrocopta procera (Gould, 1840). Reported from La Purísima (Bequaert and Miller 1973); here redetermined as *G. pellucida hordeacella.*

Hawaiia minuscula (Binney, 1840). Specimens so identified by Bequaert and Miller (1973) are here reassigned to *Hawaiia* sp.

Helix (*Macrocyclis*) *duranti* Newcomb, 1864. Record by Hemphill (1881) from near San Tomás River refers to *Haplotrema caelatum.*

Helix (or *Arionta*) *facta* Newcomb, 1864. Records from Isla Guadalupe (Binney 1879; Anonymous 1884; Cooper 1887) refer to *Micrarionta guadalupiana.*

Helix (*Arionta*) *kelletti* Forbes, 1850. Record by Hemphill (1881) from N of Todos Santos Bay probably refers to *Plesarionta stearnsiana.*

Helix remondi Tryon, 1863. Gabb's (1868) record from foothills of the Sierra de Calmallí refers to *Sonorelix peninsularis.*

Helix traskii var. *carpenteri* Newcomb, 1861. Record from Isla Guadalupe (Cooper 1892a) refers to *Helminthoglypta hannai hannai.* Records from Islas Los Coronados (Hemphill 1881; Orcutt 1886; Cooper 1892a; Gratacap 1901, as *Arionta carpenteri*) refer to *Helminthoglypta traskii coronadoensis.* Hemphill's (1881) "*Helix* (*Arionta*) *carpenteri*" from Trinidad may refer to *Sonorelix peninsularis.*

Helix (*Macrocyclis*) *voyana* Newcomb, 1865. Record by Hemphill (1881) from Todos Santos Bay refers to *Haplotrema transfuga.*

Limax guatemalensis Crosse and Fischer, 1870. Record "dans les herbes au bord des torrents de la Laguna" (Mabille 1895) may refer to *Deroceras laeve,* which has been collected at La Laguna, Sierra de la Victoria, by Miller and Christensen.

Macrocyclis sportella (Gould, 1846). Records from "near United States boundary" (Orcutt 1886; Cooper 1892a) refer to *Haplotrema transfuga.*

Pupa chordata (Pfeiffer, 1856). Records from near Bahía San Quintín (Orcutt 1886; Cooper 1892a) refer to *Pupilla sterkiana.*

Selenites duranti var. *catalinensis* Hemphill in Binney, 1890. Binney's (1890) records from Punta Banda and San Tomás River refer to *Haplotrema caelatum.*

Succinea cingulata Forbes, 1850. Hemphill's (1881) record from near mouth of San Tomás River may refer to *S. californica.*

Succinea oregonensis Lea, 1841. Record from north of 31°N (Orcutt 1886) probably refers to species here provisionally allocated to *Catinella rehderi.*

BIOGEOGRAPHY

The native land mollusk fauna of Baja California (excluding the doubtful *Polygyra behri* from beach drift) consists of 117 species and subspecies, distributed among 36 genera of 18 families (Table 1). All but the two species of the amphibious prosobranch, *Truncatella,* are pulmonates. For the numerical part of the following analysis, the operational taxonomic unit is the species. Thus, for example, the three subspecies of *Nearctula rowelli* are treated as one taxon; the endemic Baja Californian subspecies *Glyptostoma newberryanum depressum* is treated as a representative of the largely Californian species *G. newberryanum.* The analysis includes the land mollusks of the gulf islands San Esteban and San Pedro Mártir, politically parts of Sonora; the only taxon that would not otherwise be included is *Eremarionta rowelli bechteli.* Because of doubts about its true locality, *Spartocentrum eisenianum* is excluded. Four species (*Rabdotus*(?) sp., *Oxyloma nuttallianum, Sonorelix* (*Herpeteros*) *evermanni,* and *Greggelix* sp.) and one zonal occurrence of another (*Xerarionta areolata*) are known only from fossil shells. Although of interest for what they tell about distributional trends through time, these also are excluded from the numerical analysis. The final data set consists of 102 species.

The land mollusk fauna exhibits sharply distinct regional divisions (Miller 1973a, 1981b; Christensen 1979). To a large extent the molluscan zones correspond to other biological divisions proposed for the peninsula and adjacent islands. Shreve (1951) and Wiggins (1960b, 1980) recognized three major phytogeographic areas, which have met considerable acceptance by later authors: the northwest or Californian region, the Cape region, and the Sonoran Desert. Shreve (1951) divided the Baja Californian part of the Sonoran Desert into four subdivisions: Lower Colorado Valley, Central Gulf Coast, Vizcaino Region, and Magdalenan Region, each also having a vegetational and a floristic designation. Zoogeographic subdivisions proposed for the herpetofauna (Savage 1960; Murphy 1983) and scorpions (Williams 1980) have many points in common with those based on plants.

The molluscan faunal regions that we recognize (Fig. 40) depart only slightly from the phytogeographic regions. The primary divisions are the Californian, Sonoran, and Cape regions; subdivisions of the Californian and Sonoran regions are here termed "zones" (cf. Murphy 1983). All four possible types of zonal distribution occur: (a) single-zone endemics; (b) species endemic to a single zone in Baja California but also occurring extralimitally; (c) species restricted to Baja California but occurring in more than one zone; and (d) species present in more than one zone in Baja California and also occurring extralimitally (Tables 1, 2).

CALIFORNIAN REGION.—The Californian region (CA) extends west from the upper east slopes of the Sierra Juárez and Sierra San Pedro Mártir, above the (Sonoran) San Felipe Desert, to the Pacific coast and as far south as the southern margin of the Llano Santa María, inland from Bahía San Quintín. It includes the nearshore islands Los Coronados, Todos Santos, and San Martín, and also Isla Guadalupe, approximately 275 km off the west coast. The region is largely a southern continuation of Munz and Keck's (1959) California Biotic Province. Its eastern boundary is relatively sharp but the transition southward to desert is more gradual. Rainfall is mainly from the northwest, in winter and spring, decreasing southward into the desert. Plant formations include coastal sage scrub, chaparral, and, above about 1,300–1,800 m, coniferous forest, which some workers (e.g., Wiggins 1980) treat as a separate floristic region.

Three subdivisions of the Californian region can be recognized: the Northern Montane zone (NM), approximately equivalent to the Baja California Coniferous Forest of Wiggins (1980); the Northwest Coastal zone (NC), extending from the foothills below the coniferous forest on the west slopes of the Sierra Juárez and Sierra San Pedro Mártir to the Pacific coast, including the nearshore islands; and Isla Guadalupe (IG).

In the Northern Montane zone are found *Pupilla hebes, Vallonia cyclophorella,* and *Euconulus fulvus,* species with wide distributions in the cordilleran region of the western United States. Although endemic plant species are rather common in the coniferous forest, the only single-zone endemic (category a) land mollusks thus far discovered are *Helminthoglypta reederi* and the unnamed *Helminthoglypta* species from the Sierra Juárez.

The land mollusk fauna of Isla Guadalupe is highly distinctive but of a Californian character. Although the island is floristically Sonoran, except for a small zone of coniferous forest (Wiggins 1980, map 4), the fauna contains no genera or species of mollusks that are otherwise restricted to the Sonoran Desert. *Truncatella guadalupensis* may be most closely related to a Caribbean or an Indo-Pacific species (Lindberg et al. 1980). All other species either have the remainder of their distribution in the Californian region (including the part of mainland California that belongs to the Peninsular Ranges physiographic province, and the islands of the southern California borderland) or have their closest relatives there.

The Northwest Coastal Zone shares only one species (*Nearctula rowelli*) with Isla Guadalupe, but its faunal affinities are much the same: the extralimital ranges of species, or their closest rel-

TABLE 1. Distribution by region and zone of the land Mollusca of Baja California. Endemism categories: (a) single-zone endemic; (b) species endemic to a single zone in Baja California but also occurring extralimitally; (c) species restricted to Baja California but occurring in more than one zone; (d) species present in more than one zone in Baja California and also occurring extralimitally. Regions: CA, Californian; SO, Sonoran; CP, Cape. Zones: CD, Colorado Desert; GC, Gulf Coastal; IG, Isla Guadalupe; MG, Magdalenan; NC, Northwest Coastal; NM, Northern Montane; VI, Vizcaino Desert. * (asterisk) = fossil taxon.

Taxon	Endemism category	Region and zone
Prosobranchia		
Truncatellidae		
Truncatella californica	(b)	CA (NC)
T. guadalupensis	(a)	CA (IG)
Pulmonata		
Pupillidae		
Gastrocopta (*G.*) *pellucida hordeacella*	(d)	SO (MG, GC), CP
G. (*G.*) sp., cf. *G.* (*G.*) *riograndensis*	(b)	SO (GC)
G. (*Immersidens*) *allyni*	(a)	CP
G. (*I.*) *rixfordi*	(c)	SO (MG, GC), CP
Pupilla (*P.*) *hebes*	(b)	CA (NM)
P. (*Striopupilla*) *sterkiana*	(a)	CA (NC)
P. (*S.*) *goniodon*	(c)	CA (IG), SO (VI)
P. (*S.*) *guadalupensis*	(a)	CA (IG)
Pupoides albilabris	(d)	SO (MG, GC), CP
P. catalinensis	(a)	SO (GC)
Vertigo (*V.*) *berryi*	(b)	CA (NC)
V. (*V.*) *ovata*	(b)	CP
Nearctula rowelli	(d)	
diegoensis		CA (IG, NC)
catalinaria		CA (IG, NM)
guadalupensis		CA (IG)
N. degeneris	(a)	CA (IG)
Sterkia (*S.*) *calamitosa*	(a)	
calamitosa		CA (NC)
martiniana		CA (NC)
S. (*S.*) *hemphilli*	(d)	CA (NC), SO (VI)
S. (*Metasterkia*) *clementina*	(b)	CA (IG)
Valloniidae		
Vallonia cyclophorella	(b)	CA (NM)
Strobilopsidae		
Strobilops californica	(a)	CP
Subulinidae		
Lamellaxis gracilis (introduced)		CP
Opeas pumilum (introduced)		CP
Haplotrematidae		
Haplotrema (*H.*) *guadalupense*	(a)	CA (IG)
H. (*H.*) *transfuga*	(b)	CA (NC)
H. (*Geomene*) *caelatum*	(b)	CA (NC)
Bulimulidae		
Naesiotus(?) *altus*	(a)	CP
N. beldingi	(a)	CP
N. cosmicus	(a)	CP
N. dentifer	(c)	
dentifer		SO (GC)
johnstoni		SO (GC)
lamellifer		SO (VI, MG, GC)
slevini		SO (GC)
N. excelsus	(a)	CP
N. gabbi	(a)	SO (MG)

TABLE 1. Continued.

Taxon	Endemism category	Region and zone
N. gigantensis	(c)	SO (MG, GC)
N. hannai	(a)	SO (MG)
N. harribaueri	(a)	CP
N. laevapex	(a)	SO (GC)
N. montezuma	(a)	CP
N. pallidior	(a)	CP
N. rimatus	(a)	CP
N. spirifer	(a)	CP
N. veseyianus	(a)	SO (GC)
N. xantusi	(a)	CP
N.(?) sp.	(a)	CP
Rabdotus (*R.*) *ceralboensis*	(a)	SO (GC)
R. (*R.*) *chamberlini*	(a)	SO (GC)
R. (*R.*) *levis*	(a)	CP
R. (*R.*) *pilula*	(a)	CP
R. (*R.*) *sufflatus*	(c)	SO (MG, GC), CP
R. (*Plicolumna*) *abbreviatus*	(a)	CP
R. (*P.*) *artemisia*	(c)	SO (GC), CP
R. (*P.*) *inscendens*	(c)	SO (GC), CP
R. (*P.*) *perhirsutus*	(a)	CP
R. (*P.*) *ramentosus*	(a)	CP
**R.*(?) sp.	(a)	SO (GC)
Berendtia taylori	(c)	SO (MG, GC)
Spartocentrum digueti	(a)	SO (MG)
S. eisenianum		CP?
S. insulare	(a)	SO (GC)
S. irregulare	(c)	SO (MG, GC)
S. vanduzeei	(a)	SO (GC)
S. sp.	(a)	SO (MG)
Punctidae		
Paralaoma caputspinulae	(b)	CA (NC)
Helicodiscidae		
Helicodiscus (*Hebetodiscus*) *singleyanus*	(d)	SO (GC), CP
Arionidae		
Binneya (*B.*) *notabilis*	(b)	CA (NC)
B. (*Allothyra*) *guadalupensis*	(a)	CA (IG)
Succineidae		
Succinea californica	(a)	CA (NC)
S. guadelupensis	(a)	CA (IG)
S. rusticana	(d)	CA (NC), SO (VI), CP
Catinella rehderi	(d)	CA (NC), SO (VI, MG), CP
**Oxyloma nuttallianum*	(b)	SO (MG)
Helicarionidae		
Euconulus fulvus	(b)	CA (NM)
Zonitidae		
Glyphyalinia indentata paucilirata	(d)	SO (MG), CP
Striatura (*Pseudohyalina*) *pugetensis*	(b)	CA (IG)
Hawaiia sp.	(d?)	SO (MG), CP
Limacidae		
Milax gagates (introduced)		CA (NC)
Deroceras laeve	(d)	CA (NC), CP
Polygyridae		
[*Polygyra* (*Erymodon*) *behri*		SO (GC)—doubtful]

TABLE 1. Continued.

Taxon	Endemism category	Region and zone
Thysanophoridae		
Thysanophora hornii	(d)	SO (MG, GC), CP
Oleacinidae		
Pseudosubulina eiseniana	(a)	CP
P. tastensis	(a)	CP
Megomphicidae		
Glyptostoma newberryanum depressum	(b)	CA (NC)
Oreohelicidae		
Radiocentrum discus	(a)	CP
R. exorbitans	(c)	SO (MG), CP
Helminthoglyptidae		
Helminthoglypta (H.) tudiculata	(b)	CA (NC)
H. (Charodotes) hannai	(a)	
hannai		CA (IG)
diodon		CA (IG)
H. (C.) coelata	(b)	CA (NC)
H. (C.) misiona	(a)	CA (NC)
H. (C.) reederi	(a)	CA (NM)
H. (C.) traskii	(b)	
coronadoensis		CA (NC)
subsp.		CA (NC)
H. (subgenus?) sp.	(a)	CA (NM)
Micrarionta guadalupiana	(a)	CA (IG)
Plesarionta orcutti	(a)	CA (NC)
P. stearnsiana	(d)	CA (NC), SO (VI)
Xerarionta areolata	(a)	SO (MG) (*GC)
X. levis	(c)	
levis		CA (NC), SO (VI)
canescens		SO (VI)
**crassula*		SO (VI)
X. pandorae	(a)	SO (VI)
Eremarionta indioensis	(b)	SO (CD)
E. rowelli bechteli	(b)	SO (GC)
E. sp.	(a)	SO (CD)
Sonorelix (Herpeteros) chacei	(a)	CA (NC)
S. (H.) inglesiana	(a)	CA (NC)
S. (H.) peninsularis	(c)	SO (VI, MG, GC)
**S. (H.) evermanni*	(a)	SO (VI)
S. (H.) merrilli	(a)	CA (NC)
S. (H.)(?) sp.	(a)	SO (GC)
Greggelix (G.) indigena	(c)	SO (MG, GC)
G. (G.) loehrii	(a)	SO (MG)
G. (G.) punctata	(a)	SO (MG)
G. (Martirelix) babrakzaii	(a)	SO (CD)
G. (M.) huertai	(a)	SO (VI)
**G.* (subgenus?) sp.	(a)	CP

atives, occur in the Peninsular Ranges part of southern California or on the borderland islands. *Sterkia hemphilli* also occurs farther south at Punta Abreojos, the southern limit of the genus in western North America (Christensen 1979). The Baja Californian endemic subgenus *Pupilla* (*Striopupilla*) is limited to the Californian region except for the occurrence of *P.* (*S.*) *goniodon* on Isla San Benito del Oeste. The occurrences of *S. hemphilli* and *P.* (*S.*) *goniodon* in the Sonoran region are probably relicts of the formerly greater extent of the Californian region, now reduced by

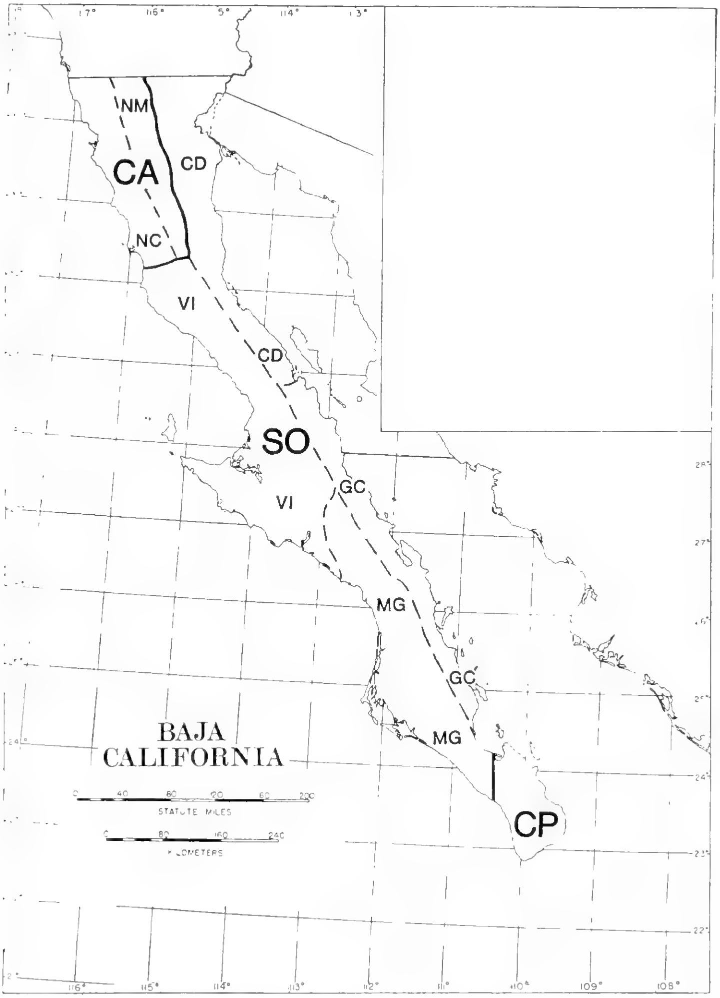

FIGURE 40. Molluscan faunal regions and zones defined in this report. Abbreviations for regions: CA, Californian; SO, Sonoran; CP, Cape. Abbreviations for zones: NC, Northwest Coastal; NM, Northern Montane; CD, Colorado Desert; VI, Vizcaino Desert; GC, Gulf Coastal; MG, Magdalenan. Not shown: IG, Isla Guadalupe zone of Californian region.

late Quaternary encroachment of the arid Sonoran environment (Axelrod 1979).

Except for one isolated, probably relict occurrence in the Sierra La Libertad, the genus *Plesarionta* is limited to the Californian region. The northern limit of *Xerarionta* in Baja California occurs slightly north of the southern interface between the Californian and Sonoran regions. The genus reappears on the southern California Channel Islands and the adjacent mainland of Los Angeles County. The present range of *Plesarionta* and *Xerarionta* coincides closely with the extent of fog from the Pacific Ocean (Miller 1973a; Christensen 1979). Pleistocene or early Holocene fossils of *Xerarionta areolata* on the east side of the peninsula and on the gulf islands of Monserrate and Espíritu Santo suggest that the influence of maritime fog was formerly more widespread.

The slug *Deroceras laeve* is shared with the Cape region; this species also ranges north to the Arctic and south to Central America. The succineids *Succinea rusticana* and *Catinella rehderi,* shared with the Cape and Sonoran regions, range to the Pacific Northwest. However, as noted earlier, these identifications based on shells alone are provisional.

Nearshore islands and island groups of the

TABLE 2. Summary of land mollusk fauna of Baja California by region, zone, and endemism category. Endemism categories as in Table 1. Numbers in parentheses = fossil taxa (additional to living taxa).

Region and zone	Regional/zonal distribution of species				
	(a)	(b)	(c)	(d)	Total
Californian (CA)	18	15	2	6	41
Northwest Coastal (NC)	8	10	1	6	25
Northern Montane (NM)	2	3	0	1	6
Isla Guadalupe (IG)	8	2	1	1	12
Sonoran (SO)	19 (2)	3 (1)	13	10	45 (3)
Colorado Desert (CD)	2	1	0	0	3
Vizcaino Desert (VI)	2 (1)	0	4	4	10 (1)
Magdalenan (MG)	7	0 (1)	9	6	22 (1)
Gulf Coastal (GC)	8 (1)	2	10 (1)	4	24 (2)
Cape (CP)	21 (1)	1	5	9	36 (1)

Northwest Coastal zone show a relatively low level of endemism. *Helminthoglypta traskii coronadoensis* on the Islas Los Coronados and *Sterkia calamitosa martiniana* on Isla San Martín are only subspecifically distinct from mainland populations. The other insular taxa do not show even this level of differentiation.

SONORAN REGION.—The truly arid region lying between the Californian and Cape regions is part of the Sonoran Desert, which also extends into Sonora, Arizona, and southeastern California (Shreve 1951; Axelrod 1979). About 70 per cent of the area of Baja California is desert (Gould and Moran 1981), including the gulf islands.

As an arid environment of regional extent, the Sonoran Desert is a young feature, emerging particularly in late Pliocene and Pleistocene interglacial stages, perhaps most strongly since the close of the Wisconsinan glacial stage (Axelrod 1979, fig. 37). Its development has interrupted the formerly continuous distribution of many plant species, such as the disjunct chaparral vegetation of California and Arizona and species of the insular and maritime flora of southern California with their nearest allies in the Sierra Madre Occidental of Mexico (Axelrod 1979:9–11). The ranges of some molluscan taxa have been similarly interrupted. *Radiocentrum,* with species in the Cape region of Baja California, in southern Arizona and New Mexico, and on Santa Catalina Island, California, shows trans-Sonoran disjunction (Hochberg et al. 1987). *Gastrocopta allyni* (allied to *G. ashmuni* (Sterki) and *G. cochisensis* (Pilsbry and Ferriss) of Arizona and New Mexico), *Vertigo ovata,* and perhaps *Gastrocopta riograndensis* may represent the same type of distribution. *Deroceras laeve* occurs in the Californian and Cape regions but not in the Sonoran region.

The Colorado Desert zone (CD) is equivalent to the Baja Californian part of the Lower Colorado Valley (=microphyllous desert, =*Larrea-Franseria* region) of Shreve (1951). It lies between the lower east slopes of the Sierra Juárez and Sierra San Pedro Mártir and the Gulf of California and extends as far south as Bahía de Los Ángeles. Beyond Baja California, the microphyllous desert extends into southern California, Arizona, and Sonora. This zone is one of the hottest and most arid of the Sonoran region. The mountains to the west isolate it from Pacific breezes; both summer and winter rainfall are sporadic. The most characteristic plant formation is *Larrea* (creosote bush) scrub, but large areas are sandy plains with little perennial vegetation.

Land mollusks are rare and confined to canyons of the larger ranges. *Eremarionta* is found in canyons on the eastern slopes of the Sierra Juárez and Sierra San Pedro Mártir. It also occurs on Isla San Esteban in the gulf and in Sonora as far south as Puerto Libertad, in zones of sarcocaulescent desert. Distribution of snails of this genus in low mountain ranges in the Mojave, Colorado, and Yuma deserts of southern California and western Arizona (Bequaert and Miller 1973, fig. 2) suggests a correlation with the northward extent of the Gulf of California in Pliocene time. Marine fossils and sediments indicate that a Pliocene gulf extended as far north as San Gorgonio Pass, in the San Bernardino Mountains, California (Allen 1957). At that time the San Gabriel and San Bernardino ranges had not yet undergone their major uplift (Axelrod 1979), and were not blocking moisture from regions to the east as they do today. Marine microfossils from drill cores taken in Cadiz and Danby dry lakes, eastern San Bernardino County, indicate a similar northward extension of marine conditions nearer to the present course of the Colorado River (Bassett et al. 1959), probably during the Pliocene. Most modern occurrences of *Eremarionta* are within or adjacent to the shoreline inferred for the maximum Pliocene extent of seas (Durham and Allison 1960, fig. 5). Thus the distribution of this, one of the most xerophilic of North American land snail genera, may originally have come about under basically maritime conditions.

The subgenus *Greggelix* (*Martirelix*) is restricted to this zone except for *G.* (*M.*) *huertai* at a single locality in the Sierra La Libertad, near the northern end of the Vizcaino Desert zone.

Because the Colorado Desert zone has no species in common with any other zone, there might be some logic in regarding it as a primary faunal division. However, in the arid environment where extreme isolation fosters a high degree of short-range, allopatric endemism, shared genera or subgenera are likely to be better indicators of faunal affinity than species. (As Page [1987] has pointed out, non-uniform taxonomic treatments hamper comparisons between biotas and, at least at present, taxonomic categories are not broadly intercomparable.) At the generic (*Eremarionta*) and subgeneric (*Martirelix*) level, the Colorado Desert zone shows closest affinity to the Gulf Coast and Vizcaino Desert zones of the Sonoran region.

The Vizcaino Desert zone (VI) is equivalent to the Vizcaino Region (=sarcophyllous desert, =*Agave-Franseria* region) of Shreve (1951). It occupies approximately the central third of the peninsula west of the crest of the mountains and shares a roughly north-south boundary with the Magdalenan zone at about 113°W. There is light winter and early spring rainfall, more sporadic in the south and interior than in the north, and rare summer rainfall in the Sierras Calamajué, San Borja, and Calmallí along the eastern edge of the zone. A narrow coastal strip about 10 km wide is influenced by the humidity of Pacific Ocean winds and fog. Vegetationally the zone is characterized by succulent-leaved plants such as *Agave* and *Dudleya,* and in many areas a dense growth of lichens. Vast areas are caliche flats or alkaline plains with *Atriplex* scrub and support no land mollusks.

Few species occur in this zone, and only two (20%), *Xerarionta pandorae* of the Islas San Benito and *Greggelix* (*Martirelix*) *huertai* from the Sierra La Libertad, are single-zone endemics. *Sonorelix* (*Herpeteros*) *evermanni,* as yet known only from fossil specimens, may be another. *Xerarionta levis,* locally abundant under favorable conditions, laps into the southern part of the Northwest Coastal zone. *Sonorelix* (*Herpeteros*) *peninsularis* has peripheral localities in the Magdalenan and Gulf Coastal zones. Related species of *Sonorelix* (*Herpeteros*) occur in the Californian region, as far north as Los Angeles County. *Plesarionta stearnsiana* and *Naesiotus dentifer,* predominantly species of the Northwest Coastal and Magdalenan-Gulf Coastal zones respectively, occur marginally within the Vizcaino Desert zone. Two succineids are shared with both the Californian and Cape regions. The 80% of taxa shared with other Baja Californian zones (category c and d species) support Christensen's (1983) characterization of the central part of the peninsula as a zone of transition between northern and southern faunas.

The islands of the Vizcaino Desert zone show a moderate level of endemism: *Xerarionta pandorae* on the San Benitos, and two subspecies (one extinct) of *Xerarionta levis* on Islas Cedros, Natividad, and San Gerónimo. Populations of *X. levis* on Isla Asunción are assigned to the nominate subspecies.

The Magdalenan zone (MG) includes the desert of the southern third of the peninsula, from the drainage divide of the Sierra de la Giganta to the Pacific coast, almost as far south as Todos Santos. Regions of arid tropical scrub and dry tropic forest in the Sierra de la Giganta have previously been excluded from the definition of Sonoran Desert (Axelrod 1979; Wiggins 1980). The parts of that range that have been explored for land mollusks have yielded a fauna that strongly resembles those of the adjacent parts of the Magdalenan and Gulf Coastal zones, and therefore we do not recognize a separate zone for the Gigantas. The coastal strip of the Magdalenan zone is subject to much the same type of marine influence as the coast of the Vizcaino

Desert zone. On the Pacific coast most rain falls in the late winter; in the interior there are summer thunderstorms as well. A diversity of plant formations is present; Shreve (1951) regarded a joint dominance of trees and large succulents to be characteristic of the zone. In the southern half of the zone the desert vegetation interfingers with dry tropic forest typical of the Cape region; in the lower foothills of the Sierra de la Giganta it grades into tropical scrub.

The zonal endemics belong to *Naesiotus* and the characteristically Baja Californian genera *Spartocentrum* and *Greggelix*. *Xerarionta areolata* is a zonal endemic as a Recent species, but occurs as Pleistocene or early Holocene fossils in the Gulf Coastal zone. The Magdalenan zone contains the only Baja Californian occurrence (as empty shells, possibly fossil) of *Oxyloma nuttallianum,* which ranges through California to the Pacific Northwest. The zone shares 11 taxa with the Gulf Coastal zone and nine with the Cape region. Four of these are wide-ranging taxa that also extend into the arid southwestern United States and for various distances into Mexico (*Glyphyalinia indentata paucilirata, Thysanophora hornii*), Central America (*Gastrocopta pellucida hordeacella*), and South America (*Pupoides albilabris*). The other shared taxa belong to the genera *Naesiotus, Rabdotus, Berendtia, Spartocentrum, Sonorelix* (*Herpeteros*), and *Greggelix* (*Greggelix*). The only island endemic in the zone is *Naesiotus hannai* on Islas Margarita and Magdalena; the only other land mollusk reported from these islands is the common peninsular *Xerarionta areolata.*

The Gulf Coastal zone (GC) includes all of the islands of the Gulf of California and a strip along the east coast of the peninsula from Bahía de Los Ángeles to the west side of Bahía de La Paz. The zone is largely equivalent to the insular and Baja Californian parts of the Central Gulf Coast (=sarcocaulescent desert, =*Bursera-Jatropha* region) of Shreve (1951). Sarcocaulescent desert vegetation also occurs in two narrow coastal strips on the extreme eastern edge of the Cape region. The molluscan fauna of these strips consists entirely of species also found farther west, in the Cape molluscan region; they are therefore included in that region. Rainfall in the Gulf Coastal zone is very low and uncertain, occurring in either late winter or midsummer but often absent for several seasons in succession. The characteristic vegetation includes shrubs and small trees with swollen-appearing trunks.

The zonal endemics belong mainly to the genera *Naesiotus, Rabdotus,* and *Spartocentrum. Pupoides catalinensis* is an endemic species related to the widespread Neotropical *P. albilabris. Eremarionta rowelli bechteli* is an endemic subspecies of a species that ranges to the Mojave and Colorado deserts. The probable *Sonorelix* (*Herpeteros*) species from Isla Ángel de la Guarda belongs to a subgenus that ranges through the Vizcaino Desert zone into the Californian region. *Gastrocopta* sp. (cf. *G. riograndensis*) may be the same species as *G. riograndensis* of Texas and northeastern Mexico. The zone shares 11 taxa with the Magdalenan zone and eight with the Cape region, with geographic affinities sorting out much like those of the Magdalenan zone.

Twenty-one taxa are recorded from the islands of the Gulf of California. Eleven (including three subspecies of *Naesiotus dentifer* and one of *Eremarionta rowelli*) do not occur anywhere on the mainland. Twelve of the 16 island occurrences of these insular endemics are on "non-land-bridge" islands—those separated from the mainland by channel depths greater than 130 m, which therefore would not have had peninsular connections during the lowest sea levels of the Wisconsinan glacial stage. In contrast, 16 of 33 island occurrences of taxa which are not insular endemics are on non-land-bridge islands.However, the difference between the two endemism categories is not significant, whether all land mollusks are considered ($\chi^2 = 2.105, 0.20 > P > 0.10$) or only those with adult shell size greater than 10 mm ($\chi^2 = 3.506, 0.10 > P > 0.05$).

CAPE REGION.—The Cape region (CP) is equivalent to the Arid Tropical Region of Wiggins (1980) plus the two strips of sarcocaulescent desert along the Cape's eastern shore, and includes the entire southern end of the peninsula south of the Sierra de la Giganta. The dominant plant formations are arid tropic scrub, dry tropic forest, and on the higher peaks of the Sierra de la Victoria, pine and oak woodland.

The rate of single-zone (category a) endemism is high (58%) and largely accounted for by diversity in *Naesiotus* and *Rabdotus.* The region shares nine taxa with the Magdalenan and eight with the Gulf Coastal zone, six of these being wide-ranging taxa extending to or through the arid southwestern United States. The slug *Dero-*

TABLE 3. Membership of monophyletic groups (each consisting of one or more Baja Californian species) in generalized tracks. Numbers in parentheses = fossil taxa (additional to living taxa).

	Generalized track				
Region and zone	Peninsular Ranges-Calif. Borderland	Cordilleran	Colorado/ Mojave Desert	Neotropical	Arizona-Northern Mexico
Californian (CA)	23	5	0	1	1
Northwest Coastal (NC)	17	2	0	0	1
Northern Montane (NM)	3	3	0	0	0
Isla Guadalupe (IG)	7	1	0	1	0
Sonoran (SO)	7 (2)	1	2	5	4
Colorado Desert (CD)	0	0	1	0	1
Vizcaino Desert (VI)	6	1	0	0	1
Magdalenan (MG)	3 (1)	0	0	3	4
Gulf Coastal (GC)	1 (1)	0	1	5	4
Cape (CP)	2	1	0	6	8

ceras laeve and two succineids are shared with the Californian region, the succineids with the Vizcaino Desert zone as well.

"TRACK RECORD"

Lines on a map connecting the taxa of Baja California with their sister taxa elsewhere—"tracks" in the parlance of vicariance biogeography, which adopted it from the Panbiogeography of Croizat (1964:7; see Rosen 1976; Page 1987)—coincide to form a small number of generalized tracks. "Sister taxa" in this context means either the disjunct populations of a species or the disjunct species of a monophyletic group. The delineation of tracks as a descriptive device does not in itself imply either a dispersal or vicariance explanation of the historical relationship between the taxa so connected.

Resolution of the biogeographic history of a monophyletic group is sometimes said to require a statement of the cladistic relationships of its component taxa—at the minimum, a three-taxon statement of the form "taxon *a* and taxon *b* are more closely related than either is to taxon *c*." Few groups of North American land mollusks have been subjected to this type of analysis; therefore, most of the sister-taxon relationships cited here are based on inspection of standard monographs of the groups involved (e.g., Pilsbry 1939–48; Christensen 1978). Future phylogenetic studies will permit refinement of the conclusions presented here. The five generalized tracks are described below; their membership is summarized in Table 3.

1. Peninsular Ranges-California Borderland Track. As previously noted, northwestern Baja California is commonly viewed as part of a Californian biotic province. Many species' ranges extend north through the Peninsular Ranges and the islands off the southern California coast at least as far as the Transverse Ranges. A substantial number of these tracks further extend to the Pacific Northwest, Alaska, and (in the case of *Paralaoma caputspinulae*) even to Kamchatka.

Vertigo berryi extends north to the Transverse Ranges and thence to the Spring Range, Nevada (Pratt 1976); as a Quaternary fossil it occurs in Arizona, Nevada, and southeastern California. The genus *Nearctula* ranges along the coast of California as far north as the San Francisco Bay area; some subspecific differentiation occurs on the Borderland islands. Both subgenera of *Haplotrema* range into coastal southern California; *Haplotrema* sensu stricto also extends northward to the North Coast Ranges in Mendocino County (Roth, in press). *Binneya* occurs on the California Borderland islands.

Succinea rusticana, Catinella rehderi, Oxyloma nuttallianum, and *Striatura pugetensis* range through southern California to the Pacific Northwest. Author Miller has dissected specimens of *Succinea* from the Salinas Valley, California, which prove to be similar or identical to *S. californica.* Affinities of the undissected *Succinea* *guadelupensis* are unknown, but conchologically similar specimens (placement in *Succinea* confirmed by Roth's dissection) occur on San Nicolas Island, California.

Helminthoglypta (*H.*) *tudiculata* extends north to the Transverse Ranges; related species extend northward along the west side of the Sierra Nevada. *Helminthoglypta* (*Charodotes*) occupies a similar range as far north as the north side of the Transverse Ranges. The distribution of *Plesarionta* and *Xerarionta* (the two genera differ anatomically only in the presence or absence of a verge at the summit of the penial sac) participates in this track and during the Pleistocene or early Holocene extended to the Gulf Coastal zone. However, a species of *Xerarionta* has been described from the Eocene of Trans-Pecos Texas (Roth 1984), where it occurs with the camaenid genus *Pleurodonte,* now restricted to the Greater Antilles. Thus, the history of *Xerarionta* and *Plesarionta* may also involve the Neotropical track. *Sonorelix* (*Herpeteros*) is endemic to Baja California, with the exception of one species, *Sonorelix* (*Herpeteros*) *angelus* Gregg, 1949, in the Transverse Ranges. The presumed sister taxon, *Sonorelix* sensu stricto, is endemic to the Mojave and Colorado deserts.

2. Cordilleran Track. Taxa of this group range through the higher mountain chains of western North America, in some cases to Arctic or Subarctic regions. Many of the genera are Holarctic. Some elements, such as *Deroceras laeve,* extend south in mesic situations as far as Central America. Others also occur in isolated montane settings such as the San Bernardino Mountains of California. Bequaert and Miller (1973, see especially pp. 57–64) summarized the ranges of many Cordilleran taxa.

Pupilla (*Striopupilla*) is an endemic Baja Californian subgenus; its presumed sister taxon is the Holarctic *Pupilla,* sensu stricto, with several species in the North American Cordillera. (Pilsbry [1948] regarded *P.* (*Striopupilla*) as representing an immigrant Asian stock, presumably by way of the North Pacific arc; however, he did not specify any plausible Asian sister-group.) *Vallonia cyclophorella* is widespread in the Cordilleran region. *Euconulus fulvus* is Holarctic, with montane southward extensions to southern California, Baja California, and Chihuahua (Bequaert and Miller 1973).

3. Colorado/Mojave Desert Track. *Eremarionta* connects the Colorado Desert and Gulf Coastal zones with southeastern California and extreme western Arizona. The sister taxon of *Eremarionta* may be *Micrarionta* of the California borderland, in which case a vicariant relationship related to the rise of the Peninsular Ranges and the San Bernardino-San Gabriel Mountains is indicated. The relationship between Baja Californian and extralimital *Eremarionta* is subspecific and readily accounted for by isolation resulting from the increasing aridity of the Sonoran desert environment (Axelrod 1979).

4. Neotropical Track. Paleontological evidence is mounting that during the late Cretaceous and early Tertiary, a land snail fauna consisting partly of genera of the modern tropics was arrayed across the southern part of North America, roughly parallel to the western limb of the Tethyan seaway (Roth 1988). Through the Cenozoic, the northern, antitropical limits of this fauna retreated southward. At the same time, the east-west ranges of taxa were more or less disrupted by tectonic events and their consequent climatic effects. Participants in an east-west Neotropical track include *Gastrocopta pellucida hordeacella*; *Pupoides*; *Sterkia,* with species in the California borderland and Mesoamerica; and probably *Helicodiscus* (*Hebetodiscus*), which ranges across the eastern United States and Mexico but is most diverse on the islands of the Greater Antilles (Pilsbry 1948). The genus *Pseudosubulina* extends to Central America and the Greater Antilles. Distribution of the genus *Strobilops* is complex (cf. Pilsbry 1948:fig. 461) and the subgeneric assignment of *S. californica* uncertain (Miller and Christensen 1980). It is tentatively referred to the group of taxa having Neotropical tracks.

Bequaert and Miller (1973) regarded *Hawaiia minuscula* and *Glyphyalinia indentata paucilirata* as part of a "pan-American" element in their Nearctic Southwestern Molluscan Province, but because of open questions regarding the taxonomy of western American records, we exclude them from further analysis here.

Truncatella guadalupensis probably participates in the Eastern Pacific-Caribbean track that is well documented with respect to marine organisms (Rosen 1976:440). Its distribution undoubtedly depends primarily on marine factors.

5. Arizona-Northern Mexico Track. This generalized track extends from Baja California to the region defined by Bequaert and Miller (1973:

fig. 1) as the Nearctic Southwestern Molluscan Province, with the exception of the Colorado and Mojave deserts. The fauna of the Southwestern Molluscan Province is itself composite and involves Cordilleran (and ultimately Holarctic), Neotropical, and Californian generalized tracks. The tracks to the California Borderland all involve disjunctions across the Colorado and/or Mojave deserts.

The track of *Gastrocopta* (*Immersidens*) *allyni* leads to sister taxa *G.* (*I.*) *ashmuni* (Sterki, 1898) and *G.* (*I.*) *cochisensis* (Pilsbry and Ferriss, 1910) of Arizona and New Mexico, across a trans-Sonoran disjunction. The sister taxon of *Gastrocopta* (*Immersidens*) *rixfordi* is probably *G.* (*I.*) *dalliana* (Sterki, 1898) of Arizona, Sonora, and northwestern Chihuahua (Bequaert and Miller 1973). The track of *Vertigo ovata* leads to the Nearctic Southwestern Molluscan Province and thence to a very large portion of the Nearctic realm (summarized by Bequaert and Miller 1973: 92–93).

The track record of the Bulimulidae is complex. According to Christensen (1978), *Berendtia, Spartocentrum,* and the *Rabdotus* of Baja California form a monophyletic group. (Breure [1979] suggested that further work might show *Berendtia* and *Spartocentrum* to be synonymous; author Christensen thinks this is highly unlikely.) Hoffman's (1988) assignment to *Naesiotus* of many Baja Californian species formerly referred to *Rabdotus* implies the presence of at least two ancestral bulimulid stocks in Baja California, both of which have undergone significant local radiation. In both cases, the extralimital sister groups appear to be taxa of the Nearctic Southwestern Molluscan Province: in *Rabdotus, Rabdotus baileyi* (Dall, 1893) and related species from Sonora; in *Naesiotus,* the group including *Naesiotus nigromontanus* (Dall, 1897), *N. christenseni* Miller and Reeder, 1984, and *N. milleri* Hoffman, 1987, from Sonora and southern Arizona. The Nearctic Southwestern group of *Naesiotus* is disjunct from other species of the genus, which are South American and Galapagan (Hoffman 1988, fig. 3).

Thysanophora hornii occurs in the Nearctic Southwestern Molluscan Province and also in Sinaloa, Jalisco, Nuevo León, Tamaulipas, and San Luis Potosí (Bequaert and Miller 1973). Additional species of *Thysanophora* occur in Central America, the West Indies, and northern South America. Its track therefore connects southern Baja California with both the Nearctic Southwestern Molluscan Province and the Neotropical region.

The track of *Radiocentrum* extends through northern Chihuahua to southern Arizona and New Mexico (Hochberg et al. 1987), with Quaternary fossils in Texas and northern Coahuila. Late Cretaceous and early Tertiary fossils extend the track northward to Alberta. A trans-Sonoran disjunction exists with respect to *Radiocentrum avalonense* (Hemphill *in* Pilsbry, 1905) on Santa Catalina Island, California. The phylogenetic relationship between *Greggelix* and other genera of Helminthoglyptidae is not known (Miller 1972); an Eocene fossil questionably referred to *Greggelix* occurs in Chihuahua, Mexico (Roth and Megaw 1989).

The various land molluscan regions of Baja California participate unequally in these generalized tracks. From Table 3 it is evident that the predominant relations of the Californian region are northward along the Peninsular Ranges-California Borderland track and secondarily (based strongly on the contribution of the Northern Montane zone) to the Cordilleran track. A minor element is Neotropical. The relations of the Sonoran region are about evenly divided between, on the one hand, the Peninsular Ranges-California Borderland track and, on the other, the Neotropical and Arizona-Northern Mexico tracks. At the level of zone, the fauna of the Vizcaino Desert zone participates most strongly in the Peninsular Ranges-California Borderland track, while that of the Gulf Coastal zone participates most strongly in the Neotropical and Arizona-Northern Mexico tracks. The Magdalenan zone fauna is more evenly balanced, reflecting the transition between northern and southern faunas pointed out by Christensen (1983). The sparse fauna of the Colorado Desert zone participates in the Colorado/Mojave Desert and Arizona-Northern Mexico tracks. The relations of the Cape region are primarily along the Arizona-Northern Mexico track and secondarily along the Neotropical track, with minor Cordilleran and Peninsular Ranges-California Borderland elements.

A striking aspect of the track record is the near-absence of species shared by the Californian region and the Nearctic Southwestern Molluscan Province (the latter being taxa with an Arizona-Northern Mexico track). *Vertigo berryi* occurs in

California and also marginally in the Southwestern Province; Pleistocene fossil remains show that it was formerly more widely distributed in the latter. The only other shared species is the "weedy" *Paralaoma caputspinulae.* Other tracks connecting the California Borderland with the Southwestern Province involve dramatic disjunctions between related species, as in *Radiocentrum,* or the still more remote relationships between genera of the Helminthoglyptidae as suggested by Bequaert and Miller (1973). Cladistic relations among helminthoglyptid genera still have not been worked out, and their phylogenetic history is probably complex. Ultimately, the phylogeny of the Helminthoglyptidae will provide valuable new information on the biogeography of Baja Californian land mollusks.

Resumen

La fauna indígena de moluscos terrestres de Baja California consiste en 117 especies y subspecies, de 36 géneros y de 18 familias. Todos ellos son Pulmonata, excepto el prosobranquio anfibio *Truncatella.* Además hay tres especies introducidas por las actividades de hombres. Se describen dos nuevas especies, *Rabdotus* (*Plicolumna*) *perhirsutus* (Bulimulidae) y *Greggelix* (*Martirelix*) *huertai* (Helminthoglyptidae). Se presentan listas de localidades, notas sinonímicas, y mapas de distribución. Se definen tres regiones malacofaunísticas: "Californian," "Sonoran," y "Cape." Además, las regiones "Californian" y "Sonoran" están divididas en zonas. Estas divisiones zoogeográficas corresponden por la mayor parte a otras divisiones botánicas y zoológicas propuestas para Baja California.

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REVIEW OF THE GRASSHOPPER GENERA *DRACOTETTIX* AND *LITOSCIRTUS* (ORTHOPTERA: ROMALEIDAE), WITH A DISCUSSION OF THEIR ORIGINS AND LIFE HISTORIES

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Abstract: The genera *Dracotettix* and *Litoscirtus* constitute the tribe Dracotettigini. The tribe is autochthonous in California, Nevada, and Baja California. Parsimony analysis indicates that *Litoscirtus* (southern) is the sister group of *Dracotettix* (northern), a finding consistent with the primarily tropical distribution of the family Romaleidae. The concealed male genitalia of all five species are similar and share characteristic laterally flared dorsal aedeagal valves.

Adult females of all Dracotettigini species can become reproductively dormant to pass the prolonged dry summers of California's Mediterranean-type climate. This ability in *D. monstrosus,* and perhaps other Dracotettigini, is geographically variable, as females from both mesic northern and some southern California localities remain reproductively active into the summer, but die soon after. In more xeric southern California populations, females enter reproductive dormancy in spring without having oviposited, become reproductively active in fall, mate, oviposit, and have adult life spans of up to 10 months. Interspecific timing of reproductive dormancy is also variable because of climatic differences at different locations. Thus, *L. insularis* from the central Baja California peninsula may be reproductively active during summer, when the area receives rain.

Litoscirtus platynotus new species, endemic to Baja California Norte, is described.

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Introduction

California supports a rich grasshopper fauna, including the 113 endemic species listed by Strohecker et al. (1968) and 11 endemic species described by Rentz and Weissman (1981, 1984). Most of the endemic species occur in the south and central coastal regions (Strohecker et al. 1968), which are characterized by a Mediterranean-type climate (Munz and Keck 1968).

Five species of *Dracotettix* Bruner and *Litoscirtus* Bruner are endemic to central and southern California, southwestern Nevada, and northern Baja California, Mexico. These grasshopper genera are biologically distinct from others in the region in having a robust body, a unique and elaborate integumental sculpturing, a tendency for flightlessness, and an unusual life-history pattern that employs reproductive dormancy, apparently adaptive to a Mediterranean climate.

Grasshoppers of the thermally moderate Mediterranean climate of central and southern coastal California and northern Baja California Norte use at least eight different life-cycle patterns (Weissman and French 1980; Rentz and Weissman 1981). One of these patterns involves an adult period of reproductive dormancy. In the only detailed ecological study of a grasshopper utilizing such a strategy, Weissman and French (1980) found an average field adult longevity in *Trimerotropis occidentalis* (Bruner) of 70 days coupled with an ovipositional delay of up to 14 weeks after becoming adults. Adult female preovipositional mortality approached 50%. This strategy exposes mobile adults, not the sessile, more desiccation-prone eggs, to the hot, dry conditions of summer. Eggs are laid in the fall after the spring and summer dry period. Adults usually die with the advent of winter freezes, although in parts of coastal southern California they persist into the following spring (Uvarov 1966b; Rentz and Weissman 1981), living up to 10 months as adults.

Adult reproductive dormancy is widespread in insects (see references in Weissman and French 1980), especially in grasshoppers from areas with: (i) a Mediterranean climate (mild winter and prolonged summer drought); (ii) a tropical climate with a predictable drought exceeding several weeks duration, as in central Africa; and (iii) a harsh winter.

While reproductive dormancy in individual grasshopper species has been previously examined, no comparative study at a tribal level has been published. In this study we confirm Rentz and Weissman's (1981) findings of reproductive dormancy in *Dracotettix monstrosus* Bruner and report on the life-history strategies of four other species composing the tribe Dracotettigini of the family Romaleidae. Although the Dracotettigini are a small group and the species generally rare, these grasshoppers provide an interesting example of a group of insects that have evolved under a Californian Mediterranean climatic regime and show how flexible grasshopper life cycles can be.

The Romaleidae are predominately neotropical, but some species have radiated into temperate climates. Study of the life cycles of these temperate species may help us to understand how tropical preadaptations, such as a reproductive dormancy, could allow these organisms reproductive flexibility in, and thus survival and colonization of, the temperate zone. The Dracotettigini evade dry and cold seasons differently than do the related *Taeniopoda eques* (Burmeister), which occurs at similar latitudes elsewhere in the United States Southwest and has a diapausing egg (Whitman and Orsak 1985), not a period of reproductive dormancy. The genus *Taeniopoda* apparently evolved in subtropical central Mexico (Rehn and Grant 1961) under a climatic regime quite different from that of northwestern Baja California Norte, where the Dracotettigini apparently originated.

Rehn and Grant (1959b, 1961) reviewed the Dracotettigini of America north of Mexico. They had little distributional data from Baja California and almost no biological information on the species. Herein we review the internal male genitalia of all four previously described taxa, describe a new species, give new distributional and ecological data for all taxa, and propose a phylogenetic history for the tribe. We then review seasonal collection records for all taxa and propose a generalized life-history scheme. Our proposed phylogeny and life-history strategy for the Dracotettigini indicate a center of evolutionary origin in southern California and northern Baja California Norte.

Most of the study specimens were collected by us and are deposited in the California Academy of Sciences (CAS). Additional specimens were kindly loaned by the CAS and the following museums: Academy of Natural Sciences of Philadelphia (ANSP), San Diego Natural History Museum (SDNHM), University of Michigan Museum of Zoology (UMMZ), the United States National Museum (USNM), and the E. L. Sleeper Collection, California State University, Long Beach (CSLB).

Geographical terminology used in this paper is mindful of, but not in complete concurrence with, Snelling (1987). Within the text, "Baja California" refers to the entire peninsula comprising Estado de Baja California ("Baja California Norte") and Estado de Baja California Sur ("Baja California Sur").

Dracotettix Bruner

Dracotettix Bruner, 1889:50 (type species *Dracotettix monstrosus* Bruner, 1889, by original designation); 1889:50; 1893:

TABLE 1. Diagnostic features of the *Dracotettix* and *Litoscirtus* species (see Fig. 1).

	D. monstrosus	*D. plutonius*	*D. newboldi*	*L. insularis*	*L. platynotus*
Anterior development of rostrum (width at eye/length)	greatly produced (0.96–1.44)	greatly produced (0.96–1.03)	weakly produced (0.95–0.99)	not produced (0.62–0.88)	not produced (0.50–0.62)
Wings surpass apex of hind femora	no	no	no	yes	yes
Fastigium rugose	yes	yes	no	no	no
Fastigium depressed at base	yes	no	no	no	no
Median pronotal crest (crest height/pron. width)	very high (0.31–0.45)	high (0.26–0.33)	high (0.24–0.35)	high (0.21–0.36)	low (0.08–0.18)
Prosternal tubercle	triangular	triangular	conical	conical	conical
Subgenital plate (male)	pointed	pointed	rounded	rounded	rounded
Number of antennal segments	16–18	16–18	22	22–23	23
Form of antennae	flattened	flattened	conical	conical	conical
Lateral margins of fastigium	bifurcate	bifurcate	entire	entire	entire

267; 1907:210, 226. Rehn and Hebard 1909:463. Hebard 1931:125. Rehn 1938:123–132. Roberts 1941:219, 239. Rehn and Grant 1959a:241–242; 1959b:131–135; 1961:178–181. Strohecker et al. 1968:22.

Roberts (1941) and Rehn and Grant (1959a) determined the phylogenetic position of *Dracotettix* based on phallic structures. Rehn and Grant (1959b, 1961) provided comprehensive taxonomic treatments of *Dracotettix* species. Subsequent references to the genus have appeared in Strohecker et al. (1968), Barnum (1964), and Rentz and Weissman (1981). *Dracotettix* was previously known from Baja California by the single species *D. newboldi* Hebard. We present new records for *D. newboldi* and *D. plutonius* Bruner, and the first records for *D. monstrosus* in Baja California. We compare the concealed male genitalia of all species because the dorsal aedeagal valves and the epiphallus are of diagnostic importance in the Dracotettigini (Rehn and Grant 1959a), and Rehn and Grant (1959a, b, 1961) did not compare the genitalia of all species in the tribe. Table 1 compares external diagnostic characters of the Dracotettigini.

Dracotettix monstrosus Bruner

(Figs. 1a, 2a, b)

Dracotettix monstrosus Bruner, 1889:50; 1907:226. Rehn and Hebard 1909:463; 1912:118. Rehn and Grant 1959b:143–156; 1961:186–189. Strohecker et al. 1968:22–23. Rentz and Weissman 1981:61–62.

Dracotettix californicus Bruner, 1907:226. Rehn and Hebard 1909:463.

CONCEALED MALE GENITALIA.—Specimens from Baja California (Fig. 2a, b) are similar to those described by Roberts (1941) and Rehn and Grant (1959a). Endophallus with dorsal aedeagal valves sclerotized, acute at apices, flaring subapically to form broad lateral plates, similar in shape to *D. plutonius*; ventral valves with simple lobes, sheath forming fleshy lobes, widely separated at ventral cleft. Epiphallus large with lophi enlarged at base and extending apically to acute points similar to that in *D. newboldi*; ancora large, extended inward and apically as bulbous lobes as in *D. newboldi*; bridge of epiphallus slightly convex at anterior margin when viewed dorsally, straighter and wider than in *D. newboldi*, more convex than in *D. plutonius*.

VARIATION.—Rehn and Grant (1959b, 1961) reported considerable size and shape variation in *D. monstrosus*, particularly in the body dimensions of females, the length of the tegmina in males, the height and shape of the pronotal crest, and the development and shape of the rostrum and fastigium in both sexes. Coloration is more variable in females than in males. The three males and one female reported here from Baja California do not deviate from this recognized variation. Body lengths of the three males range 22.6–24.6 mm, the tegmina range 10.7–11.7 mm. The rostra are greatly extended, and all four specimens have high pronotal crests similar to that in specimens from southern California.

Six specimens from Joshua Tree National Monument and two from nearby Whitewater

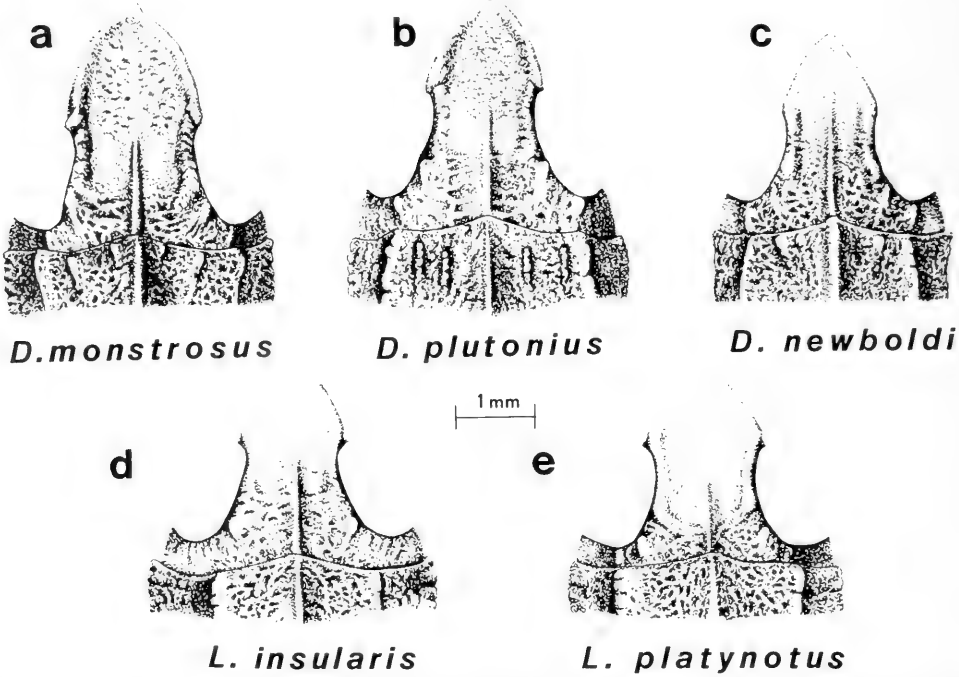

FIGURE 1. a–e. Dorsal views of adult male fastigia of Dracotettigini species (adult males). a, *Dractotettix monstrosus,* Table Mtn., Baja California Norte; b, *D. plutonius,* Panamint Range, California; c, *D. newboldi,* allotype; d, *Litoscirtus insularis,* topotype; e, *L. platynotus* holotype.

Canyon, Riverside County, California, represent the first records of *D. monstrosus* from desert areas. The six specimens from Joshua Tree National Monument were reported by Klud (1969) to be *D. plutonius.* All eight specimens are intermediate in four of six characters that Rehn and Grant (1959b, 1961) used to separate *D. monstrosus* and *D. plutonius*: metazonal crest height; fastigium length; fastigium profile; and extension of the rostrum. They are consistent with typical *D. monstrosus* for two: profile of metazonal crest; and shape of prosternal spine. These specimens are morphologically and geographically more consistent with typical *D. monstrosus* than with *D. plutonius.* We are unable to determine if the intermediacy results from genetic or environmental factors or both.

KARYOTYPE.—2N ♂ = 23, all telocentric, two large, six medium, and three small autosomes, X medium sized. The karyotype of this species has been misinterpreted. Confusion has arisen because the meiotic bivalent configuration can affect the assignment of size class. Thus, Rentz and Weissman (1981) reported four large autosomes, but their figure 92 (p. 184) clearly shows only two. In contrast, metaphase I pictured by Schroeter and Hewitt (1972) shows three large autosomes. To avoid misinterpretation, analysis should be performed on colchicine mitotic plates.

TYPE DATA.—*Dracotettix monstrosus,* lectotype, male, designated by Rehn and Hebard (1912), deposited in ANSP, type number H 83; Los Angeles, California, U.S.A. Not examined by us.

GEOGRAPHIC DISTRIBUTION.—Central and southern California Coast Ranges and inland mountains of southwestern California (Strohecker et al. 1968) and northwestern Baja California Norte (Fig. 3).

HABITAT.—Geophilous, preferring gravelly substrates where individuals are cryptic among small rocks. Rehn and Grant (1959b) reported *D. monstrosus* from near sea level to 2,400 m in California. *Dracotettix monstrosus* is generally associated with Californian chaparral or coastal sage scrub, but specimens from Joshua Tree National Monument were taken in pit-fall traps near juniper trees (Klud 1969) in a pinyon-juniper woodland.

PHENOLOGY.—Adults are known from Feb-

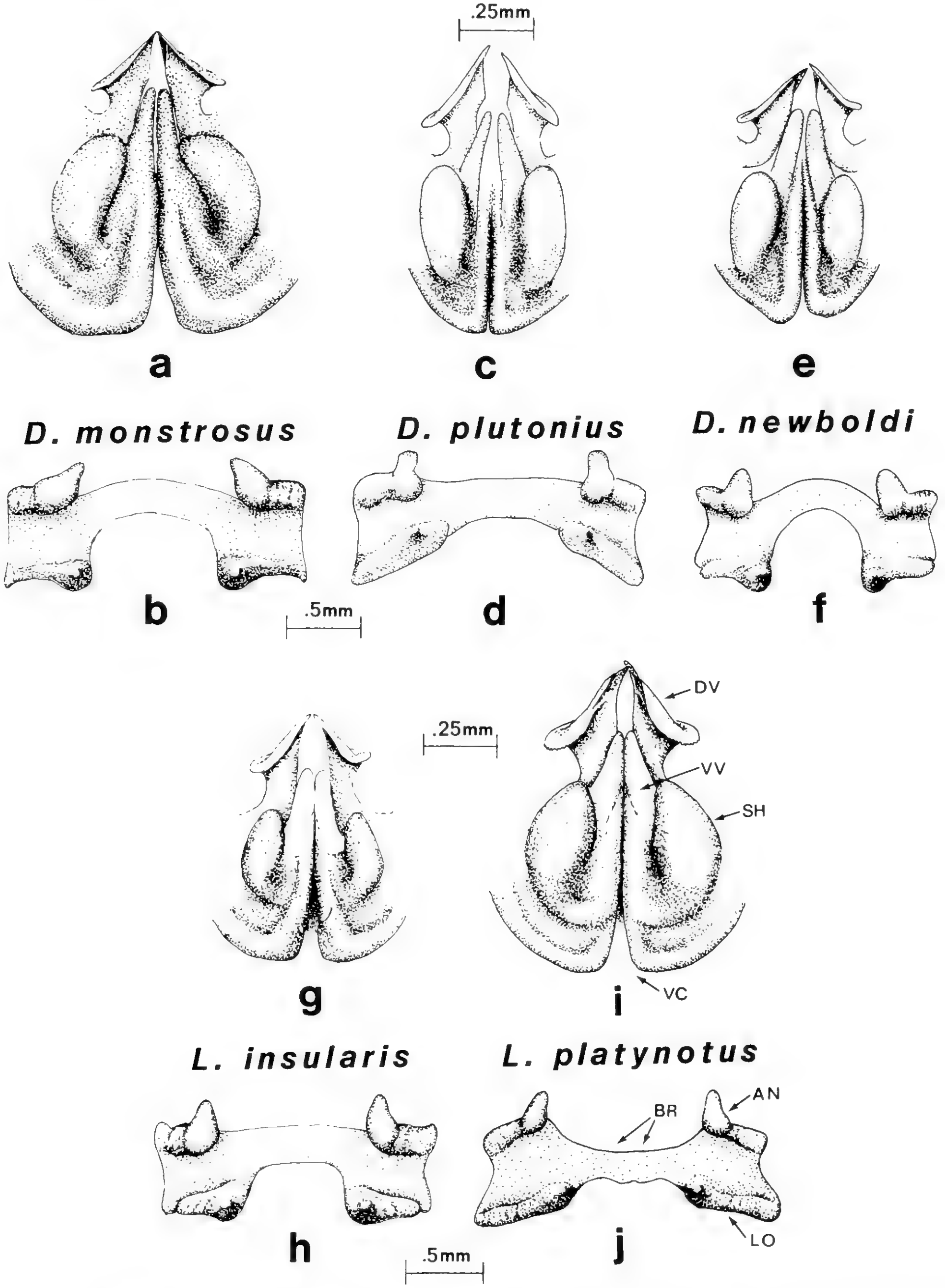

FIGURE 2. Concealed male genitalia. Posterior views of aedeagi (a, c, e, g, i): DV = dorsal valve, VV = ventral valve, SH = sheath, VC = ventral cleft. Dorsal views of epiphalli (b, d, f, h, j): AN = ancora, LO = lophus, BR = bridge. a, b, *D. monstrosus,* Table Mtn., Baja California Norte; c, d, *D. plutonius,* Panamint Range, California; e, f, *D. newboldi,* allotype; g, h, *L. insularis,* topotype; i, j, *L. platynotus,* holotype.

ruary to October, and immature stages from June to September. See discussion below on life histories.

NOTES.—One reproductively inactive adult female collected in southern California in July 1981 stridulated when held (see Strohecker et al. 1968 for similar observations). Stridulation was accomplished by a rubbing of the hind femora against the abdomen to produce a scraping sound. No other species of Dracotettigini has been reported to stridulate, but we have observed *Phrynotettix robustus* (Bruner), in the related tribe Phrynotettigini, to stridulate in a similar manner. Stridulation in the Romaleidae is discussed by Rehn and Grant (1959b:118).

SPECIMENS EXAMINED.—MEXICO. **Baja California Norte:** Table Mtn., 11.9 km E Rosarito (25 km S Tijuana), 20-IV-79 (D. K. Faulkner, 2 ♂, SDNHM); Valle de la Trinidad, Mesquite Springs, 16-III-59 (C. F. Harbison, 1 ♂, CAS); km 55 [from what city not indicated] on Mex. Hwy. 1, 6-V-62 (R. & A. R. Hardy, 1 ♀, CSLB). USA. **California:** Riverside Co.: Joshua Tree Natl. Mon., Lower Covington Flat (pit-fall trap), 9-IV-1961 (E. L. Sleeper, 1 ♀, CSLB), 5-IV-1966 (L. Garrick, 1 ♀, CSLB), 11-V-1968 (P. H. Klud, 1 ♀, CSLB), 25-X-1968 (R. A. Kramm, 1 ♀, CSLB), 12-IV-1969 (R. A. Kramm, 1 ♀, CSLB), 26-IV-1969 (E. L. Sleeper, 1 ♀, CSLB); Whitewater Canyon, 11-IV-1959 (J. C. Geest, 1 ♂, 1 ♀, CSLB).

Dracotettix newboldi Hebard

(Figs. 1c, 2e, f)

Dracotettix newboldi Hebard, 1931:125. Rehn and Grant 1959b: 135.

CONCEALED MALE GENITALIA (Fig. 2e, f).—Endophallus small relative to that in other *Dracotettix*: dorsal aedeagal valves sclerotized, acute at apices, flaring subapically forming broad plates with smooth margins; ventral valves simple, lightly sclerotized elongate lobes, relatively large; sheath forming fleshy lobes similar to that in *D. plutonius*; epiphallus small relative to that in other *Dracotettix*, with lophi enlarged at base and extended apically to acute points; ancora large, extended inward and apically to form bulbous lobes with flattened, pointed apices; bridge of epiphallus broad and strongly convex, more so than those in either *D. monstrosus* or *D. plutonius*.

VARIATION.—We examined too few specimens to assess variation. The adult female is similar to the holotype; the last instar female nymph from Todos Santos has a pronotal crest proportionately higher than those of the adult females. Late instar female nymphs of *D. monstrosus* and *Litoscirtus insularis* Bruner also have pronotal crests that are proportionately higher than the crests of adults. This condition appears to be a tribal trait.

TYPE DATA.—Holotype, female, deposited in ANSP, type number 5496; Hamilton's Ranch, near Santo Domingo Mission, Baja California Norte, Mexico. Examined by us.

GEOGRAPHIC DISTRIBUTION.—Known only from the coastal plain region of Baja California Norte (Fig. 3).

HABITAT.—Fog-influenced coastal plains and foothills of Baja California Norte. The adult female that we found was on gravelly soil among *Agave,* iceplant, cacti, and *Frankenia,* on a broad fog-desert plateau some 2.5 km from the sea.

PHENOLOGY.—Adults are known from February and July; one last instar nymph was collected in March.

SPECIMENS EXAMINED.—MEXICO. **Baja California Norte:** Hamilton's Ranch (near Colonia Guerrero), 14–17-II-30 (Newbold, Morris, 1 ♂, 1 ♀, allotype and holotype, ANSP); Santo Tomas, 32 km S, 3-III-38 (Michelacher, Ross, 1 last instar ♀, CAS); El Rosario, 4.5 km N, 9-VII-78 (D. B. Weissman, D. C. Lightfoot, 1 ♀, CAS).

Dracotettix plutonius Bruner

(Figs. 1b, 2c, d)

Dracotettix plutonius Bruner, 1893:267; 1907:226–227. Rehn and Hebard 1909:163. Rehn and Grant 1959a:241–242; 1959b:135–143; 1961:181–184. Barnum 1964:32–33. Strohecker et al. 1968:23.

This species was discussed extensively by Rehn and Grant (1959b, 1961) and does not occur in Baja California. The female spermatheca was figured by Rehn and Grant (1959a).

CONCEALED MALE GENITALIA (Fig. 2c, d; see also Rehn and Grant 1959a).—Endophallus similar in form to that in *D. newboldi,* dorsal aedeagal valves similar in shape to that in *D. monstrosus* and *D. newboldi,* but larger and more elongate, ventral valves and sheath form fleshy lobes, similar to that in *D. monstrosus* and *D. newboldi*; epiphallus with basal portion of lophi extended posteriorly as a narrow ridge; base of ancora broad, apices flattened and extended anteriorly, broadly rounded; bridge of epiphallus broader than that in *D. monstrosus* or *D. newboldi,* anterior margin almost straight.

VARIATION.—Rehn and Grant (1959b, 1961) discussed the range of morphological and color variation in *D. plutonius,* which is similar to that found in *D. monstrosus* but not as broad.

TYPE DATA.—Lectotype, male, designated by Rehn and Hebard (1912), deposited in USNM, type number 5496; Panamint Valley, Inyo County, California, U.S.A. Examined by us.

GEOGRAPHIC DISTRIBUTION.—Mountain ranges of the northern Mojave Desert, including the Panamint and Argus ranges, California, and the Mine Mountains at the Nevada Test Site, Nevada (Fig. 3).

HABITAT.—Barnum (1964:33) reported five individuals of *D. plutonius* from sagebrush (*Artemisia tridentata* Nutt.) and concluded that the species "undoubtedly feeds" on sagebrush. At Wild Rose Canyon, in the Panamint Range, we found individuals of *D. plutonius* on gravelly soil among grasses and forbs in an area between the creosotebush (*Larrea tridentata* (DC) Cov.) and pinyon pine zones. The vegetation was dominated by the shrubs box-thorn (*Lycium andersonii* Gray), blackbrush (*Coleogyne ramosissima* Torr.) and horse-brush (*Tetradymia spinosa* H. & A.), but no sagebrush was in the immediate area. We believe that *D. plutonius,* like other Dracotettigini, is primarily a geophilous species on gravelly soil, but individuals do climb onto shrubs, as Barnum (1964) observed, where they are equally well camouflaged as on gravel.

PHENOLOGY.—Adults are known from March through May, and in September. No nymphs have been found.

SPECIMENS EXAMINED.—USA. **California:** Inyo Co.: Panamint Range, Wild Rose Canyon, 1,550 m, 31-III-81 (D. C. Lightfoot, J. E. Price, 2 ♂, 2 ♀, CAS).

Litoscirtus Bruner

Litoscirtus Bruner, 1907: 210, 231 (type species *Litoscirtus insularis* Bruner, 1907, by monotypy; from a series of five syntypes from Cedros Island, Baja California, and one specimen erroneously labeled Central America [see Rehn and Grant 1959b]). Hebard 1923:326; 1931:124. Rehn 1938: 124–130. Rehn and Grant 1959b:127–129.

Hebard (1923, 1931) reported *L. insularis* from Turtle Bay on the Baja California peninsula adjacent to Cedros Island and from the Sierra San Pedro Martir, about 200 km to the north (the latter actually represents a record of the new species, *L. platynotus*). From the few specimens taken at the above localities, Rehn (1938) compared the external morphologies of *Dractotettix* and *Litoscirtus,* and Rehn and Grant (1959b) presented a comprehensive description of *Litoscirtus.* Since these works, *Litoscirtus* has appeared in the literature only in reference to *Dracotettix* (Rehn and Grant 1961). Adults of both sexes of both *Litoscirtus* species fly well, in contrast to *Dracotettix monstrosus* and *D. plutonius,* where adults of neither sex can fly. We observed one living female *D. newboldi* that could not fly, but we have not observed a living male. Because of the short wings, we do not believe that males of this species can fly.

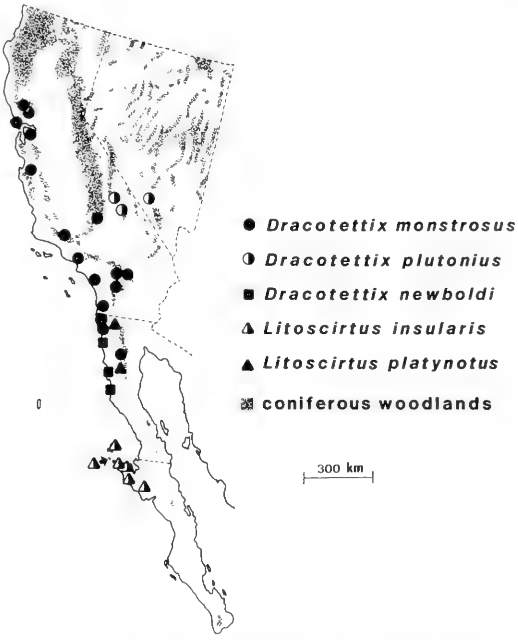

FIGURE 3. Distribution of *Dracotettix* and *Litoscirtus* species in the southwestern United States and Baja California, Mexico.

Litoscirtus insularis Bruner

(Figs. 1d, 2g, h, 4a, c)

Litoscirtus insularis Bruner, 1907:231. Hebard 1923:336; 1931: 124. Rehn and Grant 1959b:129–131.

All specimens we examined correspond with the description of Rehn and Grant (1959b). Hebard (1931) reported a single male *L. insularis* from the western slopes of the Sierra San Pedro Martir, Baja California. After examining that specimen, we conclude that it belongs to the new species *L. platynotus.* Males of the genus *Litoscirtus* were unknown before Hebard's report. He did note (Hebard 1931:124) that the male specimen "agrees closely with the female [*L. insularis,* Cedros Island], differing in being considerably smaller with pronotal cristation lower and

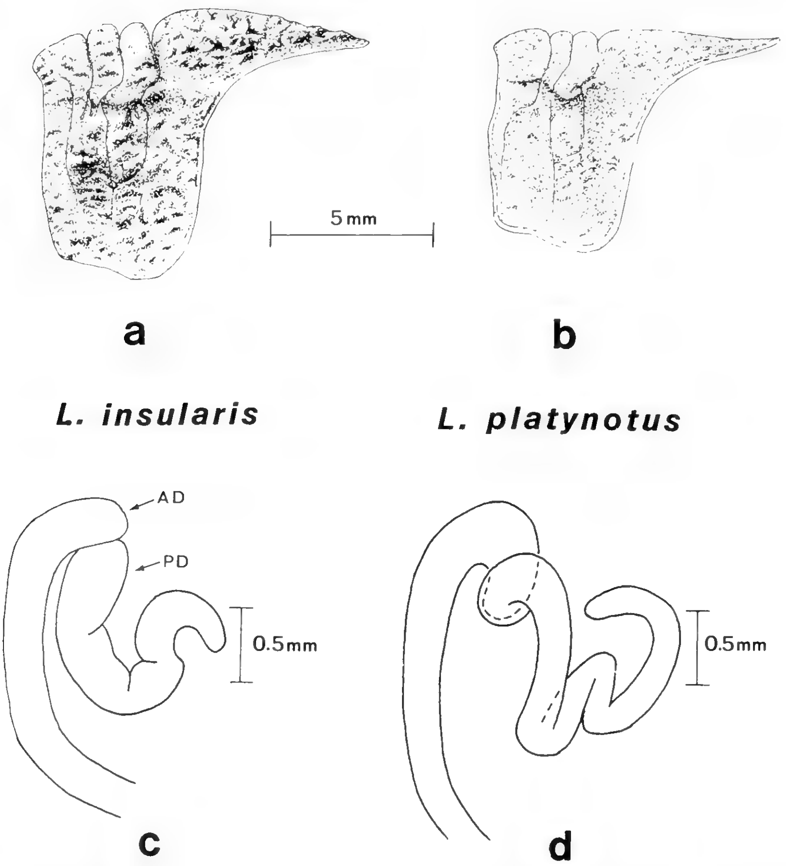

FIGURE 4. a, b. Lateral views of *Litoscirtus pronota* (females). a, *L. insularis*, topotype; b, *L. platynotus*, paratype. c, d. Lateral views of female spermathecae: AD = apical diverticulum, PD = preapical diverticulum. c, *L. insularis*, topotype; d, *L. platynotus*, paratype.

less incised." The height of the pronotal crest is actually proportionately similar in male and female specimens of *L. insularis* (Table 2).

CONCEALED MALE GENITALIA (Fig. 2g, h).—Endophallus small relative to that of other Dracotettigini, with dorsal aedeagal valves sclerotized and short, acute at apices, and flaring subapically to form broad lateral subapical plates, margins weakly serrate at apices, similar in shape to that in *Dracotettix* species; ventral valves simple, lightly sclerotized elongate lobes, sheath forming small fleshy lobes not reaching ventral cleft, proportionately smaller than *Dracotettix* species, and absolutely and proportionately much smaller than that in *L. platynotus.* Epiphallus with lophi enlarged at base, proportionately broader than in *L. platynotus,* and extended apically to acute points; ancora extended inward and apically to form bulbous lobes, proportionately broader than in *platynotus*; bridge of epiphallus broad throughout and slightly convex when viewed from above, similar to that in *Dracotettix* species.

FEMALE SPERMATHECA.—Apical diverticulum present but poorly developed, evident only before the constriction to the preapical diverticulum (Fig. 4c); preapical diverticulum short and S-shaped.

VARIATION.—Little morphological variation is evident in *L. insularis* over its limited geographic range (Table 2). The male and female specimens from Natividad Island are the smallest known specimens of each sex. The shape and height of the pronotal crest vary little. Pronotal crest shape varies in the size and angle of cuts by the three sulci, and consequently, the angles of the lobes on the prozona. The male from Natividad Island had the highest pronotal crest of all males ex-

TABLE 2. Measurements (mm) of adult male and female *Litoscirtus* species.

	Body length*	Pronotum length	Pronotum width	Pronotal crest height**	Tegminal length
Males					
insularis (n = 9)	33.6–34.9	8.0–8.7	4.9–5.9	1.2–1.8	19.3–22.2
platynotus (n = 2)	32.9–33.1	7.2–8.6	4.9–5.2	0.4–0.8	19.9–20.7
Females					
insularis (n = 12)	41.8–46.4	10.3–12.3	7.0–8.2	1.6–2.4	31.1–35.4
platynotus (n = 3)	37.9–40.5	9.4–10.6	6.1–7.5	0.5–1.2	28.4–30.6

* Rostrum to apex of tegmina.

** Lateral carinae to apex of median metazonal crest when viewed laterally.

amined. The shape of the fastigium and rostrum varies little. Coloration varies somewhat, but not to the extent found in *D. monstrosus.* Most individuals have a dark gray-brown base color, contrastingly marked with light and dark gray. Some individuals have a reddish-brown base color, with light and dark reddish-brown markings. The tegmina are generally uniform gray-brown, with several large dark spots and light spots in the cubital region, varying to that in which individuals have the principal veins darkened with numerous small spots also present. Reddish-brown individuals have the same type of tegminal pattern. The entire tegmina of the two specimens from Natividad Island are heavily patterned with dark spots and light spots. Hind tibial color varies from uniform gray or uniform brown to red with gray mottling on the external face. Most individuals from Cedros and Natividad islands had gray hind tibiae, except for two males that had red hind tibiae. In contrast, all individuals from the Baja California peninsula had brown hind tibiae.

KARYOTYPE.—2N ♂ = 23, all telocentric, two large, six medium, and three small autosomes, X medium sized. Three males collected on Cedros Island in early July had numerous meiotic divisions.

TYPE DATA.—Lectotype, male, designated by Rehn and Grant (1959b), deposited in USNM, type number 64,686; Cedros Island, Baja California Norte, Mexico. Not examined by us.

GEOGRAPHIC DISTRIBUTION.—Known only from the central west coast of Baja California in the vicinity of the Sierra Vizcaino and adjacent offshore islands, Cedros and Natividad (Fig. 3).

HABITAT.—From low coastal fog desert to high-elevation chaparral and pine forests (Cedros Island), from sea level to 1,300 m. This species occurs on open rocky soil, but is not associated with any particular vegetation type. When we sampled Cedros Island in July 1983, *L. insularis* was most abundant at high elevations, but in April 1983, the species was common at both high and low elevations (D. K. Faulkner, pers. comm.). On the Baja California peninsula, *L. insularis* occurs in the Sierra Vizcaino and along the adjacent coastline. This region is characterized by Vizcaino sarcophyllus desert scrub (Wiggins 1980) on rocky, hilly terrain.

PHENOLOGY.—Adults are known from February through August. Late instar nymphs are known from March, April, and early July.

SPECIMENS EXAMINED.—MEXICO. **Baja California Norte:** Cedros Island: Grand Canyon, 8-IV-23 (G. D. Hanna, 1 ♀, CAS); 15-VII-39 (L. L. Walker, 1 ♀, SDNHM); El Pueblo, 12-IV-83 (D. K. Faulkner, 3 ♂, 1 ♀, 3 nymphs, SDNHM); Cerro de Cedros, 3-IV-83 (D. K. Faulkner, 1 ♀, SDNHM); Cerro de Cedros, 50–1,300 m, 28-VI-83 (D. K. Faulkner, V. F. Lee, D. C. Lightfoot, D. B. Weissman, 12 ♂, 9 ♀, CAS); Pico Gill, 30-VI-83 (D. K. Faulkner, V. F. Lee, D. C. Lightfoot, D. B. Weissman, 3♂, 3 ♀, CAS). **Baja California Sur:** Turtle Bay, 24-IV-16 (U.S. Fish Comm., 1 ♀, CAS); Scammon Laguna 19–23-VII-39 (L. I. Walker, 1 ♀, CAS); Picachos de Santa Clara, 27°07′N, 113°37′W, 350 m, 3-II-73 (R. Moran, 1 ♀, UMMZ); San Andres, 5 km SE, 27°14′N, 114°22′W, 65 m, 5-II-73 (R. Moran, 1 ♀, UMMZ). Natividad Island, 1 km N lighthouse, 13-VII-83 (D. K. Faulkner, V. F. Lee, D. C. Lightfoot, 1 ♂, 1 ♀, CAS).

Litoscirtus platynotus new species

(Figs. 1e, 2i, j, 4b, d)

This species is distinct from *L. insularis* primarily in the non-overlapping pronotal crest height measurements, disproportionate wing lengths (Table 2), and geographical separation of over 150 km (Fig. 3).

SPECIES DESCRIPTION.—Asterisks refer to the holotype. Characters that do not differ from those described for *L. insularis* (see Rehn and Grant 1959b:127–128) are not mentioned here. HEAD.

Similar in shape to that of *L. insularis*; rostrum not produced forward as in *Dracotettix*; fastigium 1.2–1.5* times as wide as long, surface lightly pitted, not rugose; occiput, gena, and subocular furrow lightly rugose. THORAX. Pronotum less rugose than in *L. insularis,* females more rugose than males; median dorsal crest distinctly elevated, but less so than in *L. insularis* (Table 2, Figs. 1e, 4b); tegmina proportionately shorter than in *L. insularis,* surpassing the apices of the hind femora by a distance less than ¼ of the total tegminal length. ABDOMEN. CONCEALED MALE GENITALIA. Endophallus (Fig. 2i) largest in the Dracotettigini; dorsal aedeagal valves sclerotized and short, flaring laterally with strongly serrate margins on subapical portions; ventral valves simple, with lightly sclerotized elongate lobes; sheath forming large fleshy lobes, with ventral margins extended inward to ventral cleft; epiphallus (Fig. 2j) more slender overall than in *L. insularis*; lophi with basal portion narrowly extended below and posteriorly as a slender ridge, ancora and basal ridges slender; bridge of epiphallus narrow at midsection, rather than convex as in *L. insularis.* CONCEALED FEMALE GENITALIA. Spermatheca (Fig. 4d) with apical diverticulum barely developed, even less so than in *L. insularis,* only evident before constriction to preapical diverticulum; preapical diverticulum curved several times, recurved at apex, and longer than in *L. insularis.* APPENDAGES. Hind femora with dorsal margins weakly serrate to dentate, not undulating as in *L. insularis,* hind tibiae with 9*–10 external spines and 8–9* internal spines. COLORATION. Oval mottled gray-brown, similar to coloration in *L. insularis* except pigmented with numerous small maculations rather than a few large spots and maculations, especially the tegmina with no large spots in the cubital region as found in *L. insularis*; hind wings translucent blue-green, suffused dark brown at apices; internal face of hind femora black on basal ¾ and red* or yellow-brown on distal ¼ including the genicular lobes; hind tibiae red*, yellow, brown, or gray, with brown or gray mottling on external face.

KARYOTYPE.—2N ♂ = 23, all telocentric, two large, six medium, and three small autosomes, X medium sized. Only holotype examined, with very few meiotic divisions.

ETYMOLOGY.—From the Greek words *platy,* for flat, and *notus,* for back, in reference to the low pronotal crest relative to that in other species in the tribe Dracotettigini.

TYPE DATA.—Holotype, male. Mexico. Baja California Norte: 2 km W Ejido Ignacio Zaragoza, 0.3 km E highway km marker 65 on Mex. Hwy. 3 [ca. 45 km S Tecate], 518 m, 9-III-79 (D. K. Faulkner, J. W. Brown, D. B. Weissman, DBW #79-40, SDNHM, on permanent loan to CAS, CAS Type #16484).

GEOGRAPHIC DISTRIBUTION.—Known only from the coastal mountains and Sierra San Pedro Martir of northwestern Baja California (Fig. 3).

HABITAT.—Mountainous terrain on open rocky soil with sparse grass in chaparral areas within the Californian phytogeographic region of Wiggins (1980). The type locality is a mosaic of dry summer grassland and chaparral (including *Adenostoma fasciculatum* (H. & A.), *A. sparsifolium* Torr., *Artemisia californica* Less., and *Ceanothus* spp.) on steep rocky slopes at 518 m elevation. The region consists of extensive low mountains, deeply dissected by ephemeral drainages. Both specimens from the type locality were found in the daytime on rocky soil with a sparse grass-forb cover. On the west slope of the Sierra San Pedro Martir, the two *L. platynotus* females were found in similar habitats in open areas of mixed chaparral and pine-oak woodland. One of these females was found on the ground during the day, the other was resting on the base of a *Yucca* stalk at night.

PHENOLOGY.—Adults are known from February, March, July, and September. No immatures are known.

SPECIMENS EXAMINED.—All designated paratypes. MEXICO. **Baja California Norte:** Sierra San Pedro Martir, west slope, ca. 680 m, 25-II-30 (Newbold, Morris, 1 ♂, ANSP); km 76.6 on road to Sierra San Pedro Martir Natl. Park off Mex. Hwy. 1, 1,500 m, 27-VII-78 (D. B. Weissman, D. C. Lightfoot, 1 ♀, CAS); km 78 on road to Sierra San Pedro Martir Natl. Park off Mex. Hwy. 1, 1,500 m, 20-IX-79 (D. C. Lightfoot, R. E. Love, J. E. Price, 1 ♀, CAS); 2 km W Ejido Ignacio Zaragoza, 0.3 km E highway km marker 65 on Mex. Hwy. 3, 518 m, late Feb. 1979 (D. K. Faulkner, J. W. Brown, 1 ♀, SDNHM).

PHYLOGENY AND DISTRIBUTION OF THE DRACOTETTIGINI

Our analysis of male internal genitalia and karyotypes confirm that *Dracotettix* and *Litoscirtus* are closely related taxa. Rehn (1938) and Rehn and Grant (1959b:134) believed that either *Litoscirtus* was "ancestral to *Dracotettix* [with *D.*

TABLE 3. Character states used in the phylogenetic analysis of the Dracotettigini.

Characters	Plesiomorphic condition	Apomorphic condition
1. Integumental sculpturing	weak (few tubercles and elevated ridges)	strong (many large tubercles and ridges)
2. Pronotal crest	low (<0.2 × pronotal width)	high (>0.2 × pronotal width)
3. Rostrum	weak (<0.5 × width)	strong (>0.5 × width)
4. Wings	long (capable of flight)	short (not able to fly)
5. Number of antennal segments	many (>20)	few (<20)
6. Form of antennae	simple (conical)	modified (flat)
7. Fastigium depressed basally	no	yes
8. Lateral margins of fastigium	complete	divided
9. Prosternal tubercle	conical	triangular
10. Subgenital plate	rounded	pointed

newboldi the intermediate link], or the two genera had a common ancestor." Rehn and Grant (1959b:129) also stated that it was not possible to determine whether *Dracotettix* or *Litoscirtus* was the older evolutionary line. We propose below a hypothetical phylogenetic history for the Dracotettigini based upon parsimony analysis (Brooks 1984).

The Dracotettigini, with five species, and Phrynotettigini, with four species, are closely related tribes (Rehn and Grant 1959b). Members of these tribes are highly specialized morphologically, with robust bodies, elaborate integumental sculpturing, and wing reduction in most taxa. The high degree of secondary specialization in external morphology renders determination of plesiomorphic vs. apomorphic character states difficult for in-group and out-group comparisons using the Phrynotettigini as an out-group. We instead used the other 14 tribes in the Romaleidae (Rehn and Grant 1959a) for out-group comparisons. A list of the character states used in our analysis of the Dracotettigini is presented in Table 3. Most of the chosen characters were considered to be useful taxonomic features for the Dracotettigini by Rehn (1938) and Rehn and Grant (1959b). Those characters are mostly secondarily derived features that also appear to be variable within populations. Discrete, conservative characters, such as genitalia and chromosome configurations, do not differ enough among taxa in the Dracotettigini to be of use in phylogenetic analyses. We used MacClade algorithms (Madison and Madison 1987) to construct phylogenetic trees, because the Dracotettigini consists of a small number of species that can readily be analyzed by an interactive program like MacClade.

The most parsimonious tree resulting from our analysis and chosen to represent our hypothesized phylogeny for the Dracotettigini is presented in Figure 5. The tree reveals that *Litoscirtus* possesses the greatest number of plesiomorphic character states, and *L. platynotus* is the most primitive taxon. *Dracotettix* forms a separate group from *Litoscirtus,* but *D. newboldi* is considerably more primitive than either *D. monstrosus* or *D. plutonius.* These findings are consistent with Rehn and Grant's (1959b) conclusions that *D. newboldi* demonstrates a relationship between the two genera. Our results indicate that *Dracotettix* is probably derived from a *Litoscirtus*-like ancestor.

The Dracotettigini is a nearctic lineage apparently derived from a neotropical ancestral romaleid (Rehn 1938). Northwestern Baja California Norte is the center of geographic distribution of the Dracotettigini, where three of the five species—*D. monstrosus, D. newboldi,* and *L. platynotus*—occur (Fig. 3). Of these three taxa, *D. newboldi* and *L. platynotus* are also the most primitive members of their respective genera. *Litoscirtus insularis* is a southern isolate from *L. platynotus* in the Sierra Vizcaino and adjacent offshore islands. The Sierra Vizcaino is an elevated, fog-influenced region that is biogeographically separated from the remainder of Baja California by the Vizcaino Desert. Both species of *Litoscirtus* are likely to be relictual forms of a more widespread pre-Pleistocene ancestor. During the Pleistocene, the peninsula was cooler (Savage 1960; Breckenridge 1978), and the entire Vizcaino region was probably inhabitable by *Litoscirtus.*

Dracotettix plutonius is also likely to be a relictual form of a more widespread pre-Pleisto-

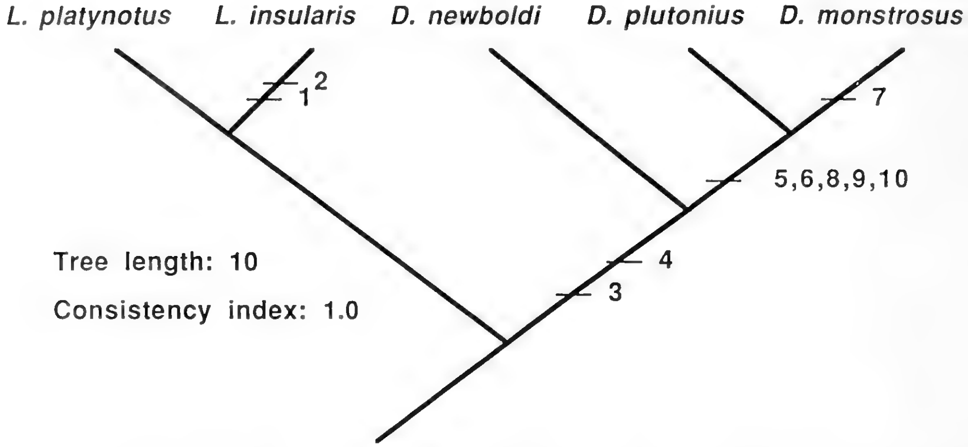

FIGURE 5. Hypothesized phylogenetic tree for the Dracotettigini based on parsimony analysis of all species in the tribe. A consistency index (Kluge and Farris 1969) of 1.0 reveals no homoplasy among characters. See Table 3 for list of characters.

cene *Dracotettix* ancestor. Suitable cooler, moister climatic conditions and associated chaparral or pinyon-juniper vegetation were prevalent across the higher elevations of the Mojave Desert during the Pleistocene (Wells and Berger 1967; Van Devender and Spaulding 1979). The ancestral form of *Dracotettix* probably dispersed east into Nevada, and populations representing *D. plutonius* apparently remained isolated in the mountains of the Mojave Desert following post-Pleistocene warming and drying trends.

The above phylogenetic and distributional scenario indicates that the Dracotettigini is an autochthonous group of species largely confined to the Mediterranean-type climatic regions of southern California and northwestern Baja California Norte. One apparent consequence of an evolutionary history in that particular climatic regime was the development of the unusual life-history pattern discussed below.

LIFE HISTORIES OF THE DRACOTETTIGINI

No species of Dracotettigini has been thoroughly studied biologically because none is found predictably in easily accessible locations. With the exceptions of the 1917–18 Nellie population of *D. monstrosus* in San Diego County, California (see below), and *L. insularis* population on Cedros Island, Baja California Norte, individuals of Dracotettigini have been rarely encountered. Long-term studies spanning several years and using marked individuals are needed to completely understand life history and reproductive strategies and to ascertain which reproductive properties are truly facultative. Nevertheless, piecemeal data are available, especially in Rehn and Grant (1959b), although those authors did not attempt to construct a hypothetical life cycle. We do so here for *D. monstrosus,* based on literature, museum and field dissections, our laboratory rearings, and certain caveats, as indicated below.

Adult female *D. monstrosus* utilize a summer reproductive dormancy period, depending upon local thermal and precipitation regimes. Most females in most populations become adult in late winter or early spring. Those at low elevations in dry, hot southern California pass the spring, summer, and early fall periods unmated and reproductively inactive. Although not proven, they apparently mate and oviposit many months after becoming adults, with the advent of fall and winter rains. They then lay eggs that probably have no dormancy period. In contrast, most females living at higher, cooler, wetter localities in San Diego County mate and oviposit shortly after becoming adults in the spring and subsequently die (see below). Their eggs probably have no dormancy period. Some females (see Table 4) from these same high-elevation San Diego populations do not become adults until summer. We predict that they enter reproductive dormancy unmated and remain reproductively inactive until fall and winter rains arrive. In northern California mating pairs of *D. monstrosus* are known from April (Strohecker et al. 1968) and June (Rehn and Grant 1959b), indicating a life cycle

TABLE 4. Seasonal data for *Dracotettix monstrosus* collected in Nellie, San Diego County, California, from 1917–18.

Life stage	Numbers of individuals/month collected				
	April	May	June	July	August
Adult ♂	24	0	7	1	12
Adult ♀	14	4	0	2	1
Adult ♀ with eggs	9*	4	0	2	1
Last instar	0	0	0	2	29
Penultimate instar	0	0	0	7	12

* Three of five without eggs had previously oviposited.

similar to spring adult females at higher elevations in San Diego County. Small nymphs have been collected in June from Santa Clara County, California (Rehn and Grant 1959b), indicating no egg dormancy.

We now report that adult females of all five species of the tribe Dracotettigini can become reproductively inactive during extended hot, dry periods. Unfortunately, we do not know if four of these species have the interpopulation reproductive plasticity seen in *D. monstrosus.* The above scheme contrasts with that used by most grasshoppers inhabiting California's Mediterranean climatic zone. Individuals of these latter taxa pass the winter in egg or early instar dormancy and become adult in late spring or early summer, mate, oviposit, and die in four to six weeks (pers. obs.).

METHODS

FEMALE MATING STATUS.—Spermathecae of adult females of all five species were examined for the presence of sperm according to Weissman (1979). We could not find dried spermatophores, as did Whitman and Orsak (1985).

FEMALE EGG MATURATION STATUS.—Terminology employed is that of Weissman and French (1980). Individuals that we collected were dissected shortly after death and examined for the presence of eggs, whereas museum specimens were dissected after their abdomens were placed in boiling water for one to two minutes. Field-captured adult females were considered reproductively dormant if they were nonteneral with extensive fat reserves and no ovarian development. Such reproductively dormant females were physically active, had full crops, and may or may not have been mated.

FEMALE OVIPOSITION STATUS.—Museum females that were obviously reproductively active (i.e., contained mature eggs) died with their ovipositor valves open, an observation previously made by Phipps for females killed with chloroform (1962) or cyanide (in litt., J. Phipps to D. B. Weissman 1986). Open ovipositor valves were seen when ovaries showed some development (i.e., Stage III of Phipps 1966), but was absent in some species (Phipps 1970).

Phipps (1966) discussed the three certain criteria of ovulation: (1) presence of eggs in the oviducts; (2) presence of traces of foam on the ovipositor valves; and (3) presence of egg resorption bodies. Criteria (1) and (2) are applicable to museum specimens, but we found (2) to be unreliable in the Dracotettigini. The absence of foam as a reliable indicator for the lack of prior oviposition is critical only for those females captured during reproductive dormancy, as reproductively active females would have eggs on dissection. We found museum specimens of *D. monstrosus* females that were obviously reproductively active before death, with ovulated eggs and gaping ovipositor valves, but no apparent traces of foam. Additionally, we have examined known laboratory-ovipositing females and found no traces of foam.

RESULTS

Dracotettix monstrosus. The most extensive natural history data are known for this species. The largest sample examined was 115 individuals collected during 1917–18 by E. P. Hewitt from Nellie, San Diego County, California, elevation 1,630 m, and borrowed from ANSP. A summary of these individuals by age, sex, and collection dates is presented in Table 4. All 21 adult females were dissected; 16 had mature eggs, including the three collected in July and August. The five without eggs were collected in April; three of these had dried foam between their ovi-

TABLE 5. Life history data for *Dracotettix monstrosus* (data from text and Rehn and Grant 1959b). X—known records; X′—known records, high-elevation localities (e.g., Nellie, Table 4); ?—hypothesized occurrences.

Stage	Month											
	J	F	M	A	M	J	J	A	S	O	N	D
Nymphs	?	?	?	?	?	X	X	X	X	?	?	?
Adults	?	X	X	X	X	X	X	X	X	X	?	?
Oviposition	?	X	X	X	X	X′	X′	X′		?	?	?
Female reproductive dormancy					X	X	X	X	X			

positor valves, indicating prior oviposition. The San Diego region had received good winter precipitation during the 1916–18 period (U.S. Department of Commerce 1916–18).

Seven individuals of *D. monstrosus* collected by D. K. Faulkner in Pine Valley (ca. 1,100 m elevation), San Diego County, California, late April 1979, were kept in the laboratory at room temperature and exposed to natural day length. The three females were gravid when collected and copulated with the males. These females oviposited in mid-May and died soon after, indicating that spring-ovipositing females probably do not live through the summer. Two of the four males survived until mid-November. In the field such long-lived males may fertilize those females that become adult during the summer (see Table 5) and remain reproductively inactive until fall, when they mate and oviposit. Unfortunately, no eggs hatched over the next year under conditions that result in hatching of other sympatric grasshopper species. Three additional females were collected at lower elevations in more arid regions of southern California in late July 1971 and mid-August 1973. None of these females had mated or had eggs, in contrast to the three reproductively active summer females from Nellie (Table 4 and above). Two males collected in northern Baja California Norte (mid-May 1979) and Los Angeles County (late June 1971) had abundant testicular meiotic division. We do not know if such males are sexually active.

Dracotettix newboldi. One non-teneral female collected in early July 1978 was unmated and without egg development. The presence of adults in February (the types) and July indicates a life history similar to that of *D. monstrosus.*

Dracotettix plutonius. The presence of adults from March to October (Rehn and Grant 1959b; Barnum 1964; and our observations) indicates a life history similar to that of *D. monstrosus.*

Litoscirtus insularis. In early April 1983, many adults and late instar nymphs were present on Cedros Island, Baja California Norte. Of three females dissected, none had ovarian development. Mating status was not determined. By early July 1983, many adults, but only two last instar nymphs, were found. Of 10 females examined, none had ovarian development, although three were mated. July males had abundant testicular division. We attempted to return to Cedros Island in September 1983, but torrential storms on Cedros prevented us. We did return to Cedros Island in late September 1984, but no individuals were found despite intensive searching. We suspect that adults were aestivating in sheltered areas awaiting fall rains that would induce reproductive activity. One of two females collected on the adjacent Baja peninsula in February 1973 had mature eggs.

Litoscirtus platynotus. Two nonteneral females collected in July 1978 and September 1979 were unmated and without eggs. The holotype male collected in early March 1979 had few meiotic divisions, but large amounts of mature sperm.

POSTULATED LIFE CYCLE OF *DRACOTETTIX MONSTROSUS*

1. Adults of both sexes and late-instar nymphs overwinter, as indicated by their appearance in late winter and early spring (see Table 5).
2. Most females from northern latitudes or high-elevation, cool, moist, southern localities mate in spring, have a period of oviposition, and die after a few months. Eggs laid in spring in central California hatch without a dormancy as indicated by the appearance of mating pairs in spring and early instars in June (Rehn and Grant 1959b).
3. Females from low-elevation, hot, dry southern localities similarly become adults in spring, but subsequently enter summer reproductive dormancy, most or all without mating. Eggs laid in fall and winter by these females apparently hatch over several months because of

cool temperatures, coupled with a long oviposition period. This accounts for the late-instar nymphs collected in spring. These adult females will be long lived, a condition found in other grasshoppers that utilize a reproductive dormancy (Uvarov 1966b; Weissman 1979; Weissman and French 1980; Rentz and Weissman 1981).

Those few females that mate in late spring and then become sexually dormant will have sperm in their spermathecae during their summer dormancy (a condition documented in *L. insularis,* but only postulated for *D. monstrosus*). The energy expenditure needed to keep these sperm alive through the summer (see similar example in LeCato and Pienkowski 1973) may be reproductively less expensive than relying on the presence of males to effect copulation in the fall, although male *D. monstrosus* can survive for seven months in the laboratory (see above). Similarly, females of the Egyptian locust store sperm during their six-month winter dormancy period between mating and oviposition (Uvarov 1966a).

4. Adult males of species whose synchronic females are in reproductive dormancy are probably never completely reproductively inactive. They usually have some meiotic divisions, even during the summer when they accumulate sperm prior to fall mating activity. It is unknown if males are sexually receptive when females are in dormancy.

Temporal aspects of the above scheme for *D. monstrosus* probably also apply to the other species of Dracotettigini, except *L. insularis,* since these four taxa all inhabit a region with similar rainfall periodicity, and all apparently have the ability to pass the summer in dormancy. The overall pattern for *L. insularis* is similar. The actual timing is different in that some females become adult in the fall and winter, mate, oviposit, and soon die. Those females becoming adult later in late winter or early spring may mate but all pass the spring and early summer reproductively dormant. These females probably become reproductively active whenever significant precipitation arrives. Such rainfall comes earlier in the year (July to January) in the central region of Baja California than farther north (October to May) in northern Baja California Norte and southern California.

SOME UNANSWERED QUESTIONS

Because of yearly fluctuations in population size of most species of Dracotettigini and our inability to simply find any individuals of certain species, parts of this study were intellectually unsatisfactory. Some gaps in our knowledge have already been referred to within the text. Entomologists in the future will unpredictably encounter populations of Dracotettigini species. To optimize such occasions, we list some questions that we attempted to answer, but could not. We concentrate on *D. monstrosus* because it is the most common and geographically widespread, and best studied of the Dracotettigini.

1. What percentage of *D. monstrosus* females overwinter as adults, and what percentage utilize a reproductive dormancy? A mark-release-recapture study (e.g., Weissman and French 1980) will probably be necessary to answer this and several other questions below.

2. How reproductively plastic are the individuals in each population of each species, since precipitation patterns in Mediterranean type climates are highly variable?

3. Is it possible that certain high-elevation females oviposit in the spring, become reproductively dormant during the summer, and oviposit again in the fall? It is known that males of the grasshopper species *Oedipoda miniata* (Pallas) with a reproductive dormancy can have these cycles reversed by appropriate changes in laboratory photoperiod and temperature (Pener and Orshan 1980). Could this reversal occur in field populations of *D. monstrosus?* Phipps (in litt. to D. B. Weissman 1986) was not aware of any African species of grasshopper, of which up to 70% of taxa utilize a reproductive dormancy during the dry season, that appeared to have oviposited and later entered reproductive dormancy.

4. Do male *D. monstrosus* from low-elevation localities employ any form of reproductive dormancy, such as reduced rate of meiosis, reduced sexual receptivity, or reduced activity level?

5. Do the eggs of *D. monstrosus* have a facultative dormancy?

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A REVISION OF *TIBOUCHINA* SECTION *LEPIDOTAE* (MELASTOMATACEAE: TIBOUCHINEAE)

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Abstract: ***Tibouchina*, with about 350 species, is the largest genus of neotropical capsular-fruited Melastomataceae, with a distribution extending from western Mexico and the West Indies to northern Argentina and Paraguay. Section *Lepidotae*, one of 11 recognized sections in the genus, is distinguished by its lepidote indument, free bracts that envelop floral buds, persistent calyx lobes, and glabrous stamens. It is closely allied to sections *Barbigerae* and *Tibouchina* but imperfectly separated from the latter as that section is currently defined. This revision of sect. *Lepidotae* includes a synoptic taxonomic history, a commentary on important taxonomic characters, a key to species, descriptions, diagnostic illustrations, and distribution maps for all taxa. As interpreted here, the section consists of nine species, three of which are newly described in this study—*T. elegantula*, *T. silvestris*, and *T. wurdackii*.**

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Introduction

Tibouchina Aublet, with about 350 species, occupies a central position among the approximately 25 genera currently assigned to the tribe Tibouchineae. It is the largest genus among neotropical capsular-fruited Melastomataceae and the most widespread, with a distribution extending from western Mexico and the West Indies to northern Argentina and Paraguay. *Tibouchina* is readily recognized by its terete hypanthia, prevailing 5-merous flowers, ventrally bilobed anther connectives, setose ovary apex, and cochleate tuberculate seeds.

In the Andes and especially in southeastern Brazil where the genus achieves its greatest diversity, many of the species with large, brightly colored flowers form a common and conspicuous element of the native vegetation. Several geographically defined tropical floras present good accounts of some of the species. The most recent monographic study of *Tibouchina* is that of Cogniaux (1891), in which 195 species were recognized. Since that time, many new species have been described, and heightened botanical exploration of the neotropics has generated a wealth of material in need of critical study.

Our attention was first drawn to sect. *Lepidotae* when one of us (FA) collected plants of some Panamanian populations that could not be placed in any of the known species of *Tibouchina* characterized by a lepidote (scaly) indument. As we extended our observations to other species in the section, we became aware of the need to recognize additional new taxa and better define the limits of others. To facilitate recognition and comparison of these novelties, sect. *Lepidotae* has been revised with a key, descriptions, and critical assessments of taxonomic characters and interspecific relationships.

Comparative data derived from vegetative and reproductive morphology, scanning electron microscopic observations of trichome morphology, and ecogeographic distributions provide a rationale for recognizing nine species, three of which are newly described in this study.

Sectional Limits, Relationships, and Taxonomic History

In his extensive treatments of *Tibouchina,* Cogniaux (1885, 1891) arranged the genus into 11 sections. Section *Lepidotae* was established for those species characterized by a lepidote indument, free bracts that envelop floral buds, persistent calyx lobes, and glabrous stamens. The section included two species, *T. lepidota* (Bonpl.) Baillon and *T. paleacea* (Triana) Cogn. The former was initially described as a *Rhexia* by Bonpland (1808). The latter was originally treated as a variety of Bonpland's species but placed in the segregate genus *Pleroma* D. Don (Triana 1871). There were no subsequent additions to sect. *Lepidotae* until Gleason (1925) described *T. lepidota* var. *intermedia,* which was later elevated to species status (Wurdack 1977). Following Gleason's paper, three additional taxa (*T. aristeguietae, T. inopinata,* and *T. narinoensis*) were added from Venezuela, Costa Rica, and Colombia respectively (Wurdack 1959, 1968, 1977). A few of the species have been treated in recent regional floras (Uribe 1972; Wurdack 1973, 1980), but an assessment of species limits and interspecific relationships was beyond the scope of those studies.

Cogniaux (1885, 1891) did not comment on the affinities of sect. *Lepidotae.* Its pervasive indument of flattened scales is shared with sections *Barbigerae* Naudin and *Tibouchina* Cogn., both of which appear to be close relatives. The limits of sect. *Barbigerae* are sharply defined because all of its approximately 18 species have staminal connectives with basal tufts of long pilose hairs. Section *Tibouchina* is also readily distinguished if we restrict it to include *T. aspera* and *T. spruceana,* the two savanna species used by Cogniaux to circumscribe the section. Plants of these two species have flowers that are individually subtended by an involucre of one or two pairs of bracts that are fused basally for ⅓–⅔ of their length. The current composition of sect. *Tibouchina* includes five additional Guayana Highland species that have the free floral bracts and glabrous staminal connectives of sect. *Lepidotae.* A critical revision of sect. *Tibouchina* will also be needed before the nature and extent of this perceived overlap can be evaluated. Pending realignment, we recognize sect. *Lepidotae* as a useful category that provides a framework for the placement of new taxa in the context of their closest relatives.

Materials and Methods

Analysis of morphological characters consisted of studying living plants of some species in the field and examining approximately 500 herbarium specimens. We have examined the types of all recognized species and their taxonomic synonyms.

For scanning electron microscope (SEM) studies of trichomes, foliar material from dried herbarium specimens was cut into square or rectangular segments, affixed to stubs with silver paste, and coated with gold under a standard vacuum evaporator. Samples were examined and photographed with an Hitachi S-520 scanning electron microscope at a voltage of 15 kV. Voucher specimens for the SEM work are cited in the figure legends.

Vegetative and Floral Morphology

Habit and Branching.—All species in sect. *Lepidotae* are evergreen shrubs or trees with opposite decussate branching. With the exception of *T. aristeguietae, T. wurdackii,* and perhaps *T. narinoensis,* all species attain tree size ranging from about 7–20 meters at maturity. Except for *T. wurdackii,* which is always shrubby and appears to be restricted to the summits of low mountains in Panama, there appears to be no absolute correlation between habit, habitat, or elevational preference.

The distal branchlets of all species are terete

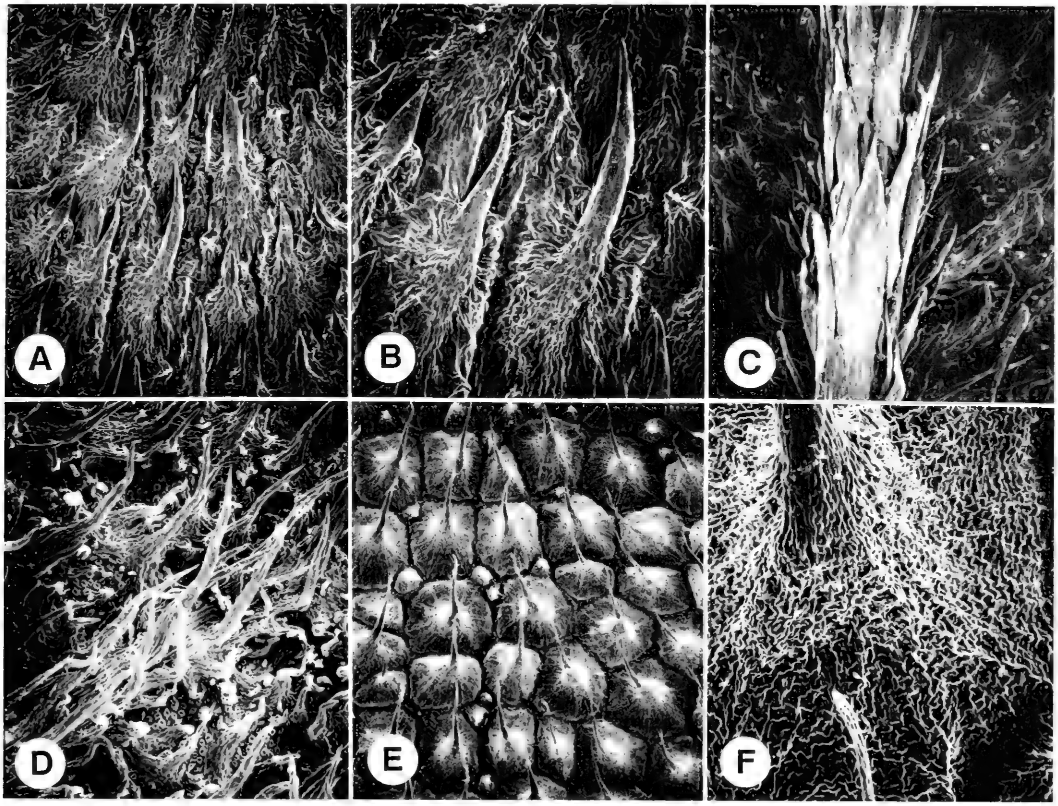

FIGURE 1. Scanning electron micrographs of foliar trichomes. A–D, *T. aristeguietae*: A, adaxial surface, ×40; B, adaxial surface, ×80; C, abaxial surface showing scales on elevated medial vein, ×40; D, abaxial surface showing trichomes on elevated secondary veins and epidermis, ×80. E–F, *T. elegantula*: E, adaxial surface showing bulla-based trichomes, ×20; F, adaxial surface showing base of one bulla-based trichome, ×150. (A–D from *Wurdack et al. 2724*, US; E–F from *Luteyn et al. 7488*, CAS.)

or subquadrate and covered with a conspicuous scaly indument. The bark on older, woody stems consists of thin, reddish-brown exfoliating strips. This condition is especially pronounced in *T. lepidota* and accounts for its common name, *siete cueros* (seven skins), in Colombia.

LEAVES.—Phyllotaxy of sect. *Lepidotae*, like that of *Tibouchina* generally, is opposite and decussate. All species have leaves with a well differentiated, entire basally symmetric blade and a canaliculate petiole. The leaves are more or less coriaceous when dry and range in shape from narrowly elliptic to elliptic-ovate, elliptic-lanceolate, or oblong-lanceolate. Foliar venation in sect. *Lepidotae* also conforms to a pattern commonly encountered in many Melastomataceae. The principal leaves have 3–5(–7) arcuate or longitudinal primary veins that arise at, or close to, a common point at the base of the blade and converge toward the apex. We employ traditional terminology in describing the venation of these species as 3–7-nerved. According to Hickey's revised classification of dicotyledonous leaves, this pattern is described as acrodromous with essentially perfect or imperfect basal venation (Hickey 1979:31, Fig. 4.3).

On the adaxial (upper) leaf surfaces, the primary veins are impressed to give the blade a grooved or furrowed effect. Without exception, the primary veins are conspicuous and elevated on abaxial (lower) foliar surfaces, but the outermost (intramarginal) pair is often depressed and inconspicuous. The reticulate network of secondary and tertiary veins on abaxial leaf surfaces is prominent and elevated in all species except *T. inopinata* and *T. wurdackii.* Leaf shape is sufficiently constant within and between populations of a species to be of diagnostic value

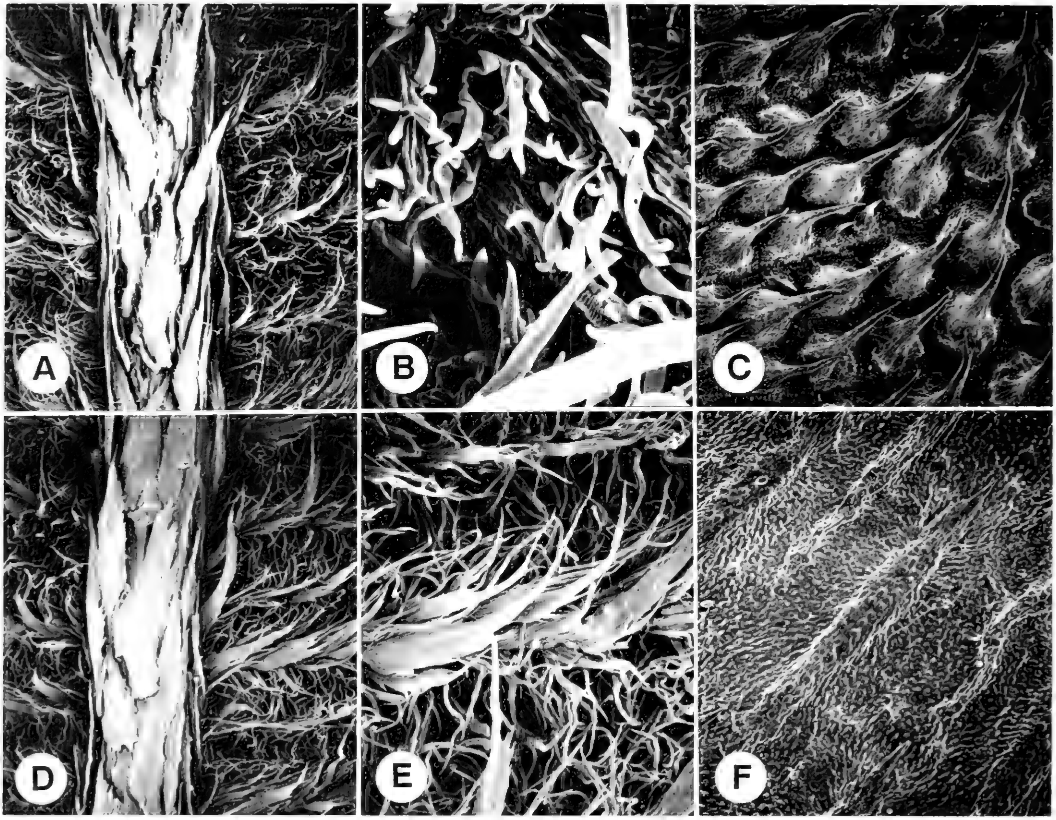

FIGURE 2. Scanning electron micrographs of foliar trichomes. A–B, *T. elegantula*: A, abaxial surface showing scales on elevated median vein and adjacent areas, ×20; B, abaxial surface showing papillose epidermal puberulence, ×500. C–E, *T. gleasoniana*: C, adaxial surface showing bulla-based trichomes, ×20; D, abaxial surface showing scales on elevated median vein and indument of adjacent areas, ×20; E, abaxial surface showing trichomes on elevated secondary veins and adjacent areas, ×50. F, *T. inopinata*, adaxial surface showing trichomes (with pustulate bases) that are partially adnate to the epidermis, ×80. (A–B from *Luteyn et al. 7488*, CAS; C–E from *Luteyn & Lebrón-Luteyn 6824*, CAS; F from *Almeda et al. 3365*, CAS.)

when correlated with other characters, such as complexity of the inflorescence, hypanthial size, and androecial details. Of greater taxonomic utility, however, is the foliar trichome complement discussed in the following section on indument.

INDUMENT.—The Melastomataceae exhibit greater trichome diversity than any other family of flowering plants (Wurdack 1986). Because of its diversity and pervasiveness, the trichome cover (indument) on the leaves, stems, and hypanthia provides some of the most important taxonomic characters for distinguishing species of sect. *Lepidotae*. For consistency, we have followed the descriptive terminology employed in Wurdack's (1986) useful atlas of melastome hairs. In some instances, however, we have applied a few of his terms somewhat differently. We have also used scanning electron microscopy to provide a visual image of intricate trichome patterns.

A notable feature of sect. *Lepidotae*, which is common in melastomes, is the range of trichome types (trichome complement) present on plants of a single species. As noted by Wurdack (1986) for melastomes in general, the typical pattern in this section includes one type of trichome on the adaxial (upper) leaf surface and one or more different ones on the abaxial (lower) leaf surface. Trichomes on the elevated primary abaxial leaf veins, on the other hand, are usually of the same kind as those on distal cauline internodes, petioles, and the inflorescence axis.

A major trend in the evolutionary modification of trichomes in this section has been com-

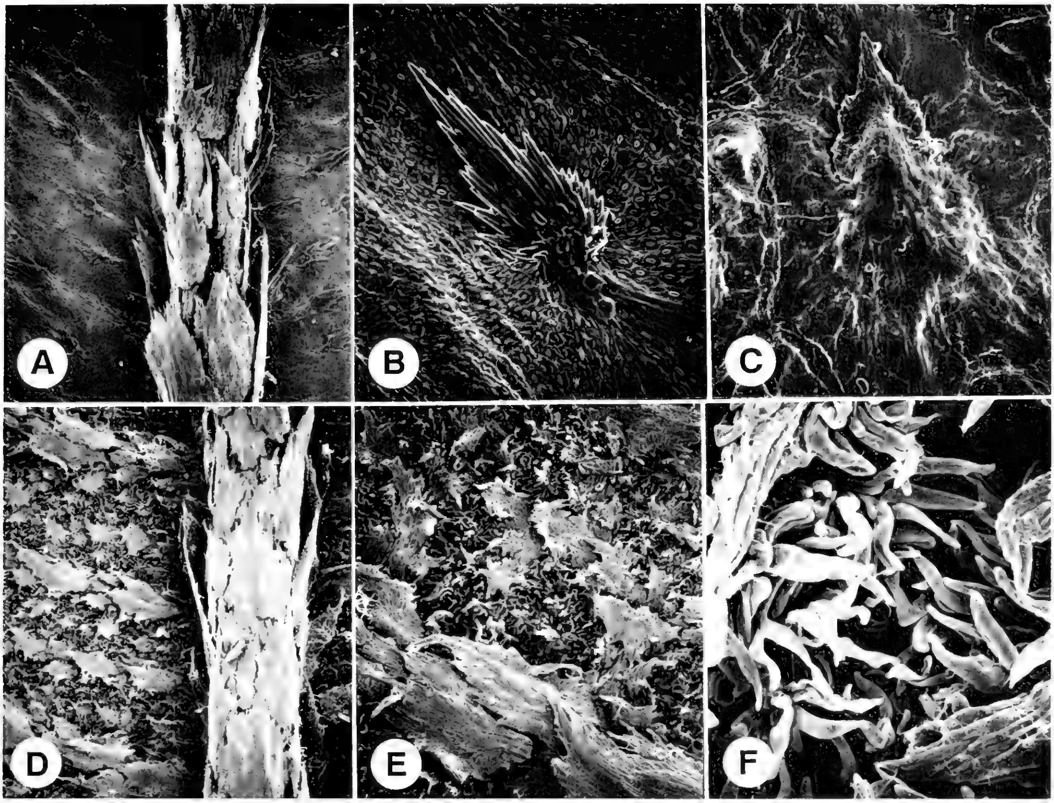

FIGURE 3. Scanning electron micrographs of foliar trichomes. A–B, *T. inopinata*: A, abaxial surface showing scales on elevated median vein and adjacent area, ×40; B, abaxial surface showing a single epidermal scale, ×200. C–F, *T. lepidota*: C, adaxial surface showing trichome partially adnate to the epidermis, ×120; D, abaxial surface showing scales on elevated median vein and adjacent area, ×30; E, abaxial surface showing scales on secondary veins and adjacent areas, ×70; F, abaxial surface showing papillose epidermal puberulence, ×500. (A–B from *Almeda et al. 3365*, CAS; C–F from *Luteyn & Lebrón-Luteyn 5557*, CAS.)

pression of hairs into sessile multicellular scales of varying size and shape. The most common type of scale on cauline internodes and elevated abaxial leaf veins is ovate to lanceolate with entire to irregularly erose or laciniate margins and basally developed lobes or a basal unlobed extension (Figs. 1C, 2D, 3D, 5C, 6D). When the base of these scales is extended into lobes or "ears" that obscure the point of attachment, we describe them as proximally attached. If no flattened basal expansion is produced below the point of attachment we describe the scales as basally attached. All species treated here have nodal cauline trichomes of this latter type (Figs. 11B, 12B). *Tibouchina lepidota* and *T. silvestris* stand apart from the others in having the proximally attached, eared cauline scales commonly intermixed with rectangular (plate-like) scales that are horizontally attached. Trichome size, shape, and basal differences provide useful characters for delimiting taxa and assessing relationships. In five of the nine species, the adaxial foliar surface is covered with trichomes that are flattened and appressed for a portion of their length. The free distal portion can be setiform as it is in *T. aristeguietae* (Figs. 1A, B) and *T. silvestris* (Fig. 5E) or compressed into a scale with irregularly erose margins as it is in *T. inopinata* (Fig. 3B), *T. lepidota* (Fig. 3C), and *T. wurdackii* (Fig. 6C). The remaining species are characterized by bulla-based hairs that are swollen basally and taper to slender terminal setae (Figs. 1E, 2C, 4A, B, 5A).

The trichome complements on abaxial foliar surfaces are more diverse than those of the adaxial surfaces. The most complex complements are found in species with bulla-based hairs on

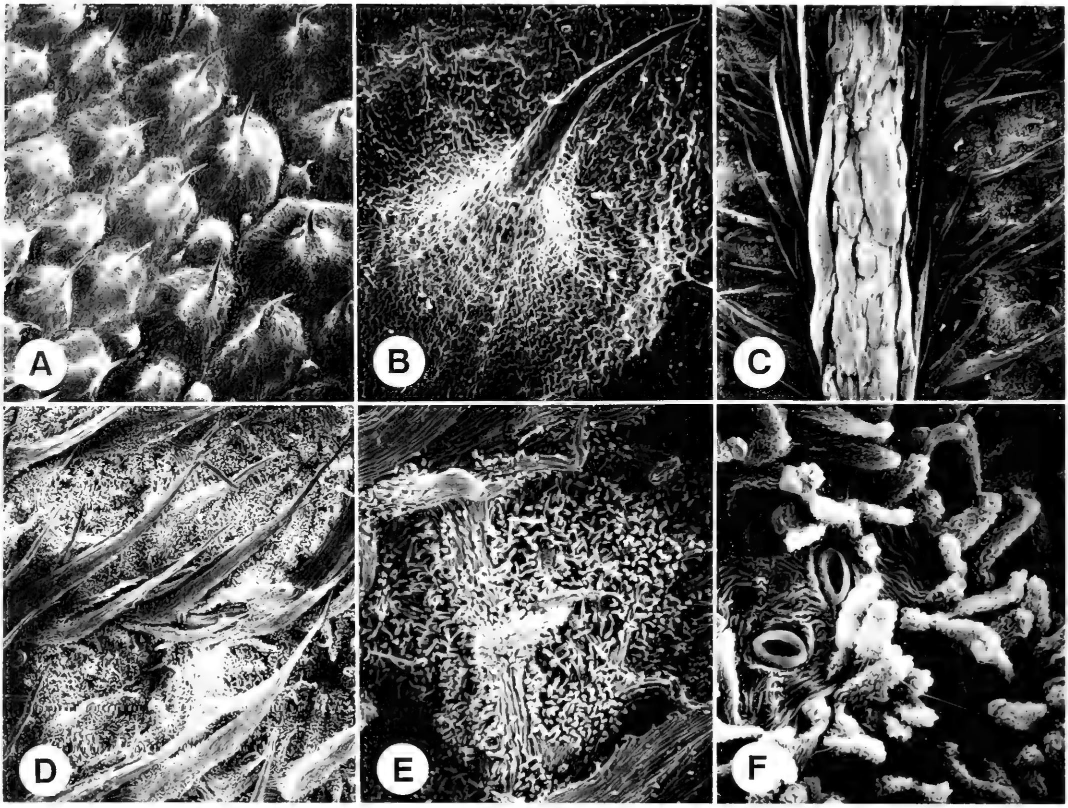

FIGURE 4. Scanning electron micrographs of foliar trichomes. A–F, *T. narinoensis*: A, adaxial surface showing bulla-based trichomes, ×20; B, adaxial surface showing a single bulla-based trichome, ×120; C, abaxial surface showing scales on elevated median vein and adjacent area, ×25; D, abaxial surface showing slender scales on secondary veins and papillose puberulence on the epidermis, ×50; E, abaxial surface showing epidermal papillose puberulence, ×150; F, abaxial surface showing papillose puberulence, ×1,000. (A–F from *Espinosa 2954,* NY.)

the adaxial surface. *Tibouchina elegantula* and *T. paleacea,* for example, have abaxial trichome complements consisting of lanceolate eared scales that grade into a mixture of slender scales, subterete hairs, and what we provisionally describe as a white papillose or farinaceous epidermal puberulence intermixed with a scattering of minute glandular hairs (Figs. 2A, B, 5C, D). This puberulence, which also occurs in *T. lepidota, T. narinoensis,* and *T. silvestris* (Figs. 3F, 4E, F, 6A, B), is a classic example of the difficulty involved in drawing sharp distinctions between papillae and unicellular trichomes (Theobald et al. 1979; Wilkinson 1979). In many respects this puberulence consists of structures that correspond to the descriptions and illustrations of papillae presented by Wilkinson (1979:148). The clustered structures in *T. silvestris* (Figs. 6A, B), however, are reminiscent of the minute dendritic trichomes with moderately long, thin-walled arms illustrated by Wurdack (1986:66, Figs. 185, 186). Within sect. *Lepidotae* these minute structures appear to be of some taxonomic significance. They are smooth walled in *T. elegantula* (Fig. 2B), *T. lepidota* (Fig. 3F), and *T. paleacea* (Fig. 5D) but consistently striate in *T. narinoensis* (Fig. 4F) and *T. silvestris* (Fig. 6B). The smooth forms are found in species from higher elevations (1,500–3,100 m), whereas the striate forms are restricted to species from lower elevations (200–1,200 m).

The simplest trichome complements on abaxial foliar surfaces are found in *T. inopinata* and *T. wurdackii.* These species have elevated primaries that are densely covered with proximally attached lanceolate scales with irregularly

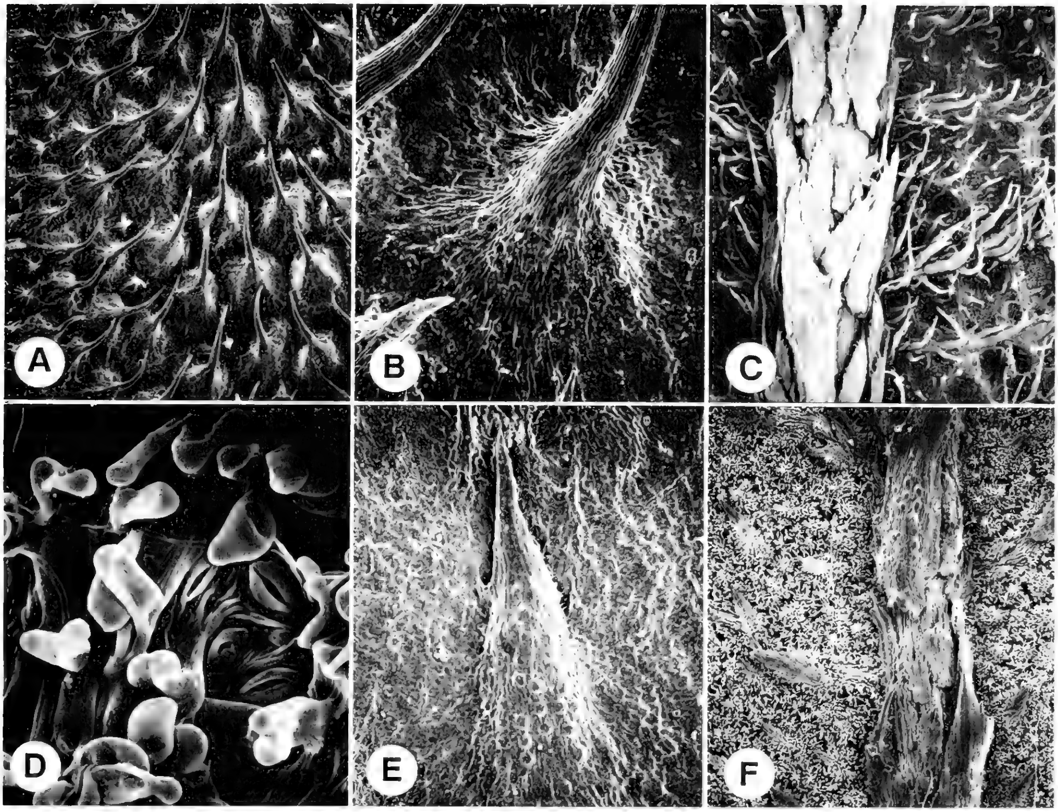

FIGURE 5. Scanning electron micrographs of foliar trichomes. A–D, *T. paleacea*: A, adaxial surface showing bulla-based trichomes, ×20; B, abaxial surface showing base of a single bulla-based trichome, ×120; C, abaxial surface showing scales on elevated median and secondary veins, ×30; D, abaxial surface showing papillose puberulence, ×1,000. E–F, *T. silvestris*: E, adaxial surface showing a single trichome (with pustulate base) that is partially adnate to the epidermis, ×120; F, abaxial surface showing scaly indument on elevated median vein and mixture of smaller scales and papillose indument in adjacent areas, ×50. (A–D from *Maguire & Maguire 44204*, US; E–F from *Køie 4808*, US.)

erose or lacerate margins and basal ears (Figs. 3A, 6D). The higher-order veins (when evident) and the leaf surface are moderately to sparsely beset with a mixture of triangular and ovate scales (Figs. 3B, 6E, F).

Indument density varies to some extent in all species. Variation is especially noticeable in the widespread *T. lepidota*, but we have been unable to detect any clinal patterns that correlate with ecology or geography.

The function and adaptive value of the scaly indument in sect. *Lepidotae* are debatable as are speculations about the significance of trichomes generally. The long-held contention is that trichomes retard water loss and alter heat exchange from plant surfaces. The extensive scaly indument may reflect light rays, thereby reducing temperature build-up at the epidermal surface. In an overview of trichome structure and function, Johnson (1975) concludes that it is no longer tenable to accept the simplistic view that transpiration reduction is a primary function of plant hairs. Levin (1973) reviews some compelling evidence to show that trichomes may play an important role in defending plants against phytophagous insects. Hence, the complex development of indument types must have evolved in response to a whole host of environmental and developmental factors (Johnson 1975).

INFLORESCENCES.—Fueled by the seminal works of Troll (1964, 1969), analyses of inflorescence structure in the Myrtales have generated more rigorous descriptions and comparisons of inflorescence types (Briggs and Johnson 1979; Sell

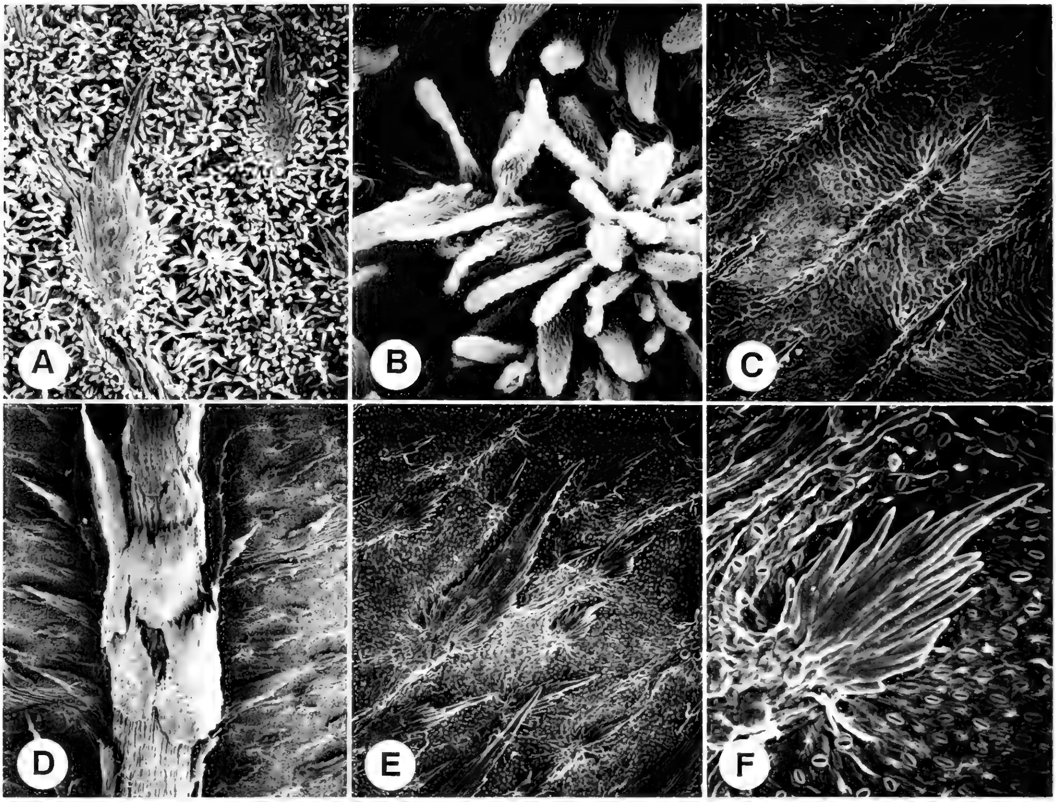

FIGURE 6. Scanning electron micrographs of foliar trichomes. A–B, *T. silvestris*: A, abaxial surface showing intercostal area with striate pustulate scales and clustered papillae-like trichomes, ×150; B, abaxial surface showing clustered papillae-like trichomes, ×1,000. C–F, *T. wurdackii*: C, adaxial surface showing trichomes (with pustulate bases) that are partially adnate to the epidermis, ×80; D, abaxial surface showing complement of large scales on elevated median vein and smaller scales on epidermis of adjacent areas, ×40; E, abaxial surface showing scale complement on intercostal area, ×80; F, abaxial surface showing a single epidermal scale, ×400. (A–B from *Køie 4808*, US; C–F from *Almeda et al. 6380*, CAS.)

and Cremers 1987; Weberling, 1988). Unfortunately, the terminology used in these studies is not uniform, but Weberling (1989) attempted to summarize much of the discursive literature on the subject. Although Briggs and Johnson (1979) focus on the Myrtaceae, the detailed nature of their study is applicable to flowering plant inflorescences generally. These workers recognize the division of inflorescences into two basic types: 1) determinate or monotelic, and 2) indeterminate or polytelic. Briggs and Johnson use anthotelic for determinate and blastotelic for indeterminate. All species in sect. *Lepidotae* have anthotelic inflorescences in which every primary, secondary, and higher-order axis ends in a flower. The species commonly show different degrees of modification from a leafy bracteose panicle with opposite and decussate branching (the frondobracteose panicle of Briggs and Johnson). As interpreted here, a panicle is an anthotelic inflorescence in which the main and at least some of the lateral axes have nodes distal to the first pair of leaves on a branch axis. Consequently, a panicle is a determinate inflorescence and not indeterminate, as it is so often used by English-language authors. Among the species treated here, *T. elegantula*, *T. gleasoniana*, and *T. inopinata* are characterized by multiflowered panicles of the kind described above (Fig. 8A). In every species the ultimate units of the primary and lateral inflorescence axes consist of what are often referred to as simple (three-flowered) dichasia (the triad of Briggs and Johnson) or some reduced derivative of this unit. A much more common inflorescence type in the section is found in *T. lepidota*, *T. narinoensis*, *T. silvestris*, and *T. wurdackii*. All of these species have fewer flowered anthotelic inflorescences representing varying reductions of the basic paniculate condition (Figs. 11, 12). In *T. lepidota,* for example, each flowering axis is terminated by what we describe as simple pedunculate dichasia or umbelliform dichasial clusters of four–six flowers. Using the multiflowered panicle as a starting point, these smaller inflorescences are readily derived by one or more of the following modifications: 1) reduction in the number of nodes and length of internodes, 2) suppression of branching on primary and secondary axes, and 3) reduction in the number of flowers (by abortion) concomitant with a reduction in the length of distal internodes. When taken to the ultimate extreme, these reductions result in the solitary flowers (monads of Briggs and Johnson) that are typical of *T. aristeguietae* and *T. paleacea.*

As in frondobracteose panicles generally, all species treated here have opposite-paired bracts that become smaller from the base of the inflorescence to the bracteoles subtending the flowers. The size, shape, and indument of bracteoles are useful characters for distinguishing species and groups of species. Like petals, they are early deciduous and not always present on dried specimens.

HYPANTHIUM AND CALYX.—The mature hypanthium, which envelops the free ovary, is terete, externally pubescent, and ranges in shape from campanulate to urceolate. It is supplied with 10 longitudinal vascular ribs that are crowned by a circular vascular plexus referred to as the torus.

The five persistent calyx lobes are ciliate, oblong to triangular, and assume a spreading to ascending posture on mature hypanthia. There is much overlap in the length and width of hypanthia and calyx lobes among species in the section. Size differences coupled with details of the indument and other traits are useful in distinguishing such species as *T. aristeguietae, T. inopinata,* and *T. narinoensis.*

PETALS.—The five petals are dextrorsely imbricate in bud and assume a more or less horizontal posture when fully expanded. Each petal is attached to a point on the torus opposing a stamen and alternating with a calyx lobe. All petals are essentially obovate with an apex that is rounded but sometimes varies to asymmetrically retuse in *T. elegantula* and *T. narinoensis.* The petals are glabrous and the margins are consistently ciliate in all species except *T. elegantula.* Differences in petal size and color are useful in characterizing several species. Like so many Melastomataceae, the petals are fugacious and difficult to rely on for species identification. Petal color is a useful field character in need of additional study. In *T. wurdackii* the petals are pink, but they are white in *T. inopinata,* its closest relative. In *T. lepidota* the petals are initially magenta or rose-red but fade to uniform lavender with age. This color change has been recorded for populations from Colombia (Uribe 1972), Ecuador (*King & Almeda 7910*), Peru (*Knapp et al. 7511*), and Venezuela (*Wurdack et al. 2753*). Floral color change following pollination or aging is reported for several flowering plants (Gori 1983), but the significance and prevalence of this phenomenon is still being explored. Because flowers that have undergone a visible change offer no food rewards (Gori 1983), pollinators picking up on this visual cue could increase their foraging efficiency by visiting only viable or unpollinated flowers. This remarkable color change is also reported for *G. gleasoniana* (*Asplund 16227*) and *T. paleacea* (*Maguire & Maguire 44204*). The diversity of flower color notes on herbarium labels suggests that this phenomenon may also be characteristic of other South American species in sect. *Lepidotae* that reportedly have purple, purple-pink, lavender, or lilac flowers. It is for this reason that we urge collectors to carefully record their field observations of petal color.

ANDROECIUM.—The 10 stamens in each flower are characterized by 2-celled, ventrally channeled, subulate anthers with ventrally inclined apical pores and anther connectives modified ventrally at the filament insertion into horizontal or upturned, bilobed ventral appendages (Fig. 8G). As is characteristic of *Centradenia* (Almeda 1977), *Pilocosta* (Almeda and Whiffin 1981), and other capsular-fruited genera in the family, each species has stamens that are differentiated into one of three size classes within a flower. These range from the strongly dimorphic condition of *T. elegantula, T. inopinata,* and *T. wurdackii* (Figs. 8G, 12G) through the weakly dimorphic staminal arrangement of *T. gleasoniana* and *T. silvestris* (Fig. 11G), to the more typical isomorphic situation found in all other species of the section. Filament insertion on the torus is like that found in most other capsular-fruited neotropical Melastomataceae. In those species with strongly dimorphic stamens, the five larger ones are inserted on the torus opposite the sepals (antesepalous) and the five smaller stamens are inserted opposite the petals (antepetalous). In the species descriptions and discussions, when the anthers are described as alternately unequal, measurements of the antesepalous anthers are listed first followed by the antepetalous ones. Connectives of the larger stamens in a flower are often conspicuously prolonged below the thecae to give anthers a pronounced curvature (Fig. 12G). In the smaller stamens, connective prolongation is shorter, and the anthers often assume an erect or ascending posture (Figs. 8G, 12G). Within the section there is also a consistent color difference between the large and small anthers in each flower, unlike the uniform yellow anthers of those species with isomorphic stamens. Even in *T. silvestris,* which has weakly dimorphic stamens, there is a consistent color difference between the antesepalous and slightly larger antepetalous anthers (Fig. 11G).

The size, color, and orientation of anthers and associated connective features are useful in species identification. We have found it difficult, however, to correlate this androecial diversity with geography, ecology, or other characters in attempts to understand patterns of floral evolution in sect. *Lepidotae.*

GYNOECIUM AND FRUIT.—The superior ovary consists of five united carpels with axile placentation. The numerous ovules in each locule are anatropous and borne on prominent peltate placental intrusions. In all species the distal third of the ovary is gently fluted and moderately to densely covered with appressed simple hairs that give the summit a setose or bristly appearance. The glabrous style terminates in a truncate to slightly expanded papillose stigma. The styles are invariably hooked or somewhat incurved apically and assume a stationary deflexed posture opposing the stamens. The mature loculicidal capsules are dry, semi-woody, and fully enveloped by the scaly hypanthia. The capsules are ellipsoid to oblong-ovoid. Aside from modal size differences, neither gynoecia nor fruits provide significant taxonomic characters for distinguishing species.

SEEDS.—The seeds of all species in sect. *Lepidotae* are cochleate (Fig. 12H) to somewhat elongate-cochleate (Fig. 11H), tuberculate, and have a terminal hilum. As is generally true for the Tibouchineae, seed morphology is remarkably uniform (Whiffin and Tomb 1972). The principal variations, although minor and of little value in distinguishing species, relate to seed length and tubercula size and shape. We have not seen mature seeds of *T. gleasoniana* and *T. paleacea* on any of the collections examined for this study. It seems unlikely, however, that they differ sufficiently to be of taxonomic significance.

CHROMOSOME NUMBERS

Chromosome numbers have been reported for only two species of sect. *Lepidotae.* Solt and Wurdack (1980) reported n = ca. 27 for *T. aristeguietae.* Raven (*in* Solt and Wurdack 1980) reported $2n$ = ca. 122 for *T. lepidota* (Bonpl.) Baillon, while Hunziker et al. (1985) reported n = ca. 62. Based on chromosome numbers of numerous species of *Tibouchina* in seven different sections (Solt and Wurdack 1980), $x = 9$ is the base number in the genus. Although additional species will have to be sampled before any generalizations can be made for the section, the chromosome numbers for these two species are clearly of secondary polyploid derivation. Based on available data *T. aristeguietae* is probably a hexaploid, whereas *T. lepidota* appears to be an aneuploid derived from a high polyploid based on $9x$.

GEOGRAPHY AND ECOLOGY

The distribution of *Tibouchina* sect. *Lepidotae* is largely centered in the tropical South American Andes from western Venezuela (Mérida) to south-central Peru (Pasco) (Figs. 7, 9, 10). Two closely related extra-Andean species, *T. inopinata* and *T. wurdackii,* are restricted to floristically related areas of Costa Rica and Panama. The center of diversity for the section is in Colombia, where six of the nine species are found. Throughout the range of sect. *Lepidotae* no more than two species occur in any other country. This high concentration of species in Colombia is a common pattern for many genera with major centers of diversity in the Andes (Cuatrecasas 1985; Gleason 1929; Luteyn 1983; Todzia 1988).

Like many neotropical Melastomataceae, high amounts of light and moisture seem to be important requirements for growth and survival of the species. The most characteristic habitat is the cool montane forests where most of the species are found growing along road cuts or forest margins. In the Andes and mountains of southern Central America this vegetational formation is commonly referred to as "cloud forest," "fog forest," "montaña," or "ceja." *Tibouchina silvestris* is exceptional in that it appears to be restricted to low elevation wet forest formations.

The only widespread species, *T. lepidota,* occurs at elevations from 800–3,200 m. High polyploidy may be an important attribute that equipped this species for widespread colonization of the tropical Andes. All other species exhibit more restricted geographical and elevational distributions. A common pattern in sect. *Lepidotae* is one in which closely related species replace each other geographically. This is apparent in the following species pairs: *T. inopinata* and *T. wurdackii* (Figs. 9, 10), *T. elegantula* and *T. paleacea* (Figs. 7, 9), and *T. gleasoniana* and *T. paleacea* (Figs. 7, 9). *Tibouchina lepidota* and *T. silvestris,* which occur in the same general area, are isolated by different elevational tolerances while *T. narinoensis* and *T. paleacea* are isolated both geographically and elevationally. Although some species are found in the same 1 degree square quadrant (*T. gleasoniana, T. lepidota,* and *T. paleacea*), label information suggests that only one species of sect. *Lepidotae* is found at any one site. The spatial relationships among these species pairs suggest that geographic and/or elevational differentiation has been a recurrent evolutionary theme in sect. *Lepidotae.* This radiation is evidently a recent phenomenon because the tropical Andes and the mountains forming the southern Central American land bridge achieved prominent uplift during the Pliocene (Raven and Axelrod 1975; Simpson 1979). Uplift, coupled with the climatic fluctuations that resulted from Pleistocene glaciations, set the stage for speciation along a lengthy corridor of cool-forest habitats. This was the environmental setting that became available to the progenitors of sect. *Lepidotae,* which probably migrated from southern and eastern areas of the South American continent.

SYSTEMATIC TREATMENT

Tibouchina sect. **Lepidotae** Cogn. *in* Martius, Fl. Bras. 14(3):371. 1885. TYPE.—*T. lepidota* (Bonpl.) Baillon.

Trees or shrubs prevailingly beset with trichomes that are compressed into flattened scales of varying sizes and shapes. Leaves opposite, decussate, petiolate, essentially entire, coriaceous, the blades of a pair essentially equal in size, 3–7-nerved, the primaries impressed adaxially and conspicuously elevated on abaxial surface. Inflorescence an anthotelic frondobracteose panicle or some modification of this structure in which the main and at least some lateral axes have nodes distal to first pair of leaves on a branch axis; bracteoles variously pubescent or glabrous, early deciduous, commonly enveloping young floral buds. Flowers perigynous; hypanthium campanulate to urceolate, mostly copiously pubescent externally, 10-nerved, and crowned by a circular vascular ring (torus) bearing calyx lobes, petals, and stamens. Calyx lobes 5, persistent. Petals 5, obovate, entire but typically ciliolate. Stamens 10, isomorphic, or weakly to strongly dimorphic with 2-celled ventrally channeled subulate anthers having ventrally inclined apical pores and glabrous anther connectives, the connectives variously prolonged and modified ventrally at filament insertion into horizontal or upturned, bilobed ventral appendages. Ovary superior, 5-celled with axile placentation. Style glabrous, hooked or incurved apically, typically declined to side of flower opposing stamens. Capsule dry, semiwoody, loculicidal. Seeds cochleate to elongate-cochleate and tuberculate with a terminal hilum.

Key to the Species of Sect. *Lepidotae*

1. Upper (adaxial) leaf surface covered with bulla-based hairs (hairs with swollen bases), the free portions of hairs spreading, awl-like.
    2. Indument of uppermost internodes appressed (rarely antrorsely spreading), proximally attached scales with irregularly shaped basal ears or flattened extensions below point of attachment; flowers borne in modified compound panicles or dichasia with up to 34 flowers (sometimes flowers solitary because of abortion of lateral buds in simple dichasia); leaf base rounded or acute; stamens isomorphic to inconspicuously dimorphic.
        3. Inflorescences composed of simple dichasia with only central flower typically persisting at anthesis; calyx lobes 8–11 mm long; hypanthial scales 3–5 mm long .... *T. paleacea*
        3. Inflorescences composed of modified panicles with 8–34 flowers; calyx lobes 2–6 mm long; hypanthial scales 1–3 mm long.

4. Scales on elevated primary veins of lower leaf surface 2–4 mm long, very narrowly lanceolate with entire margins; scales on tertiary veins straight, 1–2 mm long, flattened, very narrowly lanceolate with entire margins; intercostal areas copiously papillose pubescent, lacking twisted terete hairs; hypanthia sparsely covered with scales, margins entire, epidermal surface visible .... *T. narinoensis*
4. Scales on elevated primary veins of lower leaf surface 1.5–2.5 mm long, lanceolate with irregularly erose margins; scales on tertiary veins curved, 0.5–1 mm long, lanceolate with irregularly erose margins; intercostal areas lanate, with twisted, golden, terete hairs ca. 0.5 mm long; hypanthia densely covered with scales, the margins irregularly erose, the epidermal surface not visible .... *T. gleasoniana*

2. Indument of uppermost internodes (in part) spreading basally attached scales with prominent abaxial basal spurs or protuberances that diverge from the scale proper in nearly perpendicular fashion; flowers borne in compound panicles with ca. 50–90 flowers; leaf bases cordate to truncate; stamens dimorphic .... *T. elegantula*

1. Upper (adaxial) leaf surface covered with flattened scales, the free portions of hairs lanceolate or triangular.
5. Inflorescences much-branched panicles with up to ca. 250 flowers; calyx lobes 1–1.5 mm long; petals 0.6–1.3 × 0.4–0.7 cm; Costa Rica, western Panama (Chiriquí, Bocas del Toro) ... *T. inopinata*
5. Inflorescences consisting of solitary flowers, simple or umbelliform pedunculate dichasia with 3–6 flowers, or congested panicles with (3–)5–18 flowers; calyx lobes 3–9 mm long; petals 1.2–3.7 × 0.9–3.1 cm; Panama (Coclé, Darién, Veraguas) south to Colombia, Venezuela, Ecuador, and Peru.
6. Flowers solitary; calyx lobes 7–9 mm long; anther thecae 8–9 mm long .... *T. aristeguietae*
6. Flowers in simple or umbelliform dichasia or modified panicles; calyx lobes 3–6(–7) mm long; anther thecae 5–7.5(–9) mm long.
7. Lower leaf surface lacking a white papillose puberulence on epidermis; bracteoles 4–9 mm long, lanceolate to subulate but not enveloping and concealing young floral buds; hypanthial scales 1–2 mm long; Panama ..... *T. wurdackii*
7. Lower leaf surface with white or tan papillose puberulence; bracteoles 8–15 mm long, ovate to elliptic, typically enveloping and concealing young floral buds; hypanthial scales 3–5 mm long; Venezuela, Colombia, Ecuador, and Peru.
8. Hypanthial scales 1.5–3 mm long; lower leaf surface beset with lepidote scales; bracteoles covered with scales similar to hypanthia; stamens isomorphic, anthers yellow; western Venezuela to central Peru .... *T. lepidota*
8. Hypanthial scales 3–5 mm long; lower leaf surface beset with lanceolate scales and white or tan papillose puberulence on epidermis; bracteoles glabrous; stamens weakly dimorphic, the slightly larger anthers yellow, the smaller anthers pink or red; Colombia (Valle) .... *T. silvestris*

Tibouchina aristeguietae Wurdack, Bol. Soc. Venez. Ci. Nat. 20:360. 1959. Type.—VENEZUELA. Mérida: Arriba de Santo Domingo, 2,600 m, Aug 1958 (fl, fr), *Aristeguieta 3262* (Holotype: NY!; isotypes: NY!, US!, VEN).

Shrubs 2–5 m tall; lower branches with red peeling epidermis; distal branches terete, the internodes covered with appressed, proximally attached, lanceolate scales 1–2 mm long, usually with entire margins, sometimes with irregularly erose margins and basal ears, the nodes with similar scales mostly 4–5 mm long. Petioles 3–5 mm long, covered with lanceolate scales like those of internodes; blades coriaceous, 1.6–5 cm long, 0.9–

1.7 cm wide, narrowly elliptic to elliptic, 5-nerved, the apex apiculate, the base attenuate, the margin entire and beset with clasping, folded scales; upper leaf surface covered with scales fused to leaf surface for ¼–¾ their length, the distal portion of scale free, flattened, triangular to subulate, the fused portion covered with minute white pustules; lower leaf surface with three types of scales and hairs that nearly conceal surface; scales on elevated primary veins similar in shape and size to cauline internodal scales, the secondary and tertiary veins beset with a mixture of straight lanceolate scales 0.5–1 mm long and shorter curved or twisted hairs ca. 0.25 mm long, both free almost to base and not concealing surface, which is also randomly but sparsely beset with minute sessile glands. Flowers solitary, terminal; bracteoles conspicuous, 1.1–1.4 cm long, elliptic, enclosing bud or young flower, beset with very narrowly lanceolate scales up to 1 mm long with a broad marginal glabrous band, early deciduous; pedicels 3–5 mm long. Hypanthia (at anthesis) 7–9 mm long to torus, 7–11 mm wide, campanulate to urceolate, moderately covered with very narrowly lanceolate appressed scales 4–5 mm long. Calyx lobes, 7–9 × 3.5–4 mm, oblong, beset with scales up to 3 mm long, the scales progressively shorter toward margin, with a narrow glabrous marginal band, the margins ciliate. Petals 1.4–3.5 × 2–3.1 cm, purple to purple-pink, obovate, sparsely ciliate, otherwise glabrous. Stamens isomorphic, anther thecae 8–9 mm long with ventrally inclined pores, filaments ca. 9 mm long, white, connective extended into an upturned bifid appendage ca. 2 mm long. Ovary (at anthesis) ovoid, 7 mm long, setose and fluted in distal half. Styles 8–19 mm long, strongly hooked, declinate; stigma truncate, papillose. Seeds ca. 0.5 mm long, light brown.

Distribution and Phenology.—Endemic to western Venezuela (Fig. 7) where it is found between 1,500 and 2,600 m, primarily in wet areas along roadsides and disturbed sites. Flowering in August and October through December; fruiting in August.

Representative Specimens Examined.—VENEZUELA. Mérida: Distr. Rangel, along road near Santo Domingo (70°42′W, 8°52′N), 7 Aug 1983 (fl, fr), *van der Werff & Ortiz 6008* (MO); Distr. Rangel, Carretera Apartaderos-Sto. Domingo, 8 km antes de llegar a Sto. Domingo, 11 Oct 1983 (fl), *Aymard 2172* (CAS, MO); Distr. Rangel, Agua Caliente, a orillas de la carretera Mérida-Barinas, unos 2 km después de La Mitisús, 10 Dec 1961 (fl), *Ruiz-Terán 716* (CAS); Distr. Rangel, road between Santo Domingo and Edo. Barinas boundary, 7 Nov 1972 (fl), *Wurdack et al. 2724* (NY, US). Trujillo: between Valera and Monte Carmelo, Aug 1923 (fl, fr), *de Bellard s.n.* (US).

This species, one of two in sect. *Lepidotae* occurring in Venezuela, is distinguished by its solitary flowers, large petals (1.4–3.5 × 2–3.1 cm), long calyx lobes (7–9 mm), and hypanthia with long (4–5 mm), narrowly lanceolate scales. The leaves of *T. aristeguietae* have a unique complement of scales and hairs that link it to two different species groups within the section. In having upper leaf surfaces beset with flattened scales fused to the leaf surface for ¼–¾ their length, it is most like the group of species that includes *T. inopinata, T. lepidota, T. silvestris,* and *T. wurdackii.* The complex mixture of lanceolate scales, curved or twisted hairs, and the occasional admixture of sessile glands on secondary and higher order lower leaf veins, however, suggests a close relationship to *T. elegantula, T. gleasoniana,* and *T. paleacea.* Among this trio, *T. aristeguietae* is most like *T. gleasoniana* in its lack of the white papillose puberulence on lower leaf surfaces that is so typical of *T. elegantula* and *T. paleacea.* Wurdack (1959), in describing *T. aristeguietae,* suggested a relationship to *T. paleacea,* which differs in having larger leaves (4.2–11 × 1.6–11 cm) and an indument of bulla-based hairs on upper leaf surfaces.

Tibouchina elegantula Todzia & Almeda, sp. nov. (Fig. 8). Type.—COLOMBIA. Cauca: Parque Nac. Munchique, km 50–55 along road above Uribe, 1,875–2,256 m, 25 Apr 1979 (fl), *Luteyn et al. 7488* (Holotype: NY!; isotypes: AAU!, CAS!, CM!, COL, MO!, US!).

Frutex vel arbor 2–15 m; ramuli teretes sicut petioli inflorescentiaque dense pilis patulis squamatis eroso-ciliolatis 1–2 × 0.25–0.5 mm induti. Petioli 0.5–1.7 cm longi; lamina 7–11(–14.2) × 3.8–7.2 cm elliptica vel elliptico-ovata apice obtusa vel rotundata, basi cordata vel truncata, supra dense bullato-setulosa bullis ad basim 1–1.5 mm latis setula terminali ca. 1 mm longa, subtus in venis primariis et secundariis squamis eroso-ciliolatis 1–2.5 mm longis densiuscule obsita, subtus in superficie pilis teretiusculis plerumque 0.5–1 mm longis densiuscule obsita, 7-nervata coriacea et integra. Inflorescentia multiflora 7.5–19 cm longa; flores 5-meri, pedicellis (ad anthesim) 2–5 mm longis. Hypanthium (ad torum) 4–7 mm longum extus densiuscule paleis appressis 1.5–2 mm longis indutum; calycis lobis 3–4 × 2–2.5 mm triangularibus. Petala 1.2–1.6 × 0.9–1 cm obovata. Stamina dimorpha glabra, thecis subulatis 6 vel 5 mm longis poro ventraliter inclinato, connectivis 1 vel 0.25 mm prolongatis appendicibus ventralibus 1 vel 0.5 mm hebetibus. Ovarium 5-loculare apice modice setoso.

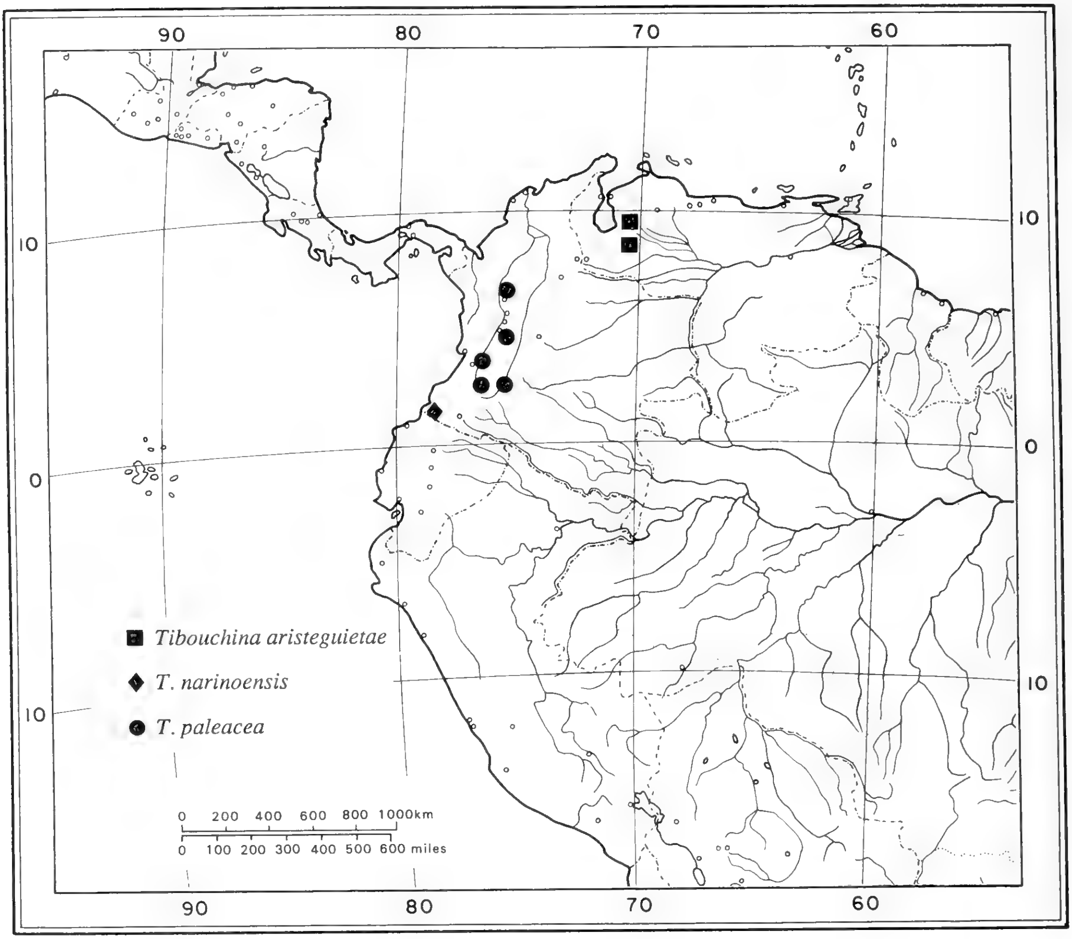

FIGURE 7. Distributions of *Tibouchina aristeguietae, T. narinoensis,* and *T. paleacea.*

Trees or shrubs 2–15 m tall; distal branches terete, the internodes densely covered with basally attached, reddish-brown scales 1–2 mm long with irregularly erose margins, the larger scales distinctly spreading and beset with a conspicuous basal knob on the abaxial surface, the nodes with similar proximally attached scales mostly 2–3.5 mm long. Petioles 0.5–1.7 cm long, covered with lanceolate scales similar to those of internodes; blades coriaceous, 7–11(–14.2) cm long, 3.8–7.2 cm wide, elliptic to elliptic-ovate, 7-nerved with the inconspicuous pair of intramarginal veins extending ca. halfway up margin, the apex bluntly rounded to obtuse, the base cordate to truncate, the margin entire and beset with overlapping, clasping, folded scales; upper leaf surface covered with bulla-based hairs with setae ca. 1 mm long; lower leaf surface with three types of scales or hairs that completely conceal surface; scales on elevated primaries appressed, proximally attached, lanceolate, 1.5–2.5 mm long, with irregularly erose or lacerate margins; scales on secondary and tertiary veins lanceolate, curved, 1–2 mm long, with irregularly erose or lacerate margins, the intercostal areas covered with twisted, golden, terete hairs 0.5–1 mm long and a ground layer of white puberulence and scattered, sessile, glandular hairs. Inflorescences terminal, much-branched panicles 7.5–19 cm long, with ca. 50–90 flowers; bracteoles 4–6 mm long, enclosing young flower buds, ovate, beset with lanceolate scales ca. 1 mm long with irregularly erose or lacerate margins and small basal ears, early deciduous; pedicels 2–5 mm long, beset with scales similar to those on hypanthia. Hypanthia (at anthesis) 4–7 mm long to torus, 5–7 mm wide, narrowly campanulate to urceolate, densely covered with appressed, proximally attached lanceolate scales 1.5–2 mm long with irregularly erose or lacerate margins and small basal ears. Calyx lobes 3–4 × 2–2.5 mm, triangular, densely beset with scales like those of hypanthia except for a very narrow glabrous marginal band, the margins ciliate. Petals 1.2–1.6 cm long, 0.9–1 cm wide, lavender, obovate, rounded to retuse at apex, glabrous, not ciliate. Stamens dimorphic, with ventrally inclined pores; larger stamens geniculate, filaments 6–7 mm long, anther thecae ca. 6 mm long, red, subulate, connective ca. 1 mm long with a yellow, erect, bifid appendage ca. 1 mm long; smaller stamens geniculate, filaments 5.5–6 mm long, anther thecae 5 mm long, subulate, yellow, connective ca. 0.25 mm long, with bifid appendages ca. 0.5 mm long. Ovary (at anthesis) ovoid, fluted at setose apex. Styles 6–8 mm long, declinate, hooked or straight at apex; stigma truncate, papillose. Seeds ca. 0.5 mm long, tan.

DISTRIBUTION AND PHENOLOGY.—Known only from Colombia (Cauca and Valle) (Fig. 9) where it occurs along roadsides in cloud forest at elevations of 1,875–2,256 m. Flowering in April; fruiting in November.

SPECIMENS EXAMINED.—COLOMBIA. Valle: Cordillera Occidental, vertiente oriental, hoya del Río Cali, vertiente derecha, entre Puente de los Cárpatos y La Margarita, 2 Nov 1944 (fr), *Cuatrecasas 18489* (NY).

In proposing this new species we emphasize its short bracteoles (4–6 mm), comparatively small, eciliate petals (1.2–1.6 × 0.9–1 cm), and unusual cauline indument consisting of basally attached spreading scales that have irregularly erose margins and subbasal callosities or protuberances on the abaxial surface (Fig. 8B). The two known collections of *T. elegantula* were previously identified as *T. gleasoniana* and *T. paleacea,* probably because of similarities in foliar pubescence. *Tibouchina gleasoniana* differs consistently from *T. elegantula* and *T. paleacea* in its lack of the white papillose puberulence that is intermixed with a scattering of sessile glandular hairs on the abaxial foliar surface. The virtually identical foliar indument of these last two species leaves little doubt that they are closely related. *Tibouchina paleacea* is separable from *T. elegantula* by the 5-nerved leaves, prevailingly appressed cauline scales with basal ears or flattened basal extensions, larger petals (1.7–2.6 × 1.5–2.7 cm), and simple dichasial inflorescence with only the central flower typically persisting at anthesis.

Occasional specimens of *T. paleacea* are superficially reminiscent of *T. elegantula* in having cauline scales that are somewhat spreading. In *T. paleacea,* however, the cauline scales are always proximally attached and have well-defined basal ears.

The name for this species is derived from *elegantulus,* Latin for elegant or very fine. It emphasizes the handsome reddish upper internodes and striking foliar indument.

Tibouchina gleasoniana Wurdack, Phytologia 35: 241. 1977. *Tibouchina lepidota* (Bonpl.) Baillon var. *intermedia* Gleason, Bull. Torrey Bot. Club 52:328. 1925. TYPE.—ECUADOR: in forests of the Andes in the temperate zone, Sep, *Jameson 87* (Holotype: NY!).

Shrubs 1.5–6 m tall; distal branches quadrangular, internodes covered with appressed, proximally attached, ovate to lanceolate scales 1–2 mm long with irregularly erose or lacerate margins, nodes beset with basally attached, lanceolate scales 3–6 mm long with mostly entire margins. Petioles 0.7–2(–4.2) cm long, beset with proximally attached lanceolate scales 1.5–3.5 mm long with irregularly erose or lacerate margins; blades coriaceous, 5–13 cm long, 2.8–6.7 cm wide, elliptic to oblong-lanceolate, 5-nerved, the apex acute, the base acute to rounded, margin entire and beset with clasping, folded scales; upper leaf surface covered with bulla-based hairs, the terminal setae 0.5–1 mm long; lower leaf surface with two kinds of scales that nearly cover the surface; scales on elevated primary veins proximally attached, lanceolate, 1.5–2.5 mm long, with irregularly erose margins; scales on elevated secondary and tertiary veins curved, 0.5–1 mm long, lanceolate with irregularly erose or laciniate margins; intercostal areas covered with twisted, golden, simple or variously branched terete hairs ca. 0.5 mm long, giving lower leaf surface a lanate appearance, lacking a white papillose puberulence. Inflorescences terminal compound panicles, 6–13.5 cm long, with 8–34 flowers; bracteoles enclosing young floral buds, 1.2–1.5 cm long, elliptic, chartaceous, the midvein sometimes beset with scales like those on hypanthium, or with a triangular patch of scales at base, otherwise glabrous, early deciduous; pedicels 2–7

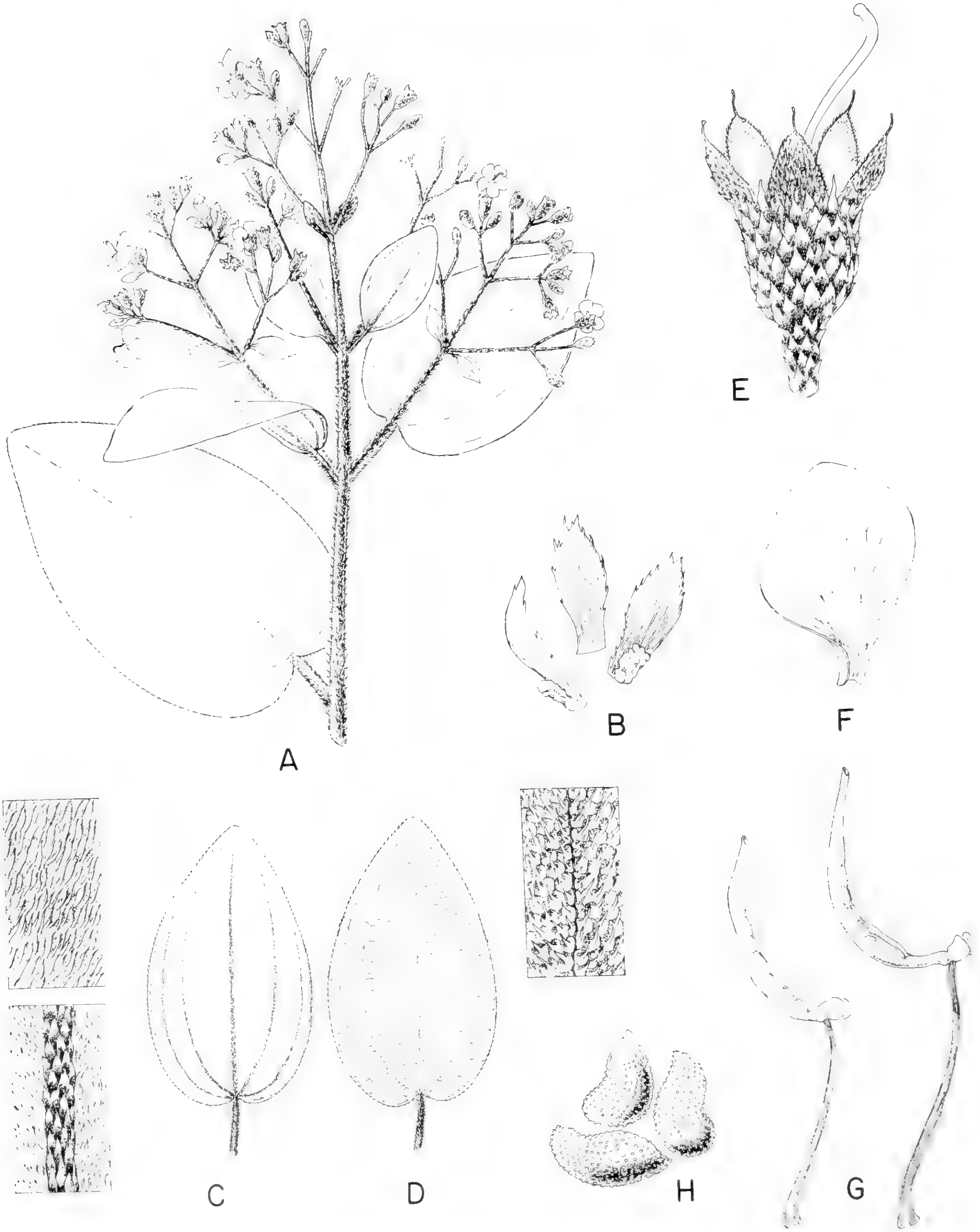

FIGURE 8. *Tibouchina elegantula* Todzia & Almeda. A, habit, × ca. ½; B, spreading cauline scales with subbasal protuberance ×9; C, representative leaf (abaxial surface) with enlargement of intercostal indument (upper left) and indument of median vein (lower left), × ca. ⅓; D, representative leaf (adaxial surface) with enlargement of indument adjacent to impressed median vein (upper right), × ca. ⅓; E, hypanthium (at anthesis) with petals and stamens removed, ×3; F, petal, × ca. 2⅙; G, antepetalous stamen, lateral view (left) and antesepalous stamen, lateral view (right), ×5; H, seeds, ×30. (A–H from *Luteyn et al. 7488*, CAS.)

mm long. Hypanthia (at anthesis) 7–10 mm long to torus, 5.5–7 mm wide, narrowly campanulate to urceolate, densely covered with appressed, proximally attached lanceolate scales (2–3 mm long) with basal ears and irregularly erose margins that conceal surface. Calyx lobes 3–6 mm long, ca. 3 mm wide, oblong to oblong-triangular, moderately beset with scales like those of hypanthia except for a narrow marginal glabrous band, the margins ciliate. Petals 2–3.2 × 1.8–2.9 cm, rose-purple fading to lavender with age, obovate, ciliate, otherwise glabrous. Stamens isomorphic to inconspicuously dimorphic, with ventrally inclined pores; filaments white, 7–8 mm long; anther thecae 5.5–8 mm long, yellow, connective 0.25–0.5 mm long, with a yellow upturned bifid appendage 0.5–1 mm long. Ovary (at anthesis) ovoid, fluted at setose apex. Styles 1.1–2 cm long, declinate, hooked or straight at apex; stigma truncate, papillose. Mature seeds not seen.

DISTRIBUTION AND PHENOLOGY.—Southern Colombia (Nariño) and north-central Ecuador (from Carchi to Bolívar) (Fig. 9) at elevations of 1,800–3,500 m, along roadsides and in disturbed areas of montane rainforest or cloud forest. Apparently flowering throughout the year.

REPRESENTATIVE SPECIMENS EXAMINED.—COLOMBIA. Nariño: Finca La Planada, near Chucunés, 13 Jan 1981 (fl), *Gentry et al. 30583* (MO); Mpio. Ricaurte, La Planada, ca. 5 km S of Chucunés, Finca of L. Salazar, 24–25 Feb 1979 (fl), *Luteyn & Lebrón-Luteyn 6824* (CAS, NY, US). ECUADOR. Bolívar: western cordillera, forest region above village of Balsapampa, Jul 1934 (fl), *Rimbach 206* (NY). Carchi: 62–75 km W of Tulcán, ca. 0°50′N, 78°5′W, 7 Jan 1985 (fl), *Luteyn & Cotton 10871* (AAU, CAS, NY). Cotopaxi: road Quevedo-Latacunga, Pilaló, 4 May 1968 (fl), *Harling et al. 9085* (F, MO, US); around Pilaló, 79°2′W, 0°57′S, 7 Jul 1968 (fl), *Holm-Nielsen & Jeppesen 1490* (AAU, US); road Echeandía-Guanujo, E of Echeandía, 79°07′W, 1°25′S, 8 Jul 1979 (fl), *Holm-Nielsen & Andrade 18584* (AAU); road Quevedo-Latacunga, 6 km before Pilaló, 16 Sep 1977 (fl), *Maas et al. 2962* (US). Imbabura: Cuichocha-Apuela road km 28, 78°28′W, 00°22′N, 5 Oct 1984 (fl), *Jorgensen & Vive 56079* (AAU); via Otavalo-INTAG, declivis occidentales del Cerro Cotacachi, 0°20′N, 78°25′W, 25 Nov 1987 (fl), *Palacios 2172* (TEX). Pichincha: Los Paysanes on road from Quito to Santo Domingo de los Colorados, 28 Jun 1939 (fl), *Asplund 7314* (LL, NY, US); Chiriboga, 5 May 1955 (fl), *Asplund 16227* (K, LL); carretera Chillogallo-Chiriboga km 36, 18 Oct 1981 (fl), *Balslev 2116* (AAU, NY); carretera Nono-Nanegalito en falda norte de Cerro Pichincha, 9 May 1982 (fl), *Balslev & Boom 2484* (AAU, NY); carretera Quito a La Concordia via Nono, Mindo, San José de las Minas y Puerto Quito, km 32, 7 Aug 1984 (fl), *Dodson et al. 15243* (MO); Tandayapa-Nono, west of Nono, 26 Jan 1974 (fl), *Harling & Andersson 11628* (AAU, US); carretera via Cotocollao-Rundupamba-Nono-Nanegalito, 6 May 1980 (fl), *Jaramillo et al. 2479* (AAU, NY); Reserva Florística-Ecológica "Rio Guajalito," km 59 de la carretera antigua Quito-Santo Domingo de los Colorados, 3.5 km al NE de la carretera, 78°48′10″W, 0°13′53″S, 11 Aug 1985 (fl), *Jaramillo & Zak 7985* (MO, TEX, US); Quito-Nono-Pto. Quito road, 13 km NW of Nono, Río Alambi valley, 27 Dec 1978 (fl), *Luteyn & Lebrón-Luteyn 6517* (NY); road from Chiriboga to Sto. Domingo, 10 km W of Chiriboga, 3 May 1985 (fl), *Stein et al. 2678* (CAS); old highway Quito-Chiriboga-Sto. Domingo, 15 Nov 1986 (fl), *Ullea 292* (AAU). Without locality, 21 Jan 1856 (fl), *Jameson 419* (BM, K, P).

This species, first described as *T. lepidota* var. *intermedia,* was known by that name for over 50 years until Wurdack (1977) recognized its distinctiveness and elevated it to species rank. *Tibouchina gleasoniana* is characterized by yellow isomorphic to weakly dimorphic stamens, appressed cauline scales with erose or lacerate margins and basal ears, and complex foliar indument. The upper leaf surface is uniformly covered with bulla-based hairs. The lower leaf surface has lanceolate scales with irregularly erose margins on the elevated primary veins, and curved scales on the secondary veins that grade into an array of narrower scales and twisted, subterete hairs on higher order veins and intercostal areas. This gives the lower leaf surface a golden, woolly appearance. Also characteristic of *T. gleasoniana* are the deciduous bracteoles that are essentially glabrous abaxially except for a scaly indument restricted to a narrow median line or basal triangular patch. Within sect. *Lepidotae* only *T. silvestris* has completely glabrous bracteoles.

Tibouchina gleasoniana is probably most closely related to *T. paleacea,* judging from their similar vegetative morphology and complex foliar indument. Although restricted to high elevations in the Andes of Colombia and Ecuador, the geographic ranges of these two species do not appear to overlap (Figs. 7, 9). It is clear from specimen identifications in herbaria that *T. gleasoniana* and *T. paleacea* have been confused in the past. In addition to longer calyx lobes (8–11 mm), *T. paleacea* is readily distinguished by shorter inflorescences (1.6–4.4 cm) with only the central flower persisting in each simple dichasium, and by the white papillose puberulence on the lower leaf surfaces.

For the most part, *T. gleasoniana* is morphologically uniform throughout its range, but a few collections representing two morphological extremes stand out. *Luteyn & Cotton 10871* (Ecuador: Carchi) and *Maas et al. 2962* and *Harling et al. 9085* (Ecuador: Cotopaxi) are unusual in

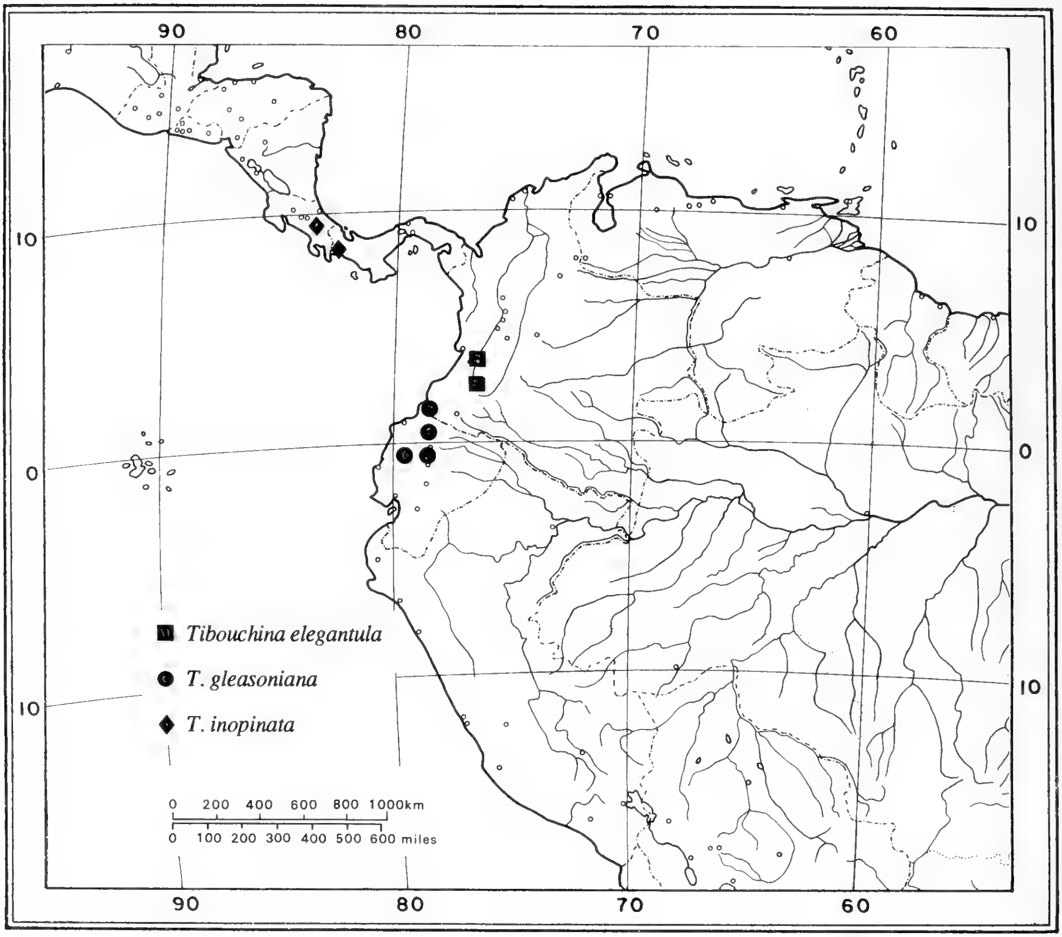

FIGURE 9. Distributions of *Tibouchina elegantula*, *T. gleasoniana*, and *T. inopinata*.

that the lower leaf surfaces have a sparser cover of shorter scales and twisted hairs. *Luteyn & Lebrón-Luteyn 6824* and *Gentry et al. 30583* (both from Colombia: Nariño) have narrowly lanceolate hypanthial scales with less pronounced lacerate margins than those of typical *T. gleasoniana*. Whether these variations are environmentally induced or the result of local genetic divergence is not known. We view these differences as well within the range of variation expected in this species and see no reason to give them formal recognition.

Tibouchina inopinata Wurdack, Phytologia 16: 169. 1968. TYPE.—COSTA RICA. Cartago: wooded slopes of Cordillera de Talamanca, 7.5 mi SW of Cartago, 5,300 ft, 15 Jul 1962 (fl, fr), *Webster et al. 12361* (Holotype: US!; isotypes: DAV!, F!, MICH!, MO!).

Shrubs to small, often spindly, arching trees 3–10 m tall; distal branches quadrangular, the internodes beset with, but not totally concealed by, appressed ovate proximally attached scales 0.5–1.5 mm long with irregularly erose or lacerate margins and truncate basal ears, the nodes with lanceolate scales 1.5–3 mm long with subentire to irregularly erose margins and small truncate basal ears. Petioles 0.6–1.4 cm long, covered with proximally attached ovate to lanceolate scales 1.5–3 mm long with truncate basal ears and sometimes with erose margins; blades coriaceous, 4.5–15 cm long, 1.6–3.6 cm wide, lanceolate to narrowly elliptic, 3-nerved with an additional inconspicuous pair of intramarginal veins, the apex narrowly and gradually acuminate, the base acute, the margin entire and beset with non-overlapping clasping folded scales; upper leaf surface beset with, but not concealed by, flattened scales fused to surface for ⅔ their length, the distal third of scale free, triangular with laciniate margins, or setiform and entire, the adnate portion covered with minute white pustules; lower leaf surface with three types of scales that do not completely conceal surface; scales on elevated primary veins similar in shape and size to petiolar scales, higher order veins (when evident) and actual surface covered with a mixture of minute ovate scales less than 0.25 mm long and lanceolate to triangular scales ca. 0.5 mm long, these obscurely auriculate at pustulate basal attachment. Inflorescences terminal much-branched panicles, 12.5–25 cm long, with up to ca. 250 flowers; bracteoles, 2–7 mm long, narrowly lanceolate to subulate, covered with scales like those of lower hypanthia; pedicels 3–9 mm long, beset with scales similar to those of hypanthia. Hypanthia (at anthesis), 3–5 mm long to torus, 3–5 mm wide, narrowly campanulate to urceolate, moderately covered with appressed, proximally attached, ovate to lanceolate scales with basal ears and irregularly erose margins. Calyx lobes 1–1.5 × 1.5–2 mm, broadly triangular, beset with scales like those of hypanthia except for a narrow marginal glabrous band, the margins ciliate. Petals 0.6–1.3 × 0.4–0.7 cm, white or pale pink, obovate, ciliate, otherwise glabrous. Stamens strongly dimorphic, with ventrally inclined pores; larger stamens geniculate, filaments 4–5 mm long, anther thecae 5–5.5 mm long, pink, subulate, connective 2–4 mm long with a yellow bifid appendage 1–1.2 mm long; smaller stamens more or less erect, filaments 4–6 mm long, anther thecae 3–4 mm long, yellow, subulate, connective strongly geniculate, 0.5–1 mm long, with a yellow, erect to incurved bifid appendage ca. 1 mm long. Ovary (at anthesis) ovoid, red and setose on upper half. Styles 6–9 mm long, more or less erect, strongly incurved distally; stigma truncate, papillose. Capsules usually upright on pendent branches; seeds ca. 0.33 mm long, light brown.

DISTRIBUTION AND PHENOLOGY.—Locally common in Costa Rica and Panama (Fig. 9) at elevations of 700–1,700 m, in disturbed montane forests. Flowering in May, June, July, and August; fruiting in July and August.

REPRESENTATIVE SPECIMENS EXAMINED.—COSTA RICA. Cartago: 1 km beyond Tapantí along road leading up the ridge to Tuis, 10 Jul 1977 (fl), *Almeda et al. 3004* (CAS, CR); mountain sides along Río Grande de Orosí between bridge over river and Tapantí, 21 Jun 1971 (fl), *Gentry 974* (F); along open trail to Tausito, 1 km NE of Tapantí, 4 Jun 1967 (fl), *Lent 1023* (F, NY, US); steep graded banks along Interamerican Hwy. on the Cordillera de Talamanca, ca. 13 km from the Tejar cutoff enroute to El Empalme, 8 Jun 1972 (fl), *Almeda & Wilbur 1635* (F, LL, NY); heavily forested slopes about 4.5 km from bridge at Tapantí above the Río Grande de Orosí, 27 Aug 1968 (fr), *Wilbur & Stone 10491* (DS, F, LL, MO, NY, US); rainforest on the steep slopes above the Río Grande de Orosí along a stretch of 9.3 km beginning 3 km from bridge at Tapantí, 9 Jul 1977 (fl), *Wilbur et al. 22286* (F); Tapantí Hydroelectric Project, 4–10 km beyond entrance to project, 25 Jun 1976 (fl), *Utley & Utley 5176* (CAS, F, MO, NY). Cartago/San José Border: ca. 8 km beyond Tejar turnoff to Interamerican Hwy. on Cordillera de Talamanca, 2 Aug 1977 (fl, fr), *Almeda et al. 3365* (CAS, CR). Heredia: 7.3 km N of Varablanca off road to Puerto Viejo, 22 Jul 1977 (fl), *Almeda et al. 3159* (CAS, CR). San José: trailside between Alto La Palma and ¾ the way to Bajo La Hondura, 13 Jul 1976 (fl), *Wilbur 20387* (CAS). PANAMA. Bocas del Toro: Cerro Colorado, 9.2 mi W of Chamí along trail E of road that leads down to stream, 8°35′N, 81°50′W, 6 Jul 1988 (fr), *Croat 69003* (CAS). Chiriquí: valley of El Hornito, vicinity of Fortuna Dam, along trail down from hwy., 8°45′N, 82°15′W, 26 May 1988 (fl), *McPherson 12529* (CAS); km 30–34 along mining road at Cerro Colorado, 9–10 Aug 1984 (fr), *Todzia & Schmalzel 2572* (CAS). Chiriquí/Bocas del Toro Border: windswept cloud forest vegetation on slopes and valleys of the Cerro Colorado region, 27 Jan 1989 (fl), *Almeda et al. 6429* (CAS, PMA); Cerro Colorado, road to Bocas del Toro, end of mountain access road, just above face of mine, 14 Aug 1977 (fr), *Folsom et al. 4731* (CAS, LL).

Tibouchina inopinata, the northernmost species in sect. *Lepidotae,* is a morphologically uniform taxon unlikely to be confused with other species. It is readily recognized by its many-flowered paniculate or highly compound dichasia with up to 250 flowers, erect broadly triangular calyx lobes, strongly dimorphic stamens, and sparse pubescence on the undersurface of the leaves. In the field it can even be recognized in sterile condition because of its distinctive, openly branched, arching habit and lanceolate leaves clustered at the ends of branches.

By virtue of its stamen morphology and mixture of large lanceolate and smaller ovate to ovate-lanceolate scales on the lower leaf surfaces, *T. inopinata* appears to be most closely related to *T. wurdackii.* Restricted to Central America, these two species are also geographically isolated from the South American species of the section.

Tibouchina lepidota (Bonpl.) Baillon, Adansonia 12:74. 1877. *Rhexia lepidota* Bonpl., Rhex. 38, pl. 15. 1808.—*Chaetogastra lepidota* (Bonpl.) DC., Prodr. 3:134. 1828.—*Pleroma lepidotum* (Bonpl.) Triana, Trans. Linn. Soc. London 28: 44, pl. 3, fig. 31k. 1871.—TYPE.—COLOMBIA or PERU. *Bonpland s.n.* (Holotype, P!; isotypes, P!, US!).

Tibouchina lepidota (Bonpl.) Baillon var. *congestiflora* Cogn., Bot. Jahrb. 8:17. 1887. Type.—ECUADOR. Pichincha: near S. Florencio at Río Pilatón, 1,800 m, Cordillera Central, 13 Jan 1881 (fl), *Lehmann 479a* (Holotype: B, destroyed, photographs F!, NY!; isotype: BR!).

Trees or shrubs 2.5–20 m tall; bark plate-like, sometimes fissured, peeling in loose flakes; distal branches terete with appressed, horizontally attached rectangular, platelike scales intermixed with or replaced by proximally attached elliptic scales 1–2 mm long with basal ears and irregularly erose margins; nodes with very narrow basally attached lanceolate scales mostly 2–3 mm long. Petioles 0.8–1.5 cm long, with scales similar to those on internodes; blades coriaceous, 4–10(–12) cm long, 0.8–4(–6.2) cm wide, oblong-ovate to elliptic, (3–)5-nerved, the apex acute, the base rounded to acute, the margin entire and beset with overlapping clasping scales; upper leaf surface beset with, but not concealed by scales adnate to surface for ⅔–¾ their length, the distal portion of flattened scale free and triangular, the adnate portion often swollen (bulla-based) and covered with minute white pustules; lower leaf surface with two types of scales that do not completely conceal epidermal surface; scales on elevated primary veins similar in size and shape to cauline scales; secondary and higher order venation and intercostal areas with irregularly erose or lacerate basally attached scales (these somewhat raised or spreading when dry), or if only sparsely covered with scales then with a ground layer of minute papillose puberulence. Inflorescences terminal, pedunculate, simple or congested umbelliform dichasia with 3–5 flowers, seldom with solitary flowers; peduncles 2.5–8(–13) cm long, beset with scales similar to those of uppermost internodes; bracteoles cucullate, 8–15 mm long, ovate to elliptic, covered with scales similar to those of hypanthia, glabrous along the margin; pedicels 1–12 mm long, beset with scales similar to those of hypanthia, early deciduous. Hypanthia (at anthesis) 4–7(–8) mm long to torus, 5–6 mm wide, campanulate, densely covered with appressed ovate to lanceolate, reddish to purplish brown, proximally attached scales (1.5–3 mm long) with basal ears and irregularly erose margins. Calyx lobes 4–6(–7) × (2.5–)3–5 mm, oblong, purple-brown to deep red, densely beset with scales like those of hypanthia except for a narrow marginal glabrous band, the margins ciliate. Petals (1.2–)1.5–2.8(–3.7) × 1–2.7 cm, crimson or rose-purple fading to lavender, obovate, the margins ciliate, otherwise glabrous. Stamens isomorphic, erect, with ventrally inclined pores; filaments 6–8 mm long, white or purple; anther thecae 5–7(–9) mm long, yellow, the connective 0.5–1 mm long with a yellow-orange, upturned bifid appendage (0.5–)1–1.5(–2) mm long. Ovary (at anthesis) 5–6 mm long, ovoid, fluted at setose apex. Styles 1–1.7 cm long, strongly declinate, hooked at apex; stigma truncate, papillose. Seeds ca. 0.5 mm long, light brown.

Distribution and Phenology.—From western Venezuela to central Peru (Fig. 10) in disturbed and undisturbed montane forest at 800–3,200 m. In Venezuela, flowering is reported from July through November while in Colombia and Ecuador flowering occurs throughout the year. In Peru flowering is more common from February through May although two flowering specimens are recorded from June and July.

Common Names.—Rondon (Venezuela); Flor de mayo, mayo, siete cueros (Colombia); Pontac, arbol de la navidad (Ecuador).

Representative Specimens Examined.—VENEZUELA. Mérida: Páramo de Zumbador, Oct 1842 (fl), *Linden s.n.* (P); Páramo de Guaraque, Cordillera de los Andes, Distr. Tovar, 6 Sep 1966 (fl), *López-Palacios 1546* (US); between Guaraque and Tovar, 12 Nov 1972 (fl), *Wurdack et al. 2753* (US). Táchira: Páramo El Zumbador, Sep 1956 (fl), *Aristeguieta 2548* (NY); Carretera Rubio-Las Delicias, 13 km above Diamante, immediately above Mata Mula, 4 Oct 1967 (fl), *Bunting 2418* (US); Quebrada El Reposo, ca. 6.7 km N of Villa Páez, at extreme NW of Páramo de Tamá, Distr. Junín, 28 Jun 1973 (fr), *Ruiz-Terán & Lopez-Figueiras 8953* (K, MO); between El Cobre and Cordero, 8 Jul 1944 (fl), *Steyermark 57127* (F, NY); between Michelena and Boca de Monte, W of Zumbador, 28 Aug 1966 (fl, fr), *Steyermark & Rabe 96797* (K, NY, US); below Páramo de La Negra on the road to Pregonero, 29–30 Aug 1966 (fl), *Steyermark & Rabe 96964* (F, NY, US); vicinity of Mata Mula, N of Delicias on road to Bramon, 7°38′N, 72°26′W, 26 Jul 1979 (fl), *Steyermark & Liesner 118683* (MO, US); brook ca. 9 km above La Grita on road to Porqueras, Serranias de Batallón, Cordillera de Mérida, Distr. Jáuregui, 31 Jul 1973 (fl), *Tillett 737-299* (MO). COLOMBIA. Antioquia: Mun. Guatapé, Vereda Santa Rita, Finca Montepinar, 6 Jun 1985 (fl), *Albert de Escobar et al. 5292* (NY); Santa Elena, near Antioquia, 9 Aug 1930 (fl), *Archer & Ramos 820* (NY, US); Medellín, La Sierra, 26 Dec 1930 (fl), *Archer 1070* (NY, US); below summit of Santa Elena, on road from Medellín to Rio Negro, 2 Apr 1949 (fl), *F. Barkley et al. 385* (NY, US); near Angelópolis, 22 Nov 1947 (fl), *F. Barkley & Gutiérrez 1676* (F, UC); Quebrada Anococsa, along Anococsa-Abriaqui road, 15 Mar 1944 (fl), *Core 445* (US); road between Robles and Guadelupe, 13 May 1944 (fl), *Core 695* (NY, US); Me-

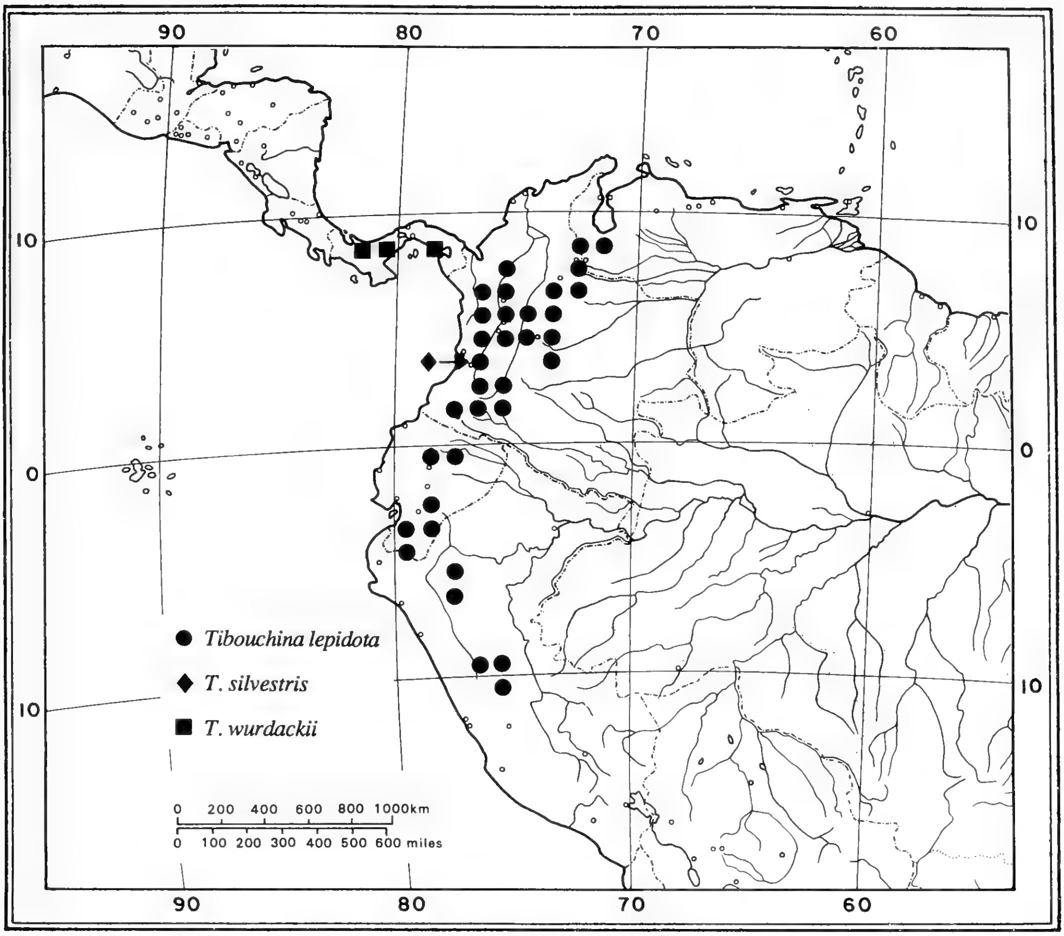

FIGURE 10. Distributions of *Tibouchina lepidota, T. silvestris,* and *T. wurdackii.*

dellín, Mount El Boquerón, Alto de los Baldíos, 9 Apr 1958 (fl), *Cuatrecasas et al. 24257* (US); "La Paloma" above Sonson, 24–25 May 1944 (fl), *Ewan 15726* (NY, US); Salto de Guadelupe, 27 Jul 1947 (fl), *Hodge 6966* (US); Santa Rosa, 27 Sep 1887 (fl), *Lehmann 7507* (F, US); Yarumal-Valdivia road, km 123, ca. 10 km N of Yarumal, 22–23 Mar 1979 (fl), *Luteyn et al. 7054* (CAS, NY); Uramita-Peque road, 20–22 km above Uranta (Las Juntas), 29 Mar 1979 (fl), *Luteyn & Lebrón-Luteyn 7174* (AAU, CAS, NY); between Yarumal and the Llanos de Cuiba, 20 Feb 1942 (fl), *Metcalf & Cuatrecasas 30134* (F, MO, NY, UC, US); Santa Barbara, Cauca Valley, 21 Sep 1922 (fr), *Pennell 10913* (NY, US); Mpio. de Granada, km 24 of San Carlos-Granada road, 06°10′N, 75°08′W, 21 May 1988 (fl), *Zarucchi et al. 6780* (CAS). Boyacá: region of Mt. Chapon, extreme western part of Dept. Boyacá, NW of Bogotá, 23 May 1932 (fl), *Lawrence 98* (F, MO, NY, US); Bosques de Arcabuco, 24 Feb 1940 (fl, fr), *Pérez Arbeláez & Cuatrecasas 8102* (NY, US); Cordillera Oriental, between Charalá and Tunja, 19 Jun 1966 (fl), *Schulz et al. 468* (US). Caldas: between Salento and Tambores, 14 Mar 1876 (fl), *André 2346* (K); Los Alpes, Aug 1944 (fl), *Dryander 2800* (F, US); Río Quindío, Salento, Cordillera Central, 27–30 Jul 1922 (fl), *Killip & Hazen 9032* (NY, US); San Bernardino, 29 Aug 1922 (fl), *Pennell & Hazen 10155* (NY, US); La Selva, Cordillera Occidental, vertiente occidental, 27 Jan 1946 (fl), *von Sneidern 5535* (F, US). Caquetá: Cordillera Oriental, vertiente oriental, Quebrada del Río Hacha, below Gabinete, 23 Mar 1940 (fl), *Cuatrecasas 8509* (F, US). Cauca: 64 km from Pital towards Popayán beyond La Plata, 21 Jan 1976 (fl), *Luteyn et al. 4972* (US); above Moroco, Río Moras Valley Paez basin, Tierra Adentro, 4 Feb 1906 (fl, fr), *Pittier 1329* (US); near the village El Tambo, in forest near Chisquio, 25 Sep 1935 (fl), *von Sneidern 445* (NY); near the village El Tambo, 16 Nov 1939 (fl), *von Sneidern 2448* (US). Chocó: Alto de Guaduas, near Carmen, 1 Mar 1944 (fl), *Core 347a* (US); along road between San José del Palmar and Cartago at Vereda San Antonio between San Jose del Palmar and jct. in road to El Cairo, 4°55′N, 76°14′W, 12 May 1983 (fl), *Croat 56660* (MO); carretera Tutunendo-El Carmen, between km. 135 and 120, Alto Río Atrato, 29 Apr 1979 (fl), *Forero et al. 6082* (US); 16–18 km W of Bolivar, near top of Cordillera Occidental and Antioquia border, 6 Jan 1979 (fl), *Gentry & Renteria 23695* (MO); Emisora La Sirena, 3 km W of La Mansa at top of Cordillera Occidental, 16 Jan 1979 (fl), *Gentry & Renteria 24200* (US); highway between El Carmen and Quibdo, 5°40′W, 76°30′W, 27 Dec 1982 (fl), *Juncosa 518* (MO). Cundinamarca: San Francisco a La Vega, 18 Sep 1961 (fl), *García-Barriga 17347* (AAU, NY); Sasaima, San Bernardo, Quebrada La María and Río Dulce, 20–30 Nov 1962 (fl), *García-Barriga 17589* (AAU, NY); Patio Bonito, Batatas Valley, Cordillera de Helicona, 12 km SE of Gachalá, 22 Sep 1944 (fl), *Grant 10291* (NY, US); "Alto Isacar," Finca 11 km S of La Palma, 11 Mar 1944 (fl, fr), *Little 7406* (NY, US); eastern Cordillera, ca. 21 km NW of Facatativá, 14 Jul 1965 (fl), *King et al. 5935* (F, NY). Huila-Com. del Caquetá: Cord. Oriental, on divide, in Gabinete, 22 Mar 1940 (fr), *Cuatrecasas 8494* (COL, F). Huila: Andaluzia, 22 Aug 1926 (fl), *Juzepczuk 6597* (NY); 12 km SE of Algeciras, SE along govt. trail to San Vincente, Cordillera Oriental, 23 Apr 1944 (fl, fr), *Little 7708* (NY, US); Balsillas, on Río Balsillas, 3–5 Aug 1917 (fl), *Rusby & Pennell 723* (NY, US). Nariño: Reserva Natural La Planada, cerca de Ricaurte, 15 Jun 1986 (fl), *León et al. 1671* (US); Ricaurte, 24 Apr 1941 (fl), *von Sneidern 631* (LL). Norte de Santander: region of Ocaña, between La María and Jurisdicciones, 25 Sep 1969 (fl), *Cuatrecasas & Rodriguez 27936* (F, NY, US). Putumayo: Valle de Sibundoy, camino de la hidráulica, 1 km N of Sibundoy, 21 Oct 1962 (fl), *Bristol 302* (COL, F); Alto de la Cordillera between El Valle de Sibundoy and Mocoa, El Portachuelo, 30 Dec 1940, *Cuatrecasas 11480* (F, US); road between El Encano and Sibundoy, páramo El Capuchino, 7 Oct 1965 (fl), *García-Barriga et al. 18600* (NY); Sibundoy, hill N of valley, 28 May 1946 (fl, fr), *Schultes & Villareal 7519* (F, K, NY, US); Valle de Sibundoy, above Santiago, 24 Jul 1964 (fl), *Soejarto 1049* (US). Quindío: between Salento and Tambores, on western slope, 14 Mar 1876 (fl), *André 2346* (NY); Mun. de Calarca, Cerro al Campanario, camino de Pinares, 3 Jun 1986 (fl), *Arbeláez 1570* (US). Santander: region about La Paz, 25 km NE of Velez, 6 May 1944 (fl), *Fassett 25191* (NY, US); Quebrada de Pois, N of La Baja, 31 Jan 1927 (fl), *Killip & A. C. Smith 18809* (F, K, NY, US). Tolima: El Fresno, "Cuchillo del Topacio," 3 Dec 1939 (fl), *García-Barriga 8223* (COL, US); El Líbano a Murillo (km 11 al 22 de la carretera), subpáramo en el Alto de Peñones, 20 Jul 1947 (fl), *García-Barriga 12260* (US). Valle: along road between Cali and Buenaventura at km 20.5 just beyond summit of road W of Dias y Ocho, 27 Aug 1976 (fl), *Croat 38558* (MO); Cordillera Occidental, filo de la Cordillera, al N de Las Brisas, Gibraltar, 25 Oct 1946 (fl), *Cuatrecasas 22515* (F, NY, US); Cordillera Central, Tenerife, hacia el cerro Pan de Azúcar, 26 Feb 1969 (fl), *Cuatrecasas et al. 27534* (F, K, NY, US); Mpio. El Cairo, El Brillante, 14 Aug 1986 (fl), *López 42* (MO); road to sea, western Cordillera, May 1939 (fl), *Dryander 2369* (F, K, NY, US); carretera San José del Palmar Chocó-Ansermanuevo, 17 km W of La Carbonera, 27 Feb 1977 (fr), *Forero et al. 3550* (MO); San Antonio, W of Cali, near summit of Cordillera Occidental, 26 Feb, 2 Mar 1939 (fl, fr), *Killip & Garcia 33659* (F, NY, US); Cordillera Occidental, Cuenca del Río Cali, Pichindé, on side of road between Brasilia and Peñas Blancas, 23 Jan 1963 (fl, fr), *López Figueiras 8264* (US); Cali-Loboguerro road, side road to San Antonio (Telecom tower) ca. km 16, 8 Mar 1979 (fl), *Luteyn & Lebrón-Luteyn 6982* (AAU, CAS, NY). ECUADOR. Azuay: Highway Cuenca-Cola de San Pablo, Sevilla de Oro, 17 Feb 1977 (fl), *Boeke & Loyola 1063* (AAU). Loja: 15 km S of Yangana on the road Loja-Zumba, 79°8′W, 4°30′S, 24 Sep 1983 (fl), *Brandbyge 42285* (AAU); 5 km SE of Loja, 7 Mar 1947 (fl), *Espinosa 1561* (F, NY, US); road Loja-Zamora, on border to Zamora-Chinchipe, 13 Apr 1974 (fl), *Harling & Andersson 13498* (AAU, MO, US); Nudo de Sabanilla, 10 Feb 1982 (fl), *Harling et al. 20545* (CAS); road Loja-Zamora, km 10.5, 79°10′W, 4°S, 17 Apr 1973 (fl), *Holm-Nielsen et al. 3656* (AAU); 2 km E of Loja on the road to Zamora, 31 Jan 1979 (fl), *King & Almeda 7910* (CAS, K, MO, US). Morona-Santiago: 3 km W of Indanza, on Gualaceo-San Juan Bosco road, 28 Jan 1981 (fl), *Gentry et al. 30980* (AAU); road Limón (General Plaza)-Gualaceo, km 16–18 from Limón, 22 Mar 1974 (fl), *Harling & Andersson 12697* (US); Lomipuero, road Gualaceo-Limón, 78°35′W, 3°3′S, 23 Sep 1979 (fl), *Holm-Nielsen et al. 20379* (AAU, K). Napo: between Cuyuja and Baeza, 26 Dec 1939 (fl), *Asplund 10146* (CAS, US); road Baeza-Tena, 8 km from Baeza, 77°50′W, 0°31′S, 27 Oct 1976, *Balslev & Madsen 10377* (AAU, CAS, F, MO, NY); Cosanga-Río Cosango, 4 Dec 1976 (fl), *Boeke & McElroy 408* (AAU, CAS, NY); km 140, Quito-Tena via Baeza, 3 Aug 1984 (fl), *Dodson et al. 14861* (MO); 2 km W of Reventador, 6 Nov 1974 (fl), *Gentry 12579* (AAU, MO, US); Borja (Virgilio Dávila), Río Quijos, 15–26 Jan 1959 (fl, fr), *Harling 3870* (LL, MO, NY); Río Borja, km 3, 77°47′W, 0°26′S, 21 Sep 1980 (fl), *Holm-Nielsen et al. 26600* (AAU, CAS); Cantón Quijos, at Río Cosanga near Cosanga, 13 Feb 1978 (fl), *Kirkbride & Chamba 4001* (NY, US). Pichincha: Los Dos Ríos on road between Chiriboga and Santo Domingo de los Colorados, 2 Jul 1955 (fl, fr), *Asplund 16813* (NY, US); km 70, old road from Quito to Santo Domingo, 13 Oct 1981 (fl, fr), *Dodson & Dodson 11851* (MO, NY); old road to Santo Domingo-Quito, Chiriboga, 8 May 1988 (fl), *Harling et al. 9237* (F, US); road Nanegalito-Pacto, km 8, 78°41′W, 0°4′N, 21 Jul 1980 (fl), *Holm-Nielsen et al. 24461* (AAU, NY); old road Quito-Santo Domingo, 12–15 km NE of turnoff to old road from junction with new road near Alluriquin, ca. 0°20′S, 78°55′W, 3 Feb 1982 (fl), *Luteyn et al. 8742* (AAU, CAS, NY). Santiago-Zamora: dense forest between Campanas and Arenillas, along Río Tintas, 10 leagues SE of El Pan, 13 Jul 1943 (fl), *Steyermark 53534* (F); along Quebrada Honda, vic. of Rancho Achupallas, 10 Oct 1943 (fl), *Steyermark 54549* (F, NY, US). Zamora-Chinchipe: Road Loja-Zamora, km 17, 79°08′W, 3°59′S, 16 Apr 1973 (fl), *Holm-Nielsen et al. 3598* (AAU, MO, NY, US); Planta Eléctrica de San Ramón, near Sabanilla, 18 km E of Loja, 3°59′S, 79°03′W, 3 Sep 1975 (fl, fr), *Little et al. 211* (US); 3 miles from Loja, on road to Zamora, 28 Sep 1959 (fl, fr), *Maguire & Maguire 44343* (NY, US). PERU. Amazonas: Prov. Bongará, 4–8 km W of Pomacocha on road to Rioja, 5°45′S, 77°53′W, 9 Feb 1984 (fl), *Gentry & Smith 45188* (CAS, MO); 4–6 km W of Pomacocha on road to Pedro Ruíz Gallo, 77°50′W, 05°50′S, 7 Feb 1988 (fl), *Gentry et al. 61330A* (CAS, MO); Prov. Bongará, 4 km N of Pomacocha on road to Brioja, trail down gorge to W of road, 5°40′S, 77°22′W, 2 Jun 1986 (fl), *Knapp et al. 7511* (CAS, TEX); Prov. Chachapoyas, Chachapoyas-Mendoza road, kms 546–549, W of Molinopampa, 11–12 Mar 1978 (fl, fr), *Luteyn & Lebrón-Luteyn 5557* (CAS, F, K, MO, NY, UC); white sand slopes along road E of Chachapoyas between Pipos and Molinopampa, 6°15′S, 77°40′W, 14 Feb 1985 (fl), *Luteyn & Cotton 11391* (CAS, NY); Prov. Bongará, 20 km on road from Pedro Ruíz to Pomacocha, 5°50′S, 77°52′W, 6 Feb 1985 (fl), *Stein & Todzia 2088* (CAS, MO); between Molinopampa and Mendoza, 10 km E of Molinopampa, 23 Feb 1978 (fl), *Wasshausen & Encarnación 1010* (K, MO, NY, US); jalca zone 3–6 km W of Molinopampa, above Laguna Pomacocha, 19 Jul 1962 (fl, fr), *Wurdack 1392* (F, NY, US). Huánuco: Prov. Huánuco, ca. 51 km NNE of Huánuco, ca. 10 km N of tunnel, 15 Jul 1981 (fl), *Dillon 2611* (F, K, MO, NY, TEX); Carpish Pass on Tingo Maria-Huánuco road, 14 Mar 1945 (fl, fr), *Hodge 6293* (US); Prov. Leoncio Prado, km 463 on Lima-Tingo Maria road, 6 Jun 1981 (fr), *Young & Sullivan 881* (CAS, MO); Tumanga, 27 Apr 1963 (fl), *Woytkowski 7995* (MO, US). Pasco: Prov. Oxapampa, Los Chacos (valley of Río Yamaquizu) near Oxapampa, 75°22′W, 11°34′S, 11 May 1982 (fl, fr), *Smith & Pretel 1509* (US). San Martín: Bongará Prov., Pedro Ruíz-Moyobamba road, km 380, near Río Nieva, 77°45′W, 5°45′S, 29 Aug 1983 (fl), *Smith 4844* (US).

Tibouchina lepidota is readily separated from other species in the section by the following combination of characters: cauline pubescence consisting of a mixture of horizontally attached platelike scales and proximally attached elliptic scales; lower leaf surfaces densely covered with erose scales and a ground layer of minute papillose puberulence (Fig. 3E, F); inflorescences typically pedunculate simple dichasia; and stamens isomorphic with yellow anthers.

In the field, *T. lepidota* stands out because its magenta to rose-red petals fade to purple or lavender with age. In sect. *Lepidotae,* petal color change also occurs in *T. gleasoniana* and *T. paleacea.*

With populations extending from the Andes of western Venezuela to central Peru, *T. lepidota* has the broadest distribution of any species in sect. *Lepidotae.* Its high chromosome number (*n* = ca. 62) indicates that it is derived, but the lack of chromosome information for other members of the section creates difficulty in assessing its affinities. Similarities in cauline and foliar pubescence, however, suggest that *T. lepidota* and *T. silvestris* are sister taxa. For an enumeration of the differences between these species, see the discussion under *T. silvestris.*

Like other widespread woody taxa confined to montane habitats in the neotropics, *T. lepidota* exhibits its share of morphological variation. Three populations possess characters at variance with the majority of specimens examined for this study. Collections from west-central Colombia (Cundinamarca and Tolima) are unusual and might, with extended study, be shown to represent a distinct taxon. They differ in having solitary flowers (vs. terminal dichasia), lanceolate hypanthial scales with fimbriate margins (vs. ovate scales with erose margins), bracteoles that are glabrous except for a thin line of scales along the midvein (vs. bracteoles that are essentially covered with scales), and anthers 8–10 mm long [vs. 5–7(–8) mm long]. Collections of this variant are as follows: COLOMBIA. Cundinamarca: Aguadita, Cordillera Oriental, 4 Feb 1876 (fl), *André 1425* (F, NY, US); San Miguel, S of Sibaté on road to Fusagasugá, between km markers 34 and 35, 13 May 1972 (fl), *Barclay et al. 3411* (US); Cuesta de Fusagasugá, 18 Feb 1940 (fl), *Cuatrecasas 8025* (F, NY, US); San Miguel á Aguabonita, 20–25 Apr 1946 (fl), *Duque-Jaramillo 3333* (CM); entre Pacho and Río Negro, 22–26 Feb 1942 (fr), *García-Barriga 10742* (US); Fusagasugá, hwy. to San Bernardo, 4 Jul 1976 (fl), *García-Barriga 21044* (F, NY, US); ca. 26 km NE of Fusagasugá, 19 Jun 1965 (fl), *King & Guevara 5669* (F, NY, US); Páramo de Guerrero, between Zipaquira and Pacho, 28 Sep 1974 (fl), *Maas & Jaramillo 1797* (US); forests between El Alto de San Miguel and La Aguadita, before Sibaté, 6 Jun 1965 (fl), *Uribe 5237* (US). Meta: Río del Nevado, below confluence of Río Arroz, S slope of W Río Humadea, Páramo de Sumapaz, 3°59′N, 73°56′W, 1 Sep 1943 (fl), *Fosberg 20944* (NY, US). Tolima: Central Cordillera, 43 km ENE of Manizales, 16–17 Jul 1965 (fl), *King et al. 5987* (NY).

The second aberrant population of *T. lepidota* is from southern Ecuador (Azuay, Moron-Santiago, Santiago-Zamora); it differs from the norm in having adaxial foliar pubescence consisting of bulla-based hairs with raised setae 0.5–1 mm long. This feature is otherwise unknown in *T. lepidota* and none of the four species in the section with bulla-based hairs are recorded from southern Ecuador. This variant is represented by the following collections: ECUADOR. Azuay: Highway Cuenca-Cola de San Pablo, Sevilla de Oro, 17 Feb 1977 (fl), *Boeke & Loyola 1063* (MO, NY, US). Morona-Santiago: 3 km W of Indanza, on Gualaceo-San Juan Bosco rd., 28 Jan 1981 (fl), *Gentry et al. 30980* (MO). Santiago-Zamora: Tambo Consuelo to Tambo Cerro Negro, E slope of the cordillera, valley of the Río Chupianza (on the trail from Sevilla de Oro to Mendez), 17 Dec 1944 (fl), *Camp E-1617* (NY); dense forest between Campanas and Arenillas, along Río Tintas, 10 leagues SE of El Pan, 13 Jul 1943 (fl), *Steyermark 53534* (F); trail between Pailas and El Pan, 10 Sep 1943 (fl), *Steyermark 54314* (F, NY).

These two anomalous populations exhibit some geographic homogeneity, but it is not clear taxa, or stabilized variants with an asexual breed-whether they represent evolving races, distinct ing system. Chromosome counts of these and other populations are also needed to determine whether observed differences are associated with heteroploidy or other cytological peculiarities.

The third and most problematic of the variants attributable to the *T. lepidota* complex is *Devia 208* (MO) from Dept. Valle in western Colombia. It is similar to *T. lepidota* in cauline indument, leaf shape, inflorescence details, and indument of the upper leaf surface. Indument of the lower leaf surface, on the other hand, varies toward, but is not identical to, *T. paleacea*. The secondary leaf veins in this collection have curved ovate scales with lacerate margins that grade into essentially terete hairs on the tertiary veins. In *T. paleacea* the straight scales on the secondary veins are slender, lanceolate and essentially entire, but they too grade into terete hairs on the tertiaries. The secondary and tertiary veins of this enigmatic collection have a scattering of the sessile reddish glands on the secondaries and higher order veins that are typical of *T. paleacea* but lacking in *T. lepidota*. Because *T. lepidota* and *T. paleacea* occur in Dept. Valle and have broadly overlapping elevational distributions, it is tempting to suggest that this variant originated from past hybridization between the two species. We have no other evidence, however, to substantiate this speculation.

Tibouchina narinoensis Wurdack, Phytologia 35: 241. 1977. Type.—COLOMBIA. Nariño: Entre Ricaurte y Diviso, carretera Pasto-Tumaco, 6 Nov 1950 (fl), *R. Espinosa 2954* (Holotype: NY!).

Shrubs or small trees to 3 m tall; distal branches terete, the internodes covered with appressed proximally attached lanceolate scales 1.5–2 mm long with irregularly erose or lacerate margins and well-developed basal ears, the nodes with similar scales mostly 2.5–4 mm long. Petioles 0.7–1 cm long, covered with scales like those of internodes; blades coriaceous, 5.7–10 cm long, 2.2–3.7 cm wide, elliptic-lanceolate, 5-nerved, the apex acute to acuminate or bluntly apiculate, the base rounded, the margins entire and beset with clasping, folded scales; upper leaf surface covered with bulla-based hairs with terminal setae ca. 1 mm long; lower leaf surface with two kinds of scales that only sparsely cover the surface; scales on elevated primary veins 2–4 mm long, straight, very narrowly lanceolate with entire margins; scales on secondary and tertiary veins 1–2 mm long with entire margins, varying from narrowly lanceolate on secondaries to nearly setiform on tertiaries; actual surface covered with a minute papillose puberulence. Inflorescences terminal modified panicles, 7.5–14 cm long, with 9–12 flowers; bracteoles ca. 3–5 mm long, narrowly lanceolate to subulate, beset with scales like those of uppermost cauline internodes, early deciduous; pedicels 0.4–1.6 cm long, beset with scales like those of hypanthia. Hypanthia (at anthesis) 6–9 mm long to torus, 4–5 mm wide, narrowly campanulate to urceolate, sparsely covered with appressed ovate to lanceolate proximally attached scales, these 1–1.5 mm long, with basal ears and irregularly erose margins, the leaf surface visible. Calyx lobes 2–4 × 1–1.5(–2.5) mm, triangular, sparsely beset with scales like those on hypanthia, the margins ciliate. Petals 1.2–1.6 × 1.1–1.4 cm, lilac to purple, asymmetrically obovate, retuse at apex, ciliate, otherwise glabrous. Stamens isomorphic, with ventrally inclined pores, the filaments 5–7 mm long, the anther thecae 6–7 mm long, yellow, subulate, the connective straight, ca. 0.5 mm long, with upturned, bifid appendages ca. 0.5 mm long. Ovary (at anthesis) ovoid, fluted at setose apex. Styles 1–1.3 cm long, declinate, incurved distally; stigma truncate, papillose. Seeds 0.25–0.33 mm long, light brown.

Distribution and Phenology.—Along roadsides and forest edges in southern Colombia (Nariño) (Fig. 7) at elevations of 200–1,450 m. Flowering reported in January, July, August, and November; two fruiting specimens from July and August.

Specimens Examined.—COLOMBIA. Nariño: Barbacoas, Corregimiento Santander (Buenavista) a Barbacoas (vertiente del Río Telembí), 3–5 Aug 1948 (fl, fr), *García-Barriga 13164* (NY, US); 2–8 km E of Junín on Tumaco-Tuquirres road, 1°15′N, 78°09′W, 26 Jul 1986 (fl, fr), *Gentry et al. 55227* (AAU); entre Altaquer y Junín, Cuyambe, 1 Jan 1957 (fl), *Idrobo & Kyburz 2357* (US); Mun. Altaquer, carretera entre Altaquer y Junín, Cuyambe, 17 Nov 1967 (fl), *Mora 4137* (COL).

Tibouchina narinoensis is known only from the type and the four collections cited here. Despite limited material, this well-defined species is easily distinguished from other South American members of the section by hypanthia with scales that do not conceal the actual surface. The foliar pubescence is also distinctive. The scales on the lower leaf surface are essentially entire, and the abaxial foliar surface is covered with a white papillose or farinaceous puberulence.

The affinities of *T. narinoensis* are with *T. paleacea*, which has a more northerly distribution in Colombia and occurs at much higher elevations (1,980–3,100 m). Differences between these two species include characters of the calyx lobes, inflorescence, and floral bracteoles. The calyx lobes of *T. narinoensis* are triangular and only 2–4 mm long whereas those of *T. paleacea* are oblong and 8–11 mm long. The compound dichasial inflorescences of *T. narinoensis* are 7.5–14 cm long. In *T. paleacea* the inflorescences consist of simple dichasia mostly 1.6–4.4 cm long, but only the central flower persists at anthesis. Although bracteoles are rarely present on fruiting collections, their size and shape are of diagnostic value. In *T. narinoensis* they are narrowly lanceolate to subulate and 3–5 mm long. In *T. paleacea* they are longer (9–14 mm) and consistently ovate.

Tibouchina paleacea (Triana) Cogn. *in* Martius, Fl. Bras. 14(3):373. 1885. *Pleroma lepidotum* (Bonpl.) Triana var. *paleaceum* Triana, Trans. Linn. Soc. London 28:44. 1871. Type. COLOMBIA. Antioquia: Río Negro, 2,300 m, *Triana s.n.* (Lectotype, here designated: K!; isolectotypes: BR!, G-DEL, K!, NY!, P!).

Trees or shrubs 2.5–10 m tall; trunks with red peeling bark; distal branches quadrangular with appressed to antrorsely spreading proximally attached lanceolate scales 1.5–2 mm long, with entire or irregularly erose margins and basal ears, the nodes with appressed basally attached lanceolate scales 2–7 mm long with entire margins. Petioles 0.5–1 cm long, covered with lanceolate spreading scales similar to those of internodes; blades coriaceous, 4.2–11 cm long, 1.6–11 cm wide, narrowly elliptic to elliptic-lanceolate, 5-nerved, the apex bluntly acute to rounded or apiculate, the base rounded, the margin entire and beset with overlapping, clasping scales; upper leaf surface covered with bulla-based hairs with terminal setae 0.25–1 mm long; lower leaf surface with two types of scales or hairs that nearly conceal surface; scales on elevated primaries proximally attached, lanceolate, 1–2 mm long with irregularly erose margins and basal ears; elevated secondary and higher order veins with an indument varying from narrowly lanceolate scales to terete hairs 0.5–1 mm long that are slightly twisted and unbranched; intercostal areas covered with a white farinaceous puberulence and a scattering of red sessile glandular hairs. Inflorescences composed of simple dichasia with only central flower typically persisting at anthesis; peduncles 1.6–2.8(–4.4) cm long with scales similar to those on uppermost internodes; bracteoles enclosing young floral buds, 1.1–1.4 cm long, ovate, with scales like those of petioles and upper internodes, glabrous along margin, early deciduous; pedicels 0.3–1 cm long, with scales like those on hypanthia. Hypanthia (at anthesis) 6–8 mm long to torus, 6–7 mm wide, campanulate to urceolate, densely covered with appressed, proximally attached, lanceolate scales 3–5 mm long with irregularly erose margins. Calyx lobes 8–11 × 3.5–4 mm, oblong, with scales like those on hypanthia, up to 5 mm long, becoming progressively shorter toward margin, with a glabrous marginal band, the margins sparsely ciliate. Petals 1.7–2.6 × 1.5–2.7 cm, deep rose-purple becoming lavender with age, obovate, sparsely ciliate, otherwise glabrous. Stamens isomorphic, with ventrally inclined pores, filaments purple, 7–9 mm long, anther thecae 6–7 mm long, yellow, connective 1–2 mm long, extended into an upturned bifid appendage 1 mm long. Ovary (at anthesis) ca. 7 mm long, fluted and setose in the distal half. Styles 1.2–1.7 cm long, slightly curved distally, stigma truncate, papillose. Seeds not seen.

Distribution and Phenology.—In central Colombia (Fig. 7) in the eastern and central cordilleras, along roadsides in disturbed and undisturbed forests at elevations of 1,980–3,100 m. Flowering reported in February, March, April, July, August, and September.

Representative Specimens Examined.—COLOMBIA. Antioquia: Río Negro, 1851–1857 (fl), *Triana s.n.* (BM). Caldas: Laguneta, Salento, 1 Apr 1942 (fl), *von Sneidern 3086* (BM, LL, NY, US). Huila: 8 km from Plata Vieja en route to Puracé, 12 Sep 1959 (fl), *Maguire & Maguire 44204* (NY, US); Moscopán, near Santa Leticia, 8 Sep 1961 (fl), *Uribe 3868* (COL, US). Quindío: Pié de San Juan, on the E slope of Mt. Quindío, 8 Mar 1875 (fl), *André 2265* (NY); Tolima: La Ceja to Agua Bonita, Old Quindío trail, 2 Aug 1922 (fl), *Killip & Hazen 9545* (NY); along Quindío Hwy., between Cajamarca and summit of Divide, 27–28 Mar 1939 (fl), *Killip & Varela 34651* (COL, NY, US); Prov. de Mariquita, La Ceja, Feb 1843 (fl), *Linden 1057* (P); ca. 30 km W of Cajamarca, 18 Aug 1959 (fl), *Maguire & Maguire 44010* (NY, US). Valle: Cordillera Occidental, Los Farallones, E slope, Almorzadero, 25 Jul 1956 (fl), *Cuatrecasas 21704* (F, NY).

The plants assigned to this species form a morphologically coherent taxon characterized by appressed to antrorsely spreading, proximally attached, cauline scales, narrowly elliptic to elliptic-lanceolate leaves with bulla-based hairs on the adaxial surface (Fig. 5A), inflorescences reduced to solitary flowers, and yellow isomorphic anthers.

An unusual variant from Dept. Valle, Colombia (*Cuatrecasas 21704*) has inflorescences consisting of simple dichasia (sometimes reduced to two flowers) on elongate peduncles reminiscent of those of *T. lepidota.* In other characters, such as leaf and cauline pubescence and stamen morphology, this collection falls well within the range of variation here attributed to *T. paleacea.*

Two collections from Dept. Chocó, Colombia (*Lozano & Diaz 3217* at F and NY and *Silverstone-Sopkin et al. 1598* at MO and US) are also anomalous. They appear to combine characters of *T. paleacea* and *T. elegantula.* In hypanthial length, petal size, androecial morphology, inflorescence details, and foliar pubescence, these two collections fit comfortably into our concept of *T. paleacea.* In other features such as leaf shape, calyx lobe length, and the unusual spreading cauline scales, they are very much like *T. elegantula. Tibouchina paleacea* and *T. elegantula* are both known from western Colombia but neither is presently recorded from Dept. Chocó. These two puzzling collections present an interesting challenge for additional field work. Until more material is available for study, we cannot place them in our taxonomy of this section with any degree of confidence.

Tibouchina silvestris Todzia & Almeda, sp. nov. (Fig. 11). TYPE.—COLOMBIA. Valle: Anchicayá, 200 m, May 1969 (fl), *Uribe-Uribe & Cortés 6280* (Holotype: COL!; isotype: US!).

Arbor parva 5–7 m; ramuli teretes sicut petioli foliorum subtus venae primariae dense pilis appressis squamatis rectangulatis vel lanceolatis obscure vel conspicue eroso-ciliolatis 0.5–1.5 × 0.5–1 mm induti. Petioli 0.5–1.4 cm longi; lamina 3–11 × 1.6–5.3 cm elliptica vel elliptico-ovata apice acuto basi obtusa vel rotundata, supra pilis ca. 1 mm longis et ½ vel ⅔ adnatis appressis sparsiuscule induta, subtus in venis secundariis squamis integris 0.5–1 mm longis sparsiuscule obsita, subtus in superficie pilis papillosis densiuscule obsita, 3–5-nervata coriacea et integra. Inflorescentia pauciflora 2.5–4.8 cm longa; flores 5-meri, pedicellis (ad anthesim) 0.2–0.7 cm longis, bracteolis glabris mox caducis. Hypanthium (ad torum) 4–5 mm longum extus densiuscule paleis appressis 3–5 mm longis indutum; calycis lobis 3–4 × 2–3 mm oblongis. Petala 1.3–1.7 × 1–1.2 cm obovata. Stamina paulo dimorpha glabra, thecis, subulatis 6 vel 5 mm longis poro ventraliter inclinato, connectivis 1 mm vel ca. 0.5 mm prolongatis appendicibus ventralibus ca. 1 mm. Ovarium 5-loculare apice modice setoso.

Trees 5–7 m tall; distal branches inconspicuously quadrate to terete, the internodes covered with appressed proximally attached, rectangular (often platelike) and lanceolate basally eared scales 0.5–1.5 mm long with irregularly erose margins, the nodes with appressed basally attached lanceolate scales 2–4 mm long with smooth margins. Petioles 0.5–1.4 cm long, covered with scales similar to those of internodes; blades coriaceous 3–11 cm long, 1.6–5.3 cm wide, elliptic to elliptic-ovate, 3-nerved with an additional pair of prominulous intramarginal veins, the apex bluntly acute, the base obtuse to rounded, the margin entire, beset with clasping folded scales; upper leaf surface with flattened scales adnate to epidermis for ½–⅔ their length, the free distal portion very narrowly triangular, the adnate portion swollen and covered with minute, white pustules; lower leaf surface covered with three types of scales that do not completely conceal surface; scales on elevated primary veins similar in size and shape to internodal scales, the secondary veins sparsely covered with lanceolate scales 0.5–1 mm long with entire margins, the tertiary veins with shorter lanceolate scales mostly 0.25 mm long, the actual surface entirely covered with white or tan papillose puberulence. Inflorescences umbelliform dichasial clusters of 3–6 flowers; peduncles 2.5–4.8 cm long; bracteoles typically enveloping and concealing young floral buds, 9–11 mm long, ovate, chartaceous, glabrous, early deciduous; pedicels 0.2–0.7 cm long, densely beset with appressed lanceolate scales mostly 2–3 mm long with small basal ears and irregularly erose margins. Hypanthia (at anthesis) 4–5 mm long to torus, 5–6 mm wide, campanulate to urceolate, concealed by appressed lanceolate scales mostly 3–5 mm long with small basal ears and irregularly erose margins. Calyx lobes 3–4 × 2–3 mm, oblong, with scales like those of hypanthia except for a narrow marginal glabrous band, the margins ciliate. Petals 1.3–1.7 × 1–1.2 cm, pink-violet to lavender, obovate, ciliate, otherwise glabrous. Stamens weakly dimorphic with ventrally inclined pores; larger stamens geniculate, filaments 6–7 mm long, anther thecae ca. 6 mm long, yellow, subulate, connective strongly geniculate, 1 mm long, with a yellow-orange, incurved, bifid appendage ca. 1 mm long; smaller stamens geniculate, filaments 6–7 mm long, anther thecae red, subulate, ca. 5 mm long, connective strongly geniculate, 0.5 mm long with a yellow-orange incurved bifid appendage ca. 1 mm long. Ovary (at anthesis) fluted at setose apex. Styles 12–14 mm long, weakly declinate, incurved distally; stigma truncate, papillose. Seeds ca. 0.5 mm long, light brown.

DISTRIBUTION AND PHENOLOGY.—Known only from the Dept. of Valle, Colombia (Fig. 10), near

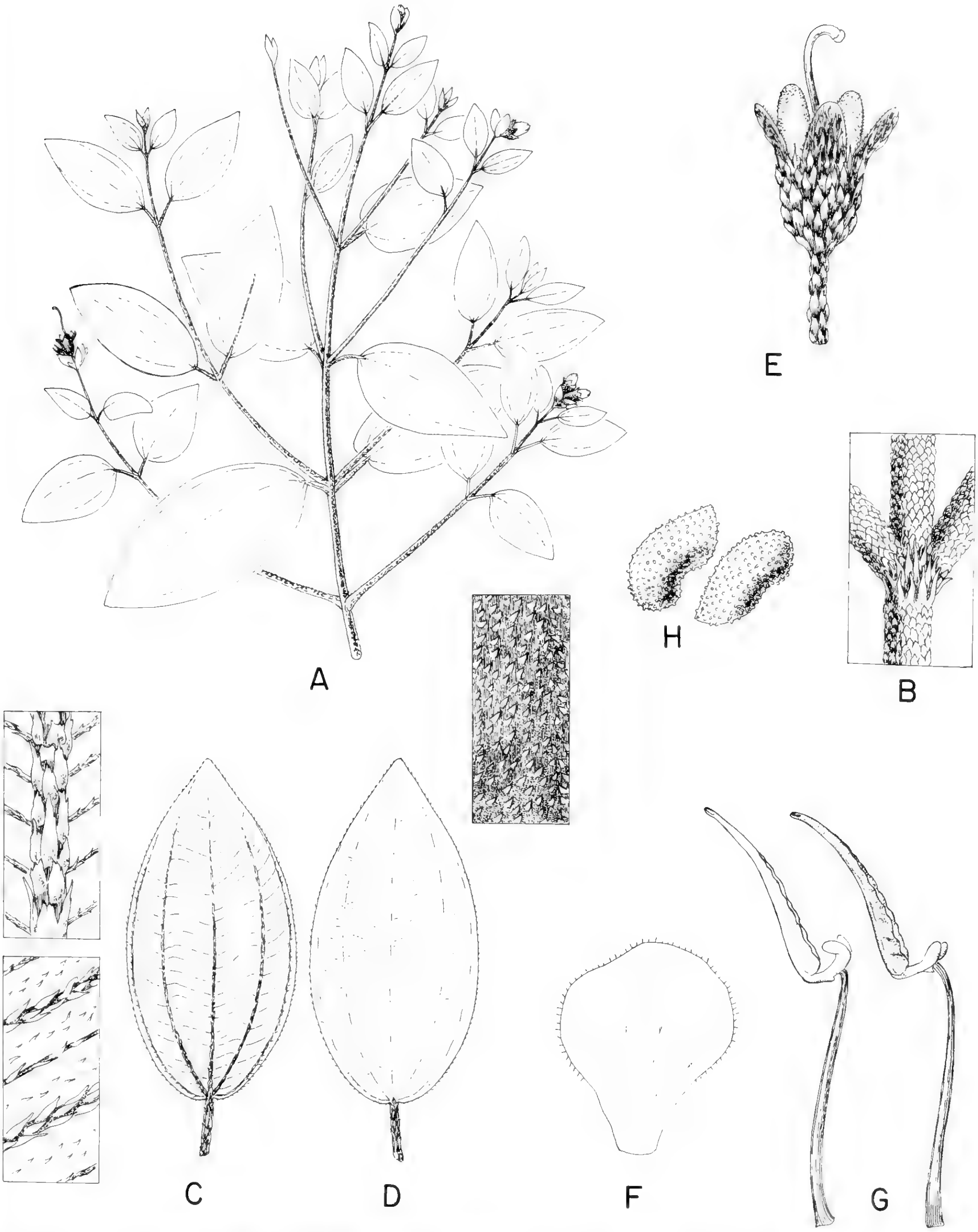

FIGURE 11. *Tibouchina silvestris* Todzia & Almeda. A, habit, × ca. ⅓; B, enlargement of cauline node; C, representative leaf (abaxial surface) with enlargement of median vein (upper left) and intercostal indument (lower left), × ca. ½; D, representative leaf (adaxial surface) with enlargement of intercostal indument (upper right), × ca. ½; E, hypanthium (at anthesis) with petals and stamens removed, ×2; F, petal ×2; G, antepetalous stamen, lateral view (left) and antesepalous stamen, lateral view (right), ×5; H, seeds, ×30. (A–D from *Køie 4808*; E–G from *Uribe-Uribe & Cortés 6280,* US.)

Anchicayá from 200–500 m in wet forest. Flowering reported in May, August, and December; fruiting reported in December.

SPECIMENS EXAMINED.—COLOMBIA. Valle: Río Anchicayá near CVC hydroelectric plant, ca. 3°40′N, 76°50′W, 15 Dec 1981 (fr), *Gentry 35662* (COL, US); Anchicayá, Cali-Buenaventura, 500 m, 11 Aug 1952 (fl), *Køie 4808* (US).

Tibouchina silvestris appears to be quite rare and occurs in a region that has been frequently visited, but perhaps not thoroughly explored, by field botanists. Although only three collections of this taxon were available for study, it is distinguished from all other species in the section by a diagnostic suite of characters: completely glabrous floral bracts and bracteoles, weakly dimorphic stamens with anther thecae that are alternately reddish-purple and yellow, essentially entire scales on the abaxial secondary leaf veins, and a conspicuous papillose puberulence on the lower leaf surfaces.

Prior to our study, the few collections of this species were identified as *T. lepidota.* Based on pubescence characters, it seems likely that *T. silvestris* is a close relative of *T. lepidota,* perhaps representing a specialized offshoot of the evolutionary line that gave rise to the latter species. In addition to its more extensive geographic range and higher elevation habitat, *T. lepidota* differs from *T. silvestris* in having shorter (1.5–3 mm), prevailingly ovate, hypanthial scales, longer calyx lobes (4–7 mm), and uniformly yellow isomorphic anthers. Within sect. *Lepidotae,* the morphological and ecogeographical relationship between *T. silvestris* and *T. lepidota* parallels that exhibited by *T. narinoensis* and *T. paleacea.* Both *T. silvestris* and *T. narinoensis* are low elevation counterparts of *T. lepidota* and *T. paleacea,* respectively. An understanding of the relationship between these species pairs is limited by the lack of chromosome counts for most species in the section.

The epithet for this species is derived from *silva,* Latin for woods, trees, or forest, to emphasize its lowland forest habitat.

Tibouchina wurdackii Almeda & Todzia, sp. nov. (Fig. 12). TYPE.—PANAMA. Coclé: forested slopes above El Copé along abandoned road leading to continental divide, 700–850 m, 8°38′N, 80°38′W, 24 Jan 1989 (fl), *Almeda et al. 6380* (Holotype: CAS!; isotypes: CR!, DUKE!, MO!, NY!, PMA!, TEX!, US!).

Frutex 1–2 m; ramuli teretes sicut petioli foliorum subtus venae primariae inflorescentia hypanthiaque dense pilis appressis squamatis lanceolatis eroso-ciliolatis 1.5–2.5 × 0.5–1 mm obsita. Petioli 2–12 mm longi; lamina 2.8–5.9 × 1–2.5 cm elliptica apice apiculato basi obtusa vel rotundata, supra pilis ca. 1 mm longis et ca. ⅔ adnatis appressis sparsiuscule induta, subtus in superficie squamis plerumque 0.5–2 mm longis obsita, 3–5-nervata nervis secundariius supra invisis subtus planis et inconspicuis. Inflorescentia pauciflora ca. 3.5–7 cm longa; flores 5-meri, pedicellis (ad anthesim) 5–12 mm longis. Hypanthium (ad torum) 6–7 mm longum extus densiuscule paleis appressis 1–2 mm longis indutum; calycis lobis 3–5 × 3 mm oblongis. Petala 1.3–1.7 × 1–1.2 cm obovata. Stamina dimorpha glabra, thecis subulatis 6 vel 5 mm longis poro ventraliter inclinato, connectivis 1 mm vel 0.5 mm prolongatis appendicibus ventralibus ca. 1 mm. Ovarium 5-loculare apice modice setoso.

Shrubs 1–2 m tall; distal branches inconspicuously quadrate to terete, the uppermost internodes covered with appressed, proximally attached, lanceolate scales 1.5–2.5 mm long with small basal ears and irregularly erose or lacerate margins, the nodes with similar scales mostly 4–6 mm long. Petioles 2–12 mm long, covered with lanceolate scales like those of internodes; blades coriaceous, 2.8–5.9 cm long, 1–2.5 cm wide, elliptic, 3-nerved with an additional inconspicuous pair of intramarginal veins, the apex apiculate, the base obtuse to rounded, the margin entire and beset with clasping, folded scales; upper leaf surface with flattened scales that are adnate for ⅔ their length, the distal third of the scale free and triangular, the adnate portion covered with minute white pustules; lower leaf surface with three types of scales that do not completely conceal the surface; scales on the elevated primary veins similar in shape and size to internodal scales, higher order veins (when evident) and actual surface covered with a mixture of ovate scales 0.5 mm long and narrowly lanceolate or triangular scales 1.5–2 mm long, these obscurely auriculate at basal attachment, lacking a white papillose puberulence. Inflorescences terminal, congested, paniculiform dichasia, 3.5–7 cm long, with (3–)5–18 flowers; bracteoles not enveloping or concealing young floral buds, 4–9 mm long, narrowly lanceolate to subulate, with scales like those of elevated lower leaf veins, early deciduous; pedicels 5–12 mm long. Hypanthia (at anthesis) 6–7 mm long to torus, 4–5 mm wide, narrowly campanulate to urceolate, densely beset with and concealed by appressed lanceolate scales 1–2 mm long, with basal ears and irregularly erose margins. Calyx lobes 3–5 mm long, ca. 3 mm wide, triangular, moderately beset with scales

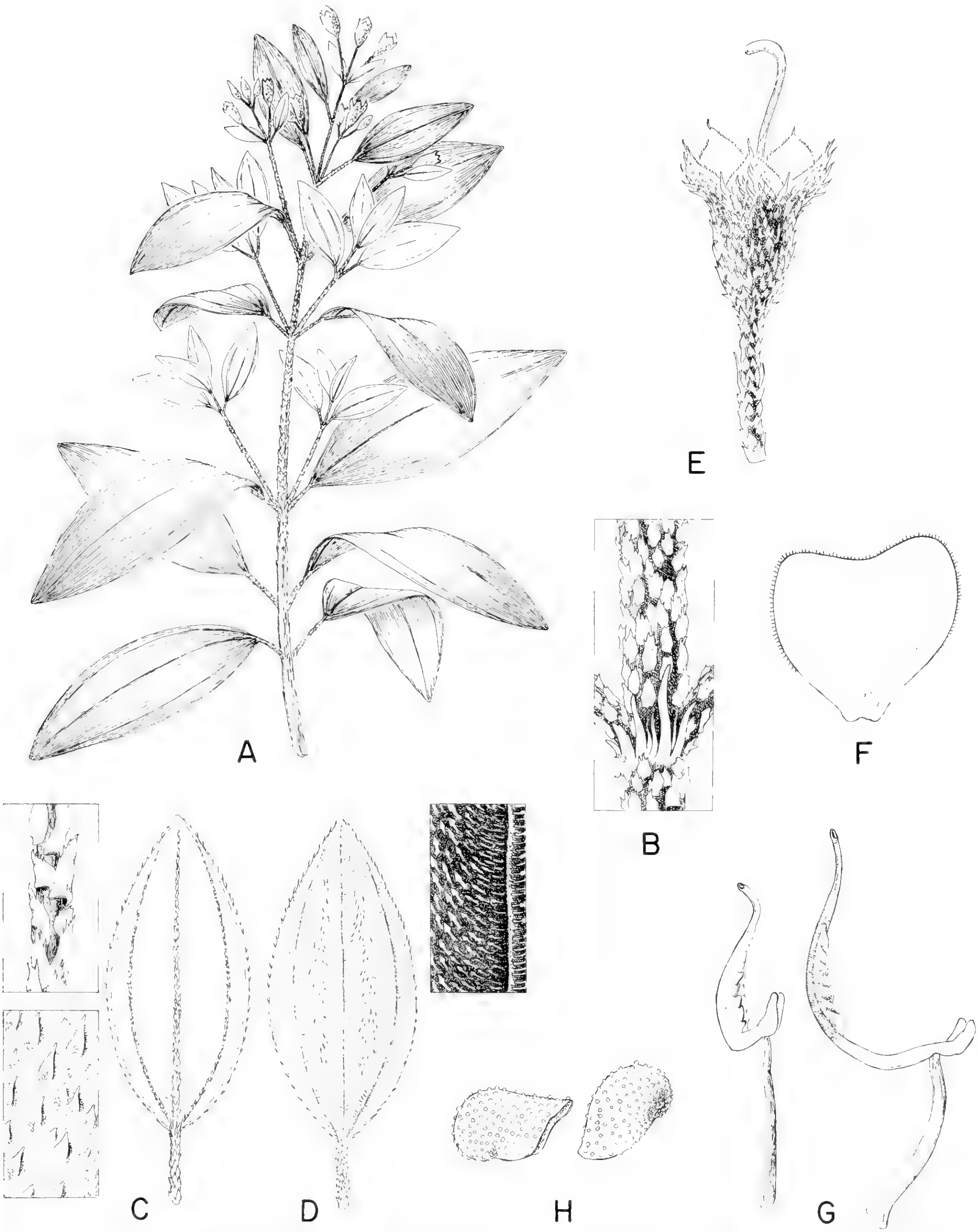

FIGURE 12. *Tibouchina wurdackii* Almeda & Todzia. A, habit, × ½; B, enlargement of cauline node; C, representative leaf (abaxial surface) with enlargement of median vein (upper left) and intercostal indument (lower left), × ca. ⅔; D, representative leaf (adaxial surface) with enlargement of indument adjacent to impressed median vein (upper right), × ca. ⅔; E, hypanthium, × ca. 2; F, petal, × ca. 17; G, antepetalous stamen, lateral view (left) and antesepalous stamen, lateral view (right), ×4; H, seeds, × ca. 50. (A–G from the holotype; H from *Almeda et al. 5928,* CAS.)

like those of hypanthia except for a narrow marginal glabrous band, the margins ciliate. Petals 1.2–1.8 × 0.9–2 cm, pink, obovate, emarginate, ciliate, otherwise glabrous. Stamens dimorphic, with ventrally inclined pores; larger stamens geniculate, filaments 9--10 mm long, anther thecae 7–7.5 mm long, red, subulate, connective 4–4.5 mm long with a yellow, upturned, bifid appendage 2 mm long; smaller stamens more or less erect, filaments 9–10 mm long, anther thecae 5–5.5 mm long, yellow, subulate, connective strongly geniculate, 1–1.5 mm long, with a yellow, erect to incurved, bifid appendage 1.5 mm long. Ovary (at anthesis) ovoid, fluted at the setose apex. Styles 10–11 mm long, declinate, strongly incurved distally; stigma truncate, papillose. Seeds 0.25–0.33 mm long, light brown.

Distribution and Phenology.—Local and uncommon in Panama (Fig. 10) at elevations of 700–1,402 m from Cerro Tute/Arizona in Prov. Veraguas to Cerro Sapo in Prov. Darién. Flowering in January and February; fruiting in January and February, April through June, and August.

Representative Specimens.—PANAMA. Coclé: Cerro Gaital, E slope and ridges leading to summit with montane rainforest and elfin woodland, 8°40′N, 80°07′W, 24 Feb 1988 (fl), *Almeda et al. 5916* (CAS, MO, PMA, TEX); forested slopes above El Copé along abandoned road leading to continental divide, 8°38′N, 80°38′W, 25 Feb 1988 (fr), *Almeda et al. 5928* (CAS, NY, PMA, TEX). Darién: NE slopes of Cerro Sapo summit, approach from Garachine, 8 May 1979 (fr), *Hammel 7250* (CAS, MO). Veraguas: top of Cerro Arizona, above Santa Fé, 22 Apr 1980 (fr), *Hammel & Kress 8560* (CAS); Cerro Tute, ca. 10 km NW of Santa Fé, on ridgetop in cloud forest, 19 May 1975 (fr), *Mori 6257* (MO); 16 Jun 1975 (fr), *Mori 6751* (MO); 3 Aug 1975 (fr), *Mori 7566* (MO).

Although this species was first collected in 1975, its exact identity remained an enigma until flowering material was gathered in 1988. *Tibouchina wurdackii* and the closely related *T. inopinata* are restricted to southern Central America, but their ranges replace one another (Figs. 9, 10), and they have different peak flowering times. Based on our field experience, *T. inopinata* flowers most profusely from May through August, whereas *T. wurdackii* is at its peak in January and February. The resemblance between *T. wurdackii* and *T. inopinata* is most evident in details of the scaly foliar indument (Figs. 2F, 3A, B, 6C–F). Both species are also characterized by a dimorphic androecium and petals that do not undergo a significant color change with age. In *T. wurdackii* the longer petals (1.2–1.8 cm) are pink and the anthers are alternately 7–7.5 and 5–5.5 mm long. In contrast, the petals of *T. inopinata* are shorter (0.6–1.3 cm), typically white, and the anthers are alternately 5–5.5 and 3–4 mm long. Other subtle, but consistent, differences between the two species include foliar size and shape. The shorter blades of *T. wurdackii* are elliptic with an apiculate apex and an obtuse to rounded base, whereas the modally longer blades of *T. inopinata* are lanceolate to narrowly elliptic with a gradually acuminate apex and an acute base. In collections lacking diagnostic flower parts, careful attention to the size and complexity of the inflorescence will make confusion between the two unlikely. In *T. wurdackii* the relatively short (3.5–7 cm) few-flowered dichasia are crowded by subtending leaves. In *T. inopinata* the many-flowered compound panicles (12.5–25 cm long) are well exserted beyond the leaves at nodes initiating the inflorescence.

We take pleasure in naming this species for John J. Wurdack, friend, mentor, and colleague, in recognition of his many significant contributions to the taxonomy of neotropical Melastomataceae.

Acknowledgments

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RESUMEN

El género *Tibouchina,* con 350 especies, es el más grande de los géneros neotropicales de la familia Melastomataceae cuyos frutos son cápsulas. *Tibouchina* se distribuye desde la parte oeste de México, continuado a través de Centro América y Las Antillas hasta la parte norte de Argentina y Paraguay. La sección *Lepidotae* es una de las 11 secciones del género *Tibouchina.* Las características vegetativas y florales que se pueden usar para distinguir la sección son: indumento de pelos escamosos, bracteolas florales libres, sépalos persistentes, y estambres glabros. Las secciones *Lepidotae, Barbigerae,* y *Tibouchina,* las únicas secciones en el género con pelos escamosos, están intimamente relacionados. Se provee una revisión de la sección *Lepidotae* que incluye una sinopsis de la historia taxonómica, un comentario sobre las características vegetativas y florales importantes, una clave, descripciones, discusiones, ilustraciones y mapas de distribución para todas las especies. Se reconocen nueve especies y se describen tres especies nuevas, *T. elegantula* y *T. silvestris* de Colombia, y *T. wurdackii* de Panamá.

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MACROURID FISHES OF THE SUBGENUS *CHALINURA*, GENUS *CORYPHAENOIDES*, FROM THE INDIAN OCEAN

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Abstract: The subgenus *Chalinura* Goode and Bean, 1883, of the large macrourid genus *Coryphaenoides* Gunnerus, 1765, is represented in the Indian Ocean by six species. *Coryphaenoides grahami* is described from seven specimens from the Indian Ocean, the Atlantic off South Africa, and the Pacific off New South Wales, Australia. Its closest relative appears to be *C. striaturus* Barnard, formerly known only from South Africa, but now known from the southeastern Atlantic across the Indian Ocean into the western Pacific. *Coryphaenoides murrayi* Günther is newly recorded from the Indian Ocean off Australia. Three geographic populations of *C. serrulatus* Günther are recognized: one in the New Zealand area, a second in the Australian Bight, and a third in the central and western Indian Ocean. The last population is described as a new subspecies, *C. serrulatus oceanus*. *Coryphaenoides mcmillani* is described from 16 specimens taken off Cape Agulhas and Whale Ridge in the South Atlantic, the western and central Indian Ocean, off New South Wales and South Australia, and off New Zealand. It most closely resembles *C. subserrulatus* Makushok, a species somewhat peripheral to the Indian Ocean that has been captured only at the extreme southeastern and southwestern margins of the basin, as well as off Argentina and New Zealand.

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INTRODUCTION

Over the past two decades, Soviet fishery and oceanographic expeditions have investigated extensively the continental slope fauna of the Indian Ocean. The resulting biological collections have greatly increased our knowledge of the Indian Ocean deep-sea fauna, which has long remained poorly known. Expeditions in the past have concentrated on the continental margins, with few extending their work to the many geologic features far offshore.

The extent to which Soviet expeditions have helped to fill the gaps in collection sites in the Indian Ocean can be appreciated by comparing the maps in Figures 1 and 2. The benthic trawl and dredge hauls at which macrourids were taken by six different vessels between the late 1800s and the mid-1900s are plotted in Figure 1. Figure 2 shows the sites at which macrourids were collected by Soviet vessels. This map is far from comprehensive, in that the plots represent only those stations at which we have examined ma-

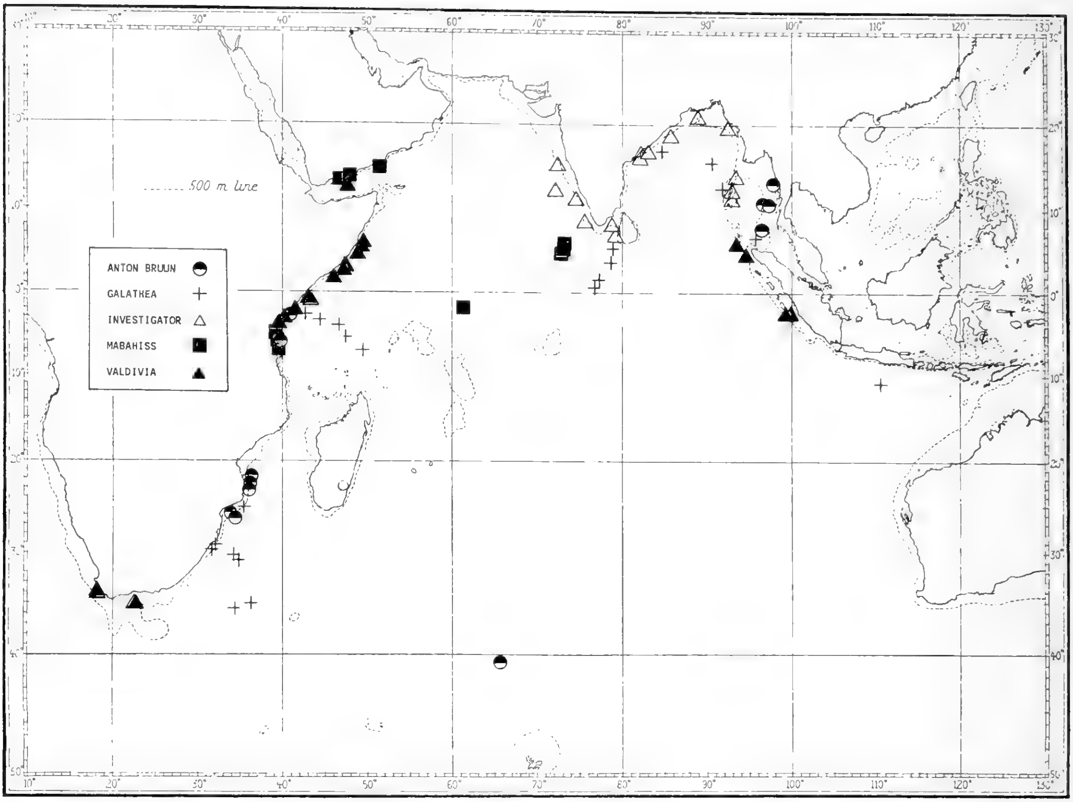

Figure 1. Sites at which grenadiers were collected in the Indian Ocean by the ships *Anton Bruun, Galathea, Investigator, Mabahiss,* and *Valdivia.*

crourids. Shcherbachev (1987) provided a map showing general areas in the Indian Ocean where trawling has been conducted by Soviet expedition ships. Conversations with colleagues suggest that collecting along the coasts of southern Africa and Australia by regional fisheries and other scientific agencies has increased considerably in recent years. We have examined some, albeit limited, macrourid specimens accumulated by a few of these entities; those in the Australian Museum (AMS), National Museum of Victoria (NMV), and National Museum of New Zealand (NMNZ) are of particular importance in this report.

Macrourids have been among the most numerous of the fishes collected by the many expeditions at which trawls were dragged at slope depths of the Indian Ocean. Shcherbachev (1987) listed more than 30 species of macrourids (in 21 genera), but based on our studies of collections housed mainly in Moscow, we estimate that the Indian Ocean is home to more than 100 species of macrourids, most in the genera *Coryphaenoides* (about 20 species) and *Coelorinchus* Giorna, 1810 (about 25 species). *Nezumia* Jordan, 1904, and *Ventrifossa* Gilbert and Hubbs, 1920, constitute the next most speciose genera with about 10 species each, with *Gadomus* Regan, 1903, *Bathygadus* Günther, 1878, *Hymenocephalus* Giglioli, 1884, *Mataeocephalus* Berg, 1898, and *Trachonurus* Günther, 1887, having representatives of about three to six species (*Gadomus* and *Bathygadus* may not be grenadiers; see Howes 1989 and Howes and Crimmen 1990). When collections in Australia and South Africa are studied closely, we predict that the total number probably will rise by 10% or more.

This paper is the 11th treating Soviet collections of macrourid fishes of the Indian Ocean. Previous ones include Merrett et al. (1983); Sazonov (1981); Sazonov and Shcherbachev (1982a, b, 1985); Shcherbachev et al. (1986); Shcherbachev (1987); Shcherbachev and Piotrovskyi

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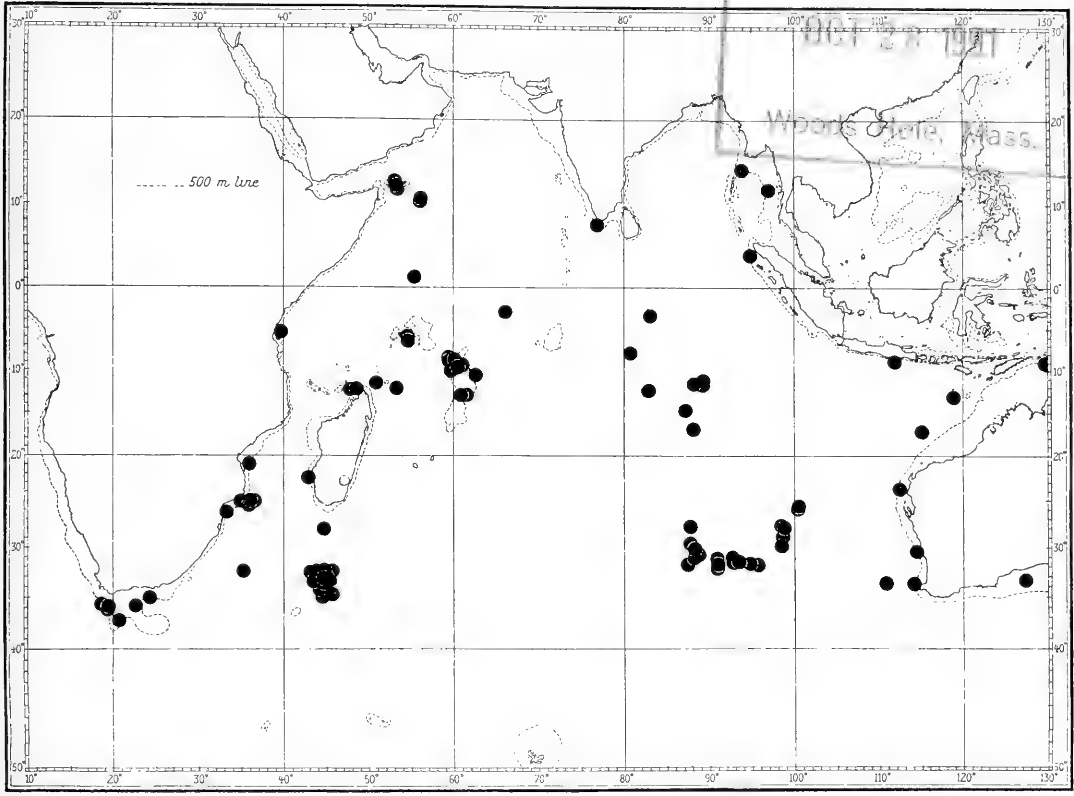

FIGURE 2. Sites at which grenadiers were collected in the Indian Ocean by Soviet vessels.

(1982); Shcherbachev et al. (1979); and Trunov (1980). Iwamoto's participation in this project began with a 3.5-month visit to the P. P. Shirshov Institute of Oceanology in Moscow in 1988, on an invitation from Dr. Nikolai V. Parin, head of the Institute's Laboratory of Oceanic Ichthyofauna. Treatment of the genera *Coryphaenoides* sensu lato and *Coelorinchus* will be by Shcherbachev and Iwamoto. The remaining macrourid genera will be treated jointly by Shcherbachev, Yuri I. Sazonov, and Iwamoto. The purpose of the current paper is to report new collections of four common southern hemisphere species, *Coryphaenoides serrulatus* Günther, 1878, *C. murrayi* Günther, 1878, *C. subserrulatus* Makushok, 1976, and *C. striaturus* Barnard, 1925, and to describe a new subspecies of the first, and two new species related to the last two.

METHODS AND MATERIALS

Methods for taking and abbreviating measurements and counts follow Iwamoto (1970) and Iwamoto and Sazonov (1988). One difference, however, is the measurement of postorbital length, which in this and subsequent papers is the greatest distance from posterior rim of orbit to upper posterior angle of opercle. Institutional abbreviations follow Leviton et al. (1985), and later, Leviton and Gibbs (1988), except for NZOI, New Zealand Oceanographic Institute, Wellington, which they do not list. Literature references to generic names are not listed in the Literature Cited unless otherwise cited; they can be obtained from Eschmeyer (1990).

Most of the Soviet collections used here are, or will be, deposited in the Zoological Museum of Moscow State University (ZMMGU). Significant representatives have also been deposited in the California Academy of Sciences (CAS). Other collections still in the Shirshov Institute of Oceanology (IOAN) will eventually be deposited in ZMMGU or in other institutions as they are studied. The Zoological Institute of the Academy of Sciences in Leningrad (ZIN) will be the main repository of primary types. Representative sam-

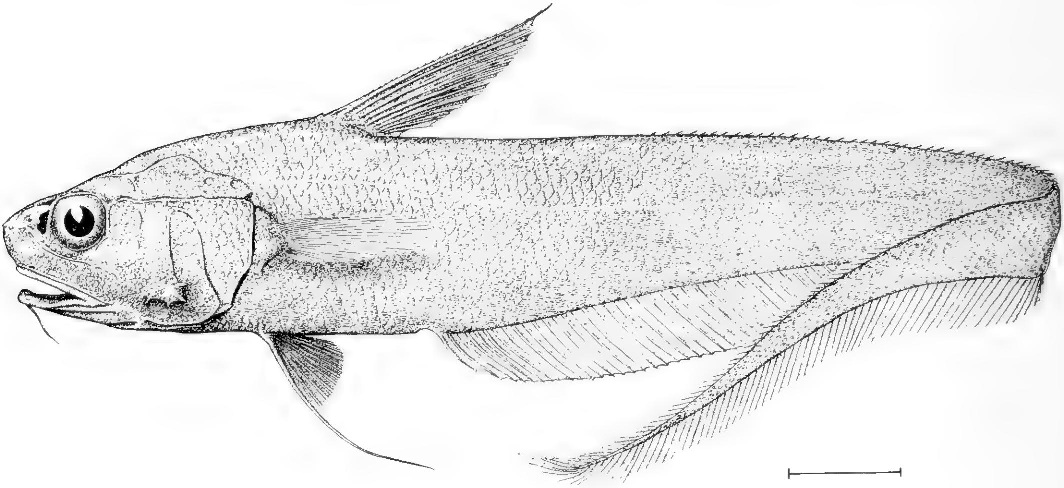

FIGURE 3. *Coryphaenoides grahami* n. sp. Holotype, ZIN 49766, from Broken Ridge (30°58′S, 93°42′E) in the Indian Ocean, 1,060–1,100 m. Scale bar equals 25 mm.

ples will be sent to museums outside the Soviet Union.

Genus *Coryphaenoides* Gunnerus, 1765, sensu lato

The genus (and subgenera) as used here follows definitions given by Iwamoto and Stein (1974) and Iwamoto and Sazonov (1988).

Coryphaenoides grahami new species

(Figs. 3, 4)

Coryphaenoides armatus [non Hector, 1875]: Shcherbachev 1987:7 (listed from Indian Ocean: Madagascar and West Australian ridges, 1,060–1,280 m).

TYPE MATERIAL.—Holotype: ZIN 49766 (unripe ♀, 59.3 mm HL, 390+ mm TL); 30°58′S, 93°42′E; 1,060–1,100 m; *Fiolent* cr. 7(9), tr. 44; 4.VIII.1977. Paratypes: CAS 73237 (unripe ♂, 54.7 HL, 340+ TL); 33°56.8′S, 45°27.8′E; 1,270–1,280 m; *Zvezda Kryma* cr. 6, tr. 90; 31.VII.1976. ZMMGU P-17615 (unripe ♂, 53.2 HL, 337 TL); SE Atlantic off South Africa, 33°36′S, 15°38′E; 1,200–1,225 m; *Poltava* tr. 450 (or 430?). AMS I.29742 (56.0 HL, 340+ TL); off New South Wales, 32°09′S, 153°09′E; 1,079–1,143 m; FRV *Kapala* sta. K-89-1707; 17.VIII.1989. AMS I.29737 (58.2 HL, 347+ TL); off New South Wales, 35°28′S, 150°56′E; 1,116–1,134 m; FRV *Kapala* sta. K-89-1901; 31.VIII.1989. AMS I.29745 (55.5 HL, 367 TL); off New South Wales, 34°54′S, 151°16′E; 1,097–1,143 m; FRV *Kapala* sta. K-89-1802; 22.VIII.1989. AMS I.29798 (55.2 HL, 330+ TL); New South Wales NE of Tuncurry, 33°08′S, 153°16′E; 1,034–1,079 m; FRV *Kapala* sta. K-89-1204; 15.VI.1989.

DIAGNOSIS.—Underside of snout completely scaled; V. 12; teeth small, weak, rather deciduous in most individuals, in a single row in lower jaw; head about 6 in TL; preopercle with 4 spikelike struts.

COUNTS AND MEASUREMENTS (see also Tables 1–4).—D. II,9 (8) + about 100; A. about 110; 1P. i19–i21 (23); scales below 1D. 7.5–9, below mid-base 1D. 5.5–6.5, below 2D. 8–9.5, lat.l. 26–31.

The following in percent HL: pre-A. 159–167; pre-1D. 126–130; pre-V. 101–107; greatest body depth 76–84; depth over A. origin 61–73; length 1P. 60–71; length V. 76–86.

DESCRIPTION.—Body deep behind anal fin origin, gradually tapering into long, laterally compressed tail. Head rather short, broad, its greatest width about equal to postorbital length, its length 6 or more in total length. Vertical diameter of orbit more than horizontal diameter, less than snout length, about 5 in head length. Snout broad, bluntly rounded, scarcely produced beyond large mouth and lacking terminal or lateral scutes. Interorbital broad, width greater than snout length. Mouth subterminal, upper jaw extends to below hind edge of orbit or beyond, rictus extends to below posterior one fourth of orbit. Barbel slender, length about equal to orbit diameter. Suborbital region deep, almost vertical except for narrow crooked suborbital shelf, which is much broader anteriorly than below midorbit. Preopercle with posteroventral margin forming a slight lobe with hind edge inclined forward and a shallow inflection above angle; preopercle ridge with prominent spikes at posteroventral angle, the spikes formed from the struts that in other species are covered by a bony rounded shield. Interopercle with a slender posterior tip that protrudes slightly beyond preopercle. Sensory pores on head slightly developed, most prominent along ventral margins of snout and suborbital, and along lower jaw. Posterior nostril large, length about equal to diameter of eye lens.

Gill membranes narrowly attached to isthmus, the gill opening extending forward to below hind edge of maxillary. Outer gill slit fairly wide; outer series of rakers on first arch developed, as in most species of subgenus *Chalinura,* into short lappet-like structures; other rakes more ridgelike. Length of gill filaments about two-thirds diameter of orbit.

Scales large and highly deciduous over most of body and head, but those on snout and underside of head much smaller. Entire dorsal and ventral surfaces of snout apparently covered with small scales, without naked lunate patches behind leading edge of snout or a file of small scales along leading edge characteristic of most other species of subgenus *Chalinura.* Scales on underside of snout mostly nonimbricate and beset with 2 or 3 short rows of low spinules. Body scales (Fig. 4) with multiple (as many as 9 or 10) parallel longitudinal rows of short, sharp, recumbent spinules. Head ridges lacking strong stout scales. A row of slightly thickened but very small scales along suborbital ridge, flanked above and below by small, thinner, looser scales.

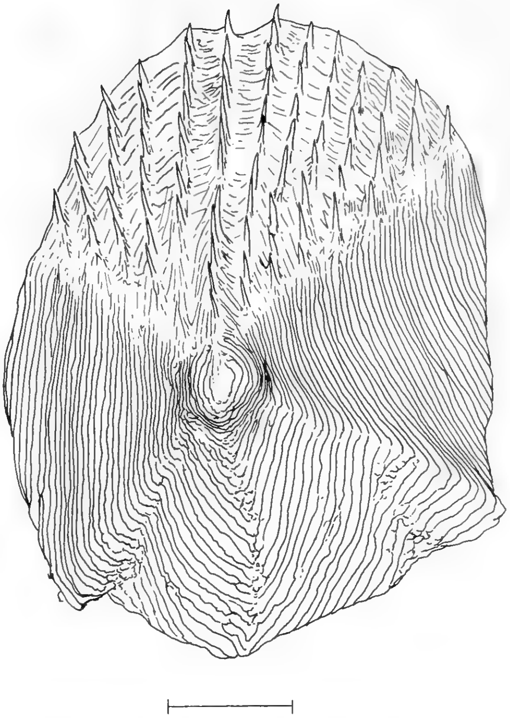

Figure 4. Scale from flank (near lateral line) below interspace between first and second dorsal fins of *Coryphaenoides grahami.*

Teeth all small, short, conical, slightly recurved in both jaws. Teeth weak and appear to be infirmly attached to jaws; those on holotype almost entirely missing, and many found lodged in gill rakers of CAS paratype. (In most paratypes

Table 1. Gill Rakers Counts in Four Species of *Coryphaenoides.* Asterisks indicate counts of holotype.

	Total gill rakers, first arch												
	Outer series							Inner series					
	7	8	9	10	11	12	13	11	12	13	14	15	16
striaturus	4	6	11	4	3	—	—	—	1	4	21	1	1
grahami	—	1	2	3	—	—	—	1	3	—	2	—	—
mediterraneus	—	—	—	3	2	1	1	—	—	—	—	3	4
murrayi	—	—	2*	—	3	—	—	—	—	—	1*	6	1

	Total gill rakers, second arch											
	Outer series						Inner series					
	11	12	13	14	15	16	11	12	13	14	15	16
striaturus	1	6	15	6	—	—	2	11	12	2	1	—
grahami	1	2	2	1	—	—	1	3	2	—	—	—
mediterraneus	—	—	—	2	3	2	—	—	—	2	3	2
murrayi	—	—	—	2*	2	1	—	1	2*	3	2	1

TABLE 2. Pelvic Fin Ray Counts in Four Species of *Coryphaenoides.*

	Pelvic fin rays			
	10	11	12	13
striaturus	—	4	52	—
grahami	—	12	13	—
mediterraneus	—	—	7	6
murrayi	2	6	5	—

the empty tooth sockets were the only evidence of the former presence of teeth.) Premaxillary teeth in narrow band, scarcely protruding above gum papillae; an outer, widely spaced series of slightly enlarged teeth. Mandibular teeth similarly small and arranged in a single row.

Fins rather well developed; first dorsal high, the serrated spinous ray about equal to head length; outer pelvic fin ray filamentous and extending past anal origin. Pectoral and pelvic origins about on same vertical; first dorsal origin well behind that vertical; anal origin below interspace of first and second dorsal fins, at a vertical passing a short distance behind first dorsal fin; second dorsal origin far posterior.

Ten slender (longest measured 14.8 mm) pyloric caeca in ZMMGU P-17615, an unripe female. Stomach of this individual empty; stomach of CAS paratype everted and could not be examined without damaging specimen.

Color in fresh specimens ivory-white with silvery sheen, edged in different places with black. In alcohol, color fades to dark gray to dark brown, with abdomen and ventral parts of head and gill cover blackish. Lips, gill membranes, mouth, and gill cavities black. Barbel dark brownish basally, pale distally. Paired and first dorsal fins blackish, anal fin dusky.

DISTRIBUTION (Fig. 5).—Known from seven specimens collected in the eastern and western Indian Ocean, the Atlantic off South Africa, and the Pacific off New South Wales, Australia.

SIZE.—To 39 cm.

ETYMOLOGY.—Named for Ken Graham of the New South Wales State Fishery Agency, who has collected numerous valuable fish specimens, including the four AMS paratypes.

REMARKS AND COMPARISONS.—*Coryphaenoides grahami* most closely resembles *C. striaturus.* The two species are apparently sympatric off South Africa and Australia, where two paratypes were discovered among collections of *C. striaturus.* The general shape, counts, and proportional measurements (Tables 1–3) are similar in the two species; the complete scale covering

TABLE 3. Comparison of Preoral Length, Interorbital Width, and Posterior Nostril Diameter in Four Species of *Coryphaenoides.*

	Preoral length (% HL)											
	9	10	11	12	13	14	15	16	17	18	$\bar{x}$	SD
striaturus	—	1	2	9	6	8	6	3	—	1	13.50	1.6987
grahami	—	1	1	2	2	—	1	—	—	—	12.17	1.7224
mediterraneus	1	2	2	2	—	—	—	—	—	—	10.71	1.1127
murrayi	—	—	—	—	1	—	2	—	—	—	14.33	1.1547

	Interorbital width (% HL)													
	23	24	25	26	27	28	29	30	31	32	33	34	$\bar{x}$	SD
striaturus	1	8	9	11	9	11	5	2	—	—	—	—	26.46	1.7474
grahami	—	—	—	—	—	1	2	—	4	—	—	—	30.00	1.1952
mediterraneus	1	—	2	2	1	2	—	—	1	—	—	—	26.56	2.1660
murrayi	—	—	—	—	—	1	2	—	2	—	1	1		

	Posterior nostril (% HL)									
	3	4	5	6	7	8	9	10	$\bar{x}$	SD
striaturus	4	15	20	6	3	—	—	—	4.77	0.9944
grahami	—	—	—	—	—	—	4	1	9.20	0.4472
mediterraneus	1	1	—	—	—	—	—	—	3.50	0.7071
murrayi	1	—	2	—	—	—	—	—	4.33	1.1547

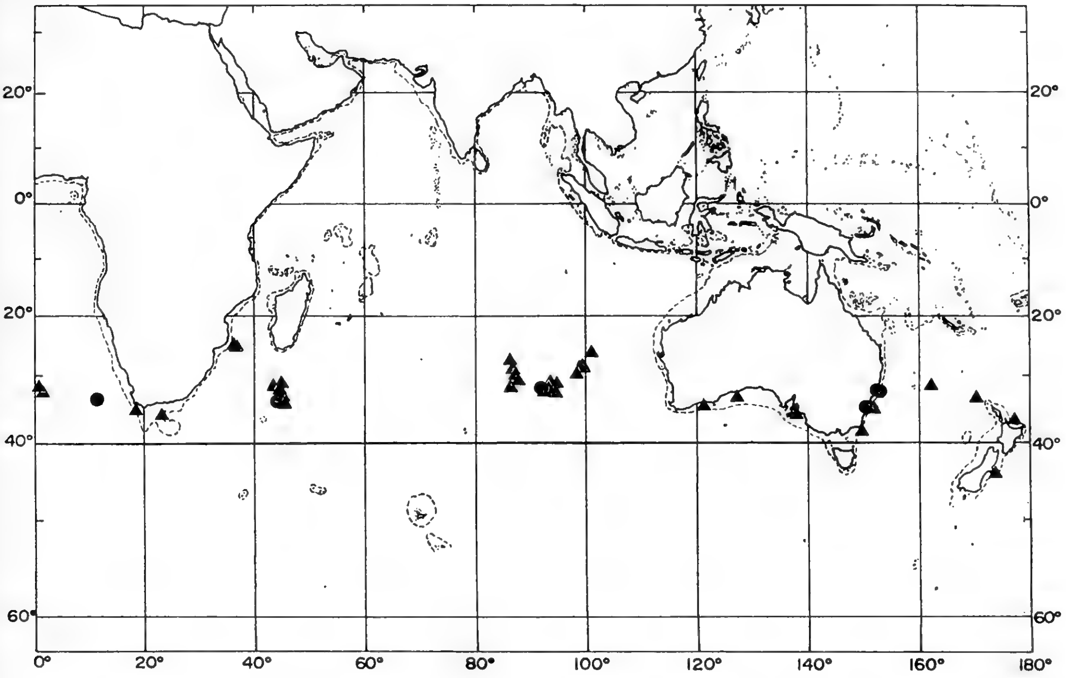

FIGURE 5. Catches of *Coryphaenoides grahami* (circles) and *C. striaturus* (triangles) in the Indian Ocean and adjacent waters.

on the snout, suborbital, and lower jaw contrasts the two from other close members of the subgenus (but not *C. serrulatus*). The new species can be distinguished from *C. striaturus* by its overall darker color; larger posterior nostril (9.1–9.3% HL cf. 3.0–5.5%); slightly broader interorbital (29.3–31.4% cf. 23.0–29.8%); slightly longer distance V.-A. (61–69% cf. 42–62%) and distance isth.-A. (110–119% cf. 90–109%); smaller, weaker teeth; and the spikelike processes on the

TABLE 4. Selected Measurements of Type Specimens of *Coryphaenoides grahami* n. sp.

	ZMMGU P-17515	CAS 73237	AMS I.19798–010	AMS I.29745–005	AMS I.29742–003	AMS I.29737–002	ZIN 49766 (holotype)
TL (mm)	337	340+	330+	367	340+	347+	290+
HL (mm)	53.2	54.7	55.2	55.5	56.0	58.2	59.3
			The following in percent of head length				
Snout	25.0	28.9	26.8	27.6	26.3	28.0	27.0
Internas.	21.4	25.6	21.6	21.4	23.6	23.0	22.9
Interorb.	29.3	31.0	31.2	29.0	28.2	31.4	31.2
Orbit	22.6	23.4	22.6	23.4	22.3	21.0	22.3
Suborb.	11.7	13.2	10.7	13.5	12.5	11.7	13.2
Postorb.	56.4	53.9	56.2	53.9	54.5	56.2	58.0
Orb-preop.	47.6	49.4	46.0	49.2	47.3	48.5	52.6
Up. jaw	41.7	39.1	40.8	40.5	42.9	40.5	42.5
Barbel	19.7	12.8	20.7	17.3+	19.8	22.5	21.6
Gill slit	18.6	16.8	20.1	19.8	20.9	–	20.2
V.-A.	69	69	65	63	64	65	61
Isth-A.	114	119	107	108	109	110	110
1D.-2D.	98+	82	91	95	105	95	94

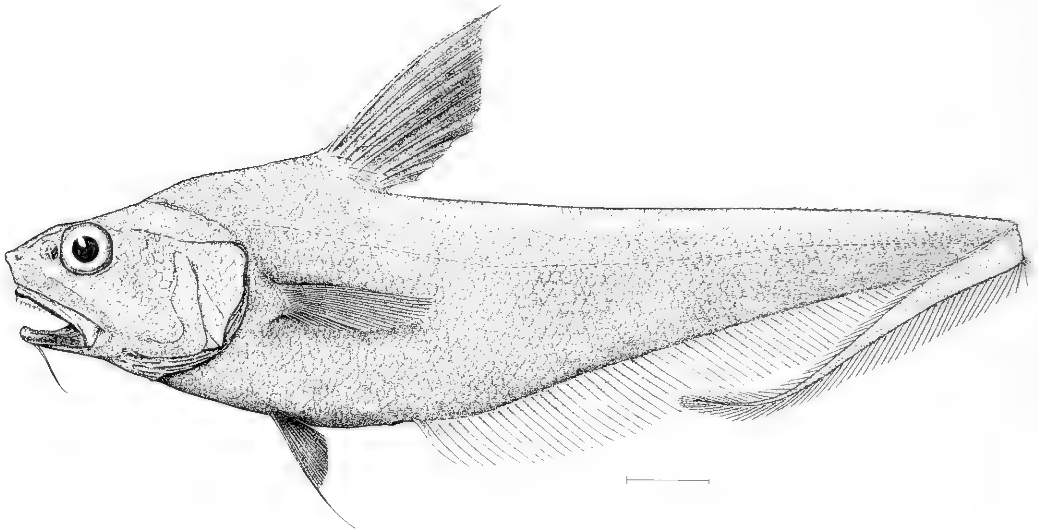

FIGURE 6. *Coryphaenoides striaturus.* Specimen CAS 66471 (79.3 mm HL, 450 mm TL) collected by the *Vityaz'* from Walters Shoals (31°59′S, 45°11′E) in the western Indian Ocean, 1,950–2,050 m.

preopercle. It also differs considerably in the dorsal profile of the head and nape, the latter being much more humped in the larger specimens of *C. striaturus.*

The nearly toothless condition of most specimens was surprising, but Merrett and Karrer (1988) recently documented edentulate specimens of nine adult *Coryphaenoides* referable to *C.* (*Chalinura*) *brevibarbis* Goode and Bean, 1896, *C.* (*Chalinura*) *mediterranea* Giglioli, 1893, and *C.* (*Lionurus*) *carapinus* (Goode and Bean, 1883). These nine specimens were ripe adult males with much enlarged nasal rosettes. We determined the sex of only three specimens of *C. grahami,* but not all had a relatively large posterior nostril (Table 3). The CAS and ZMMGU paratypes are males with moderately developed gonads and well-developed intestines; the holotype is a female. Merrett and Karrer (1988) were unable to offer an explanation for edentulate macrourids. Nor can we.

Coryphaenoides striaturus Barnard, 1925

(Figs. 5–7)

Coryphaenoides (*Chalinura*) *striatura* Barnard, 1925a:500–501 (off Cape Point in 823–1,737 m); 1925b:337–338, pl. 13, Fig. 4, 4a. Iwamoto 1986:335.

Coryphaenoides striatura: Smith 1949:133, Fig. 237. Shcherbachev 1987:7 (in part; listed from Indian Ocean: Madagascar Ridge, Ninety East Ridge, West Australian Ridge; specimens from Naturaliste Plateau, 2,320–2,350 m, represent *C. murrayi*; ZMMGU P-17633).

Coryphaenoides (*Nematonurus*) *armatus*: McCann and McKnight 1980:29–31, Figs. 11, 12 (misidentification of a specimen of *C. striaturus* from sta. E437 off New Zealand, 1,547 m).

Coryphaenoides (*Chalinura*) *murrayi*: McCann and McKnight 1980:34 (in part; specimen from sta. F892; the other specimen is *C. murrayi*).

DIAGNOSIS.—All of snout surfaces uniformly covered with small scales; pelvic fin rays 11–12 (usually 12); premaxillary teeth in broad cardiform band about 4 rows wide, flanked by an outer row of enlarged, slender, widely spaced canines; mandibular teeth irregularly uniserial; orbit diameter 18–24% of HL, interorbital 23–30%, preoral 10–16%; barbel 18–26%; posterior nostril 3.0–7.1%.

MATERIAL EXAMINED.—**Pacific Ocean.** Tasman Sea: ZMMGU P-17616 (65.0 HL, 356 TL); 30°24′S, 161°57′E; 1,210 m; *Dmitry Mendeleev* cr. 16, sta. 1245; 29.XII.1975. Australia: NMV A6569 (49.7 HL, 240+ TL); Victoria, 85 km S of Pt. Hicks, 38°31.4′S, 149°21.5′E; 1,986–1,360 m. AMS uncat. (88.0 HL, 500+ TL); off New South Wales, 34°54′S, 151°16′E; 1,097–1,143 m; *Kapala* sta. 89-1,802; 22.VIII.1989. New Zealand: NZOI (52.7 HL, 325+ TL); E coast of South Is., 42°13.0′S, 174°33.0′E; 1,547 m; sta. F892. NZOI (68.1 HL, 365 TL); N coast of North Is., 36°58.5′S, 176°41.0′E; 1,280–1,196 m. ZMMGU P-17617 (37.1 HL, 231 TL); NW of North Is., 33°56′S, 170°47′E; 2,005–2,010 m; *Dmitry Mendeleev* cr. 16, tr. 1264.

Indian Ocean. South Africa: ZMMGU P-17618 (6, 21.6–32.4 HL, 124–167 TL); 35°44′S, 22°34′E; 1,260–1,350 m; *Ob* cr. 2, sta. 264; 18.III.1957. Mozambique Channel: IOAN (57.0

HL, 295+ TL); 25°28.3′S, 35°28.7′E; 1,260–1,230 m; *Vityaz'* cr. 17, sta. 2629; 23.XI.1988. CAS 66478 (4, 42.3–53.0 HL, 250–302 TL); 25°07′00″S, 36°49′24″E; 2,220–2,140 m; *Vityaz'* cr. 17, sta. 2639; 27.XI.1988. West Indian Ridge: IOAN (51.3 HL, 310 TL); 45°51′S, 41°54′E; 1,700 m; *Fiolent* cr. 5, tr. 121; 28.XI.1974. Madagascar Ridge: ZMMGU P-17619 (2, 38.6–46.7 HL, 240–280 TL); 32°12′S, 43°15.5′E; 1,460–1,470 m; *Prof. Mesiatzev* cr. 7, tr. 135; 14.VI.1979. ZMMGU P-17620 (2, 66.6–76.2 HL, 345+–400 TL); 32°19′S, 44°03′E; 1,210–1,240 m; *Zvezda Kryma* cr. 7, tr. 50; 21.I.1977. CAS 66463 (5, 21.1–71.0 HL, 95+–398 TL); Walters Shoals, 32°53′00″S, 45°11′30″E; 1,310–1,265 m; *Vityaz'* cr. 17, sta. 2672; 9.XII.1988. CAS 66471 (79.3 HL, 450 TL) and IOAN (3, 44.8–57.3 HL, 245+–341 TL); Walters Shoals, 31°59′00″S, 45°11′00″E; 1,950–2,050 m; *Vityaz'* cr. 17, sta. 2772; 25.XII.1988. CAS 66427 (2, 21.0–90.6 HL, 133–493 TL), CAS 66428 (53.6 HL, 303+ TL), and IOAN (3, 23.2–65.3 HL, 149+–334 TL); Walters Shoals, 34°41′48″S, 45°28′00″E; 1,518–1,750 m; *Vityaz'* cr. 17, sta. 2742; 20.XII.1988. IOAN (4, 27.8–65.0 HL, 183–353 TL); 32°45′S, 45°31′E; 1,760–1,700 m; *Vityaz'* cr. 17, sta. 2673; 9.XII.1988. Ninety East Ridge: ZMMGU P-17621 (2, 53.9–82.9 HL, 319–410+ TL) and CAS 71479 (2, 80–87.1 HL, 452+–447+ TL); 27°37.9′S, 87°49′E; *Prof. Mesiatzev* cr. 7, tr. 18; 26.III.1979. ZMMGU P-17622 (37.0 HL, 208+ TL) and CAS 71484 (3, 48.0–69.7 HL, 270+–382 TL); 29°38′S, 88°06′E; 1,300–1,500 m; *Prof. Mesiatzev* cr. 7, tr. 19; 26.III.1979. ZMMGU P-17624 (86.1 HL, 470 TL); 31°50′S, 87°22′E; 1,600–1,624 m; *Prof. Mesiatzev* cr. 7, tr. 21; 29.III.1979. ZMMGU P-17623 (72.4 HL, 430 TL); 30°22′S, 88°43.9′E; 1,320 m; *Prof. Mesiatzev* cr. 7, tr. 20; 28.III.1979. Broken Ridge (West Australian Ridge): IOAN (87.0 HL, 467+ TL); 31°08′S, 88°15′E; 1,380 m; *Ikthyandr* cr. 4, tr. 34. ZMMGU P-17625 (72.7 HL, 412 TL); 30°51′S, 93°46′E; 1,320–1,360 m; *Fiolent* cr. 7(9), tr. 40; 3.VIII.1977. ZMMGU P-17626 (88.0 HL, 505 TL); 28°46.8′S, 98°20′E; 1,270–1,320 m; *Fiolent* cr. 7(9), tr. 36; 25.VII.1977. ZMMGU P-17627 (90.0 HL, 525 TL); 31°09′S, 93°57′E; 1,050 m; *Fiolent* cr. 7(9), tr. 39; 3.VIII.1977. ZMMGU P-17628 (69.3 HL, 340+ TL); 30°58′S, 93°42.3′E; 1,060–1,100 m; *Fiolent* cr. 7(9), tr. 44; 4.VIII.1977. ZMMGU P-17629 (84.3 HL, 470 TL); 31°06′S, 93°49′E; 1,050 m; *Fiolent* cr. 9, tr. 45; 4.VIII.1977. ZMMGU P-17630 (77.1 HL, 430 TL); 25°35.7′S, 100°30′E; 1,624 m; *Prof. Mesiatzev* cr. 7, tr. 43; 19.IV.1979. IOAN (95.0 HL, 510 TL); 31°40′S, 95°37′E; 1,080–1,180 m; *Ikthyandr* cr. 4, tr. 39. IOAN (2, 83.0–85.0 HL, 485–503+ TL); 30°45′S, 94°16′E; 1,425 m; *Ikthyandr* cr. 4, tr. 50. IOAN (2, 83.0–88.0 HL, 460–510+ TL); 30°56′S, 94°42′E; 1,460 m; *Ikthyandr* cr. 4, tr. 51. IOAN (97.0 HL, 550+ TL); 28°38′S, 98°51′E; 1,280 m; *Ikthyandr* cr. 4, tr. 54; 22.III.1978. IOAN (68.9 HL, 390+ TL); 31°08′S, 93°49′E; 1,050 m; *Fiolent* cr. 7(9), tr. 38; 30.VIII.1977. IOAN (2, 46.0–52.0 HL, 260–290 TL); 28°28′S, 98°41′E; 1,260 m; *Fiolent* cr. 7(9), tr. 35; 24–25.VII.1977. IOAN (48.0 HL, 292 TL); 28°39′S, 98°36′E; 1,140 m; *Fiolent* cr. 7(9), tr. 30; 23.VII.1977. Great Australian Bight: ZMUC P-373096 (49.8 HL, 279 TL); 37°28′S, 138°58′E; 1,340–1,320 m; *Galathea* sta. 554; 5.XII.1951. ZMMGU P-17646 (4, 47.5–80.6 HL, 282–447+ TL); 33°48.3′S, 127°17′E; 1,080–1,100 m; *Dmitry Mendeleev* cr. 16, sta. 1373; 28.II.1976. NMV A6197 (81.9 HL, 421+ TL); Western Australia, 34°35.5′S, 121°19′E; 1,015–1,030 m.

South Atlantic Ocean. ZMMGU P-17631 (2, 62.5–72.5 HL, 360–320+ TL); off Namibia (South-West Africa); 1,000 m; *Poltava* tr. 425; 24.I.1970. ZMMGU P-15645 (50.8 HL, 286 TL); 32°41.4′S, 1°48.4′E; 1,060–1,125 m; *Prof. Mesiatzev* cr. 8, tr. 23; 3.IX.1979. ZMMGU P-15644 (57.8 HL, 305 TL); 33°17.7′S, 2°14′E; 923–1,115 m; *Prof. Mesiatzev* cr. 8, tr. 22; 22.IX.1979. IOAN (86.7 HL, 388+ TL); 35°28′S, 18°40′E; 990–1,000 m; *Fiolent* cr. 3, tr. 244; 28.X.1973. ZMMGU P-15656 (91.8 HL, 405+ TL); Discovery Seamount, 1250 m; *Prof. Mesiatzev* tr. 159. ZMMGU P-13879 (2, 67.8–85.6 HL, 330–445 TL); Rio Grande Plateau, 30°25′S, 35°09′W, 1,350 m; *Prof. Mesiatzev* cr. 2, tr. 12; 7.VII.1974; ZMMGU P-17644 (57.5 HL, 306 TL); Rio Grande Plateau; *Zvezda Kryma* cr. 3; ZMMGU P-17645 (92.1 HL, 502+ TL); 30°25′S, 34°04′W; 1,130–1,175 m; *Prof. Mesiatzev* cr. 1, tr. 23; 12.VII.1974. RUSI 10324 (50.4 HL, 254+ TL) and RUSI 10330 (72.5 HL, 400+ TL), no specific locality, but presumably off southern Africa.

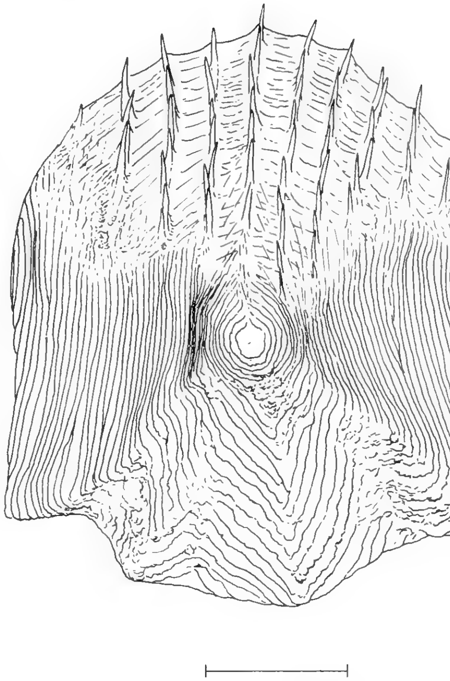

FIGURE 7. Scale from dorsum below interspace of first and second dorsal fins of *Coryphaenoides striaturus*. Scale bar equals 1.0 mm.

COUNTS AND MEASUREMENTS (see also Tables 1–3).—1D. II,8–10 (usually II,9); 1P. i18–i24 (usually i19–i22); V. 11–12 (1 spec. with 13); total GR-I (outer/inner) 7–11/12–16, GR-II 11–14/11–15; scales below 1D. 7.5–10, below mid-1D. 5–7.5, below 2D. usually 8–9, lat. l. usually 30–36; caeca 9–12 (in 15 spec. examined).

Total length 120+–550 mm; HL 21.0–97.0 mm. The following in percent HL: postrostral 70.4–76.5; 26.2–30.2; preoral 10.4–16.3; posterior nostril 3.0–7.1; internasal 19.7–28.3; interorbital 23.0–29.8; orbit 18.2–24.0; suborbital 10.5–14.7; postorbital 50.6–57.2; orbit-preop.

45.7–53.4; upper jaw 38.2–45.8; barbel 18.0–26.4; gill slit 15.5–22.9; V.-A. 42–74; isth.-A. 83–119; depth over A. origin 67–91; 1D.–2D. 63–106; 1D. height 81–109; 1P. 56–68; V. 65–97.

Description.—Body deep, compressed; in most specimens examined, depth at origin of first dorsal fin about equal to head length; depth about half head length over anal fin origin; body tapers gradually from about halfway along length of anal fin, then rather quickly to end of tail. Head rather robust, its greatest width about equal to postorbital length; its length about 5.5 into total length. A pronounced dip in dorsal profile over orbits, followed by a distinct hump over nape. Orbit small, diameter ¼–⅕ of head length, considerably smaller than snout length. Snout scarcely protruding, rather low, its length about equal to interorbital width or slightly greater; no stout scutelike scales at angles. Head ridges prominent, but not reinforced by stout scales. Mouth large, upper jaw extends posteriorly to below posterior edge of orbit, rictus extends to below midorbit. Chin barbel long and slender, about equal to orbit diameter. Suborbital with a rather broad, pronounced shelf. Preopercle margin slightly inclined posteriorly, forming a moderate, crenulated lobe at angle; interopercle scarcely protruding beyond lobe as a thin, narrow flap; preopercle ridge forming a distinct angle posteroventrally. Sensory pores on head small, inconspicuous; snout surfaces covered with numerous small, low sensory tubercles. Posterior nostrils small, 3.5 or more into orbit.

Gill membranes narrowly attached to isthmus, opercular opening extends forward to below posterior end of lower jaw, slightly behind vertical through hind edge of orbit; no free fold across isthmus. Gill rakers short, lappet-like, distally spinous; outer series of first arch not elongated. Gill filaments moderate in length, longest almost equal to diameter of eye lens.

Body scales (Fig. 7) relatively large, thin, and deciduous. Short, greatly reclined, needlelike spinules arranged in discrete parallel rows, about 9–14 rows, depending on size of fish, in specimens examined. Scales of head generally smaller and with spinules more erect than those on scales of body; scales on snout, suborbital, and underside of head, including mandibular ramus, very small.

Inner teeth of premaxillary in about 4 irregular diagonal rows forming a moderately wide band, flanked by a wide-spaced series of short, slender canine-like teeth. Mandibular teeth consist of a single row of small, erect, spaced teeth.

Second spinous ray of first dorsal fin compressed and armed with sharp, slender, reclined teeth along leading edges, its length about equal to head length; its origin somewhat behind vertical through pectoral and pelvic origins, which are about on same vertical. Outer pelvic ray prolonged into a filament that extends well posterior to anal fin origin, usually to base of 6th–11th anal ray. Anal fin well developed, its origin slightly behind vertical through base of first dorsal fin. Origin of second dorsal fin far posterior, about at distal tip of depressed first dorsal fin; rays scarcely developed over most of anterior half, relatively low over remainder.

Intestinal tract long, with at least 4 major bends. Pyloric caeca numerous, long, slender, directed posteriorly or posteroventrally. Stomach and intestinal tracts of several specimens of *C. striaturus* from Walters Shoals contained remains of bottom-living polychaetes (family Polynoidae), shrimps, gammarids, isopods, crabs, octopods, and cuttlefish (*Heteroteuthis dispar*) (contents determined by I. V. Nikitina and T. A. Gorelova, IOAN).

Color in alcohol overall dark brown to swarthy, although some small to medium-sized specimens of less than 30 cm TL pale to somewhat tawny. Outline of scale pockets in dark specimens quite prominent, but inconspicuous in pale specimens. Head areas, especially snout, mouth, gill covers, and undersides darker in all specimens; a thin, dark orbital rim. Operculum and branchiostegal membranes blackish; lips blackish, but gums pale to gray. Barbel light to medium brown, generally darker near base. Oral, branchial, and abdominal cavities black or dark gray, gill rakers dusky, gill filaments pale. Fins blackish in dark individuals, pale to dusky in pale individuals, although in these latter, outer pelvic ray, uppermost pectoral ray, and membrane between second spinous ray and first segmented ray dark.

Distribution (Fig. 5).—Widespread in southern hemisphere, from the Rio Grande Rise in the southeastern Atlantic, to the southern tip of South Africa and the Mozambique Channel, across the Indian Ocean (Madagascar Ridge, Ninety East Ridge, Broken Ridge) to Australia (Naturaliste Plateau, Western Australia, Victoria, New South Wales) and into the Pacific in the Tasman Sea and off New Zealand. Depth range 823–2,010 m, although most captured between 1,000–1,400 m.

SIZE.—To at least 55 cm TL and 97 mm HL.

REMARKS AND COMPARISONS.—*Coryphaenoides striaturus* had been poorly known and recorded from only two specimens (Iwamoto 1986) until our examination of Soviet collections from the Indian Ocean and others in Australian and New Zealand museums. The species is actually abundant and widespread in slope waters at depths of 1,000–1,400 m.

Coryphaenoides striaturus is very similar to *C. mediterraneus* (Giglioli, 1893) of the North Atlantic, but the two are immediately distinguished by differences in the snout squamation: *C. mediterraneus* is completely naked on the underside of snout and has lunate naked patches above; *C. striaturus* is completely scaled in those areas. Pelvic fin ray counts are somewhat higher in *C. mediterraneus,* 12–14 (compared with 11–12). *Coryphaenoides mediterraneus* also appears to grow considerably larger, attaining at least 670 mm TL and 129 mm HL (ZMMGU uncat. from off northwestern Africa, 22°40′N, 17°20′W, 1,370–1,430 m), compared with the maximum of 550 mm TL and 97 mm HL of specimens of *C. striaturus* we have examined.

Coryphaenoides murrayi is another closely related congener that has also been captured in the Indian Ocean, as well as off New Zealand, where a specimen of *C. striaturus* was identified by McCann and McKnight (1980) as *C. murrayi.* The almost completely naked snout of that species (but a characteristic row of small scales along leading edge) readily distinguishes specimens of *C. murrayi* from those of *C. striaturus. Coryphaenoides murrayi* also has a slightly larger and higher snout (length 29–31% HL, preoral length 11–17%), somewhat broader interorbital width (28–34%) and suborbital (13–17%).

McCann and McKnight (1980) erroneously identified a specimen of *C. striaturus* as *C. armatus,* but that species is readily distinguished by its naked underside of snout, premaxillary teeth broadly conical and in one or two rows, shorter barbel (11–15% HL), body scales with a slightly enlarged median spinule row, scales of head stouter, more adherent, sensory pores well developed and prominent, and snout more protruding and pointed.

Coryphaenoides murrayi Günther, 1878

(Fig. 8)

Coryphaenoides Murrayi Günther, 1878:26 (E of New Zealand, *Challenger* sta. 168, 1,100 fm [2,012 m]); Gilbert and Hubbs 1916:143. *Macrurus* (*Chalinurus*) *murrayi*: Günther 1887: 144, pl. 34A.

Chalinura murrayi: Goode and Bean 1896:412; Grey 1956: 170 (in part; records).

Coryphaenoides (*Chalinura*) *murrayi*: McCann and McKnight 1980:32, Figs. 14–16 (in part; specimen from sta. F126; the other specimen is *C. striaturus*).

DIAGNOSIS.—All ventral and most dorsal surfaces of snout naked; a naked strip behind leading horizontal edge of snout on each side; pelvic fin rays 11–12 (usually 12); premaxillary teeth in broad cardiform band about 6 rows wide, flanked by an outer row of enlarged, slender, widely spaced canines; mandibular teeth uniserial; snout 28–31% of HL, interorbital 28–34%, orbit 20–23%, barbel 23–26%, outer gill slit 20–22%.

MATERIAL EXAMINED.—BMNH 1887.12.7.113 (Holotype; 62.6 mm HL, 373 mm TL); off New Zealand; 2,012 m; *Challenger* sta. 168. ZMMGU P-17633 (2, 28.5–61 HL; 175–324 TL) and CAS 73238 (35.5 HL, 187 TL); 33°42′S, 110°53′E; 2,320–2,350 m; *Dmitry Mendeleev* cr. 16, sta. 1388. LACM 10978 (4, 26.5–48.0 HL, 110+–265 TL); W of Auckland Is., 51°07′S, 162°03′E; 1,665 m; 10-ft Blake trawl; 8.II.1965. NZOI (73 HL, 365 TL); N of North Is., New Zealand, 36°58.5′S, 176°41.0′E; 1,280–1,196 m. NMV A6793 (200 TL); 85 km S of Pt. Hicks, Victoria, Australia; 38°31.4′S, 149°21.1′E; 1,986–1,360 m.

COUNTS AND MEASUREMENTS (see also Tables 1–3).—1D. II,8–10; 1P. i18–i20; V. 10–12; total GR-I (outer/inner) 9–11/14–16, GR-II 14–16/12–16; scales below 1D. 9–11, below mid-1D. 6–7, below 2D. 9–11, lat.1. about 33.

Total length 110–373 mm; HL 26.5–62.6 mm. The following in percent HL: postrostral 73–75.4; snout 28.3–29.6; preoral 11–17; internasal 19.7–34.0; posterior nostril 4.6–5.3; interorbital 28.9–33.3; suborbital 13–17; postorbital 53–60; orbit-preop. 49–57; upper jaw 42–45; V.-A. 45–56; isth.-A. 87–100; body depth 79–84; depth over A. 63–71; 1D.-2D. 34–81; 1D. height 77–91; 1P. 60–71; V. 87–101.

DESCRIPTION (mostly of holotype, supplemented by other specimens).—Trunk rather short, distance isthmus to origin of anal fin usually less than length of head. Head relatively broad, greatest width almost two-thirds its length. Snout broad, blunt, subvertical. Orbits small, about 1.5 into snout, 1.5 into broad interorbital space, 5.0 into head length. Mouth large, almost

FIGURE 8. Photograph of holotype of *Coryphaenoides murrayi*, BMNH 1887.12.7.113 trawled by the *Challenger* east of New Zealand in 2,012 m. Photograph by Geert Brovad.

terminal; upper jaw extends to below posterior margin of pupil. Suborbital region wide, subvertical, weakly ridged. Barbel slender, slightly longer than orbit diameter. Anterior nostril free, septum separating anterior and posterior nostrils not forming a hood. Preopercle somewhat lobelike, its vertical margin steeply oblique, posteroventral margin crenulated, with tips of interopercle and subopercle slightly exposed beyond.

Gill openings wide, membranes of opposite sides join on isthmus below posterior margin of orbits, about at vertical of posterior end of maxillary. Gill rakers and filaments about as described for those of *C. striaturus.*

Head mostly covered with scales, but naked on lips, gill membranes, nasal fossae, underside of snout, and ventrally on anterior portion of suborbital; a single transverse row of small, embedded scales marking leading edge of snout, behind which is a narrow, naked strip; mandibles finely scaled posteriorly, but naked at anterior end. Head scales with low, small spinules arranged in 3–6 divergent rows; those on body with 5–8 weakly divergent to parallel rows.

Teeth prominent, an outer enlarged row (18 + 20 teeth in holotype) on premaxillary, medial to which is a broad, tapered band of villiform teeth, about 6 rows wide at symphysis, 2 wide posteriorly. Mandibular teeth in a single row (19 + 21 teeth in holotype).

Length first dorsal fin less than length of head; the first ray a short sharp spike, the second ray spinous, armed along leading edge with short, sharp, reclined teeth; fin origin well behind those of pectoral and pelvic fins; second dorsal poorly developed, its origin often indistinct and far posterior to first dorsal base. Pectoral fin about three-fifths of head length, origin about on same vertical as that of pelvic fin. Outer pelvic ray prolonged, about equal to head length in some specimens, extended posteriorly about to base of 6th–12th anal fin ray. Anal origin below hind end of first dorsal fin base.

Holotype with 9 long pyloric caeca, the longest caecum measuring about 27 mm. In small (110+ mm TL) specimen from LACM 10978, longest of 10 flaccid caeca measured only 3 mm. Swimbladder of holotype (already dissected out when examined in October 1986) had six thin retia, each tipped with a small peltate gas gland.

Color in alcohol light to medium brown; mouth bluish brown; gill cavity dark brown, lips and all rays yellowish brown to grayish brown.

DISTRIBUTION.—Western Indian Ocean to southern Australia, New Zealand, and Fiji, in depths of 1,196–2,350 m.

SIZE.—To at least 37 cm.

REMARKS AND COMPARISONS.—The Indian Ocean collections here reported are the first records from waters west of New Zealand. The type series apparently included five specimens, but only two were examined in BMNH, the putative holotype and a single 129+ mm TL paratype that represents a specimen of *C.* (*Lionurus*) *carapinus* (Goode and Bean, 1883). The holotype is in good condition, and salient diagnostic features are readily apparent. The illustration given in Günther (1887: pl. 34A) is excellent and accurate.

The species was confused in the past with *C. mediterraneus* (Giglioli, 1893), but that species has more pelvic fin rays (13–14, rarely 12), a longer barbel (27–37% HL), a slightly shorter snout (25–29% HL), and perhaps a slightly narrower band of premaxillary teeth (4–5 rows wide) (see Marshall 1973:593–595). The widespread *C. leptolepis* (Günther, 1887) is closely similar, but has somewhat fewer pelvic fin rays (9–11), shorter barbel (16–23% HL), and longer outer gill slit (23–28% HL). See the description of *C. striaturus* for a comparison with that species.

Coryphaenoides serrulatus Günther, 1878

Coryphaenoides serrulatus Günther, 1878:26 (type locality NE of New Zealand, *Challenger* sta. 169, 700 fathoms; 3 specimens). Whitley 1968:38. Ayling and Cox 1982:165. Last et al. 1983:243, Fig. 21.17 (description; Tasmania and Victoria, Australia). Paxton et al. 1989:326 (Australian records).

Macrurus (*Macrurus*) *serrulatus*: Günther, 1887:133, pl. XXX, Fig. A.

Macrourus serrulatus: Phillipps 1927:22.

Coryphaenoides (*Coryphaenoides*) *serrulatus*: McCann and McKnight 1980:37–39 (description; New Zealand records).

DIAGNOSIS.—Seven pelvic fin rays; large, prominent, spiny scutes at terminal and lateral angles of snout; spinules on body scales leaf-shaped or lanceolate; outer gill rakers relatively long and somewhat tablike; a well-developed chin barbel.

REMARKS.—We have been able to distinguish three populations of the species: one confined to oceanic areas of the Indian Ocean; another to the Australian Bight; and the last to the western South Pacific in the Tasman Sea and off New Zealand. The first population in the Indian Ocean is here recognized as a new subspecies and is readily distinguished from the nominate subspecies from the western Pacific. The population in the Australian Bight area appears to be intermediate in most of the characters that separate the populations on either side (Tables 5, 6; Fig. 9). It thus suggests that the Australian Bight may be an area of intergradation. The distributions of character states generally follow a steplike progression, with the Australian Bight population intermediate. In three characters (distance from orbit to angle of preopercle, interorbital width, and counts of gill rakers), however, the Australian Bight population is skewed away from the others—suggesting that perhaps it, too, deserves subspecific recognition. Our recognition of subspecies serves to highlight the geographical differences we found in the species. It is beyond the scope of the present work to pursue this problem further, but it is worthy of closer study by persons having access to material from along the entire continental slope of Australia.

Coryphaenoides serrulatus serrulatus Günther, 1878

(Figs. 9, 10)

DIAGNOSIS.—Outer pelvic ray 50–80% of HL, usually falling near or slightly beyond origin of anal fin, but seldom beyond base of fifth or sixth ray. Orbit diameter (30) 32–36 (37%) of HL, suborbital 11–13 (14)%, upper jaw (39) 40–44%, barbel (20) 21–26 (28, 30)%, orbit to angle of preopercle 37–45 (47)%. Inner gill rakers first arch (total) 11–13 (14).

MATERIAL EXAMINED.—**Pacific Ocean.** New Zealand: ZMMGU P-17634 (53.0 mm HL, 286+ mm TL); 43°35′S, 161°25′W; 670 m; *Kamenskoe* tr. 31; 16.VII.1978. ZMMGU P-17647 (61.5 HL, 353 TL); 43°04′S, 175°17′E; 810 m; *Poseidon* tr. 99 ("122E"). ZMMGU P-17648 (2, 45.3–68.0 HL, 242+–330+ TL); 43°05′S, 174°56′W; 900 m; *Poseidon* tr. 100

TABLE 5. Frequency Distributions of Selected Proportional Measurements for Three Populations of *Coryphaenoides serrulatus.*

Preoral length (% HL)

	12	13	14	15	16	17	18	$\bar{x}$	*SD*
Indian Ocean	2	7	10	13	12	3	—	14.74	1.2933
Australian Bight	1	3	3	7	7	2	2	15.20	1.5275
New Zealand	—	1	1	1	4	2	1	15.80	1.4757

Interorbital width (% HL)

	18	19	20	21	22	23	24	$\bar{x}$	SD
Indian Ocean	—	9	12	11	6	1	1	20.52	1.2192
Australian Bight	—	—	1	4	5	1	1	21.75	1.0553
New Zealand	1	7	8	5	1	—	—	19.91	0.9714

Greatest orbit diameter (% HL)

	27	28	29	30	31	32	33	34	35	36	37	$\bar{x}$	SD
Indian Ocean	4	2	10	10	11	8	3	—	—	—	—	30.21	1.6106
Australian Bight	—	—	—	—	—	4	7	6	6	3	1	34.00	1.3868
New Zealand	—	—	—	1	—	1	5	—	1	2	—	33.40	1.8379

Suborbital width (% HL)

	10	11	12	13	14	$\bar{x}$	SD
Indian Ocean	14	21	9	1	—	10.93	0.7804
Australian Bight	—	3	12	11	1	12.37	0.7415
New Zealand	—	2	6	1	—	11.89	0.6009

Barbel length (% HL)

	20	21	22	23	24	25	26	27	28	29	30	31	32	33	$\bar{x}$	SD
Indian Ocean	—	—	—	1	2	8	8	7	2	6	3	—	1	1	27.00	2.2243
Australian Bight	—	—	—	1	3	—	2	—	1	—	1	—	—	—	25.63	2.3867
New Zealand	1	2	1	1	1	3	—	—	—	—	—	—	—	—	22.89	1.9650

Orbit to angle of preopercle (% HL)

	37	38	39	40	41	42	43	44	45	46	47	48	$\bar{x}$	SD
Indian Ocean	—	—	—	—	2	6	13	13	10	1	—	1	43.67	1.3342
Australian Bight	3	3	6	3	3	5	—	1	1	—	—	—	40.04	2.1307
New Zealand	—	—	—	1	5	1	1	1	—	—	1	—	42.10	2.0790

Upper jaw length (% HL)

	39	40	41	42	43	44	45	46	$\bar{x}$	SD
Indian Ocean	—	1	1	11	16	10	6	1	43.20	1.2040
Australian Bight	1	2	5	6	5	2	—	—	41.86	1.3148
New Zealand	1	3	6	—	—	—	—	—	40.50	0.7071

("87E"). ZMMGU P-17649 (86.3 HL, 445+ TL), *Poseidon* (no trawl number) ("173E"). ZMMGU P-17650 (90.1 HL, 440+ TL); *Poseidon* (no trawl number) ("176E"). ZMMGU P-17651 (70.7 HL, 386 TL); 42°51′S, 177°49′W; 1,050 m; *Poseidon* tr. 97; 8.II.1978. ZMMGU P-17652 (59.5 HL, 340 TL); 52°33′S, 171°35′E; 540 m; *Poseidon* tr. 155 ("92E"). ZMMGU P-17635 (2, 60.5–63.1 HL, 342–360 TL); 43°01′S, 174°22′E; 850–860 m; *Dmitry Mendeleev* cr. 16, sta. 1268. Australia: AMS I.24054-013 (318 TL); New South Wales off Kiama, 34°39′S, 151°18′E; 869 m; 1983.

Indian Ocean. Great Australian Bight: ZMMGU P-17653 (24, 68.2–82.1 HL, 235+–449 TL); 33°48′S, 127°17′E; 1,080–1,100 m; *Dmitry Mendeleev* cr. 16, sta. 1373; 28.II.1976. NMV A.3400 (3, 61.5–69.0 HL, 341+–370 TL); off Portland, Victoria, 38°38′S, 141°04′E; 990–1,100 m. Tasmania: AMS I.25477-001 (69.0 HL, 365 TL); W coast off Pieman R.

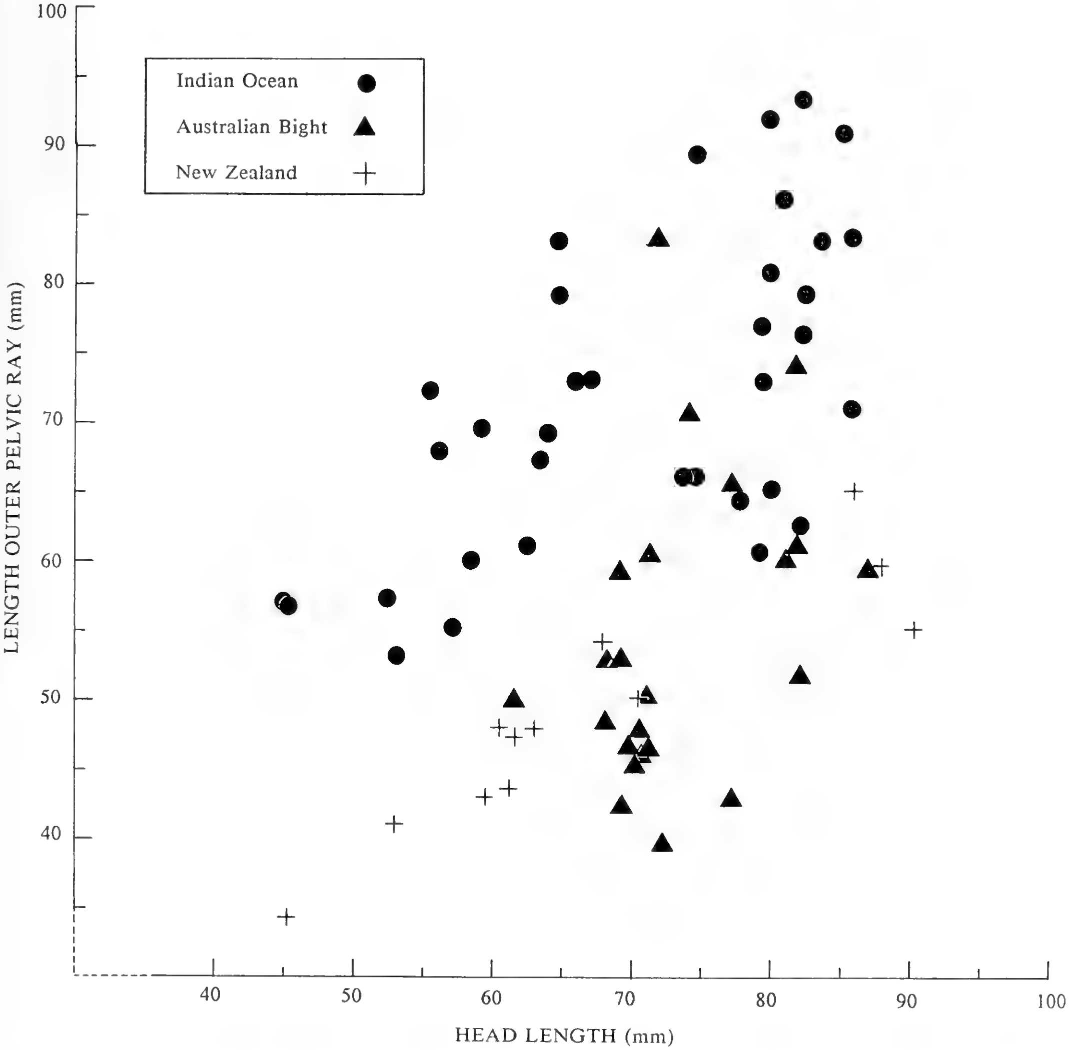

FIGURE 9. Scatter diagram showing relationship of length of outer pelvic fin ray to head length in three populations of *Coryphaenoides serrulatus*.

DISTRIBUTION (Fig. 10).—Off New Zealand, in the Tasman Sea off New South Wales, Australia, in the Indian Ocean off Tasmania and the Great Australian Bight, in depths of 540–1,100 m.

REMARKS AND COMPARISONS.—Specimens from New Zealand and the Tasman Sea tended to be more uniformly brown and paler than the darker, violet-hued subspecies from the Indian Ocean, the scale pockets and the suborbital ridge were not as prominently delineated, and the scales were somewhat more adherent. Most specimens from the Australian Bight were in poor condition, and several important characters (such as barbel length and length outer pelvic ray) could not be properly measured. The consequence of this is apparent in the wide dispersion of points in the scatter diagram (Fig. 9). When evaluating this diagram, one should consider the maximal proportional lengths plotted for each population as having greater import, because the shorter lengths usually represent measurements of broken fin rays. Bearing this in mind, the New Zealand specimens appear to have a distinctly shorter outer pelvic fin ray.

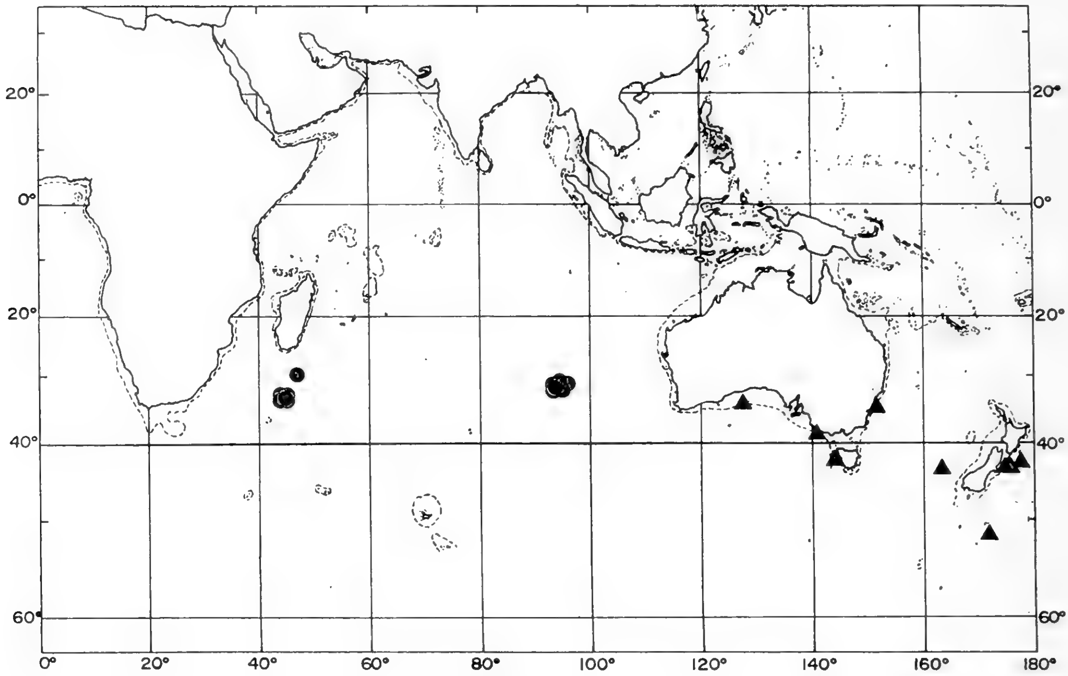

FIGURE 10. Catches of *Coryphaenoides serrulatus oceanus* (circles) and *C. s. serrulatus* (triangles).

Coryphaenoides serrulatus oceanus new subspecies

(Figs. 9–11)

Coryphaenoides serrulatus: Shcherbachev 1987:41 (listed from Indian Ocean: Madagascar Ridge and West Australian Ridge [=Broken Ridge]; 870–1,250 m).

DIAGNOSIS.—Outer pelvic fin ray 85–120% HL, extends well beyond anal fin origin, usually to about 8th–16th anal ray. Orbit diameter (27) 29–33% of HL, suborbital 10–12 (13)%, upper jaw 42–45 (46)%, barbel (23) 25–30%, orbit to angle of preopercle (41) 42–45 (48)%. Inner gill rakers on first arch (total) (12) 13–14 (15).

MATERIAL EXAMINED.—Holotype: ZIN 49797 (88.5 mm HL, 482+ mm TL); Walters Shoals, 33°01′S, 44°30′E; 970–980 m; *Vityaz*' cr. 17, sta. 2706; 15.XII.1988. Paratypes: Broken Ridge (West Australian Ridge): ZMMGU P-17636 (57.1 mm HL, 358 mm TL); 31°10′S, 93°56′E; 1,120–1,250 m; *Fiolent* cr. 7(9), tr. 39; 3.VIII.1977. ZMMGU P-17637 (2, 52.5–77 HL, 308–437+ TL); 31°09′S, 93°49′E; 1,050 m; *Fiolent* cr. 7(9), tr. 38; 3.VIII.1977. ZMMGU P-17639 (83.6 HL, 465 TL); 31°32.5′S, 95°16′E; 1,050 m; *Zvezda Kryma* cr. 6, tr. 133; 19.IX.1976. ZMMGU P-17640 (5, 53.2–67.0 HL, 305–391 TL); 30°59′S, 93°35′E; 1,050 m; *Fiolent* cr. 7(9), tr. 43; 4.VIII.1977. ZMMGU P-17641 (52.4 HL, 371 TL); 31°06′S, 93°49′E; 1,050 m; *Fiolent* cr. 7(9), tr. 45; 4.VIII.1977. IOAN (6, 53.1–74 HL, 292–385 TL); 31°03′S, 93°08′E; 1,049–1,064 m; *Prof. Mesiatzev* cr. 7, tr. 26; 2.IV.1979. IOAN (4, 75.7–85.4 HL, 407–477 TL); 31°04′S, 95°38′E; 1,000–1,120 m; *Ikthyandr* cr. 4, tr. 38. IOAN (2, 78.5–84.6 HL, 422–485 TL); 30°59′S, 93°35.7′E; *Ikthyandr* cr. 4, tr. 48; 17.III.1978. IOAN (2, 78.4–82.5 HL, 425–480 TL); 30°45′S, 94°16′E; 1,255 m; *Ikthyandr* cr. 4, tr. 49. Madagascar Ridge: ZMMGU P-17638 (55.6 HL, 337 TL); 33°08′S, 44°15′E; 870–888 m; *Fiolent* cr. 11, tr. 18; 14.IV.1979. ZMMGU P-17654 (81.0 HL, 480+ TL); 30°02.8′S, 46°02.5′E; 960–1,010 m; *Zvezda Kryma* cr. 1(6), tr. 13; 2.VII.1976. ZMMGU P-17655 (81.7 HL, 420 TL); 32°19′S, 44°03′E; 1,210–1,240 m; *Zvezda Kryma* cr. 7, tr. 50; 22.I.1977. IOAN (2, 47.5–72.2 HL, 266–392 TL) and CAS 66468 (7, 57.6–71.0 HL, 332–415 TL); 33°01.2′S, 44°36.8′E; 1,010 m; *Vityaz*' cr. 17, sta. 2668; 8.XII.1988. IOAN (2, 71.0–88.5 HL, 402–480+ TL) and CAS 66432 (80.2 HL, 450 TL); 33°01′00″S, 44°30′00″E; 970–980 m; *Vityaz*' cr. 17, sta. 2706; 15.XII.1988. IOAN (2, 28.8–50.5 HL, 158+–294 TL) and CAS 66464 (56.1 HL, 282+ TL); Walters Shoals, 33°16′42″S, 43°41′00″E; 920–900 m; *Vityaz*' cr. 17, sta. 2764; 24.XII.1988. IOAN (38.6 HL, 234 TL) and CAS 66481 (45.3 HL, 290 TL); Walters Shoals, 33°01′48″S, 44°23′36″E; 910–925 m; *Vityaz*' cr. 17, sta. 2707; 15.XII.1988. IOAN (20, 35.3–65.8 HL, 213–388 TL); Walters Shoals; *Vityaz*' cr. 17, sta. 2765; 24.XII.1988.

COUNTS AND MEASUREMENTS (see also Tables 5, 6).—D. II,9–11 + 112–119; 1P. i18–i24 (usually i19–i22); V. 7; total GR-I (outer/inner) 8–11/12–15 (usually 13 or 14), GR-II 12–15/10–15 (usually 13 or 14); scales below mid-1D. 5.5–7.5, below 2D. 7–10, lat.l. 35–41; caeca 14–23.

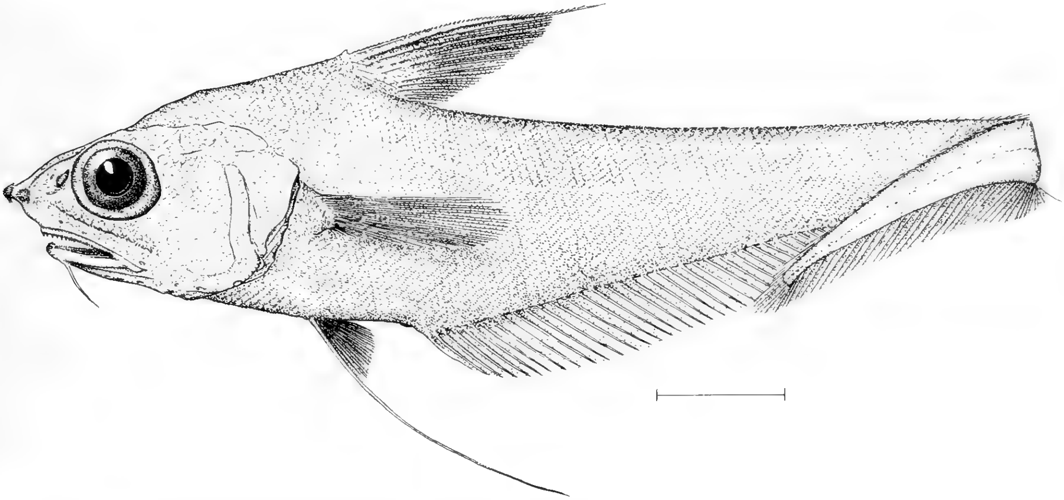

FIGURE 11. *Coryphaenoides serrulatus oceanus* n. subsp. CAS 66464 (56.1 mm HL, 282+ mm TL) collected by the *Vityaz'* from Walters Shoals in the western Indian Ocean, 920–900 m. Scale bar equals 25 mm.

Total length 158+–485 mm, HL 26.8–88.5 mm. The following in percent HL: postrostral 72.4–76.2; snout 26.3–30.5; preoral 11.5–16.8 (usually 13–15); internasal 16.2–18.8; posterior nostril 6.2–9.2; interorbital 18.6–24.0 (usually 19–22); orbit 26.8–33.0 (usually 30–32); suborbital 9.5–12.1; postorbital 43.0–49.5; orbit-preop. 40.9–47.4 (usually 42–45); upper jaw 40.5–46.4; barbel 23.3–33.4 (usually 25–29); gill slit 16.1–22.7; pre-A. 148–186; V.-A. 44–67; isth.-A. 86–116; body depth 74–108; 1D.–2D. 57–107; 1D. 76–102; 1P. 50–74; V. 77–133 (usually more than 100).

DESCRIPTION.—Head short, compressed and deep, width about equal to distance between snout tip and hind edge of orbit; length about 6 in total length. Body deep, compressed, width across pectoral bases about 2 in greatest depth (under first dorsal origin); body tapers rapidly behind anal origin. Orbits large, round to somewhat oval in outline, diameter more than snout, about 1.4–1.5 into postorbital, upper anterior margin flush with dorsal profile. Snout rather short but prominently pointed, its tip and lateral angles accentuated by large, spiny, tuberculous scales; width across lateral angles of snout more than inter-

TABLE 6. Gill Raker Counts for Three Populations of *Coryphaenoides serrulatus*.

	Total gill rakers, first arch									
	Outer series					Inner series				
	7	8	9	10	11	11	12	13	14	15
Indian Ocean	—	9	20	14	3	—	2	12	30	2
Australian Bight	5	16	17	—	—	2	14	11	1	—
New Zealand	2	6	—	2	—	—	1	9	—	—

	Total gill rakers, second arch											
	Outer series						Inner series					
	10	11	12	13	14	15	10	11	12	13	14	15
Indian Ocean	—	—	9	11	30	10	1	1	3	18	14	2
Australian Bight	2	3	9	11	3	—	1	8	14	4	1	—
New Zealand	—	—	1	8	1	—	—	—	8	2	—	—

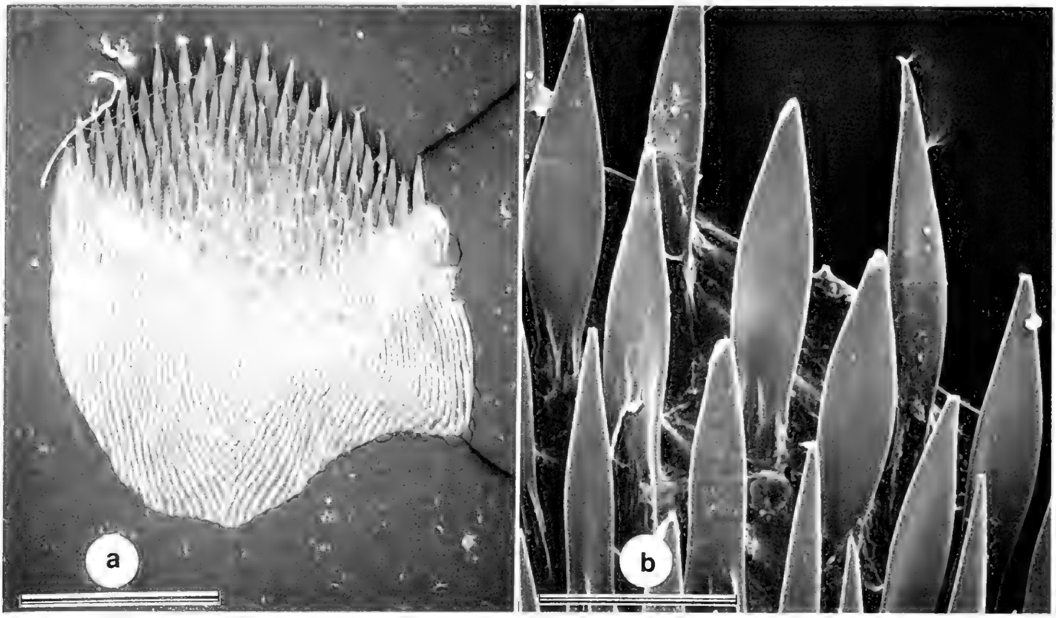

FIGURE 12. Scale from dorsum below interspace between first and second dorsal fins of *Coryphaenoides serrulatus oceanus* (CAS 66481). Scale bar in (*a*) equals 1.0 mm; that in (*b*) equals 0.15 mm.

orbital width, but least width across lateral nasal ridges (internasal width) much less than interorbital width. Mouth large, subterminal, upper jaw extends posteriorly just short of vertical through hind edge of orbit, rictus to below midorbit or beyond. Barbel very slender, tapering to hair-fine tip. Plane of suborbital almost vertical, but area traversed by a stout ridge extending from below anterior nostril to below hind border of orbit. Preopercle margin slightly lobed posteroventrally, with a slight inflection above angle, the ridge closely paralleling free edge. Interopercle rather broad, its tip exposed beyond preopercle. Cephalic sensory pores well developed, especially along ventral margin of suborbital, margin of preopercle, and on mandibular rami, and to a lesser degree along postorbital ridge and over interorbital.

Gill openings wide, extending forward to below end of maxillary; a narrow free posterior fold across isthmus. Outer gill slit moderately restricted; outer rakers on first arch numerous and developed into flat, tablike structures, the free distal tips bristling with small spinules, inner rakers somewhat more ridgelike, with proportionately less free margins; gill filaments relatively short, their greatest free length about equal to or more than length posterior nostril.

Scales on body (Fig. 12) large and densely covered with small, sharp, greatly reclined lanceolate spinules. Head scales more variable, those ventrally and over surfaces of interorbital, snout, and suborbital smaller; the large terminal and lateral snout scutes bluntly conical with multiple rows of stout spines radiating from apex; gap between these scutes and between lateral scutes and suborbital ridge covered with small, loose scales; suborbital ridge marked with a row of strong, thickened, coarsely spined scales; a second or third row of smaller, thickened scales above, forming ventral edge of orbit. Underside of snout, suborbital, and lower jaw covered with small, rather deciduous scales, the loss of which may suggest nakedness in these areas, especially under tip of snout.

Teeth in premaxillary in a moderately wide band, the inner teeth small and flanked externally by large, recurved conical teeth having flanged, arrowhead-shaped tips. Mandibular teeth slightly smaller than outer teeth of premaxillary and aligned in a uniform single row except at symphysis, where they stand in two rows.

Dorsal fin with a strong, laterally compressed spine, the leading edge armed with small, sharp, tightly spaced, imbricate teeth, the spine terminating in a short filament. Outer pelvic ray slen-

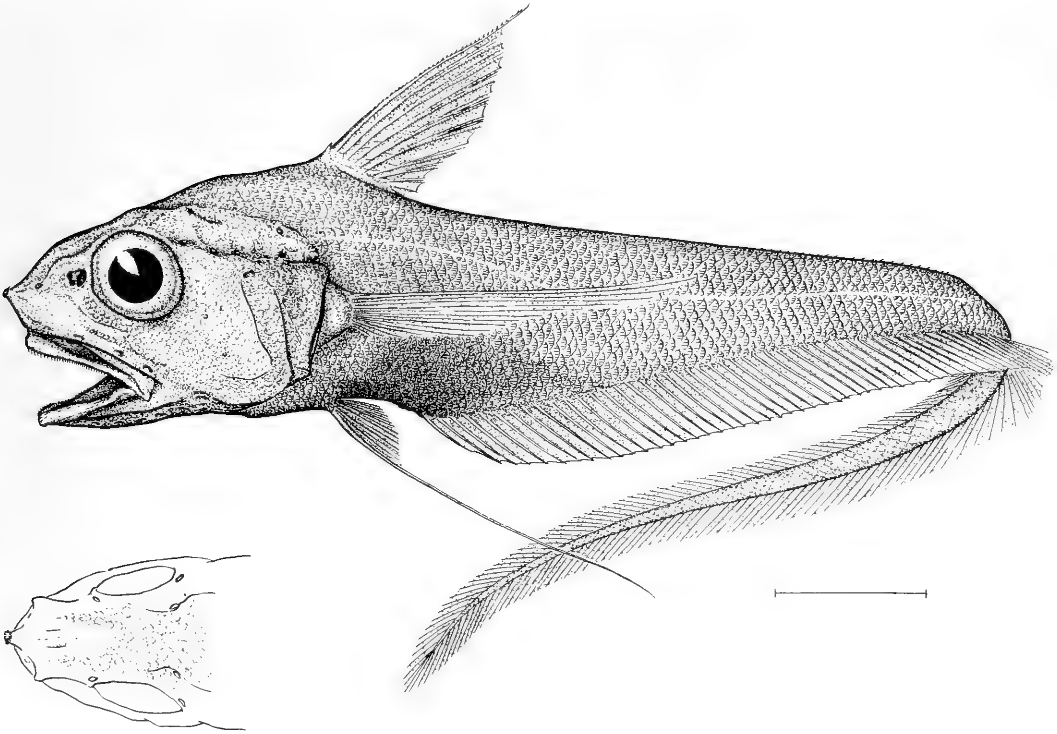

FIGURE 13. *Coryphaenoides mcmillani* n. sp. Holotype, NMV A.6794 (54.0 mm HL, 285+ mm TL), from off New South Wales, Australia, in 1,009–817 m. Scale bar equals 25 mm. Fins and scales partially reconstructed.

der, produced into a hair-fine filamentous tip that, if complete, extends beyond base of 10th anal ray. Pelvic and pectoral origins about on same vertical, slightly in front of first dorsal origin. Anal origin slightly behind vertical of hind end of first dorsal fin base. Origin of rudimentary second dorsal fin far posterior, often obscure.

Vent encircled by a black margin, which is broadened anteriorly and highly suggestive of a luminescent organ, but structure not histologically examined. Pyloric caeca long, slender, about equal to orbit diameter, directed posteriorly and ventrally; 14–23 in 27 specimens. Five or 6 retia mirabilia in 3 specimens. Stomach and intestinal tract of 38 specimens examined during *Vityaz'* cruise 17 contained only pelagic animals (determined by T. A. Gorelova, IOAN): decapods, amphipods, cephalopods, and mesopelagic fishes (*Argyropelecus* sp., *Stomias* sp., *Maurolicus muelleri*).

Color in alcohol medium gray-brown with a distinct underlying violet hue overall; surface over abdominal and gill cavities bluish to blackish. Gill membranes, snout, and underside of head often irregularly peppered with small melanophores, giving a dirty appearance; underside of snout above symphysis of jaws often blackish. Lips, fins (except second dorsal and basal portion of outer pelvic ray), rim of orbit, and anterior edge of posterior nostril blackish, the last two areas variably pigmented, however, Linings of mouth and gill cavity black; gill arches and rakers dusky.

DISTRIBUTION.—Indian Ocean, from Walters Shoals south of Madagascar to Broken Ridge (West Australian Ridge) (Fig. 10), in depths of 870–1,255 m.

SIZE.—To more than 48 cm.

ETYMOLOGY.—The subspecific name alludes to the oceanic distribution of the subspecies, compared with the more continental distribution of the nominate subspecies.

Coryphaenoides mcmillani new species

(Figs. 13–15)

TABLE 7. Selected Measurements of 13 Specimens of *Coryphaenoides mcmillani*. Asterisk indicates holotype.

	ZMMGU 17642	NMNZ J10/9/84	NMNZ J7/40/83	CAS 73236	NMNZ J10/9/84	NMV A.4277	NMNZ J10/9/84	NMNZ J10/9/84	NMV A.6794*	NMNZ J7/40/83	NMNZ A1/57/83	NMNZ J7/40/83	NMV A.6893
TL (mm)	207+	248	221	225+	223+	233	334	243+	285+	302+	325	320	273+
HL (mm)	40.5	41.6	41.8	44.6	49.0	50.7	51.2	53.8	54.0	55.2	55.9	56.1	56.4
The following in percent of head length													
Snout	28.4	30.0	29.4	28.7	30.4	31.2	29.1	29.7	29.8	28.1	28.1	29.8	29.1
Preoral	13.8	13.9	12.9	12.8	13.5	12.6	13.7	12.8	12.2	12.5	11.8	13.9	11.9
Internas.	20.0	22.8	20.3	23.1	22.7	20.7	22.3	21.0	22.0	21.9	21.3	20.1	21.5
Interorb.	25.7	26.4	26.3	28.0	28.8	26.4	30.3	28.6	26.7	27.2	27.7	26.4	26.8
Orbit	30.1	27.9	29.9	30.5	27.6	27.8	27.0	27.6	27.2	29.5	28.8	27.5	26.6
Suborb.	11.4	12.5	12.7	12.3	12.7	10.7	12.9	12.2	12.4	12.1	11.4	11.8	11.2
Postorb.	47.4	47.4	45.5	47.3	47.6	47.1	47.7	47.3	47.8	46.9	48.3	47.1	47.9
Orb-preop.	43.5	45.9	41.4	43.9	45.1	49.2	45.5	43.6	45.4	44.0	44.4	45.6	44.1
Up. jaw	49.9	47.1	46.2	49.8	47.3	46.4	46.3	46.4	47.4	46.6	47.4	48.1	46.3
Gill slit	25.2	22.8	23.2	26.5	22.7	23.3	21.5	21.0	20.4	24.1	22.9	23.2	22.7

DIAGNOSIS.—Snout naked except for small spiny scutes at terminal and lateral angles; head pores prominent; orbit 26.6–30.5% HL, internasal 20.0–23.1%, interorbital 25.7–30.3%, suborbital 10.7–12.2%; barbel rudimentary; pelvic fin rays 8 (rarely 9), length outer ray usually more than 100% HL; pectoral fin rays i17–i20 (rarely i16), length usually about 70–90% HL; inner gill rakers on first arch 16–18 (rarely 19); spinules on body scales thin, needlelike.

MATERIAL EXAMINED.—Holotype: NMV A6794 (♂, 54.0 mm HL, 285+ mm TL); Australia, New South Wales, 56 km ENE of Nowra, 34°44′S, 151°14.3′E; 1,009–817 m. Paratypes: Australia. NMV A4277 (50.7 HL, 233 TL); South Australia off Kingston, 37°36′S, 139°00′E; 1,060 m. NMV A6893 (56.4 HL, 273+ TL); Tasmania, 41 km NE of Cape Tourville, 41°54.5′S, 148°42.6′E; 1,273–119 m. **Central and western Indian Ocean.** ZMMGU P-17642 (40.5 HL, 207+ TL); Broken Ridge: West Australian Ridge, 30°50′S, 92°29′E; 1,400 m; *Prof. Mesiatzev* cr. 7, tr. 24; 1.IV.1979. CAS 73236 (44.6 HL, 225+ TL); Walters Shoals, 33°01.6′S, 44°49.2′E; 1,100–1,090 m, *Vityaz*' cr. 17, sta. 2670; 8–9.XII.1988. IOAN (32+ HL, 166+ TL); 32°53′S, 45°11′05″E; 1,210–1,265 m; *Vityaz*' cr. 17; 9.XII.1988. **South Atlantic.** ZMMGU P-17643 (34 HL, 180 TL) and ZMMGU P-14363 (59.1 HL, 338+ TL); off Cape Point, 35°48′S, 19°16′E; 950–1,000 m; *Fiolent* cr. 5, tr. 82; 8.XI.1974. IOAN (45 HL, 261 TL); Whale Ridge, 31°46′S, 02°10′E; 110 m; *Ikthyandr* tr. 72; 15.III.1987. **New Zealand.** NMNZ P.26958 (3, 41.8–56.1 HL, 221–320 TL); Challenger Plateau, 42°58.6′S, 168°21.9; 1,142–1,147 m; bottom trawl; sta. J7/40/83; 9.VII.1983. NMNZ P.26957 (55.9 HL, 325 TL); Challenger Plateau, 41°25.3′S, 168°05.2′E; 1,138–1,141 m; bottom trawl; sta. A1/57/83. NMNZ P.26956 (4, 41.6–53.8 HL, 223+–334 TL); Chatham Rise, 44°49.8′S, 172°48.5′E; 1,180–1,184 m; sta. J10/9/84; 9.VI.1984. NMNZ P.26959 (55.1 HL, 338 TL); Chatham Rise, 44°52.1′S, 175°24.4′E; 1,068–1,085 m; sta. J9/7/85; 7.V.1985.

COUNTS AND MEASUREMENTS (see also Table 7).—D. II,9–11 + about 125; V. 8 (rarely 9); scales below 1D. 7.5–9.0; below mid-1D. 4.5–6.5 (usually 5–6); below 2D. 6.5–9.5; lat.1. 31–36 (usually 31–34); caeca 9–10.

Total length 180–338 mm, HL about 34–56.1 mm. The following in percent HL: postrostral 72.2–74.6; posterior nostril 6.4–7.8; pre-A. 135–159; V.-A. 30–53; isth.-A. 65–93; body depth 68–85; 1D.–2D. 23–58; 1D. 73–94; 1P. 63–99; V. about 125–146.

DESCRIPTION.—Head short, moderately compressed, width slightly more than postorbital, length about 5–6 in total length. Body width across pectoral bases about 2 in greatest depth; dorsal profile tapers sharply below first dorsal, then levels off to end of tail. Snout bluntly pointed, scarcely produced beyond the large mouth, its

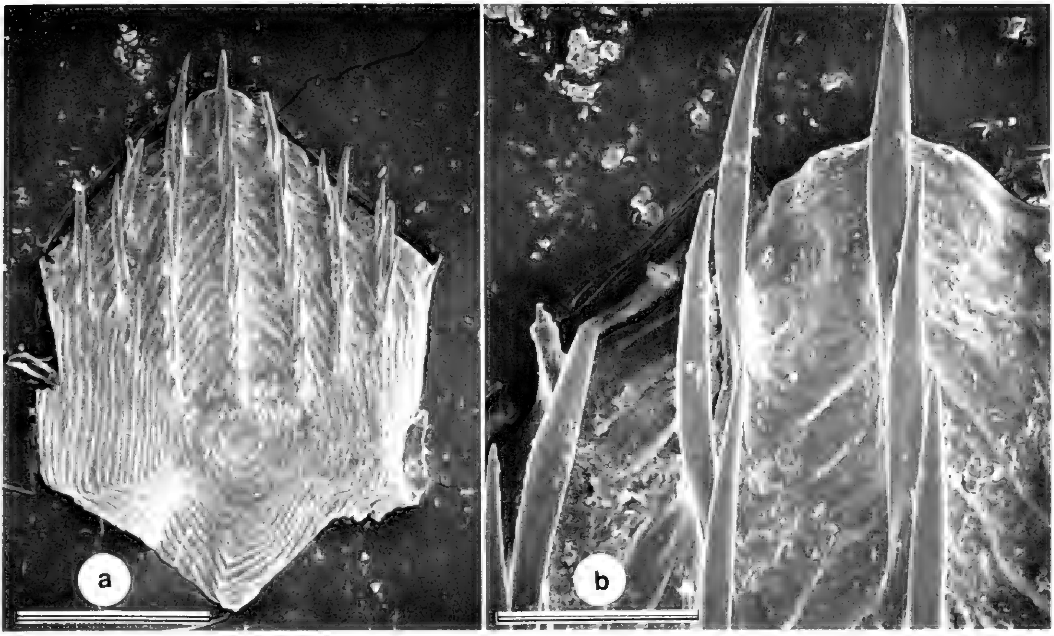

FIGURE 14. Scale from dorsum below interspace between first and second dorsal fins of *Coryphaenoides mcmillani* (NMNZ J10/9/87). Scale bar in (*a*) equals 0.75 mm; that in (*b*) equals 0.15 mm.

width across lateral angles about equal to least interorbital width, tipped with a small, buttonlike spiny scute, the apex of which is directed anterodorsally; smaller scutes at each lateral angle. Orbit round to somewhat oblate, the anterodorsal margin scarcely if at all entering dorsal profile; its greatest diameter about equal to least interorbital width. Mouth large, upper jaw extends posteriorly to below hind edge of orbit, rictus to midorbit or beyond. Barbel a tiny stump, scarcely developed.

Suborbital with a narrow, almost vertical shelf, least width about half of orbit diameter, half of interorbital width. Preopercle margin slightly lobed posteroventrally, the preopercle ridge notably more angular. Interopercle narrow, its posterior tip minimally exposed beyond preopercle margin. Cephalic sensory pores large, well developed, particularly on mandibular ramus, along lower margin of subopercle, and along dorsal edge of postorbital ridge.

Gill openings wide, extending forward to under posterior end of maxillary; gill membranes narrowly attached to isthmus, with a broad free fold. Outer gill slit moderately restricted, the opening slightly less than internasal width. Outer series of rakers on first arch relatively long, flat, from broadly triangular ventrally on arch to saber-shaped in dorsalmost ceratobranchial rakers; inner margin beset with small sharp spines. Rakers on inner series of first arch and in other arches generally shaped somewhat like short, laterally flattened, wide-based clubs, the distal margin of the "clubhead" bristling with sharp needlelike spines. Gill filaments short, their length about equal to length of longest outer gill rakers.

Scales highly deciduous, most relatively small, those on body below anterior end of second dorsal fin covered with extremely thin, needlelike, strongly recurved spinules arranged in approximately 8–10 almost parallel rows (Fig. 14). The terminal and lateral snout scutes rather small, each isolated around a broad region of naked skin, the naked surfaces of snout extending dorsad along broad avenues on medial sides of internasal ridges, interrupted on each side by a narrow peninsula of small scales projecting forward along either side of supranarial ridge. Lateroventrally the naked surfaces extend below suborbital shelf to near posterior end of upper jaw, although a narrow wedge of small scales extends forward to below nostrils. Mandibular

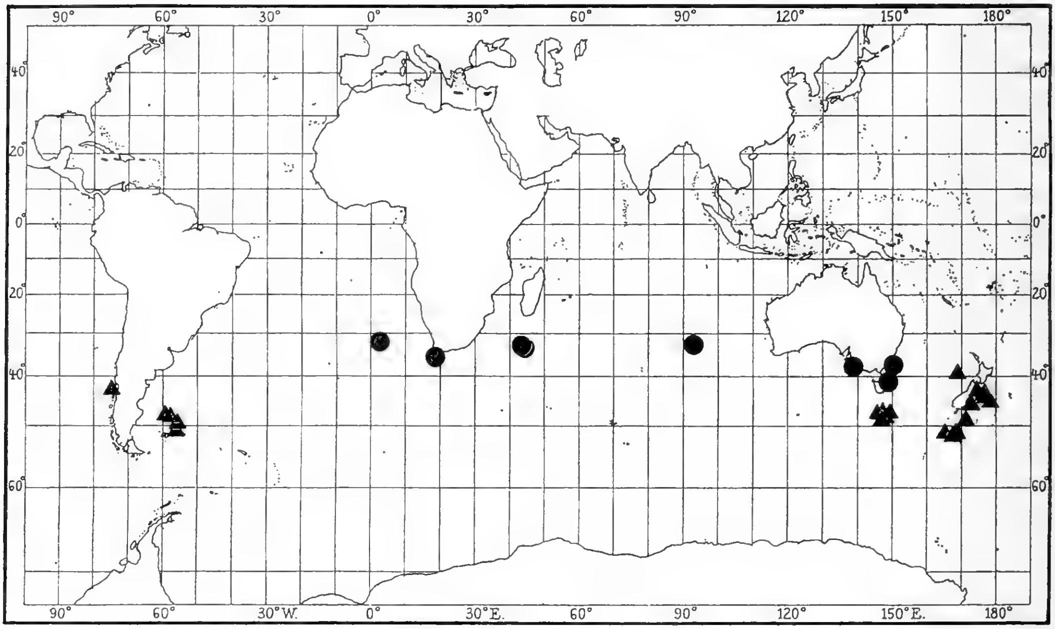

FIGURE 15. Catches of *Coryphaenoides mcmillani* (circles) and *C. subserrulatus* (triangles). Southwest Atlantic plots of *C. subserrulatus* after Trunov and Konstantinov (1985).

rami have single file of small, loose scales. Scales along suborbital shelf small, not especially stout, only 1 or 2 rows deep.

Teeth in premaxillary in a narrow band with a close-set outer series of slightly enlarged teeth. Mandibular teeth small, in an irregular row laterally, in a narrow cluster at symphysis. A distinct gap at symphysis separating left and right tooth bands of both jaws.

First dorsal fin with a sharp spikelike first spinous ray followed by a long compressed ray armed with a sharp ridge of small serrations along leading edge; fin base rather steeply inclined; fin origin about on same vertical as that of pectoral fin, or slightly behind. Second dorsal fin rudimentary over anterior half or so; origin difficult to determine in some specimens because anteriormost rays rudimentary. Pectoral fins long, when intact almost as long as head; upper middle rays longest, distally hairlike and easily broken. Pelvic fin with an elongated outer ray that exceeds length of head in almost all specimens (those shorter probably a result of having been broken off); fin origin under hind edge of operculum, slightly ahead of pectoral origin. Anal fin well developed, although distal tips of rays weak and easily broken; origin under posterior edge of first dorsal fin or somewhat more posterior.

Vent situated immediately anterior to anal fin origin; no trace of a luminescent organ in CAS paratype, although abdomen between pelvic and anal fins black. Peritoneum ivory but overlain by black pigmentation. Pyloric caeca short, fat, directed generally ventrally; 9, 9, 10, and 10 counted in 4 paratypes. Intestinal bending pattern simple in a NMNZ specimen (41.6 HL), with two major bends between pylorus and anus, and a small "S" bend near rectal end. A 55.2 mm HL female (NMNZ) had large ovaries with well-developed eggs ranging 0.6–1.2 mm diameter. Swim bladder of ZMMGU P-14363 (♀, 59.1 mm HL) well developed; five slender short retia attached to small, bean-shaped gas glands. Stomach in this specimen packed with shrimplike crustaceans.

Color in alcohol brownish gray to swarthy overall, with pronounced blackish area over abdomen behind pelvic fins and extending posteriorly to over first several anal fin rays. Margins of scale pockets darkly marked in denuded specimens. Operculum and branchiostegal membranes black. Most of head membranes blackish and thinly covered with small melanophores. Jaws dark gray to blackish. A narrow black orbital ring. Fins dusky to blackish, first dorsal and pelvic fins generally darkest. Linings of mouth and gill cavities black. Gill arches and rakers dark gray.

DISTRIBUTION (Fig. 15).—Whale Ridge and tip of South Africa in Atlantic, west through southern Indian Ocean and South Pacific to New Zealand. Depth range 950–1,400 m.

ETYMOLOGY.—Named after Peter McMillan of the Fishery Research Agency in Wellington, New Zealand, who independently recognized the species as new and was planning to describe it as such, but kindly deferred to us and allowed us to study his material.

REMARKS AND COMPARISONS.—*Coryphaenoides mcmillani* is very similar to *C. subserrulatus* and was mistakenly identified as that species by Shcherbachev (1987). On initial examination, the first specimen we examined from Broken Ridge appeared to be simply a darker, damaged representative of *C. subserrulatus*. Closer study, however, revealed pronounced differences in lengths and counts of pelvic and pectoral fin rays, and the size of several head parts. Subsequently, two badly damaged specimens were discovered in IOAN, and a fourth specimen was taken by the *Vityaz'* off Walters Shoals in 1988. In November 1989, one of us (TI) discovered three relatively undamaged southern Australian specimens in the collections of the NMV, and Peter McMillan had nine New Zealand representatives. Surprisingly, no specimens were found in the extensive collections of the Australian Museum in Sydney.

The new species shares with *C. subserrulatus* a similar head and body morphology, with a large subterminal mouth, short, blunt snout tipped with a prominent terminal scute that is directed anterodorsally, high gill raker counts, relatively long outer gill rakers on first arch, elongated outer pelvic fin, rudimentary barbel, and similar dentition. The new species differs notably in lacking the elongated pectoral fin ray of *C. subserrulatus*, in having needlelike spinules on body scales (cf. leaflike), a substantially broader suborbital, somewhat shorter preoral length and orbit diameter, and somewhat greater snout length, internasal width, interorbital width, postorbital length, and length orbit to angle of preopercle. *Coryphaenoides mcmillani* is also a darker fish overall, the region around the mouth and gill membranes being notably darker than in *C. subserrulatus*.

The new species is readily distinguished from *C. serrulatus* by its elongated outer pelvic fin ray, its rudimentary chin barbel (well developed in *C. serrulatus*), its deciduous scales that have needlelike spinules (relatively adherent scales densely covered with leaflike spinules in *C. serrulatus*), its extensive naked areas on the snout (vs. mostly scale covered), and its anterodorsally directed terminal snout scute (vs. anteriorly directed).

Coryphaenoides mcmillani and *C. subserrulatus* are apparently sympatric off New Zealand, southeastern Australia and Tasmania, and possibly also off southern Africa (two specimens of the latter species recorded by Iwamoto [1986] must be rechecked). Specimens of *C. subserrulatus* have been captured much shallower than specimens of the new species, but at greater depths the depth distributions overlap. Surprisingly, *C. subserrulatus* has not been recorded from oceanic elevations of the Indian Ocean far from continental influences, and the species appears to be entirely replaced there by *C. mcmillani*.

Coryphaenoides subserrulatus Makushok, 1976

(Figs. 15–17)

Coryphaenoides subserrulatus Makushok, 1976:144–155, figs. 1–7 (holotype ZIN 42639A plus 5 paratypes, S of New Zealand off Campbell Plateau; 52°20′S, 166°13′E; 1,148–1,180 m). Ayling and Cox 1982:166. Last et al. 1983:243–244, Fig. 21.18 (recorded off Australia [Tasmania and Victoria], apparently common off Tasmania in 900–1,050 m). Trunov and Konstantinov 1985:153–155 (recorded off SE coast of South America; 730–860 m; description, slight differences in morphometry found between Atlantic and New Zealand specimens). Iwamoto 1986:335, Fig. 93.13 (2 spec. off South Africa [Agulhas Bank]; 980 m). Pavlov and Andrianov 1986: 158–159 (28 spec., recorded from Mill submarine elevation [South Tasman Rise]). Paxton et al. 1989:326 (listed; recorded off SE Australia [New South Wales, Tasmania, Victoria]).

Coryphaenoides (*Coryphaenoides*) *quadripennatus* McCann and McKnight, 1980:41–42, Figs. 18, 21–23 (holotype NZOI 190, plus 8 paratypes; all from New Zealand area, 739–1,212 m).

DIAGNOSIS.—Pelvic fin rays 7, the outer stout greatly elongated, usually more than 1.5 times length of head; pectoral fin rays i13–i18 (usually i14–i15), second uppermost ray stout and greatly elongated, much longer than head length; inner gill rakers on first arch 16–19; chin barbel rudimentary, scarcely visible; spinules on body scales lanceolate to shield-shaped (Fig. 17).

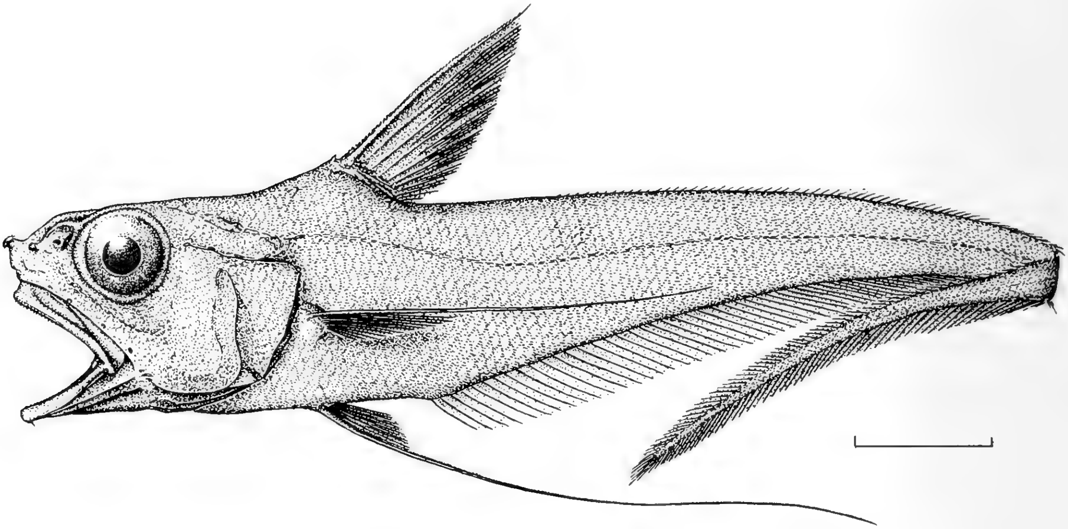

FIGURE 16. *Coryphaenoides subserrulatus.* LACM 11485-1 (310 mm TL) collected by the *Eltanin* off New Zealand (43°48.2′S, 174°24′W) in 497 fm (909 m). Scale bar equals 25 mm. Fins and scales partly reconstructed.

MATERIAL EXAMINED (58 spec.).—South Tasman Rise [Mill submarine elevation]: ZMMGU P-16266 (19, 34.8–60.2 HL, 210–340 TL); 47°27′S, 148°26′E, *Prof. Mesiatzev* cr. 12, tr. 39; 27.IV.1983. LACM 11449-5 (2, 56.0–57.5 HL, 339–320 TL); 47°11′S, 147°47′E; 1,034 m; *Eltanin* sta. 1983; 24.II.1967. LACM 11447-1 (59 HL, 370 TL); 47°21′S, 147°52′E; 915 m; *Eltanin* sta. 1981; 24.II.1967. NMV A5029 (5, 52.6–63.0 HL, 314+–352 TL); 47°29.0′S, 147°59.0′E. ZMMGU P-16273 (9, 17.9–23.8 HL, 96–161+ TL); 47°17′S, 148°15′E; 900–920 m; *Prof. Mesiatzev* cr. 12, tr. 41; 28.IV.1983. ZMMGU P-16287 (26.2 HL, 140+ TL); 47°19′S, 148°22′E; 930 m; *Prof. Mesiatzev* cr. 12, tr. 40; 27.IV.1983.

New Zealand. LACM 11085-6 (8, 47–59 HL, 270–330 TL); Campbell Plateau, 53°49′S, 169°57.2′E; 971 m; *Eltanin* sta. 1990; 1.I.1968. IOAN (56.7 HL, 310 TL); Campbell Plateau, 48°55′S, 171°15′E; 680 m; *Poseidon* 85E. IOAN (52.5 HL, 300+ TL) and CAS 71485 (2, 47.4–49.8 HL, 280–292+ TL); Campbell Plateau, 53°20′S, 167°14′E; 1,020–1,026 m; *Dmitry Mendeleev* sta. 1281; 17.I.1976. IOAN (48.8 HL, 265 TL); Chatham Rise, 44°S, 178°05′E; 960 m; *Poseidon* 110E. CAS 71490 (58.9 HL, 350+ TL); Chatham Rise, 42°55′S, 177°09′E; 860 m; *Poseidon* 139E. IOAN (55.9 HL, 333 TL); Chatham Rise, 42°30′S, 175°E; 250–600 m; *Poseidon* 11E. IOAN (58.0 HL, 330 TL); Chatham Rise, 44°30′S, 177°39′E; 820 m; *Poseidon* 100E. IOAN (58.0 HL, 356 TL); Chatham Rise, 44°53′S, 173°11′E; 990–1,000 m; *Poseidon* 135E. CAS 71496 (54 HL, 305 TL); Norfolk Rise, 39°17′S, 167°02′E; 880 m; *Poseidon* 146E. IOAN (53.9 HL, 315 TL); *Poseidon* 112E. IOAN (46.1 HL, 250+ TL); *Poseidon* 265D.

South Atlantic. Off Argentina, IOAN (52.5 HL, 200+ TL; dried spec.); 47°25.5′S, 60°03′W; 790 m; *Gizhiga* tr. 213; 14.IX.1975. ZIN 48737 (2, 53.0–58.4 HL, 325–315+ TL); 47°17′S, 59°49.3′W; 825–830 m; *Patriot* tr. 225; 22.XI.1984. ZIN 48732 (52.3 HL, 290+ TL); 50°55′S, 56°05′W; 740–760 m; *Gizhiga* cr. 27, tr. 190; 22.VIII.1985.

Southeastern Pacific. Off Chile, ZIN 48715 (9, 56.8–65.3 HL, 287+–372 TL); 42°24.3′S, 74°45′W; 470–440 m; *Akademik Knipovich* cr. 12, sta. 128; 26.II.1973.

Other specimens not examined in detail; all South Tasman Rise: NMV A.5830 (148 TL); 47°00′S, 147°45′E. NMV A.3625 (1 spec.); 47°32′S, 148°16′E; 1,100 m. NMV A.5011 (4, 116–250 TL); 47°01′S, 148°04′E. NMV A.5831 (206 TL); 47°31′S, 148°30′E. NMV A.3621 (1 spec.); 47°29′S, 148°30′E; 1,056 m. NMV A.5029 (5, 312–348 TL); 47°29′S, 147°59′E. NMV A3708 (3, 310–330 TL).

COUNTS AND MEASUREMENTS.—D. II,9–11 + about 120–133; GR-I (outer) 10–14, GR-II (outer/inner) 16–18/14–17; scales below 1D. 8–9, below mid-1D. 4.5–6.5, below 2D. 6.5–8.5, lat.l. 29–37; caeca 12–14.

Total length 96+–370 mm, HL 17.8–63.0. The following in percent HL: postrostral 72.7–77.4; snout 25.0–29.4; preoral 10.0–13.9; internasal 16.3–19.5; post. nostril 5.5–8.6; interorbital 19.8–25.2; orbit 29.6–34.3; suborbital 7.3–9.6; postorbital 43.3–46.7; orb.-preop. 36.1–42.7; upper jaw 44.1–49.0; gill slit 20.5–26.7; pre-A. 143–175; V.-A. 33–51; isth.-A. 77–108; body depth 73–86; 1D.–2D. 40–79; 1D. height 81–96; 1P. 115–214; V. 158–221.

SIZE.—Attains at least 37 cm.

DISTRIBUTION.—New Zealand, South Tasman Rise, southeastern Australia off New South Wales and Victoria, Agulhas Plateau, the Atlantic off Argentina, and the southeastern Pacific off Chile. The species is apparently peripheral to the Indian Ocean, having been captured only at the extreme

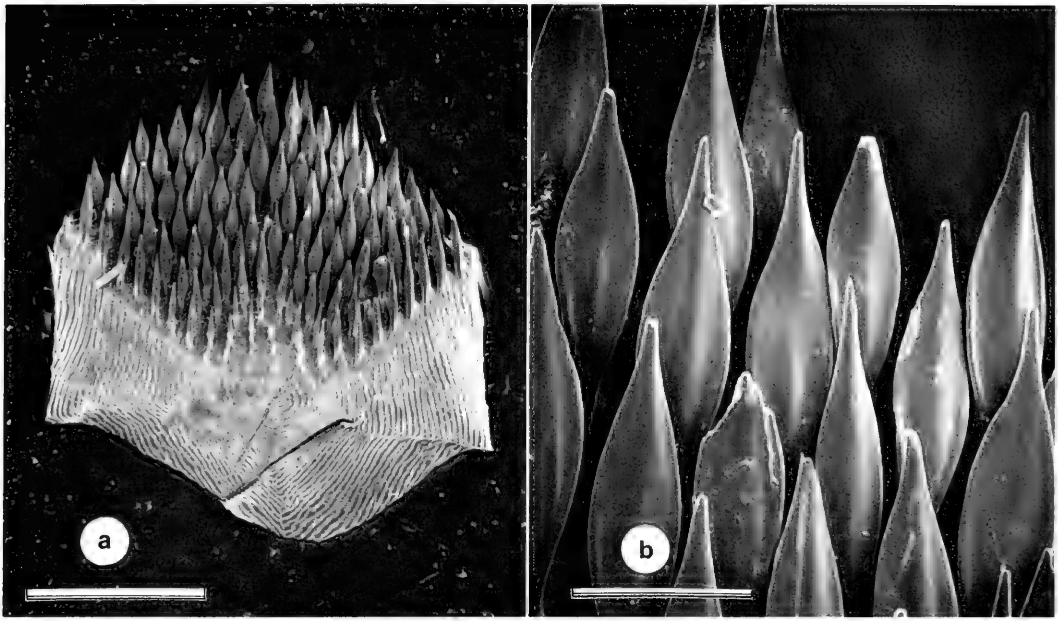

FIGURE 17. Scale from dorsum below interspace between first and second dorsal fins of *Coryphaenoides subserrulatus* (CAS 71485) from off New Zealand. Scale bar in (*a*) equals 1.0 mm; that in (*b*) equals 0.2 mm.

southeastern and southwestern borders. Shcherbachev's (1987:7) report of it from the Broken Ridge was based on a 205 mm specimen, described above as *C. mcmillani.* The presence of *C. subserrulatus* off the Atlantic coast of Argentina and the Pacific coast of Chile is surprising and creates quite a disjunction in the geographic distribution of the species. In reporting on their South Atlantic specimens, Trunov and Konstantinov (1985) noted several differences between their material and those from the New Zealand area. They attributed the differences to geography and habitat. In light of the discovery of a new Indian Ocean species related to *C. subserrulatus,* further examination of their material might be worthwhile.

REMARKS.—*Coryphaenoides subserrulatus* has been well described and illustrated by several workers (see synonymy), and another detailed description is unnecessary. This species is so distinctive that it is not likely to be confused with any other species except *C. mcmillani.* The two species, however, are readily distinguished by differences in pelvic fin ray numbers, the length and development of elongated pectoral fin ray, and several morphometric features, as described in the description of *C. mcmillani.*

DISCUSSION OF RELATIONSHIPS.—In their cladogram of *Coryphaenoides* and relatives, Iwamoto and Sazonov (1988: Fig. 1) had the *C. serrulatus* group on a branch with *Albatrossia* and *Hyomacrurus* based on the presence of only two retia mirabilia in the gas gland, compared with four or more in most *Coryphaenoides* and other closely related genera and species groups. The count of two retia in the *C. serrulatus* group was based on Trunov and Konstantinov's (1985) report of that number in two specimens of *C. subserrulatus.* Our subsequent examination of several specimens of *C. subserrulatus, C. serrulatus,* and *C. mcmillani* has shown six, a number that would place the group in the clade with subgenera *Chalinura, Lionurus,* and *Nematonurus.* We cannot account for the differences in counts between our findings and those of Trunov and Konstantinov; their specimens should be reexamined. Often, the individual retia and gas glands appear to be coalesced into one or two structures and must be teased apart to show the separate parts. Perhaps this was the situation in their specimens. The leaf-shaped scale spinules, initially thought to be a synapomorphy of the *C. serrulatus* group, are absent in *C. mcmillani.* The needlelike scale spinules of that species probably represent a plesiomorphic condition, similar to the condition in other members of the subgenus *Chalinura.* Based primarily on dentition and gill raker shape, the *C. serrulatus* group most closely agrees with subgenus *Chalinura,* but our assignment is tentative and awaits confirmation or contradiction from other sources.

Trunov and Konstantinov's (1985) report of the presence of a small light organ immediately anterior to the anus of *C. subserrulatus* marks the first record of such a gland in a species of *Coryphaenoides,* although light organs are common to all *Coelorinchus* species and three other genera with six branchiostegal rays. (All macrourines with seven branchiostegal rays appear to have light organs.) We interpret its presence as a retention of a plesiomorphic state common in the Malacocephalini, as well as in members of *Coelorinchus,* but secondarily lost in *Coryphaenoides.* It would be well to examine histologically other members of *Coryphaenoides* to determine if light organs are represented more widely than currently assumed.

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A REVISION OF *APHELANDRA* (ACANTHACEAE) IN MEXICO

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Abstract: Twelve species of *Aphelandra* are treated as occurring in Mexico: *A. aurantiaca, A. gigantiflora, A. guerrerensis, A. heydeana, A. hintonii, A. lineariloba, A. madrensis, A. scabra, A. schiedeana, A. speciosa, A. verticillata,* and *A. wendtii.* Six of these, *A. guerrerensis, A. hintonii, A. lineariloba, A. madrensis, A. verticillata,* and *A. wendtii,* are endemic to the country. *Aphelandra wendtii* is newly described from rain forests in Veracruz, Tabasco, and Chiapas. A neotype is selected for *Hemisandra aurantiaca,* and lectotypes are designated for *A. acutifolia, A. aurantiaca* var. *roezlii, A. gigantiflora, A. haenkeana, A. madrensis,* and *A. schiedeana.* Pollen of all 12 species is tricolpate. Chromosome numbers of six species of Mexican *Aphelandra* are all $n = 14$. Keys to the genera of Mexican Aphelandreae and the species of Mexican *Aphelandra* are provided.

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Introduction

Aphelandra R. Brown is a genus of about 175 species of perennial herbs, shrubs, and small trees restricted in distribution to the neotropics. The genus is well known to horticulturists in temperate regions because some of the species are cultivated for the ornamental value of the brightly colored inflorescences (e.g., *A. chamissoniana* Nees) or the variegated or colored leaves (e.g., *A. squarrosa* Nees, the zebra plant). Recent systematic studies of the genus include a comprehensive taxonomic revision by Wasshausen (1975) and a monograph of the Central American species of the *A. pulcherrima* complex by McDade (1984). Most of the species are confined to South America (especially southeastern Brazil and the Andes of Bolivia, Peru, Ecuador, and Colombia); however, 31 are known to occur in Central America and Mexico.

In the only comprehensive account of Acanthaceae, Nees (1847) noted the occurrence of seven species of *Aphelandra* in Mexico: *A. acutifolia* Tafalla ex Nees, *A. aurantiaca* (Scheidw.) Lindl., *A. deppeana* Schlecht. & Cham., *A. haenkeana* Nees, *A. pectinata* Willd. ex Nees, *A. pulcherrima* (Jacq.) Kunth, and *A. schiedeana* Schlecht. & Cham. The Mexican report of *A. pulcherrima* was based on a collection made by Haenke from Acapulco now assigned to another species (*A. scabra*), and the report of *A. pectinata* was based on specimens from Colombia and Costa Rica that were erroneously attributed to Mexico. In the related genus *Lagochilium* Nees, considered by Bentham (1876) and subsequent authors to be congeneric with *Aphelandra,* Nees (1847) treated another Mexican collection of Haenke as *L. spicatum* Nees. The holotype of *L. spicatum* at PR is not an *Aphelandra*; rather, it appears to be a species of *Justicia* and was so annotated by Wasshausen in 1971. Hemsley (1882) treated nine species of *Aphelandra* in Mexico, the seven noted by Nees (1847) under *Aphelandra* and two treated by Nees under other genera (*A. hydromestus* (Nees) Hemsley and *A. verticillata* Nees ex Hemsley). Standley (1926) synonymized *A. hydromestus* and *A. acutifolia* with *A. aurantiaca,* synonymized *A. pectinata* and *A. haenkeana* with *A. deppeana,* and recognized *A. madrensis* Lindau and *A. speciosa* T. Brandegee for a total of seven Mexican species. Wasshausen (1975) recorded 10 species of the genus as occurring in Mexico. He excluded Mexico from the range of *A. pulcherrima* and added *A. guerrerensis* Wasshausen, *A. heydeana* J. D. Smith, *A. hintonii* Wasshausen, and *A. lineariloba* Leonard. He also placed *A. hydromestus* into the synonymy of the Brazilian species, *A. prismatica* (Vellozo) Hiern, and he discounted a Mexican origin for the cultivated material on which the former species was based.

This study presents a taxonomic revision of all species of *Aphelandra* known to occur in Mexico. Data were obtained from more than 1,200 herbarium specimens from 38 herbaria and from living plants observed in the field and greenhouse. Twelve species, consisting of the 10 treated by Wasshausen (1975), one newly described, and one range extension into the country, are recognized as occurring in Mexico in my study. Among the 12 species, six are endemic to Mexico (*A. guerrerensis, A. hintonii, A. lineariloba, A. madrensis, A. verticillata,* and *A. wendtii*), four are restricted to southern Mexico and northern Central America (*A. gigantiflora, A. heydeana, A. schiedeana,* and *A. speciosa*), and two are wide-ranging taxa that attain the northernmost extent of their respective ranges in Mexico (*A. aurantiaca* and *A. scabra*). Information on the 10 species endemic to Mexico and northern Central America was gathered throughout their respective ranges. Studies of *A. aurantiaca* and *A. scabra* were limited to Mexican representatives of these species. Whereas only representative specimens are cited for commonly collected species, all specimens utilized in this study are listed in Appendix B.

In spite of this and other recent work on the genus, knowledge of Mexican *Aphelandra* remains incomplete. For example, *Aphelandra hintonii* is known from only a single collection; fruits are unknown for *A. heydeana* and *A. hintonii*; and unusual plants from the poorly collected Sierra Madre Sur in southern Mexico remain difficult to treat. It is likely that additional species will be discovered in the remote regions of southern Mexico.

SUBFAMILIAL CLASSIFICATION.—Both Lindau (1895a) and Bremekamp (1965) included *Aphelandra* in the subfamily Acanthoideae, tribe Aphelandreae. This tribe is characterized by having tricolpate pollen, four monothecous stamens, and a corolla with a distinct upper lip. Genera of Aphelandreae in Mexico can be distinguished by the following key.

1. Corolla 6.5–24 mm long; stamens 1.2–11 mm long, filaments inserted in distal ⅔ of corolla tube (0.36–0.77 the distance up tube from base), usually included in corolla tube; $x = 13$.
    2. Corolla zygomorphic, lobes of upper lip dissimilar to those of lower lip; lobes of upper lip not obovate and usually not more than ½ the length of the lip; plants caulescent; corolla yellow, pinkish, or white; anthers at least partially exserted from corolla tube; stigma bilobed or funnelform. .... *Holographis.*
    2. Corolla subactinomorphic, lobes more or less similar in form (or upper lip reduced in size relative to lower lip in *S. cordatum, S. chamaeranthemoideum,* and *S. nanum*), upper lip divided nearly to its base into 2 prominent, obovate lobes greater than 2.5 mm long; plants acaulescent (leaves clustered at or near ground) or caulescent; corolla pinkish or purplish (sometimes white); anthers included in corolla tube; stigma funnelform. .... *Stenandrium.*
1. Corolla 30–80 mm long; stamens 23–60 mm long, filaments inserted in proximal ⅓ of corolla tube (0.14–0.33 the distance up tube from base; or up to 0.40 in *A. verticillata*), always exserted from corolla tube; $x = 14$. .... *Aphelandra.*

More than 50 species of the New World genus *Stenandrium* Nees have been described, largely from Brazil, the West Indies, and Mexico (Daniel 1985). *Holographis* Nees comprises 15 species confined to Mexico (Daniel 1983, 1988). Relationships among these three genera of Aphelandreae have been discussed by Daniel (1983, 1985) and are further considered with respect to chromosome numbers by Daniel et al. (1984, 1990).

A species of the primarily Brazilian genus

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Geissomeria Lindl. of the Aphelandreae was described from an unidentified locality in Mexico by Lindau (1895b). Unfortunately, the type of *G. mexicana* Lindau was destroyed at B. No photographs of the holotype, isotypes, or recent collections of the species have been located.

Subgeneric Classification.—There is no recent subgeneric classification of *Aphelandra.* Nees (1847) recognized two sections now regarded as artificial: *Stenochila* with the lateral lobes of the lower lip of the corolla less than one-third as long as the lower-central lobe and *Platychila* with the lateral lobes one-third or more as long as the central lobe. In the former section he included *A. scabra* (as *A. pulcherrima, A. pectinata, A. haenkeana,* and *A. deppeana*) and *A. schiedeana. Aphelandra aurantiaca* (including *A. acutifolia*) was included in section *Platychila.* Section *Platychila* was further divided by Nees into subsections "*Genuinae*" with entire leaves and "*Acanthoideae*" with dentate or pinnatifid leaves. Although Lindau (1895a) followed this subgeneric classification, it was ultimately rejected, without being replaced, by Wasshausen (1975). The only group of related taxa recognized since Wasshausen's (1975) monograph is the informal *A. pulcherrima* complex of about 40 species (McDade 1984).

Mexican species of *Aphelandra* are diverse and appear to segregate into seven recognizable groups or alliances: 1) *A. scabra* (in the *A. pulcherrima* complex) with bracteal nectaries and lateral lobes of the lower lip of the corolla reduced and fused to the upper lip; 2) *A. aurantiaca* with the younger stems flattened and the bracts pectinately dentate; 3) *A. verticillata* with quaternate leaves and pollen with bifurcating colpi; 4) *A. speciosa* with bracts large, leathery, arching, glabrous, and apically apiculate; 5) *A. heydeana* and *A. wendtii* with conspicuously reflexed bracts; 6) *A. lineariloba* and *A. madrensis* with relatively short corollas, unequally bilobed stigmas, and filaments with conspicuously flattened trichomes; and 7) *A. gigantiflora, A. guerrerensis,* and *A. schiedeana* with large reddish corollas, erect bracts, and filaments lacking flattened trichomes. *Aphelandra hintonii,* with large corollas and conspicuously flattened staminal trichomes, combines characteristics of the latter two alliances. Additional studies of the genus will be needed in order to place the Mexican species into a subgeneric framework.

Distribution in Mexico.—Of the 12 species of *Aphelandra* in Mexico, seven occur in the southernmost state, Chiapas. Five species are now known from each of the southern states Oaxaca and Guerrero. The numbers of species per state decreases to the north. The majority of species occurs in moist to wet habitats; however, at least *A. scabra* and *A. verticillata* can occur in relatively dry habitats as well.

Several indirect lines of evidence support a hypothesis that *Aphelandra* radiated to Mexico from South America: 1) the greatest concentration and diversity of species is encountered in South America; 2) in most instances, there are clear relationships between the Mexican species or species-groups and South American species; 3) the greatest abundance of Mexican species is in the southernmost regions of the country; 4) both *A. scabra* and *A. aurantiaca,* which attain the northern limit of their distributions in Mexico, exhibit greater morphological diversity in South America; and 5) the monophyletic *A. pulcherrima* complex is most diverse and abundant in South America with only one highly derived species, *A. scabra,* in Mexico (McDade 1984). The presence of six species endemic to Mexico suggests the possibility of some secondary radiation of the genus in that country. If Guatemala, Belize, and El Salvador are considered together with Mexico, 10 of the 12 species of *Aphelandra* occurring in the region are endemic there.

Reproductive Biology.—Mexican species of *Aphelandra* are conspicuous by their large, densely bracteate, and brightly colored inflorescences. The large, tubular, and nectariferous flowers appear to be adapted for pollination by hummingbirds. McDade (1984) reported that hummingbirds pollinated flowers of 10 species in southern Central America, including *A. scabra* (as *A. deppeana*), the range of which extends into Mexico. Hummingbird visitors to *A. scabra* in Mexico were noted on one herbarium level (*Calzada 1626-B*). Nectar quantity of 10 flowers of *A. guerrerensis* grown in a greenhouse, determined according to the method of Baker (1979), was in each instance considerably greater than 8.7 μl (mean ± standard deviation of spot diameter: 22.3 mm ± 3.32). Analysis of nectar sugar composition of *A. aurantiaca, A. gigantiflora, A. guerrerensis, A. lineariloba, A. scabra,* and *A. wendtii* by Dr. C. E. Freeman reveals all to have considerably greater percentages of sucrose than fructose or glucose and usually about twice as much fructose as glucose (Daniel and

Freeman, in prep.). High percentages of sucrose and a hexose imbalance are typically found in flowers known or suspected to be hummingbird-pollinated (Baker and Baker 1983; Freeman and Worthington 1985).

Individuals of most Mexican species of *Aphelandra* flower during November, December, and January, that is, immediately following the wet season in most of southern Mexico. Fruiting usually occurs simultaneously or somewhat later with individuals of most species bearing fruits from December through March. Relatively few fruiting collections are known for most Mexican species. It is not known whether this is a result of poor reproductive success or failure by field-workers to collect the slightly less conspicuous fruiting plants.

Aspects of the reproductive biology of the Central American species of the *A. pulcherrima* complex were summarized by McDade (1984, 1985). She noted that among these species autogamy is prevented by exsertion of the stigma beyond the anthers during anthesis. She also demonstrated that whereas several species (or populations) are fully self-compatible, others are partially self-incompatible. Four collections representing three species of *Aphelandra, A. lineariloba* (*Daniel 2138cv*), *A. guerrerensis* (*Daniel 5376cv*), and *A. scabra* (*Daniel 5328cv* and *Daniel et al. 5476cv* [Panama.—Canal Area: along "Vine Road" to Fort Kobbe beach, W of Bridge of the Americas, CAS]), were grown from cuttings in a greenhouse during this study and tested for self-compatibility and autogamy as described by Daniel (1990). Fruiting did not occur in any of the artificially self-pollinated flowers nor in any undisturbed flowers. These results suggest that under greenhouse conditions, these three species of *Aphelandra* are neither self-compatible nor autogamous.

Several additional aspects of the floral biology of Mexican species cultivated at the San Francisco Conservatory of Flowers were noted. In *A. scabra* (*Daniel 5328cv*), about 24 hours prior to anthesis, the distal four–five mm of the central lobe of the lower lip curved away from the upper lip with the apex of the lobe recoiling. At anthesis, the entire lower-central lobe separated from the upper lip and over four–five hours progressively reflexed until the distal portion contacted the corolla tube. During the subsequent 24–48 hours, the lower-central lobe continued to recoil from the apex overlapping itself several times. Corollas persisted on the plants for four–six days following the onset of anthesis. In *A. lineariloba* (*Daniel 2138cv*) anthesis began with the lower lip spreading away from and becoming more or less perpendicular to the upper lip. Within 24 hours, the three lobes of the lower lip were reflexed and thereafter withered. The lower lip of *A. guerrerensis* (*Daniel 5376cv*) remained in a position more or less perpendicular to the upper lip from the onset of anthesis until the corolla fell from the plant, a period of from four–eight days for undisturbed corollas and from two–three days for artificially self-pollinated corollas.

Palynology.—Previous palynological studies of *Aphelandra* in this century (Raj 1961; Wasshausen 1975; McDade 1984) reveal some diversity in grain shape (spherical to perprolate), exine sculpturing (verrucose, reticulate, psilate), and apertures (tricolpate or polyrugate). Most species examined have prolate to perprolate and tricolpate pollen with variegated exine sculpturing. Untreated pollen from herbarium specimens representing all 12 species of *Aphelandra* occurring in Mexico was examined with the scanning electron microscope in this study (Figs. 1, 2). Grain size ranges from 35–60 μm in length (polar axis) and from 20–42 μm in width (equatorial axis). Grain shape is prolate (varying from subprolate to perprolate) with a ratio of polar to equatorial axes varying from 1.2–2.4. The grains are tricolpate with colpi extending from the equator nearly to or to both poles. In most species the colpi become narrowed as they approach the poles. In some instances (e.g., some grains of *A. madrensis*), the colpi fuse at the poles. In *A. verticillata* (Fig. 1a), the colpi bifurcate into two short segments as they approach the poles. McDade (1984) noted colpi that bifurcate and subsequently fuse with adjacent colpi near the poles in some collections of *A. golfodulcensis* McDade of southern Central America. Colpi that bifurcate near the poles are known in some, but not all, species of the related genus *Holographis* (Daniel 1983; see discussion above and under *A. verticillata*). In addition to the three equatorially positioned colpi, pollen of *A. gigantiflora, A. heydeana, A. lineariloba, A. madrensis, A. schiedeana,* and *A. speciosa* has a three-armed aperture at each pole. The arms of these apertures extend from the poles toward the equator, alternate with the colpi. Their length can be up to one-quarter of the length (polar axis) of the entire grain. These polar apertures are evident in Wass-

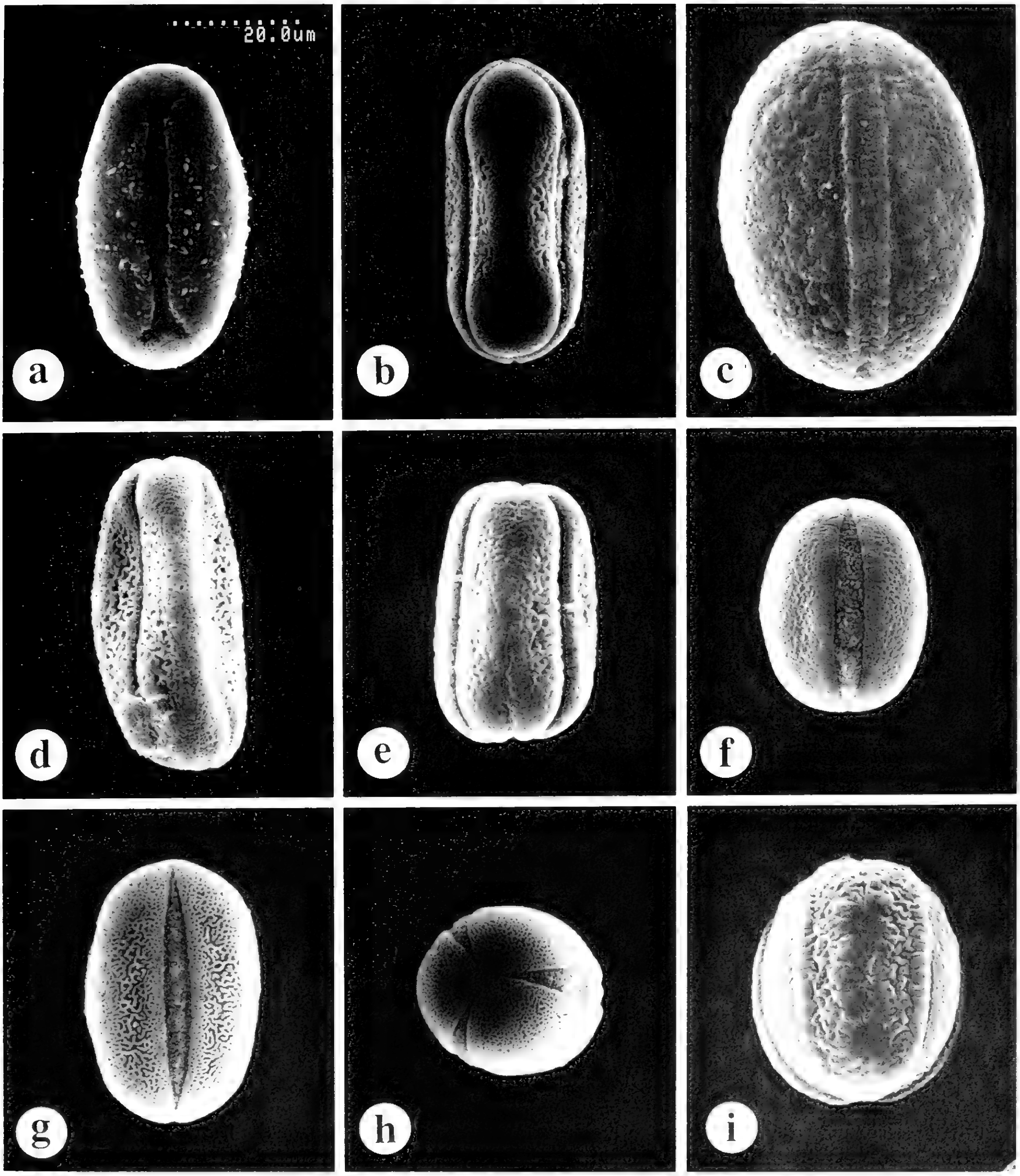


FIGURE 1. Scanning electron micrographs of *Aphelandra* pollen. a, *A. verticillata* (*Daniel et al. 3295*), colpal view; b, *A. scabra* (*Daniel 5328*), intercolpal view; c, *A. aurantiaca* (*Breedlove & Daniel 71287*), colpal view; d, *A. speciosa* (*Croat 40837*), intercolpal view; e, *A. lineariloba* (*Daniel 2138cv*), intercolpal view; f, *A. madrensis* (*Langlassé 806*), colpal view; g, *A. wendtii* (*Breedlove & Smith 22121*), colpal view; h, *A. wendtii* (*Breedlove 22121*), polar view; i, *A. hintonii* (*Hinton et al. 16049*) intercolpal view. Scale in b–i same as in a.

hausen's (1975) micrographs of pollen of *A. lineariloba, A. madrensis,* and *A. schiedeana,* and *A. verticillata* from Mexico and in *A. flava* Nees from South America. Wasshausen's (1975) micrograph of *A. verticillata* (based on *Moore 5503*) is likely mislabeled. Pollen of *A. verticillata* from four specimens (*Daniel et al. 3295, Hinton 13486, Moore 5503,* and *Rzedowski 27991*) examined in my study was homogenous, lacked polar apertures, and had bifurcating colpi. Exine sculp-

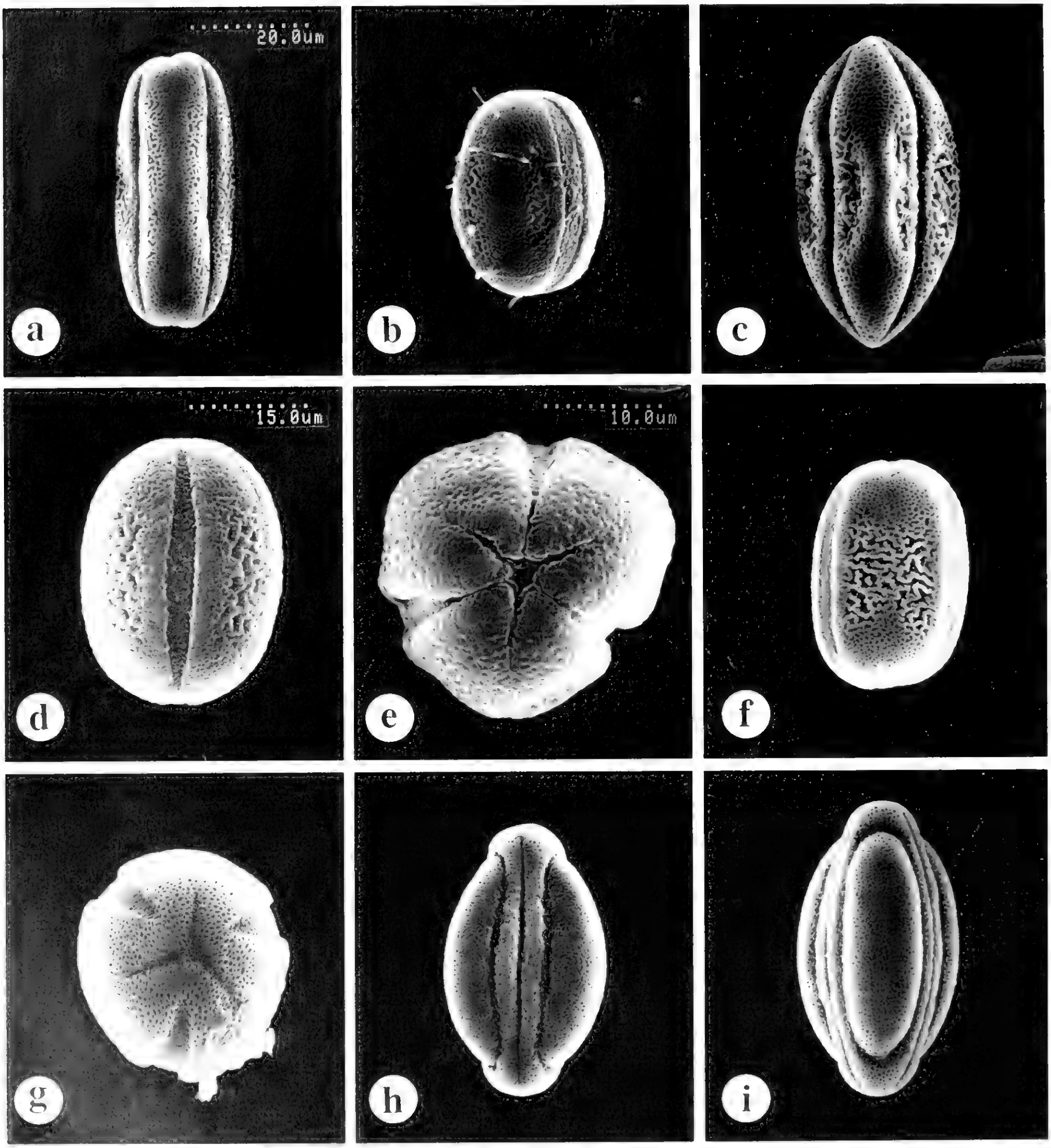


FIGURE 2. Scanning electron micrographs of *Aphelandra* pollen. a, *A. heydeana* (*Breedlove 65803*) intercolpal view; b, *A. guerrerensis* (*Hinton et al. 11199*) intercolpal view; c, *A. guerrerensis* (*Daniel 5376*), intercolpal view; d, *A. gigantiflora* (*Breedlove & Daniel 70900*), colpal view; e, *A. gigantiflora* (*Standley 19771*), polar view; f, *A. schiedeana* (*Ventura A. 12241*), intercolpal view; g, *A. schiedeana* (*Ventura A. 12241*), polar view; h, *A. sp.* (*Delgado S. 655*), colpal view; i, *A. sp.* (*Delgado S. 655*), intercolpal view. Scale in b, c, and f–i same as in a.

turing of Mexican *Aphelandra* generally agrees with that shown by Wasshausen (1975) and McDade (1984). Sculpturing over the colpi varies from psilate in *A. verticillata* to gemmate or verrucate in all other species; that of the mesocolpia varies from foveolate to fossulate (e.g., *A. verticillata*) to more or less evenly reticulate (e.g., *A. madrensis*) to unevenly reticulate with conspicuous, more coarsely rugulate bands or regions flanking the colpi (most species).

Pollen of a single Mexican collection that otherwise greatly resembles *A. gigantiflora* is unique among species of the genus studied to date. It has a pseudocolpal (or colpoid) ellipse in each mesocolpium (Fig. 2h, i and see discussion under *A. gigantiflora.*)

CHROMOSOME NUMBERS.—Chromosome numbers have been determined for six species of Mexican *Aphelandra*: *A. aurantiaca, A. gigantiflora, A. guerrerensis, A. leariloba, A. madrensis,* and *A. scabra.* Like most previous counts for species occurring outside of Mexico, all counts for the Mexican species have been $n = 14$ (Daniel et al. 1990, Daniel and Chuang, in prep.). This number appears to be the base number for *Aphelandra* and clearly delimits the genus from its Mexican relatives in the Aphelandreae, *Holographis* and *Stenandrium,* which appear to have a base number of $x = 13$ (Daniel et al. 1984, 1990).

TAXONOMIC TREATMENT

Aphelandra R. Brown, Prodr. Fl. Nov. Holl. 1:475. 1810. TYPE.—*A. cristata* (Jacq.) R. Brown in Aiton (1812) (*Justicia cristata* Jacq.).

Hemisandra Scheidw. Bull. Acad. Roy. Sci. Bruxelles 9:22. 1842. TYPE.—*H. aurantiaca* Scheidw. (1842) (= *A. aurantiaca* (Scheidw.) Lindl.).

Erect perennial herbs, shrubs, or small trees; cystoliths absent; stems terete to quadrate or sometimes somewhat flattened. Leaves opposite (rarely alternate, ternate, or quaternate), subsessile to petiolate, blades often decurrent along petiole (petiolar wings excluded from leaf blade data in following descriptions), entire, sinuate, lobed, or dentate, flat to undulate. Inflorescence of terminal, simple or branched, usually densely flowered spikes; flowers relatively large, sessile, subtended by paired isomorphic bractlets and a bract; bracts usually subfoliose, green to brightly colored, entire or dentate, often with nectaries on abaxial surface. Calyx divided nearly to or to base into 5 subequal to unequal lobes; corolla variously colored (mostly shades of red, orange, and yellow in ours), tube straight to curved, usually ampliate apically, sometimes bearded within, limb bilabiate, the upper (posterior) lip innermost in bud, often conduplicate and enclosing stamens during anthesis, apically entire to bilobed, margin often flaring outward at base or sometimes for entire length of vertical sides, the lower (anterior) lip spreading to ± perpendicular to upper lip to reflexed to recoiled, conspicuously trilobed or with lateral lobes much reduced to vestigial; stamens 4, usually inserted in basal third of corolla tube (at a point 0.14–0.33[–0.40] the distance up tube from base in ours), didynamous with pairs inserted at slightly different positions in tube (posterior pair inserted up to 1 mm distal to anterior pair in ours), filaments and anthers usually exserted from tube, anthers monothecous, connivent (often in pairs), pairs presented at ± same height or with one pair extending beyond the other, lacking basal appendages, often pubescent, pollen generally subprolate to perprolate, tricolpate, staminode usually present, consisting of a slender short filament, a small triangular projection, or a small callous region, inserted between posterior pair of stamens (i.e., dorsal-most in corolla tube, alternate with 2 fused lobes of upper lip of corolla), glabrous or pubescent; stigma symmetrically to asymmetrically funnelform or shallowly to deeply bilobed, lobes unequal. Capsule ovoid to ellipsoid to subglobose; seeds 4, flattened to subglobose, subelliptic to subcircular to somewhat squarish to subtriangular in outline.

DISTRIBUTION.—*Aphelandra* extends from the state of Sinaloa in northwestern Mexico (ca. latitude 25° N) southeastward through regions of both wet and dry forests to the state of Santa Catarina in southeastern Brazil (ca. latitude 28° S). The greatest concentrations of species are in the Andes of Colombia, Ecuador, Peru, and Bolivia.

Key to the Species of *Aphelandra* in Mexico

1. Leaves whorled (4 per node); corolla yellow, 25–35 mm long; pollen with colpi bifurcating toward each pole. .... 1. *A. verticillata.*
1. Leaves opposite (rarely subopposite); corolla red, orange, or (rarely) yellowish, 30–85 mm long; pollen with colpi tapering toward each pole.
    2. Bracts with 2 submarginal clusters of padlike nectaries (up to 16 per cluster) on abaxial

surface; lower-central lobe of corolla becoming recoiled, the lateral lobes reduced to vestigial toothlike appendages up to 2.5 mm long and attached to upper lip. ..... 2. *A. scabra.*

2. Bracts without padlike nectaries on abaxial surface; lower-central lobe of corolla spreading to reflexed, the lateral lobes conspicuous (3.5–25 mm long) and attached to lower lip.
   3. Young stems somewhat flattened; bracts dentate with 7–15 teeth per side; corolla orange to yellowish. ..... 3. *A. aurantiaca.*
   3. Young stems subterete to quadrate; bracts entire or dentate with 1–2 teeth (sometimes inconspicuous) per side; corolla red or reddish (one collection of *A. heydeana* reported as orange-red with yellowish veins on lower lip).
      4. Inflorescence rachis glabrous; bracts arching away from rachis at maturity, abaxially glabrous, abruptly apiculate (to cirrhous) at apex, the apiculum usually reflexed-coiled; corolla externally glabrous. ..... 4. *A. speciosa.*
      4. Inflorescence rachis pubescent; bracts erect to spreading but not arched, abaxially pubescent (rarely nearly glabrate in *A. wendtii*), rounded to acute to accumulate to aristate at apex, the apical portion sometimes spreading to reflexed but lacking a reflexed-coiled apiculum; corolla externally pubescent.
         5. Corolla 30–42 mm long, the upper lip 6–13 mm long, the lower lip 3.5–13 mm long; stigma unequally bilobed, 0.5–2 mm long; corolla discolorous with limb darker than tube; filaments with conspicuously flattened trichomes.
            6. Lower lip of corolla reflexed, with lobes linear, the lateral 0.6–1 mm wide, the lower-central 0.8–2 mm wide; anterior pair of thecae dorsally glabrous. ..... 5. *A. leariloba.*
            6. Lower lip of corolla ± perpendicular to upper lip, with lobes narrowly to broadly elliptic to subcircular to obovate, the lateral 1.8–6 mm wide, the central 4–9.5 mm wide; anterior pair of thecae dorsally pubescent with flattened trichomes. ..... 6. *A. madrensis.*
         5. Corolla 41–85 mm long, the upper lip 16–36 mm long, the lower lip 17–39 mm long; stigma funnelform, 0.2–0.5 mm long; corolla concolorous; filaments glabrous or with filamentous trichomes (or if flattened trichomes present, as in *A. hintonii,* then with corolla 60–80 mm long).
            7. Inflorescence appearing subcapitate (rarely elongate); bracts lanceolate to strap-shaped, 5–11 times longer than wide, gradually attenuate at apex; thecae 6.5–8.1 mm long (bracts 28–65 mm long, see below). ..... 7. *A. wendtii.*
            7. Inflorescence elongate; bracts lanceolate to ovate to elliptic to obovate, 1.1–4.9 times longer than wide, rounded to acute to acuminate to caudate at apex; thecae 3–5.5 mm long (or if up to 7 mm long, as rarely in *A. heydeana,* then with bracts 14–26 mm long).
               8. Two filaments distally pubescent with conspicuously flattened trichomes; bractlets 2.5–4 mm wide; lateral lobes of lower lip of corolla obovate–elliptic, 4.5–8 mm wide; inflorescence rachis densely sericeous with silky, flexuose to antrorsely appressed glandular and eglandular trichomes up to 1.5 mm long. ..... 8. *A. hintonii.*
               8. Filaments lacking conspicuously flattened trichomes; bractlets 0.8–2 (–2.5) mm wide; lateral lobes of lower lip of corolla lanceolate to linear-elliptic to oblanceolate, 0.5–5.5 mm wide; inflorescence rachis variously pubescent with glandular and/or eglandular trichomes but not as described above.
                  9. Bracts attenuate-caudate to caudate at apex, the distal portion spreading to reflexed; thecae 5–7 mm long, all apically pubescent (inflorescence rachis eglandular, see below). ..... 9. *A. heydeana.*
                  9. Bracts rounded to acute to acuminate to subfalcate at apex, the distal portion erect; thecae 3–5.5 mm long, only 2, if any, apically pubescent (or if all apically pubescent, as sometimes in *A. gigantiflora* from outside of Mexico, then with inflorescence rachis glandular).

10. Thecae glabrous; pollen lacking 3-armed polar apertures. .... 10. *A. guerrerensis.*
10. At least 2 thecae (i.e., posterior pair) apically and/or dorsally pubescent; pollen with 3-armed polar apertures.
    11. Rachis viscid with conspicuous glandular trichomes; seeds covered with apically branched or dendritic trichomelike papillae. .... 11. *A. gigantiflora.*
    11. Rachis pubescent with eglandular trichomes only; seeds nearly smooth or covered with low, rounded encrustations. .... 12. *A. schiedeana.*

1. **Aphelandra verticillata** Nees ex Hemsley, Biol. Centr. Amer. Bot. 2:513. 1882. (nom. nov. for *Crossandra haenkeana* Nees, based on herbarium name cited by Nees as a synonym of *C. haenkeana*).

Crossandra haenkeana Nees in DC. Prodr. 11:281. 1847. (non *Aphelandra haenkeana* Nees, 1847). Type.—MEXICO. Western Mexico, 1791, *T. Haenke s.n.* (Holotype: PR!, photo at US!; isotype: PRC!, photo at US!).

Perennial herb or shrub to 3 m tall. Young stems terete to subquadrate, more or less evenly pubescent with flexuose to retrorse eglandular trichomes 0.1–1.2(–2) mm long, becoming glabrate. Leaves whorled, 4 per node, sessile (and sometimes subauriculate) to petiolate, petioles to 45 mm long (naked portion to 2.5 mm long), blades lanceolate to ovate 27–150 mm long, 9–70 mm wide, 2–4.4 times longer than wide, acuminate at apex, rounded to attenuate-decurrent along petiole with a tapering or nontapering wing extending nearly to or to node and sometimes subauriculate to auriculate at base, surfaces pubescent or glabrate, margin entire. Spikes axillary or terminal, elongate, up to 100 mm long (excluding flowers), 13–33 mm wide (excluding flowers) near midspike, rachis puberulent with straight eglandular trichomes 0.05–0.2 mm long. Bracts entirely green or sometimes reddish distally, ovate to elliptic, 11–19 mm long, 3–8.5 mm wide, 1.8–3.7 times longer than wide, acute to acuminate, usually mucronate and erect to somewhat twisted-spreading at apex, abaxial surface pubescent with straight to antrorse, eglandular trichomes 0.05–0.6 mm long, margin conspicuously ciliate with flexuose eglandular trichomes to 2 mm long, entire. Bractlets lanceolate, 10–17 mm long, 1–2 mm wide, aristate at apex, pubescent like bracts. Calyx 12–18 mm long, lobes lanceolate, 1.5–2 mm wide at base, aristate at apex, abaxial surface pubescent like bracts and usually also with inconspicuous glandular trichomes to 0.1 mm long (margin with occasional glandular trichomes to 0.2 mm long). Corolla yellow, 25–35 mm long, externally pubescent with eglandular trichomes 0.05–0.2 mm long, upper lip 8–15 mm long, bilobed with triangular-ovate to linear-elliptic lobes at apex, 3–6.8 mm long, 2.1–2.5 mm wide, margin flared apically if at all, lower lip spreading or ± perpendicular to upper lip, 9–15 mm long, lateral lobes linear to oblanceolate to obovate, 7–13.5 mm long, 1.8–4 mm wide, lower-central lobe elliptic to obovate, 7.5–13 mm long, 4–8 mm wide, 1–1.3 times longer and 1.6–2 times wider than lateral lobes. Stamens 23–28 mm long, posterior pair inserted ca. 1 mm distal to anterior pair, filaments proximally pubescent with filamentous eglandular trichomes, distally glabrous, thecae 2.3–3 mm long, pairs presented at ca. same height, all apically and dorsally pubescent with cobwebby trichomes; staminode 0.5–1.5 mm long, pubescent. Style 24–35 mm long, pubescent (at least proximally) with eglandular trichomes; stigma obliquely funnelform, 0.2–0.5 mm long or unequally bilobed with one lobe 0.1–0.2 mm long and the other 0.2–0.3 mm long. Capsule 10.5–11 mm long, pubescent with mostly straight eglandular trichomes 0.2 mm long. Seeds not seen.

Distribution and Habitat.—West-central Mexico (Guerrero, México, Michoacán, and Morelos; Fig. 3) in regions of tropical deciduous forest to oak forest at elevations from 500 to 1,550 m.

Phenology.—Flowering: November–December; fruiting: November.

Using the morphological attributes in the above key to Mexican Aphelandreae, this species should be treated in *Aphelandra*. In many characteris-

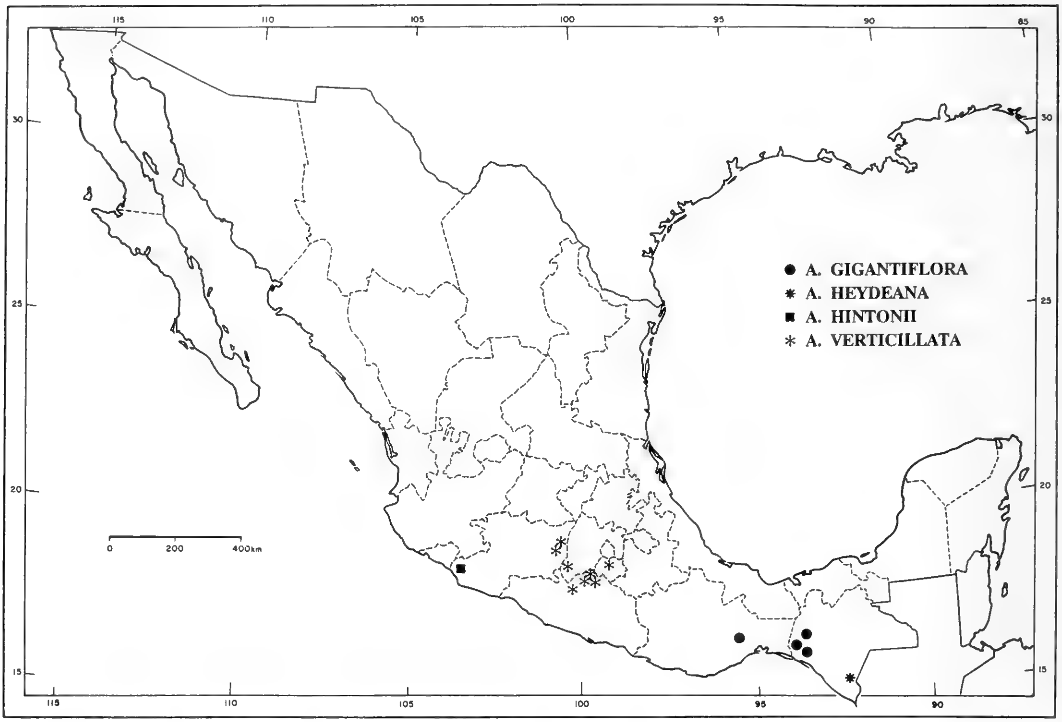


FIGURE 3. Distribution of *Aphelandra gigantiflora, A. heydeana, A. hintonii,* and *A. verticillata* in Mexico.

tics, however, *A. verticillata* links *Aphelandra* and *Holographis,* and with some justification, might be treated equally well in the latter genus. Character states of *A. verticillata* suggestive of *Holographis* include quaternate leaves, yellow corollas, and pollen with colpi bifurcating toward the poles. The reddish coloration often present on the bracts and the long stamens are character states more reflective of species of *Aphelandra.* Corolla length and position of insertion of the stamens in the corolla tube represent features of *A. verticillata* that are somewhat intermediate between Mexican species of the two genera. A chromosome number determination for this species is highly desirable and will likely determine its ultimate generic placement. At this time, treating this species in *Aphelandra* rather than *Holographis* is somewhat arbitrary, but follows a conservative taxonomic and nomenclatural course.

ADDITIONAL SPECIMENS EXAMINED.—MEXICO. **Guerrero:** Taxco (Purisima-Pantheon), *R. Abbott 506* (ENCB, GH); Distr. Adama, Temisco, cañón of Río Achotla, *Y. Mexia 8904* (NY); Río de los Sabinos near Los Sabinos, 36–38 km toward Teloloapan from Iguala, *H. Moore 5503* (BM, G, GH, UC, US); near Taxco, *L. Rowntree s.n.* (ARIZ); camino a la torre de microondas Tuxpan, ca. 10 km NE de Iguala, *J. Rzedowski 37165* (ENCB, MEXU). **México:** Distr. Temascaltepec, Ypericones, *G. Hinton 2971* (BM, G, GH, K, MO, NY, TEX, US). **Michoacán:** 14 mi SSW of jct. Hwy. 15 in Zitacuaro toward Huetamo, *T. Daniel et al. 3295* (CAS); Zitacuaro-Enandio, *G. Hinton et al. 13486* (ARIZ, F, GH, K, MICH, MO, NY, TEX, US, W); 3 km S de Paricuaro, sobre la carr. a Tuxantla, *J. Rzedowski 27991* (ENCB). **Morelos:** Cañón de Lobos, KM 120 de la carr. Cuernavaca-Cuautla, *J. Flores C. 246* (ENCB); Sierra Chalchi, S de Tepostlán, *F. Miranda 3807* (MEXU); without locality, *L. Paray s.n.* (MEXU). **State undetermined:** without locality, Expedicíon Malaespina, *L. Neé s.n.* (MA).

2. Aphelandra scabra (Vahl) Smith in Rees, Cyclop. 39(1): *Aphelandra* n. 3. 1818. *Justicia scabra* Vahl, Enum. 1:120. 1804. TYPE.—Without specific locality, date, or collector (on the reverse side of the specimen are the following notations: "Justicia scabra tetrandra" and "Spec: singulam quod possid. Brugm. dedit"); the protologue notes only, "Habitat in America meridionali" (Holotype: C!, photo at US!).

Aphelandra deppeana Schlecht. & Cham. Linnaea 5:96. 1830. TYPE.—MEXICO. **Veracruz:** Hacienda de la Laguna [ca. 15 mi S of Jalapa], September, *C. Schiede 119* (Holotype: B, destroyed, photos at F!, NY!, US!).

Aphelandra haenkeana Nees in DC. Prodr. 11:298. 1847. Type.—MEXICO. **Veracruz:** Cordillera de Veracruz, Mirador, Tacuapan, près des ruisseaux, June–October 1840, *H. Galeotti 909* (Lectotype: K!; see discussion; isolectotypes BR!, G!, P!, US!, W!).

Aphelandra pectinata Willdenow ex Nees in DC. Prodr. 11: 297. 1847. Type.—COLOMBIA. **Córdoba:** mouth of the Río Sinú, *H. Cuming 1099* (Lectotype: K!, designated by McDade in 1984).

Aphelandra fulgens Decaisne, Rev. Hort. ser. 3, 1:21. 1847. Type.—MEXICO. **Veracruz:** Mirador, September 1842, *A. Ghiesbreght 57* (Holotype: P!, photo at US!; isotype P!).

Branched shrub to 3.6 m tall. Young stems subterete to quadrate-sulcate, often with scattered blistery tubercules on the surface, pubescent with (flexuose to) retrorse to retrorse-appressed to antrorse to antrorse-appressed eglandular, often golden or straw-colored trichomes 0.3–1 mm long (at least some antrorse trichomes always present, sometimes restricted to near inflorescence), becoming glabrate. Leaves opposite, subsessile to petiolate, petioles to 85 mm long (naked portion to 35 m long), blades ovate to elliptic to obovate, 50–260 mm long, 19–103 mm wide, 1.4–4.1 times longer than wide, (rounded to) acute to acuminate at apex, gradually to more or less abruptly attenuate-decurrent (often to node) at base, surfaces pubescent with cauline type trichomes (adaxial surface often sparsely so or glabrate), margin entire to sinuate-crenate. Spikes terminal (and often in axils of distal leaves as well), elongate, up to 210 mm long (excluding flowers), 8–25 mm in diameter (excluding flowers) near midspike, rachis pubescent with antrorse eglandular trichomes 0.2–0.9 mm long. Bracts green, often tinged with red or orange, often spreading with age, ovate to elliptic to obovate, 7–18 mm long, 3–7 mm wide, 1.6–2.8 times longer than wide, acuminate, erect or occasionally somewhat spreading at apex, abaxial surface pubescent with antrorse to antrorse-appressed eglandular trichomes 0.05–1 mm long and with 2 clusters of padlike nectaries near margin (one on each side), nectaries (1–)3–10(–16) per cluster, elliptic to circular in outline, 0.2–0.8 mm long, margin ciliate with straight to flexuose eglandular trichomes to 1.2 mm long, coarsely dentate with (1–)3 teeth per side, teeth 0.3–3 mm long. Bractlets lance-subulate to lanceolate, 5–12 mm long, 0.8–1.9 mm wide, attenuate to aristate at apex, abaxial surface pubescent like bracts. Calyx 6–12 mm long, lobes lanceolate, 1.6–3 mm wide at base, acuminate to aristate at apex, abaxial surface sparsely pubescent with trichomes like those of bracts concentrated near distal portion of midvein. Corolla dull red to red-orange, 30–45 mm long, externally pubescent with eglandular trichomes 0.05–2 mm long, upper lip 9–14 mm long, bilobed with lobes triangular, 2–8 mm long at apex, margin not flaring, lower lip 12–17 mm long, lateral lobes appearing attached to upper lip, reduced and often inconspicuous, erect to slightly spreading, triangular to linear 0.2–2.5 mm long, 0.3–1 mm wide, lower-central lobe recurved or coiled, lance-ovate to elliptic, 10–15 mm long, 3–5.5 mm wide, 7.3–24 times longer and 2.8–8 times wider than lateral lobes. Stamens 26–32 mm long, posterior pair inserted 0.5 mm distal to anterior pair, filaments proximally pubescent with filamentous eglandular trichomes, distally glabrous, thecae 3–4.4 mm long (including a short [0.05 mm] basal, spurlike appendage that is sometimes present), anterior pair extended up to 1 mm beyond posterior pair, all 4 apically and dorsally sparsely pubescent with cobwebby or flexuose eglandular trichomes, often becoming glabrate; staminode absent. Style 29–36 mm long, glabrous; stigma asymmetrically funnelform, 0.3–0.7 mm long. Capsule 11–17.5 mm long, glabrous, shiny, often punctate-pitted. Seeds somewhat flattened, subcircular to subtriangular, 3.5–5.3 mm long, 3.3–4.5 mm wide, pubescent with simple to bifurcate to dendritic trichomes 0.05–0.1 mm long (sometimes becoming very sparse or the surface glabrate).

Distribution and Habitat.—Mexico (Campeche, Chiapas, Guerrero, Oaxaca, Quintana Roo, Tabasco, Tamaulipas, Veracruz, Yucatán; Fig. 4), Guatemala, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Venezuela, Guyana, Surinam, and Brazil; plants occur in vegetation types varying from dry to wet (including thorn scrub, tropical deciduous forest, oak forest, pine-oak forest, montane rain forest, and lowland rain forest) at elevations from 10 to 1,200 m. Plants often are found in disturbed habitats as well.

Phenology.—Flowering throughout the year; fruiting: January–April.

Local Names.—“Cola de gallo” (*Chavelas P. et al. ES-2391,* Ver.); “Flor de coyililló” (*Sousa 2058,* Ver.); “Hoja de espanto” (*Menéndez et al. 400,* Tab.); “Palo blanco” (*Boege 497,* Gro.); “sucsumucuy” (*Hernández G. 1517,* Oax.); “sucsumuycuy” (*Hernández G. 920,* Oax.); “Vara blanca” (*Boege 374,* Gro.); “Vara de San José” (*Herrera C. 35,* Gro.).

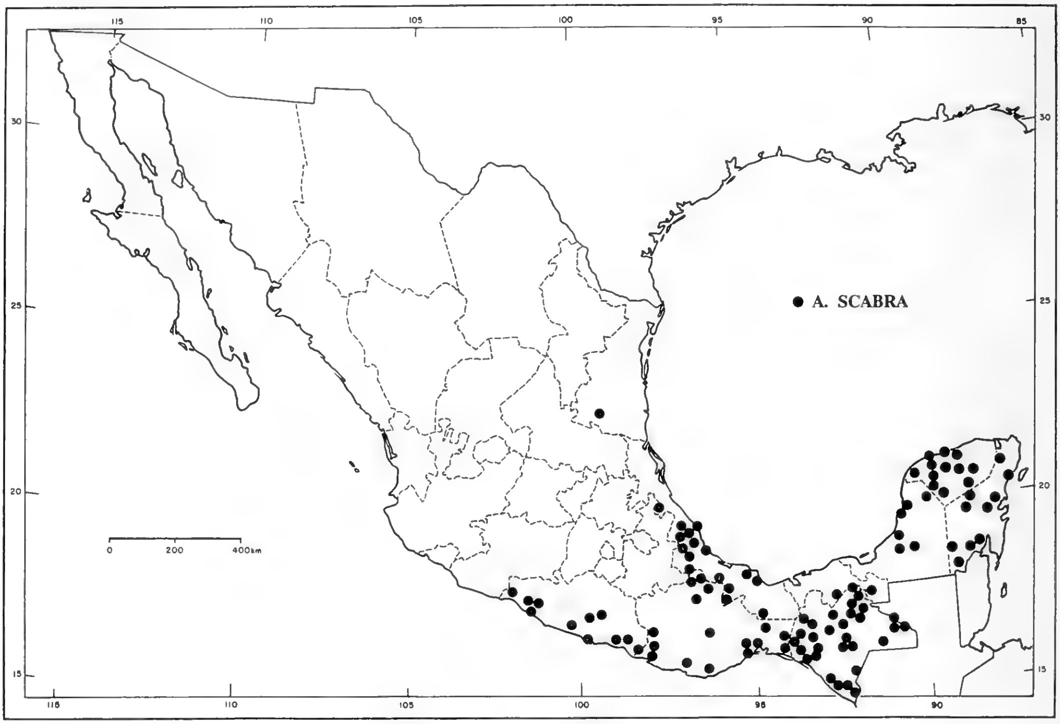


FIGURE 4. Distribution of *Aphelandra scabra* in Mexico.

McDade's (1984) selection of *Galeotti 909* at US as the lectotype of *A. haenkeana* is not in agreement with Article 7.4 of the International Code of Botanical Nomenclature (Greuter et al. 1988) because she designated an isosyntype rather than a syntype. Article 8.1(b) permits another lectotype (i.e., one of the syntypes) to be designated. Thus Galeotti's specimen at K is herewith selected as the lectotype of *A. haenkeana.*

Aphelandra pectinata is listed as a Mexican synonym above because two of the syntypes cited by Nees (1847) were attributed to Mexico. In fact both of these were collected elsewhere in Latin America; Humboldt's collection from the Río Sinú is from Colombia and Sinclair's collection from "Nicoza" is undoubtedly from the vicinity of the Gulf of Nicoya in Costa Rica.

Aphelandra scabra has the most extensive range of any species in the genus, and its ecological amplitude varies from wet to dry forests. Its ability to colonize disturbed habitats likely has been a contributing factor to both its abundance and wide distribution. McDade (1984) noted considerable variation in leaf size and corolla color (pink, orange, and red) in this species. Plants from Mexico vary in leaf size but have only dull or orangish red corollas. It is probably the most easily distinguishable Mexican species of *Aphelandra* due to the presence of nectaries on the abaxial surface of the bracts. Bracteal nectaries are unknown among other Mexican species of *Aphelandra.* Also, the lower lip of the corolla in *A. scabra* (with the lateral lobes small or vestigial and fused to the upper lip and the central lobe becoming recoiled) is unlike that in the other Mexican species.

The distinctive morphology of the corolla and the bracteal nectaries align *A. scabra* with the *A. pulcherrima* complex as delimited by McDade (1984). Among the 13 Central American species in this alliance, McDade (1984) showed that *A. scabra* (as *A. deppeana*) was most closely related to the Panamanian endemic *A. panamensis* McDade, which differs primarily by its longer corollas.

REPRESENTATIVE SPECIMENS EXAMINED.—MEXICO. **Campeche:** Mpio. Champotón, Yohaltun, 18°53′N, 90°20′W, *C. Chan & E. Ucan 871* (F); Monterrey, *C. Lundell 1227* (F); Mpio. Campeche, 15 km NW de Campeche, camino a Mérida, *E. Martínez S. 2977* (MEXU); beyond Hoplachen on Campeche-Mérida rd., *H. Moore 8078* (BM, CAS, US); 16 km SE of Champotón, *J. Taylor & C. Taylor 12667* (NY, US); KM 17 de la carr. Escarcega-Champotón, *O. Téllez et al. 6298* (BM, MO); 15 km S de Campeche sobre la carr. de Champotón a Campeche, *O. Téllez et al. 6394* (CAS). **Chiapas:** 1.5–3.5 mi N of Tuxtla Gutiérrez on rd. to Sumidero, *W. Anderson & C. Laskowski 4224* (DUKE, MICH, US); Mpio. Tapachula, Rancho Santa Isabel, 8 km W de Tapachula, *R. Arcos V. 151* (MEXU); Palenque, *A. Armor V30* (F); Mpio. Tenejapa, Shaki 'Uk'um, paraje of Mahben Chauk, *D. Breedlove 7609* (DS, F, MICH, US); 9 km N of Tuxtla Gutiérrez along rd. to El Sumidero, *D. Breedlove 13879* (DS, F, MICH, US); Mpio. Terán, 6.5 km W of Tuxtla Gutiérrez along Hwy. 190, *D. Breedlove 20154* (DS); Mpio. Ocozocoautla de Espinosa, 32 km SW of Ocozocoautla, *D. Breedlove 27476* (CHAPA, DS, DUKE, MICH, MO, NY); Mpio. Arriaga, 13 km N of Arriaga, *D. Breedlove 28299* (DS, DUKE MICH, MO); Mpio. Las Margaritas, W side of Laguna Miramar, E of San Quintín, *D. Breedlove 33349* (DS, DUKE, F); Mpio. Catazaja, 18 km E of Catazaja, *D. Breedlove 47219* (CAS); Mpio. La Libertad, 15–20 km toward Chancala on rd. to Bonampak from Palenque-Ocosingo rd., *D. Breedlove 49152* (CAS); Mpio. Bachajon, 3 km N of Bachajon-Ocosingo rd. at Temo on rd. to Palenque, *D. Breedlove 52486* (CAS); Mpio. Socoltenango, 30 km ESE of Pugiltic on rd. to Comitán, *D. Breedlove 53638* (CAS, DUKE); Mpio. Ocosingo, near El Real, E of Ocosingo, *D. Breedlove 56376* (CAS, LL); 11 km SW of Fronteras Comalapa along rd. to Motozintla, *D. Breedlove 65534* (CAS); Mpio. Berriozábal, Rancho Cruz Ancho at Pozos de Berriozábal, *D. Breedlove 70400* (CAS); Mpio. Huixtla, 6–8 km NE of Huixtla on rd. to Motozintla, *D. Breedlove & A. Smith 22544* (CHAPA, DS, MO); 2 mi S of Tuxtla Gutiérrez along rd. to Villa Flores, *D. Breedlove & P. Raven 13351* (DS, MICH, US); Mpio. Villa Corzo, along Colonia Vicente Guerrero on rd. to Finca Cuxtepec, *D. Breedlove & J. Strother 46596* (CAS); Mpio. Cintalapa, La Mina Microwave Station, 12 km S of Hwy. 190 near Rizo de Oro, *D. Breedlove & R. Thorne 20667* (DS, DUKE, MO); Mpio. Mapastepec, 10 km SE of Mapastepec, *D. Breedlove & R. Thorne 30734* (CHAPA, DS, MICH); carr. Ocosingo-Palenque, 25 km N de la desviación al Parque Natural Cascadas de Agua Azul, *E. Cabrera & H. de Cabrera 6199* (NY); Tuxtla Gutiérrez, El Zapotal, *C. Cowan 5025* (CAS, TEX); along Hwy. 190, 2.4 mi NE of Oaxaca border, *T. Daniel 1282* (CAS, MICH); along Hwy. 190, 56 km SW of Cintalapa toward Tehuantepec, *T. Daniel et al. 5867* (CAS); Mpio. Tonalá, Cerro Bernal, ca. 25 km SE of Tonalá, *G. Davidse et al. 30143* (CAS, DUKE); 7 km al NE de Belisario Domínguez, carr. Huixtla-Motozintla, *A. Delgado S. et al. 799* (DS, MEXU); Sierra de Soconusco, from Escuipulas to Canada Honda, *E. Hernández X. & A. Sharp X-301* (DS); 6 km al SE de Escuintla sobre la carr. al Panteon, *L. Hilerio A. 5* (MICH); Mpio. Venustiano Carranza, Soyatitán, along rd. from Pinola Las Rosas to Pugiltic, *R. Laughlin 2024* (DS, US), *A. Ton 3106* (DS, DUKE, F); Río Lacantun, several mi above mouth, *C. Lundell 17855* (LL, MO); Ocozocoautla, La Roblada, *T. MacDougall H5* (US); Cintalapa, Rizo de Oro, *T. MacDougall s.n.* (F, NY); El Sumidero, Tuxtla Gutiérrez, *T. MacDougall s.n.* (NY); Simojovel, *T. MacDougall s.n.* (NY); Mpio. Ocosingo, 10 km SE de Crucero Corozal, camino a Boca Lacantum, *E. Martínez S. 7430* (MEXU, NY); Escuintla, *E. Matuda 151* (MICH, MO, US); Mt. Ovando, near Escuintla, *E. Matuda 6162* (F, LL, MO, US), *6198* (LL, MO); San Pedro, *C. Mell 561* (NY, US); Mpio. Amatenango del Valle, 17 km N de Amatenango, *O. Téllez & R. Pankhurst 7071* (MEXU); Mpio. Tenejapa, Tih Ha', paraje of Mahbenchauk, *A. Ton 1395* (DS, F, MICH, US); Mpio. Chiapa de Corzo, El Chorreadero, 5.6 mi SE of Chiapa de Corzo, *A. Ton 2950* (DS, DUKE, NY, US), *3256* (DS, DUKE, F, MICH, NY); Mpio. Simojovel de Allende, along rd. from El Bosque to Simojovel, *A. Ton 3076* (DS, DUKE, MICH, NY); Mpio. Venustiano Carranza, above Finca Carmen along rd. from Acala to Pugiltik, *A. Ton 3211* (DS, MICH, NY); Mpio. Tapachula, La Trinidad, *E. Ventura & E. López 816* (BM); Mpio. Frontera Comalapa, ca. 2.25 km (air) S of Col. Vera Paz, *B. Voorhies & A. Sanchez 72–29* (DS). **Guerrero:** vicinity of Acapulco, *G. Barclay 1973* (BM), *W. Boege 497* (MEXU), *G. Lay & A. Collie s.n.* (BM), *L. Neé s.n.* (MA), *E. Palmer 174* (BM, E, F, K, MO, NY, UC, US), *A. Sinclair s.n.* (E), *Voyage de la Venus s.n.* (P); 5–6 mi E of Acapulco on Hwy. 95, *M. Carlson 3066* (DUKE, F, NY, US); along Hwy. 134 between La Salitrera and Coyuca de Catlán, 18.5–18.9 km NE Hwy. 200, *T. Daniel 5328* (CAS), cuttings from this locale grown at San Francisco Conservatory of Flowers, *T. Daniel 5328cv* (CAS); Mpio. Cuajinicuilapa, camino a Huajintepec a 49 km de la desviación a Cuajinicuilapa, *G. Gaxiola 190* (MEXU); Mpio. San Luis Acatlán, 8 km NE de Horcastitas, *J. González L. 276* (MEXU); Mpio. Cuautepec, San Agustín Cuilutla, *N. Herrera C. 35* (MEXU); Vallecitos, *G. Hinton et al. 9903* (ARIZ, K, NY, US, W), *11477* (ARIZ, DS, K, NY, US, W); Atoyac, *G. Hinton et al. 10919* (ARIZ, F, K, MO, NY, UC, US); Carrizo-El Río, *G. Hinton et al. 14691* (ARIZ, DS, NY, US, W); Mpio. La Unión, 8 km N de La Unión, *S. Koch & P. Fryxell 83117* (CAS, CHAPA, TEX); area del Jardín Zihuatanejo, cerro a 1 km del pueblo de Zihuatanejo, *M. Lad. O. et al. 247* (CAS); La Botella, *E. Langlassé 679* (K, US); La Roqueta Island off Acapulco, *I. Langman 3309* (US); beyond Acahuizotla on hwy. to Acapulco, *H. Moore 5108* (BM, UC, US); between Copala and Juchitango, *E. Nelson 2297* (US); Mpio. Chilpancingo, "Poza azul," 11.7 km W del Ocotito camino a Sta. Bárbara, *R. Torres C. et al. 1857* (CAS, CHAPA); Mpio. Quechultenango, 4 km NE de Colotlipa, *M. Zamora M. 5273* (MEXU, NY). **Oaxaca:** Voca del monte inter Tehuantepec et sinum Mexicanum, *G. Andrieux 131* (K, P, W); Distr. Tuxtepec, Temascal lado E de la Presa Miguel Alemán, *R. Cedillo T. & R. Torres 1044* (LL, MEXU); Chiltepec, *R. Cedillo T. et al. 1649* (CAS, MEXU); Distr. Juchitán, Cerro Santo Domingo, *C. Conzatti 3735* (US); along Hwy. 125 between Pinotepa Nacional and Tlaxiaco, *T. Croat 45777* (CAS, MO); along Hwy. 131 between Puerto Escondido and Sola de Vega, 22.4 km N jct. Hwy. 200, *T. Daniel 5374* (CAS); E of Soledad (near Mitla), *W. Ernst 2555* (MEXU, MICH, US); Mpio. Sta. María Chimalapa, ca. 4–5 km N de Sta. María, *H. Hernández G. 342* (CAS, CHAPA); Mpio. Ixtaltepec, 25 km N de Juchitán, *S. Koch et al. 78292* (MEXU, US); Comaltepec, *F. Liebmann s.n.* (K); Tapesco, S of Tres Cruces, Tehuantepec, *T. MacDougall H56* (US); Putla, S. Vicente, *T. MacDougall s.n.* (F, MICH, NY, US); Tehuantepec, Potrero Villalobos, *T. MacDougall s.n.* (F, NY); Distr. Tuxtepec, Chiltepec and vicinity, *G. Martínez C. 254* (MEXU, UC, US), *808* (MICH); Mpio. Salina Cruz, Santa Cruz Hidalgo, el lado E de Cerro Marimba, *C. Martínez R. 263* (CAS); Mpio. Tehuantepec, Rancho El Limon, 17 km O de Tehuantepec, *C. Martínez R. 926* (CAS); Mpio. Matías Romero, Los Angeles, 20 km NO del entronque con la carr. Matías Romero-Acayucan, *C. Martínez R. 1098* (CAS); Mpio. San Miguel Chimalapa, Arroyo El Caracol, ca. 1 km NO de Congregación Benito Juárez, 16°43′N, 94°09′W, *S. Maya J. 525* (CAS); Cafetal Concordia (Cerro Espino), *B. Reko 3626* (US); Temascal, *M. Sousa s.n.* (MEXU);

El Cerro de Cosolapa, Cosolapa, *J. Vera S. 2617* (MEXU, MICH, US); Dto. Jamiltepec, 3 km NE de Flores Mágon, *P. Tenorio L. et al. 2718* (CAS); Dto. Jamiltepec, Dos Caminos, 12 km del entronque brecha a San Agustín Chayuco con la carr. Jamiltepec-Pinotepea Nacional, *P. Tenorio L. 3066* (CAS); Mpio. Ayautla, 4 km NE de Ayautla, *P. Tenorio L. & G. Dieringer 10695* (CAS, MEXU); Mpio. Sta. María Jacatepec, 28 km SO de Tuxtepec, *R. Torres C. & E. Martínez S. 11077* (CAS); 2.5 km N de Sta. Cruz Flores Mágon y 19 km N de Jamiltepec, *R. Torres C. et al. 1678* (MEXU). **Quintana Roo:** 4 km S de Nuevo Xcan, rumbo a Cobá, *E. Cabrera & L. Cortez 269* (BM, MEXU, NY); 4 km N de Estero Franco, en el camino a Tomás Garrido, *E. Cabrera & H. de Cabrera 3301* (MEXU, MO); en la brecha de Divorciados a La Pantera, por la vía corta a Mérida, *E. Cabrera & G. Durán 750* (CAS, MEXU); en la brecha a Chanca, Ver., 9 km S de Carrillo Puerto, *E. Cabrera & R. Torres 1073* (BM, CAS, MEXU); Hwy. 186, 15 mi W of jct. Hwy. 186 with Hwy. 307, *D. Dreyer 343* (CAS, MEXU); Chichankanab, *G. Gaumer 1488* (F, US); Lake Chichankanab, *G. Gaumer et al. 23650* (BM, K, US); 3 km ENE de F. Carrillo Puerto, camino a Vigía Chico, *H. Quero et al. 2816* (MEXU, MO); 36 km S of Dzuiche on Hwy. 164, 19°40′N, 88°35′W, *K. Roe et al. 1349* (US); 3 km SE de Chunhuhub, *O. Téllez & E. Cabrera 1758* (MEXU, MO, NY); Chetumal, Cenote Azul junto a la Laguna de Bacalar, *A. Villamar s.n.* (DS); KM 6 carr. F. Carrillo Puerto-Cancún, *R. Villanueva 845* (MEXU). **Tabasco:** San Pedro, Ejido López Zamora, *J. Calzada & A. Gómez-Pompa 2304* (F); Mpio. San Pedro Balancán, limite E de la zona de Reserva Federal sur del Plan Balancán-Tenosique, *J. García F. & J. Palma G. 84* (CHAPA); Cerro de Tortugero, 7 km S of Macuspana, *C. Gilly & E. Hernández X. 393* (MICH); 3 km del C-30 sobre la brecha W-0 (Norte 33), Balancán, *F. Menéndez et al. 400* (CAS, MEXU, MO); Balancán, carr. 20, 4 km de la carr. 0 (Cerro) en dirección W, *A. Novelo et al. 32* (K, MO); Parque Nacional de Agua Blanca, Macuspana, KM 64 carr. Villahermosa-Escárcega, 17°38′N, 92°30′W, *L. Ruíz P. 8* (CHAPA); Mpio. Balancán, El Arenal, *F. Ventura A. 20921* (CAS). **Tamaulipas:** near Gómez Farias, ca. 0.5 mi N on rd. to Aguacates, *A. Richardson 946* (TEX). **Veracruz:** El Salto de Eyipantla, 8 km de Sihuapan, San Andrés Tuxtla, *J. Calzada 1052* (CAS, F, NY), *1626-B* (BM, CAS, CHAPA); Mpio. Playa Vicente, Ejido Piedra de Cal, *J. Chavelas P. et al. ES-4281* (MEXU); 17 km de Palma Sola, hacia Cardel, *F. Chiang 334* (MEXU); Dos Ríos, Cerro Gordo, *J. Dorantes 367* (F, MO); ladera NE del Cerro Monte de Oro, *J. Dorantes et al. 922* (CAS, F); Laguna Verde, Alto Lucero, *J. Dorantes et al. 5082* (BM, F, MEXU); Region of San Andrés Tuxtla, *R. Dressler & Jones 230* (BM, MICH, MO, NY, UC, US); Mpio. Jesus Carranza, along Río Jaltepec, *C. Gilly 36* (MICH); Laguna near Veracruz, *J. Greenman 71* (F, NY); Río Antigua ca. 38 km WNW of Veracruz toward Xalapa, 19°18′N, 96°28′W, *H. Iltis & A. Lasseigne 843* (F, US); Zacuapan, *F. Liebmann s.n.* (K); Consoquitla pr. Mirador, *F. Liebmann s.n.* (K); Mirador, *J. Linden 189* (G, K); Atoyac, NO de Cordoba, *A. Lot 555* (CAS, F); Mpio. de Cosamaloapan, Aleman, *G. Martínez C. 1150* (BM, CAS, F, MEXU, MICH, MO, NCU, US); Mpio. Coatepec, 5 km (air) SE of Tuzamapan, *M. Nee & K. Taylor 26016* (NY); Zacuapan, *C. Purpus 1938* (BM, E, F, MO, NY, UC, US); Banos del Carrizal, *C. Purpus 6073* (E, UC); Zacuapam, Rancho Viejo, *C. Purpus 10878* (BM, DS, M, MICH, UC, US); Buenaventura, *H. Ross 1077* (M); Salta de Ayipantla, 5 km S of San Andrés Tuxtla, *S. Solheim & V. Powers 868* (WIS); Mpio. Zapata, La Laja, entre Corral Falso-Pinoltepec, carr. Jalapa-Veracruz, *L. Trejo 85* (MEXU); Mpio. San Pedro Soteapan, 2 km Soteapan camino Las Cascadas, 18°14′N, 94°52′W, *F. Vasquez B. & D. Hernández L. 89* (F); Mpio. Hidalgotitlán, Río Soloxuchil entre Hermanos Cedillo y La Escuadra, *M. Vasquez et al. 985* (MEXU, NCU); Mpio. de Dos Ríos, Miradores de Poblado, *F. Ventura A. 2544* (DS, MICH, NY); Puente Nacional, *F. Ventura A. 2637* (CAS, MICH, NY); Mpio. Totutla, Encinal, *F. Ventura A. 7049* (MICH); Mpio. Puente Nacional, La Ceiba, *F. Ventura A. 9235* (MICH); Mpio. Alto Lucero, Blanca Espuma, *F. Ventura A. 9326* (MICH); Mpio. Actopan, Villa Nueva, *F. Ventura A. 12101* (MEXU); Mpio. Emiliano Zapata, "La Laja," 16 km SE de Xalapa, *L. Villarreal 79949* (IBUG). **Yucatán:** Cenote Ainil ca. 6 mi N of Muna, *M. Butterwick 184* (LL); 8 km O de Cacalchen, carr. Texkokob-Tekanto, *E. Cabrera & H. de Cabrera 9474* (MEXU); Sayil, 36 km SO de Oxkutzcab, *E. Cabrera & H. de Cabrera 9562* (MEXU); Coba, *R. Crockett 150* (US); vic. of Sayil, *S. Darwin et al. 2166* (F, MO); Uxmal, near ruins, *O. Degener & I. Degener 26785* (NY, US, W), *A. Schott 671* (BM); Mpio. Oxkutzcab, 4 km W de Sayil, *A. Espejo et al. 1233* (CHAPA); Uayma, ca. 20 km NW von Valladolid, 20°44′N, 88°19′W, *H. Flügel & E. Geiseler 7017* (B); near Izamal, *G. Guamer 300* (ARIZ, BM, CAS, DS, E, F, K, MICH, MO, NY, UC, US, W), *s.n.* (F), *C. Seler & E. Seler 3932* (F); Kancabconot, *G. Guamer et al. 23587* (F, MA, MO, UC, US); Mpio. Valladolid, 2.5 km del Poblado Unión Libre a Yaxcabá, *M. Magaña & S. Zamudio 524* (CHAPA, MEXU); rd. to Tepakaam, *C. Millspaugh 91* (CAS, F, US); Mpio. Chablekal, Dzibichaltun, *M. Ordonez 43* (F); Col. 18 km N of Colonia, *R. Read et al. 79-005* (US); Chichén Itzá, *V. Rudd 2033* (US), *W. Steere 1481* (MICH); Mpio. Santa Elena, 0.5 km SW of entrance rd. to Kabah archaeological site on Hwy. 261, between Hopelchén and Mérida, *A. Sanders et al. 9619* (CAS); Muna, *W. Steere 2151* (F, MICH, MO); Progreso, *W. Steere 3012* (MEXU, MICH, US); Hacienda Chunchucmil, 30 km NW of Maxcanu, ca. 20°41′N, 90°13′W, *L. Ortega T. & E. Mena P. 746* (CAS); Mpio. Dzoncauich, Chacmay, 21°02′N, 88°57′W, *P. Yam P. & L. Yam O. 40* (F). **State undetermined:** without locality, *Grisebach s.n.* (K), *E. Kerber s.n.* (US), *J. Linden s.n.* (MICH), *M. Sessé et al. 280* (MA), *290* (MA), *300,* (F, MA), *s.n.* (BM, OXF).

3. **Aphelandra aurantiaca** (Scheidw.) Lindl. Bot. Reg. 31:pl. 12. 1845. *Hemisandra aurantiaca* Scheidw. Bull. Acad. Sci. Bruxelles 9: 22. 1842. Type.—Bot. Reg. 31:t. 12. 1845 (Neotype, designated here; see discussion).

Aphelandra acutifolia Tafalla ex Nees in DC. Prodr. 11:299. 1847. Type.—MEXICO. **Oaxaca:** Sierra S. Pedro Nolasco, Talea, etc., 1843–44, *C. Jürgensen 648* (Lectotype: K ex hb. Hooker!, designated here; isolectotypes: BM!, G!, photo at US!; see discussion).

Aphelandra aurantiaca var. *roezlii* Ortgies ex L. Van Houtte, Fl. Serres Jard. 17:53. 1868. (as "roezli"). Type.—Fl. Serres Jard. 17:t. 1741–1742. 1868 (Lectotype, designated here; see discussion).

Aphelandra roezlei E. Carrière, Rev. Hort. 44:100. 1872. Type.—(see discussion).

Mostly unbranched (monocaulous) perennial herb to 1.2 m tall. Young stems somewhat flattened, glabrous or rarely sparsely pubescent with retrorse eglandular trichomes 0.1–0.3 mm long.

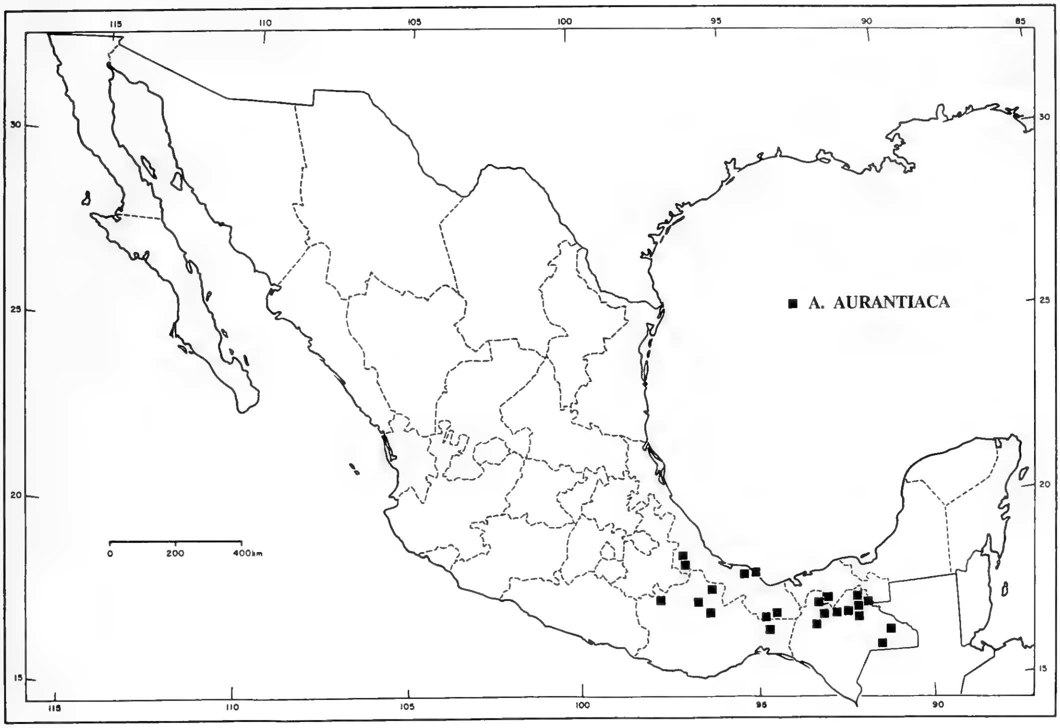


FIGURE 5. Distribution of *Aphelandra aurantiaca* in Mexico.

Leaves opposite, petiolate, petioles to 50 mm long (naked portion to 35 mm long), blades ovate to ovate-elliptic to elliptic, 55–260 mm long, 25–115 mm wide, 1.7–3.8(–6.3) times longer than wide, acuminate (to rounded-apiculate) at apex, rounded to abruptly or gradually attenuate-decurrent (sometimes nearly to node) at base, surfaces glabrous or with scattered trichomes along midvein on abaxial surface, margin entire to subcrenate. Spikes terminal (and sometimes in axils of distal leaves as well), elongate, up to 200 mm long (excluding flowers), 15–33(–55) mm in diameter (excluding flowers) near midspike, rachis pubescent with straight to flexuose to antrorse eglandular and glandular (sometimes absent) trichomes 0.1–0.4 mm long. Bracts green or reddish (sometimes green with reddish coloration at margin and apex), sometimes spreading with age, lance-ovate to ovate-elliptic to elliptic, 15–37 mm long, 6–15 mm wide, 2.3–4.2 times longer than wide, acuminate and erect at apex, abaxial surface sometimes impressed punctate, pubescent with antrorse (near base of bract) to straight eglandular trichomes 0.05–0.2 mm long and glandular trichomes 0.05–0.2 mm long (the latter sometimes not evident on older bracts), proximal bracts sometimes also pubescent with antrorse to antrorse-appressed eglandular trichomes to 0.4 mm long, margin ciliate with eglandular trichomes to 0.4 mm long, dentate with 7–15 teeth per side, teeth 0.1–2 mm long. Bractlets subulate to lance-subulate to lanceolate, 7–15 mm long, 0.5–2 mm wide, subaristate to aristate at apex, abaxial surface pubescent like bracts (although with glands often more conspicuous). Calyx (sometimes bilabiate with posterior 2 lobes fused nearly to apex) 10.5–16.5(–19) mm long, lobes lanceolate to lance-subulate, 1.5–3 mm wide at base, attenuate to aristate at apex, abaxial surface pubescent like bractlets. Corolla orange to reddish orange (often with yellow markings on inner surface of lips) or yellow, 50–63 mm long, externally pubescent with eglandular and glandular (often absent) trichomes 0.05–0.2 mm long, upper lip 17–25 mm long, entire to emarginate with rounded lobes up to 0.3 mm long at apex, margin flaring along most or all of the 2 vertical sides, lower lip ± perpendicular to upper lip, 17–25 mm long, lateral lobes obovate to elliptic to ovate-elliptic, 9.5–15 mm long, 5–10.5 mm wide, lower-central lobe ovate-elliptic to elliptic to obovate, 14–25 mm long, 7–16 mm wide, 1.5–1.8 times longer and 1.4–2.2 times wider than lateral lobes. Stamens 39–51 mm long, posterior pair inserted ca. 0.5 mm distal to anterior pair, filaments pubescent with eglandular trichomes throughout their length (more abundant distally than proximally), thecae 4–5 mm long, pairs presented at ca. same height, all apically and dorsally pubescent (sometimes sparsely so) with cobwebby trichomes; staminode reduced to a thickened callous. Style 45–57 mm long, pubescent (especially proximally, becoming less so distally) with eglandular trichomes; stigma unequally bilobed (often appearing obliquely funnelform) with 1 lobe 0.4–1 mm long, the other nearly obsolete or 0.1–0.2 mm long. Capsule 12.5–17 mm long, pubescent with straight to flexuose to retrorse to antrorse eglandular and glandular (at least on distal portion) trichomes 0.05–0.2(–0.5) mm long. Seeds flattened, subcircular to somewhat squarish, 3.3–5.5 mm long, 2.8–4.5 mm wide, covered with coarse, mostly appressed, often apically bifurcate trichomelike papillae 0.05–0.2 mm long.

Distribution and Habitat.—Southern Mexico (Chiapas, Oaxaca, Tabasco, Veracruz; Fig. 5), Guatemala, Belize, Honduras, Costa Rica, Panama, Colombia, Surinam, French Guiana, Ecuador, Peru, Brazil, Bolivia; plants occur in lowland and montane rain forests at elevations from 50 to 1,700 m

Phenology.—Flowering: throughout the year; fruiting: November–March.

In the protologue of *Hemisandra aurantiaca* a type was not designated and neither specimens nor illustrations were cited. Scheidweiler (1842) noted that plants of this species were grown in the Royal Greenhouses at Laeken and at the Jardin Botanique de Bruxelles in 1839 from seeds procured in Mexico. The only specimen originating from cultivation at BR is a sheet from the Martin Martens collection received in 1932 with the notation, "ex horto 1852." It is not known whether this collection was made from plants originally introduced in Belgium in 1839. In the absence of a holotype or any materials from which to choose a lectotype, the first illustration of this species to be published—that accompanying Lindley's new combination—is selected as the neotype. Further information concerning the origin of the plants cultivated in Belgium was provided by Van Houtee (1868). He noted that the plant treated by Lindley as *A. aurantiaca* was discovered in Tabasco, near Teapa, at an altitude of 2,500 feet by Linden. The plant was sent to Belgium and propagated there. Two of Linden's collections of this species from near Teapa are extant in various herbaria (see below).

Syntypes from Mexico, Peru, and Surinam were cited by Nees for *A. acutifolia.* Wasshausen (1975) included all of the syntypes (or isosyntypes) within *A. aurantiaca.* A specimen of the Mexican collection is selected here as the lectotype.

The protologue of *A. aurantiaca* var. *roezlii* indicates that the name is based on cultivated plants obtained by Benedict Roezl in Mexico (Van Houtte 1868). McVaugh (1972) noted that Roezl rarely, if ever, preserved herbarium specimens of his American collections for European gardens. In any event, the location of Van Houtte's herbarium and types is unknown (Stafleu and Cowan 1986). The colored plate (1741–1742) opposite page 53 in the protologue is herewith designated as the lectotype of *A. aurantiaca* var. *roezlii* because it is the only known element from the original material eligible to serve as the nomenclatural type (Greuter et al. 1988, Art. 7).

Wasshausen (1975) treated the name *A. roezlei* as a combination based on *A. aurantiaca* var. *roezlii.* Undoubtedly the name is derived from Van Houtte's variety; however, because he neither indicated the name as a new combination nor listed the basionym, Carrière's name must be treated as designating a new species rather than comprising a new combination. The protologue of *A. roezlei* appears to be based largely on cultivated plants. No specimens or illustrations were cited. A neotype would have to be selected in order to typify this name.

Both *A. aurantiaca* var. *roezlii* and *A. roezlei* were distinguished primarily by the light-colored regions of the leaves. Although some collectors of *A. aurantiaca* from adjacent countries (e.g., Belize: *Schipp 1063,* MICH) have noted a light-colored mottling on the leaves of some plants, such was not noted on labels of Mexican collections examined in this study. Some conspicuous whitish or grayish coloration along the major veins is evident among dried specimens of several Mexican collections (e.g., *Martínez C. 397,* MICH), however. This type of variation in leaf coloring is particularly evident in some South American representatives of *A. aurantiaca* (e.g.,

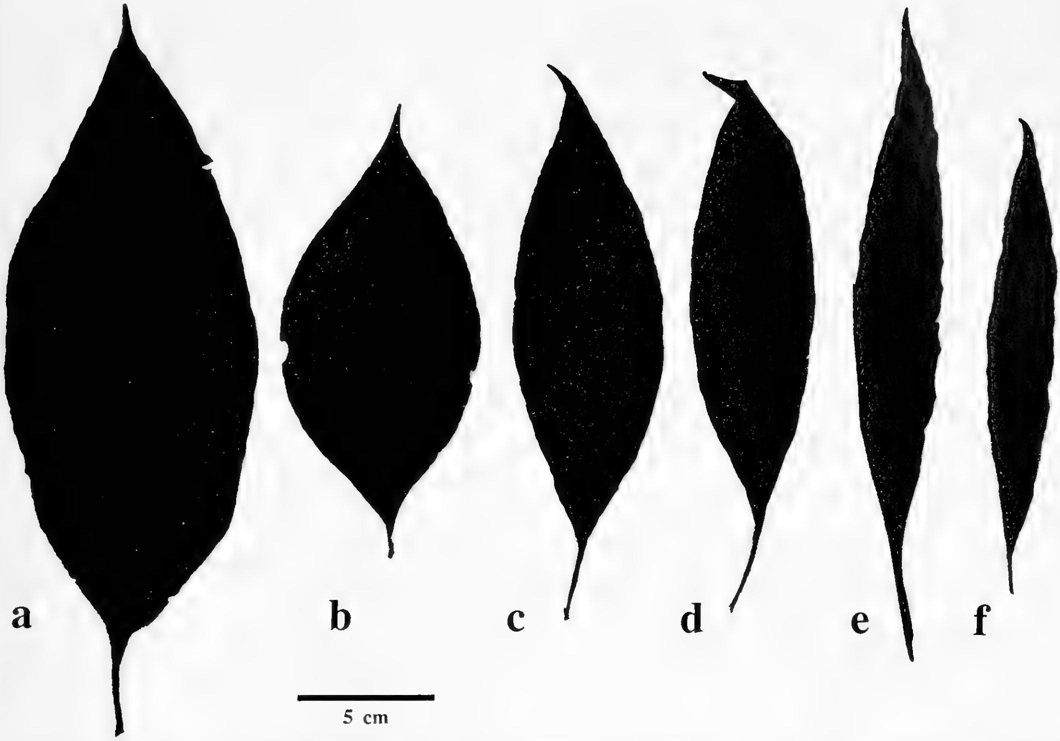


FIGURE 6. Leaf variation among Mexican specimens of *A. aurantiaca.* a, *Daniel & Wendt 5808* (Veracruz); b, *Nava Z. s.n.* (Veracruz); c, *Hernández G. 1591* (Oaxaca); d, *Calzada 59* (Veracruz); e, *Hernández G. 1463* (Oaxaca); f, *Hernández G. 1463* (Oaxaca). All leaves are from one of the distalmost three nodes.

those described as *A. fascinator* Linden & André) and is noted below for *A. speciosa.*

Aphelandra aurantiaca is the second most widely distributed species of the genus and is commonly cultivated for ornament. In Mexico its distribution is limited to regions with abundant rainfall. The species is readily recognizable by the combination of its somewhat flattened young stems and pectinately dentate bracts. There is some variation in corolla and perhaps leaf coloration as noted above, but otherwise, Mexican plants are generally homogeneous. Plants resembling *A. aurantiaca* but with somewhat narrower, sinuately margined leaves were described from Peru as *A. repanda* Nees and from northern Central America as *A aurantiaca* var. *stenophylla* Standley. Wasshausen (1975) treated such plants from Guatemala to Peru as var. *stenophylla,* whereas Gibson (1974) recognized them as *A. repanda.* Standley (1929) noted that narrow-leaved plants frequently occur with broader leaved ones and that "intermediate forms" were not encountered in various localities where the two were growing together. Indeed, the narrow-leaved plants appear to be a sporadic form that occurs with the more typical form throughout the range of the species. Therefore it is not surprising that narrow-leaved individuals have recently been collected in Mexico as well (e.g., *Hernández G. 1463*). Figure 6 illustrates some of the variation in leaf form among Mexican specimens of *A. aurantiaca.* Such variation is suggestive of a continuum within a single species.

REPRESENTATIVE SPECIMENS EXAMINED.—MEXICO. **Chiapas:** Mpio. Rayon, 10 km above Rayon Mezcalapa along rd. to Jitotol, *D. Breedlove 26116* (DS); Mpio. Solosuchiapa, 3–5 km above Solosuchiapa along rd. to Tapilula, *D. Breedlove 26460* (DS, MO); Mpio. Berriozábal, 13 km N of Berriozábal near Pozo Turipache and Finca El Suspiro, *D. Breedlove 31250* (DS); Mpio. Palenque, vicinity of Agua Azul, *D. Breedlove & F. Almeda 57256* (CAS); Mpio. Palenque, 6–12 km S of Palenque on rd. to Ocosingo, *D. Breedlove & R. Dressler 29788* (DS, MEXU); Mpio. La Libertad, 15–20 km toward Chancala on rd. to Bonampak from the Palenque-Ocosingo rd., *D. Breedlove 49151* (CAS, TEX); Mpio. Chilon, along rd. to Pozo Cuevas above Agua Azul, *D. Breedlove & F. Almeda 57212* (CAS); Mpio. La Trinitaria, KM 21–23 along rd. from Lago Tzicao to Santa Elena, *D. Breedlove & T. Daniel 71287* (C, CAS, K, MEXU, MO, NY, TEX); Mpio. Ocosingo, Arroyo Nayte, 8 km NE de Crucero Corozal, camino Palenque-Boca Lacantum, *E. Martínez S. 8484* (MEXU, NY); Cerro Tres Picos, N.O. Simojobel, *F. Miranda 5661* (MEXU); between Tumbala and El Salto, *E. Nelson 3377* (US). Oaxaca: 10 mi from Huajuapan de León toward Tehuacán, *R. Barr & Dennis 65–373A* (ARIZ); Chinantla près Lacoba, *H. Galeotti 914* (BR); Lalana, *H. Galeotti 946* (BR, G, P, W); Mpio. Santa María Chimalapa, Arroyo Milagrito, ca. 6 km SE de Sta. María, *H. Hernández G. 440* (CAS, CHAPA); Mpio. Sta. María Chimalapa, Arroyo Monte Rico, ca. 18 km E de Sta. María, 16°55′N, 94°34′W, *H. Hernández G. & C. Gonzâlez L. 1591* (CAS); Lobani, Chinantla, *F. Liebmann 10603* (C), *s.n.* (K); San Pedro Tepinapa, Chinantla, *F. Liebmann 10604* (C); Comaltepeq, *F. Liebmann s.n.* (K); entre Puerto Eligio a Comaltepec, KM 153 entre Tuxtepec a Oaxaca S. Juarez, *G. Martínez C. 397* (DS, F, MEXU, MICH, UC, US). **Tabasco:** Mpio. Teapa, KM 4 de la carr. Teapa-Tapijulapa, *M. Magaña & S. Zamudio 987* (MO); Teapa, *J. Linden 177* (G, K, P), *540* (BR, G); Mpio. Teapa, El Madrigal, *F. Ventura A. 20990* (MEXU), *F. Ventura A. 21223* (CHAPA). **Veracruz:** Sierra de Tuxtla, 4 mi ENE of Tapalapa, *R. Andrle 87* (US); Mpio. Catemaco, lado NE de Lago Catemaco en cerros al E de Coyame, *J. Beaman 5195* (CAS, F, MEXU, US); Valle de Cordova, *E. Bourgeau 1998* (BR, C, K, P, US); Estación de Biología Tropical Los Tuxtlas, *J. Calzada 59* (CAS, F, MEXU, MICH, US); Mpio. Minatitlán, Zona de Uxpanapa, 13.7 km E of La Laguna toward Uxpanapa, then 6.5 km N toward Belisario Domínguez, *T. Daniel & T. Wendt 5808* (CAS, CHAPA); Estación de Biología Tropical Los Tuxtlas, UNAM camino a la Laguna Escondida, 18°35′N, 95°01′W, *M. Dillon et al. 1781* (F, US), *A. Villegas H. 29* (F); between Sontecomapan and Montepio, *A. Faberge s.n.* (MEXU, TEX); Playa Escondida, *B. Hawkins 102* (MIN); Est. Biol., Sontecomapa, *R. Hernández et al. 483* (DS, LL, MEXU, MO, NY, US); Catemaco, *T. MacDougall 31* (US); Buena Vista, Catemaco, *T. MacDougall 564.S* (F, MICH, NY), *s.n.* (US); Est. Biol. San Andrés Tuxtla, *G. Martínez C. 1774* (CAS, CHAPA, F, MEXU, MICH, MO, US), *2198* (F); 5.7–6 mi from Catemaco on rd. to Sontecomapan, *H. Moore & G. Bunting 8930* (UC, US); Cordova, *F. Müller 2189* (NY), *2215* (NY, W); Mpio. Hidalgotitlán, Río Solosúchil, 2–3 km SE of Augustín Melgar, 17°14′N, 94°33′W, *M. Nee & K. Taylor 29945* (F); Mpio. San Andrés Tuxtla, Balzapote, *G. Shapiro 262* (MEXU); El Vijía de Santiago Tuxtla, *M. Sousa 2580* (MEXU); al pie del Cerro Cochinitos, muy cerco de Coyame, al NE de la Laguna de Catemaco, *M. Sousa & M. de Sousa 94* (CAS, MEXU, US); Mpio. Santiago Tuxtla, Loma Quemada, *F. Ventura A. 14894* (MA), *15612* (MEXU); La Sierra de Lobardia, vic. of Ejido de Pueblo Nuevo, 15–25 km N of Campo Exp. de Hule, El Palmar, Zongolica, *J. Vera S. 2370* (MICH); Mpio. Hidalgotitlán, Manchon al N del Capamento La Laguna, 17°17′N, 94°30′W, *T. Wendt et al. 2725* (CAS, TEX). COUNTRY UNDERMINED.—Nueva Espagna, *J. Mociño & M. Sessé s.n.* (OXF); without locality, *M. Sessé & J. Mociño 281* (F, MA).

4. Aphelandra speciosa T. Brandegee, Univ. Calif. Publ. Bot. 6:196. 1915. TYPE.—MEXICO. **Chiapas:** Finca Mexiquito, July 1913, *C. Purpus 6995* (Holotype: UC!; isotypes: see discussion).

Shrub to 4 m tall. Young stems terete to quadrate or somewhat flattened, glabrous or sparsely pubescent with antrorse eglandular trichomes 0.2–0.3 mm long. Leaves opposite, petiolate, petioles to 140 mm long (naked portion to 135 mm), blades ovate-elliptic to elliptic to obovate-elliptic, 135–340 mm long, 32–140 mm wide, 1.8–4.9 times longer than wide, acuminate to subfalcate at apex, (acute to) gradually attenuate at base, surfaces glabrous or nearly so, margin entire. Spikes terminal, elongate, up to 210 mm long (excluding flowers), 30–70 mm in diameter (excluding flowers) near midspike, rachis glabrous. Bracts reddish, arching away from rachis, elliptic to obovate, 26–45(–55) mm long, 15–30 mm wide, 1.3–2.1 times longer than wide, abruptly apiculate (to cirrhous) at apex with apiculum usually reflexed-coiled (except on lowermost bracts) and often breaking off, abaxial surface glabrous, margin sparsely ciliate with straight to flexuose eglandular and glandular trichomes 0.1–0.5 mm long or becoming glabrate, entire or rarely irregularly and inconspicuously toothed with 1–2 teeth (0.1–0.3 mm long) per side. Bractlets lanceolate, 9–18 mm long, 1.7–2.8 mm wide, attenuate at apex, abaxial surface glabrous. Calyx 13–17 mm long, lobes linear to lanceolate, 2.8–3.9 mm wide at base, abruptly acuminate at apex, abaxial surface glabrous. Corolla red, 55–62 mm long, externally glabrous (Mexican specimens, see discussion below), upper lip 17–22 mm long, entire at apex, margin apprently flared along most of the vertical sides, lower lip apparently somewhat reflexed, 19–27 mm long, lateral lobes obovate, 10–14 mm long, 4.5–5.5 mm wide, lower-central lobe elliptic 19–26 mm long, 10–14 mm wide, 1.7–2 times longer and 2.8–2.9 times wider than lateral lobes. Stamens 45–55 mm long, posterior pair inserted ca. 1 mm distal to anterior pair, filaments proximally pubescent with filamentous eglandular trichomes, distally glabrous, thecae 6–8 mm long, pairs presented at ca. same height, apically glabrous, posterior pair often dorsally pubescent; staminode 15 mm long, pubescent. Style 54-58 mm long, glabrous; stigma symmetrically funnelform, 02.–0.3 mm long. Capsule 18–23 mm long, glabrous, punctate-pitted. Seeds somewhat flattened, subelliptic, 5.2–7.5 mm long, 4.2–5.5 mm wide, surface covered with subclavate papillae that are prominent on immature seeds and become less so or mostly restricted to margin on mature seeds.

DISTRIBUTION AND HABITAT.—Southern Mexico (Chiapas; Fig. 7) and Guatemala; plants occur in regions of wet forest at elevations from 900 to 1,800 m.

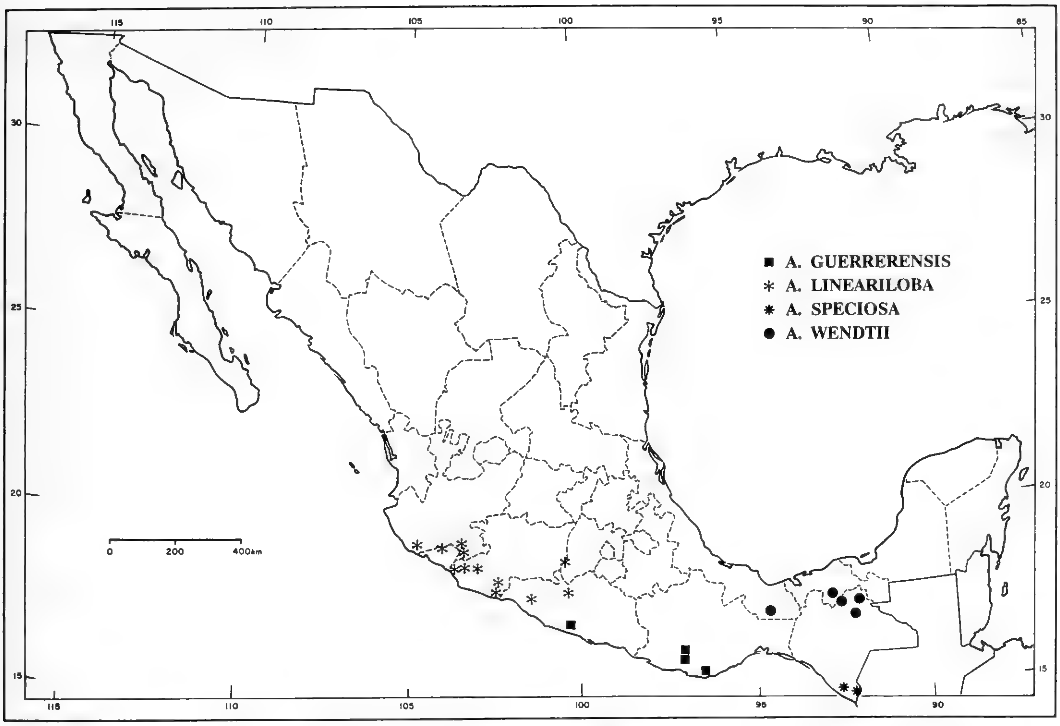


FIGURE 7. Distribution of *Aphelandra guerrerensis, A. lineariloba, A. speciosa,* and *A. wendtii* in Mexico.

PHENOLOGY.—Flowering: May-October and January; fruiting: March, July, August, October.

LOCAL NAMES.—"Flor de mayo" (Gibson 1974, Guatemala); "flor de la Santa Cruz de Mayo" (Gibson 1974, Guatemala).

The locality provided on *Purpus 6995* at the herbaria cited below is given as Finca Irlanda and the date of collection as June 1914. Because the locality and date are at variance with the holotype at UC, these specimens may not represent isotypes. Sousa S. (1969) noted that these localities are different and that Purpus collected at Finca Mexiquito (15°06′N, 92°16′W) during June through September of 1913 and at Finca Irlanda (15°09′N, 92°19′W) during August through September of 1913 and May through June and September of 1914.

The above description includes information from Central American collections as well as those from Mexico. Although there are few collections of this species with well preserved flowers, some variation in corolla pubescence was noted. Corollas of *Skutch 1496* have glands up to 0.2 mm long on the abaxial surface of the lower lip. *Walker 448* has a few sparse eglandular and glandular trichomes on the lower lip. Both of these collections are from Guatemala. Other collections from Guatemala and Mexico with corollas appear to have glabrous lower lips. Variability in leaf coloration was observed in a population of this species in Guatemala. Skutch noted on his flowering collection *1496* that the midvein and the basal portion of the secondary veins were white. This coloration is still evident on the dried specimen. On his subsequent collection (*1538*) of fruiting material from this population a few days later, he noted that the white coloration was no longer evident.

Possible relatives of *A. speciosa* are unknown. The species, with its bracts that are brightly colored, leathery in texture, arching away from the rachis, apically apiculate to cirrhous, and abaxially essentially glabrous, is morphologically unlike other species from Mexico and northern Central America. Species from southern Central America and South America with a superficial resemblance (e.g., large leathery bracts) to *A. speciosa* include: *A. darienensis* Wassh., *A. hirta* (Klotzsch) Wassh., *A. liboniana* Linden ex Hooker, and *A. martiusii* Wassh.

ADDITIONAL SPECIMENS EXAMINED.—GUATEMALA. **Quezaltenango:** 3 km S. of Sta. María Planta Eléctrica on Hwy. 9s, 14°40′N, 91°30′W, *K. Roe et al. 720* (US); Finca St. John, ca. 5 km S of Sta. María de Jesus on slopes of Volcán Sta. María, *J. Walker 448* (GH). **San Marcos:** La Trinidad, ca. 2 km from Finca Armeria above San Rafael, *T. Croat 40837* (MEXU); Canjutz, *G. Salas 16* (US). **Suchitepequez:** Finca Moca, *A. Skutch 1496* (A, US). *1538* (A, US); Volcán Santa Clara, 1.5–2 mi W of Finca El Naranjo, *J. Steyermark 46800* (US). MEXICO. **Chiapas:** El Mango, Guatimoc, Cacaohoatan, *R. Hernández M. 2354* (MEXU); Corcega, Pueblo Nuevo Com., *E. Matuda 17656* (DS, F, MEXU); Finca Irlanda, *C. Purpus 6995* (A, BM, F, GH, MO, NY, US); Finca Irlanda, Soconusco, *H. G. 11* (DS), *16* (DS).

5. **Aphelandra leariloba** Leonard, Kew Bull. 1938:63. 1938. TYPE.—MEXICO. **México:** Distr. Temascaltepec, Villaneda, 22 February 1935, *G. Hinton et al. 7412* (Holotype: K!; isotypes: ARIZ!, BM!, F!, G!, GH!, MO!, NY!, US!).

Erect branched shrub or small tree to 3 m tall. Young stems terete to subquadrate-fluted, pustulate (i.e., with protruding blisterlike lenticels), glabrous or distally pubescent with ascendant-appressed eglandular trichomes to 0.4 mm long. Leaves opposite, petiolate, petioles to 120 mm long (naked portion to 50 mm long), blades elliptic to ovate, 50–200 mm long, 18–105 mm wide, 1.7–2.4 times longer than wide, acuminate to falcate at apex, gradually to abruptly attenuate-decurrent (often nearly to node) at base, surfaces pubescent with antrorse eglandular trichomes (especially along major veins), margin entire to subcrenate. Spikes terminal (and sometimes in axils of distal leaves as well), elongate, up to 300 mm long (excluding flowers), 18–30 mm in diameter (excluding flowers) near midspike, rachis pubescent with straight to flexuose eglandular and glandular trichomes 0.05–0.5 mm long. Bracts reddish with green veins, sometimes spreading with age, obovate to elliptic to subcircular, 13–25 mm long, 7–14 mm wide, 1.6–2.3 times longer than wide, acute-mucronate and erect at apex, abaxial surface and margin pubescent like rachis, margin entire (or sometimes with a tooth to 0.4 mm long along 1 or both sides). Bractlets lanceolate to lance-subulate, 7–13 mm long, 1–2.5 mm wide, aristate at apex, abaxial surface pubescent like bracts. Calyx 10–15 mm long, lobes lanceolate, 1.5–3.5 mm wide at base, subaristate to aristate at apex, abaxial surface pubescent like bracts. Corolla reddish (proximal portion of corolla tube greenish yellow, distal portion of tube reddish, throat and external surface of lips faded red to cream, limb internally maroon except pale red to cream at apices of lips), 30–42 mm long, externally pubescent with glandular and eglandular trichomes 0.05–0.2(–0.5) mm long, upper lip 6–13 mm long, entire or bilobed with rounded lobes 0.5–1 mm long at apex, margin not flared, lower lip at first ± perpendicular to upper lip, soon reflexed, 3.5–9 mm long, lateral lobes linear, 2.5–8 mm long, 0.6–1 mm wide, eventually withering during anthesis, lower-central lobe linear, 3–9 mm long, 0.8–2 mm wide, 1.2–1.3 times longer and 1.3–2.2 times wider than lateral lobes. Stamens 27–32 mm long, posterior pair inserted ca. 1 mm distal to anterior pair, filaments pubescent (at least proximally) with filamentous eglandular trichomes, anterior pair also distally pubescent with conspicuously flattened eglandular trichomes, thecae 2–3 mm long, pairs presented at ca. same height, all apically (and posterior pair dorsally) pubescent with cobwebby eglandular trichomes; staminode a triangular callous 0.3 mm long. Style 30–35 mm long, pubescent with eglandular trichomes proximally and becoming glabrous distally; stigma unequally bilobed with 1 lobe 1.5–2 mm long and the other 0.4–0.6 mm long. Capsule 14–18 mm long, pubescent with mostly straight eglandular trichomes 0.1–0.2 mm long. Seeds flattened, subcircular, 3–4.5 mm long, 2.7–3 mm wide, pubescent with stiff, simple to dendritic trichomes 0.1–0.2 mm long. (Fig. 8).

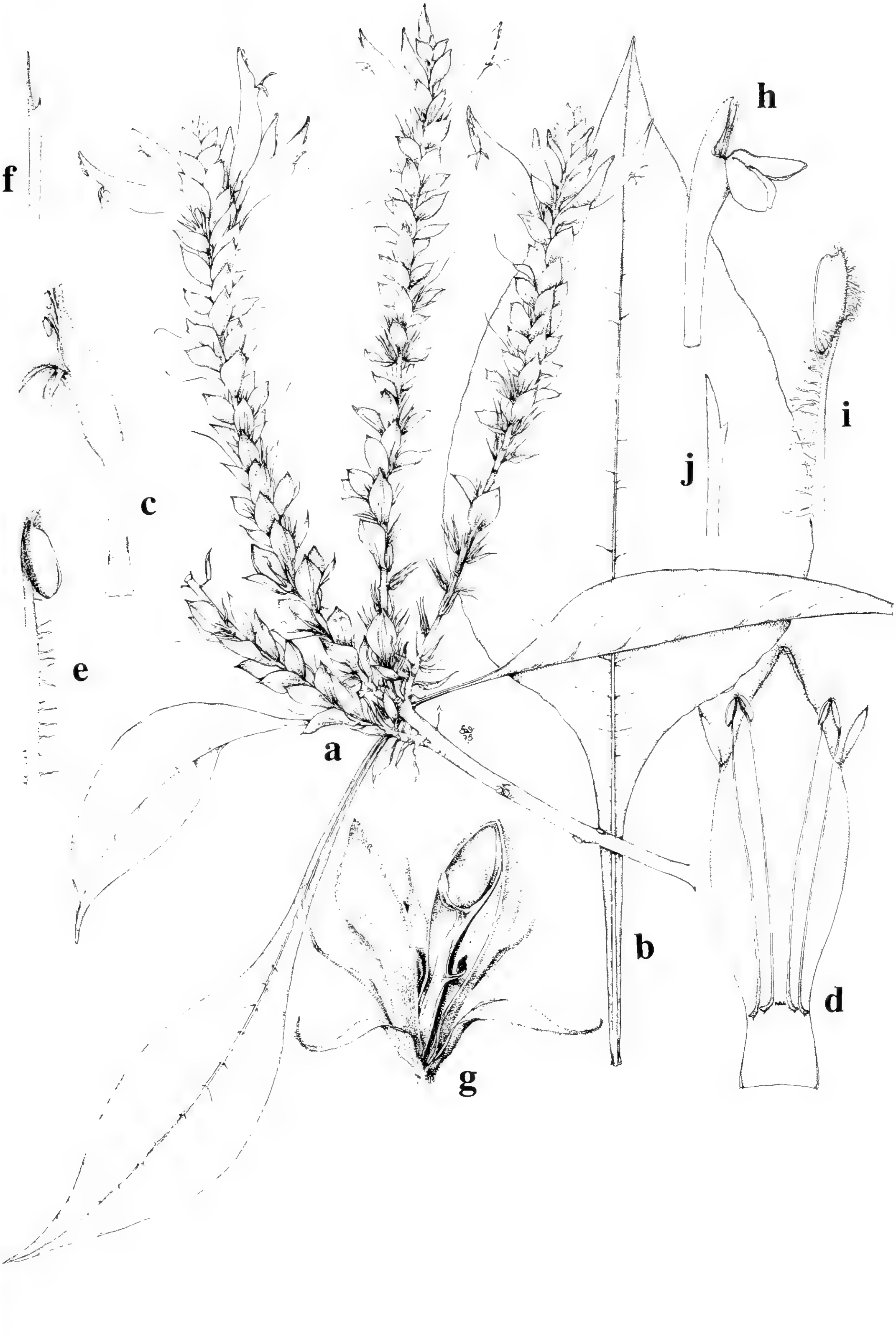
DISTRIBUTION AND HABITAT.—West-central Mexico (Jalisco, Colima, Michoacán, México, and Guerrero; Fig. 7); plants occur in rocky canyons in regions of tropical subdeciduous forest, oak forest, and pine-oak forest at elevations from 150 to 1,300 m.

PHENOLOGY.—Flowering: December–March; fruiting: December–April.

Aphelandra leariloba and *A. madrensis* both

→

FIGURE 8. *Aphelandra leariloba* (a–e, *McVaugh & Koelz 1751*) and *A. madrensis* (h–j, *Feddema 2568*). a, Branch with spikes, ×0.5; b, Leaf, ×0.5; c, Flower with calyx removed, ×1; d, Corolla (with lower-central lobe removed) cut open to reveal androecium, ×1.5; e, Distal portion of stamen, ×5; f, Distal portion of style with stigma, ×5; g, calyx and capsule, ×2; h, Flower with calyx removed, ×1; i, Distal portion of stamen, ×5; j, Distal portion of style with stigma, ×5. Drawn by Karin Douthit for McVaugh's *Flora Novo-Galiciana*; copyright reserved to the University of Michigan Herbarium, used with permission.


f
c
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occur in west-central Mexico, flower during the dry season, and share a combination of morphological attributes that readily distinguishes them from all other Mexican species of the genus. These morphological features include discolorous and relatively short corollas with short lips, elongate and unequally bilobed stigmas, and large, flattened trichomes on the filaments. Because the only mutually exclusive characters that distinguish them from each other all pertain to characters of the flower, the identification of strictly fruiting plants can be problematic. In such instances, the tendency of most individuals of *A. madrensis* from Sinaloa, Nayarit, Jalisco, and Colima to lack glands (or at least to lack conspicuous glands) in the inflorescence (i.e., rachis, bracts, bractlets, calyx, and corolla) is often helpful (see discussion under *A. madrensis*). In contrast, *A. lineariloba* always exhibits conspicuous glands in the inflorescence.

In addition to *A. lineariloba* and *A. madrensis,* only one other species, *A. hintonii,* is known from the Nueva Galicia region of west-central Mexico. Like the former two species, *A. hintonii* has large and conspicuously flattened trichomes on the filaments. Unlike them, however, it has longer calyces, corollas, and thecae (see discussion under *A. hintonii*).

ADDITIONAL SPECIMENS EXAMINED.—MEXICO. **Colima:** Sierra de Manantlán, Cerro Grande between Juluapan to Los Sauces, 29 km (air) NW of Colima, *T. Cochrane et al. 11722* (IBUG, UCR); 9–10 km ESE of Minatitlán, *R. McVaugh 26224* (MICH). **Guerrero:** Distr. Montes de Oca, Vallecitos, *G. Hinton et al. 11648* (F, GH, K, LL, MO, US); Sierra Madre Sur, Distr. Adama, N of Río Balsas, Temisco, Barranca del Consuelo, *Y. Mexia 8952* (ARIZ, B, CAS, F, G, GH, K, MO, UC, US); Achotla, *B. Reko 5047* (US). **Jalisco:** Mpio. Tuxpan, La Higuera, *A. Alvarez G. 23* (IBUG); along Hwy. 110, 2.2 mi N of Pihuamo, *T. Daniel 2138* (ASU, CAS, MICH), cuttings from this locale grown at San Fransisco Conservatory of Flowers, *T. Daniel 2138cv* (CAS); 3 km S de Pihuamo, *Diaz L. 9406* (ENCB); 21.2 km SW de Atenquique, *E. Lott et al. 985* (ASU, MEXU, MO); hwy, to Autlán, 9 mi N of rd. jct. at W end of Bahía de Navidad, *R. McVaugh & W. Koelz 1751* (MICH); Mpio. Pihuamo, S del rancho El Tule, *B. Mora N. s.n.* (IBUG). **México:** Distr. Temascaltepec, Acatitlán, *G. Hinton 3156* (BM, G, GH, K, MO, US). **Michoacán:** Hacienda Coahuayula, *G. Emrick 52* (F); Distr. Coalcomán, Coalcomán, *G. Hinton et al. 12881* (GH, LL, US), *13623* (F, GH, MO, US); Distr. Coalcomán, Huixontla, *G. Hinton et al. 15794* (B, F, G, K, LL, M, MO, MICH, US, W); 8 km S of Arteaga, *B. Leuenberger & C. Shiers 2708* (B); ca. 45–48 km S of Arteaga, 12–15 km N of Playa Azul, *R. McVaugh 22609* (MICH); ca. 8 km NW of Aguililla, rd. to Aserradero Dos Aguas, *R. McVaugh 22650* (MICH).

6. Aphelandra madrensis Lindau, Bull. Herb. Boiss. ser. 2, 4:326. 1904. TYPE.—MEXICO. **Guerrero:** Sierra Madre, 1,600 m, 27 January 1899, *E. Langlassé 806* (Holotype: B, destroyed; lectotype: P!, designated here; isotypes: G!, GH!, K!, US!).

Branched shrub to 3.5 m tall. Young stems terete to subquadrate, multi-fluted, pubescent with antrorse to ascendant to ascendant-appressed eglandular trichomes to 0.8 mm long or glabrate. Leaves opposite to subopposite, petiolate, petioles to 110 mm long (naked portion to 45 mm long), blades (narrowly elliptic to) ovate to broadly ovate, 55–220 mm long, 20–110 mm wide, 1.6–3.4(–5.2) times longer than wide, acuminate to subfalcate at apex, abruptly to gradually attenuate-decurrent (sometimes nearly to node) at base, surfaces sparsely pubescent (especially along midvein) with eglandular trichomes or glabrate, margin entire to subcrenate. Spikes axillary (in axils of distal leaves) and/or terminal, elongate, up to 155 mm long (excluding flowers), 14–50 mm in diameter (excluding flowers) near midspike, rachis pubescent with ascendant (especially near base of spike) to straight to flexuose eglandular and glandular (sometimes inconspicuous or absent) trichomes 0.1–0.8 mm long. Bracts green proximally and red distally (red coloration often not evident on fruiting individuals), often spreading with age, broadly ovate to ovate to elliptic to obovate-elliptic, 9–30 mm long, (3.5–)5–12(–17) mm wide, (1.3–)1.7–2.9 times longer than wide, rounded (often apiculate) to acute to subacuminate (sometimes mucronate), erect at apex, abaxial surface and margin pubescent with an understory of straight eglandular trichomes 0.05–0.2 mm long and an overstory (sometimes absent) of straight to flexuose eglandular and/or glandular (sometimes inconspicuous or absent) trichomes 0.2–1.2 mm long, margin entire or rarely sporadically and irregularly toothed with 1–2 teeth per side, teeth 0.2–0.5 mm long. Bractlets lanceolate to subulate, (3–)4.5–15 mm long, (0.5–)1.2–1.6 mm wide, attenuate to aristate at apex, pubescent like bracts. Calyx 7–12(–16) mm long, lobes ovate to lanceolate to linear, 1.6–3.3 mm wide at base, acute to acminate to attenuate to subaristate at apex, pubescent like bracts (overstory trichomes often sparse or absent except near apex). Corolla red with limb conspicuously darker than tube, 33–

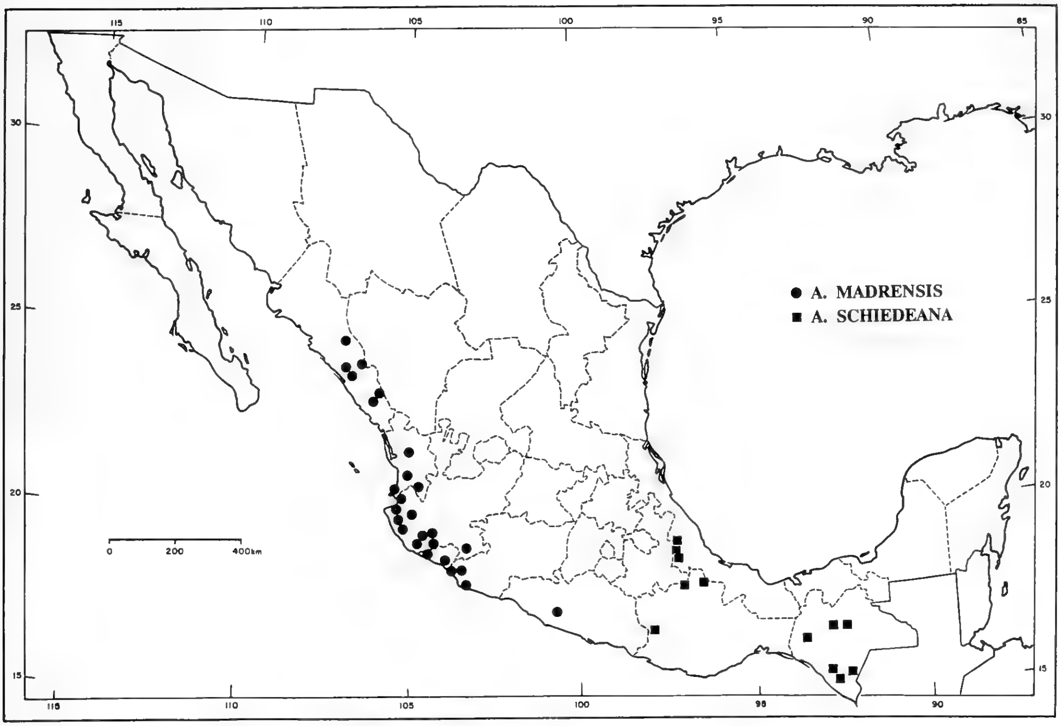

FIGURE 9. Distribution of *Aphelandra madrensis* and *A. schiedeana* in Mexico.

42 mm long, externally pubescent with eglandular and sometimes glandular trichomes to 1 mm long, glandular trichomes, when present, sometimes restricted to lower lip, upper lip 6.5–11.5 mm long, entire or bilobed with rounded lobes 0.4–0.7 mm long at apex, margin not flared, lower lip ± perpendicular to upper lip, 7–13 mm long, lateral lobes narrowly elliptic to subcircular to obovate, 5.5–12 mm long, 1.8–6 mm wide, lower-central lobe subcircular to broadly elliptic to obovate-elliptic, 6–12.5 mm long, 4–9.5 mm wide, 1–1.7 times longer and 1.4–2.2 times wider than lateral lobes. Stamens 26–31 mm long, posterior pair inserted ca. 1 mm distal to anterior pair, anterior (longer) filaments proximally pubescent with conspicuously flattened and/or filamentous eglandular trichomes, distally pubescent with flattened trichomes, posterior (shorter) filaments proximally pubescent with flattened or filamentous eglandular trichomes, distally glabrous, thecae 2.2–3.7 mm long, anterior pair extended up to 1 mm beyond posterior pair, apically pubescent with cobwebby eglandular trichomes, dorsally pubescent with cobwebby (posterior pair) or flattened (anterior pair) eglandular trichomes; staminode 0.3–0.8 mm long, pubescent. Style 24–33 mm long, pubescent with eglandular (and sometimes glandular) trichomes throughout; stigma unequally bilobed with one lobe 0.05–0.3 mm long and the other 0.5–1.9 mm long. Capsule 12–17.5 mm long, externally pubescent with straight to flexuose to retrorse eglandular trichomes 0.1–0.3 mm long. Seeds flattened, subelliptic to somewhat squarish, 3.5–5 mm long, 3–4.3 mm wide, covered with apically bifurcate or branched to dendritic trichomelike papillae 0.1–0.3 mm long. (Fig. 8).

DISTRIBUTION AND HABITAT.—West-central Mexico (Sinaloa, Nayarit, Jalisco, Colima, Michoacán, and Guerrero; Fig. 9); plants occur in ravines and stream valleys in regions of tropical deciduous, subdecidous, oak, and pine-oak forest at elevations from near sea level to 2,500 meters.

PHENOLOGY.—Flowering: November–March; fruiting November–March.

Locality information provided on the type of *A. madrensis* is not very precise. Between the

13th and 31st of January, 1899, Langlassé traveled from Tecpan to the summit of the Sierra Madre Sur in Guerrero and back by way of the route to Ajuchitlán on the Río Balsas (McVaugh 1951). The type was apparently collected during the descent of the Pacific slope on the return to Tecpan.

The type of *A. medrensis* was collected approximately 300 km southeast of the main portion of the range of the species and differs from most collections from Sinaloa, Nayarit, Jalisco, and Colima in several features including: longer bractlets (12–15 mm vs. 3–8.5 mm), longer calyces (12–16 mm vs. 7–11 mm), and more glandular corollas (external surface evenly and densely glandular vs. external surface eglandular or with glands restricted to the lower lip only) with the lateral lobes of the lower lip broader (elliptic to subcircular and 5–6 mm wide vs. narrowly elliptic to obovate and 1.8–5.5 mm wide). The type differs even more conspicuously from most of these collections by its conspicuously glandular inflorescences (vs. inconspicuously glandular or eglandular) with thin and membranous textured bracts (vs. thicker and stiffer). However, several collections from the vicinity of Coalcomán in Michoacán either exhibit character states that bridge some of the morphological gaps between the more northerly collections and the type or randomly combine character states from each. For example, in *Hinton et al. 11062* and *12675*, the bractlets vary from 7.5 to 10.5 mm in length and are thus intermediate between the type and the more northerly collections. In most other characters (e.g., calyx length, corolla pubescence, lateral lobe shape and size, and inflorescence pubescence) *Hinton et al. 12675* resembles the northern collections. It has thin, membranous bracts like those of the type, however. *Hinton et al. 11062* resembles *Hinton et al. 12675* in most of these features except it has thicker and stiffer bracts. *Hinton et al. 16062* resembles the northern collections in its pubescence and lateral corolla lobes, resembles the type in length of the calyces, and is intermediate between the two in bractlet length and bract texture. *Hinton et al. 15912* and *16042* have prominent glandular trichomes throughout the inflorescence and on the entire external surface of the corolla, bractlets 7–10 mm long, calyces 10.5–12 mm long, elliptic to obovate lateral corolla lobes 4–4.8 mm wide, and membranous- to stiff-textured bracts.

Further studies may reveal that the northern populations represent a taxon other than that represented by the type of *A. madrensis*. Considering the overlap in character states noted above and the lack of any collections from Guerrero since that of Langlassé, it seems premature to propose such at this time. It is not known whether Hinton's series of collections from Michoacán represents hybrids between two such similar taxa or merely local variation in a wide-ranging species.

The most morphologically similar species, and undoubtedly the closest relative of *A. madrensis*, is *A. lineariloba*, which is also endemic to western Mexico. Further consideration of these species is provided in the discussion of the latter.

Representative Specimens Examined.—MEXICO. **Colima:** Mpio. Tecomán, Tecolapa, Cerro el Alcomun, *F. Leger 1033* (CAS, IBUG); 13–15 km W of Santiago, *R. McVaugh 25026* (MICH); gorge of Río Cihuatlán (Moravasco), rd. to Durazno, Jalisco, 13 mi N of Santiago, *R. McVaugh & W. Koelz 1652* (MICH). **Jalisco:** N end of Valley of Purification, KM 228 on Hwy. 100, SW of Autlán, *R. Alva & S. Cook 1677* (UC); Sierra de Manantlán, Sn. Miguel, *O. Angel R. s.n.* (IBUG); ca. 19 km S of Puerto Vallarta toward Tuito, *T. Croat 45415* (MO); Cuautitlán, 2–3 km NW de Telcruz, 50 km NW de Colima, 19°29′N, 104°8′W, *R. Cuevas & G. Nieves 2141* (IBUG); 20.9–23.7 mi NE of La Huerta and 11.9–14.7 mi SW of turn to Ahuacapan S of Autlán, *T. Daniel 2114* (ASU, CAS, MICH, UCR); 20.1–22.9 km S of Talpa de Allende toward La Cuesta, *T. Daniel 5251* (CAS); along Hwy. 80, 14.1 km N jct. Hwys. 80 and 200 near Melaque, *T. Daniel 5276* (C, CAS, IBUG, K, MEXU, TEX); ca. 3 km NE of Puerto Vallarta, upriver from Playa Grande, *C. Feddema 2568* (MICH); 10 km NE of Puerto Vallarta near Milagro on rd. to Mascota, *C. Feddema 2590* (MICH); 18 km ESE of Tomatlán, 19°53′N, 105°05′W, *H. Iltis & M. Nee 1640* (US); Sierra Manantlán, ca. 9 km N de Casimiro Castillo, 19°41′N, 104°25′W, *E. Judziewicz et al. 5173* (US); 29 km SW de Autlán, carr. a Melaque, ca. 4 km N de Ejido El Rincon, *E. Lott & J. Magallanes 865* (CAS, CHAPA, TEX); 6–10 mi SW of Talpa de Allende, above Aranjués in valley of Río Charco Verde, *R. McVaugh 14345* (MICH); Mpio. Tomatlán, 5 km NE of Piloto, *R. McVaugh 25449* (MICH); Sierra del Halo, 7–9 mi from Colima-Tecalitlán hwy. near lumber rd. leaving hwy. 7 mi SSW of Tecalitlán, *R. McVaugh & W. Koelz 1266* (MICH); S of Puerto Vallarta near seashore, *Y, Mexia 1134* (CAS, E, F, MICH, UC, US); Santa Cruz de Vallarta, *Y. Mexia 1259* (BM, DS, US); Mpio. Casimiro Catillo, 4 km NE de El Zapotillo, *F. Santana M. 2540* (IBUG); 3 km adelante de Los Mazos, entre Autlán y Casimiro Castillo, *F. Santana M. & Cházaro B. 2649* (MEXU); camino de las matequillas a la Cascada de las Juntas, Las Loyas, Autlán, *A. Vasquez 3759* (MEXU). **Michoacán:** Distr. Coalcomán, Aquila, *G. Hinton et al. 11062* (US), *16042* (US), *16062* (K, LL, MICH); Distr. Coalcomán, S. Naranjillo, *G. Hinton et al. 12675* (DS, K, US); Distr. Coalcomán, Tizupan, *G. Hinton et al. 15912* (US); Mpio. Coahuayana, rd. summit between San Telmo and San Juan de lima, *J. MacDougal & J. Miley 494* (DUKE, IBUG). **Nayarit:** 8 km N of Real de Zopilote on rd. to San

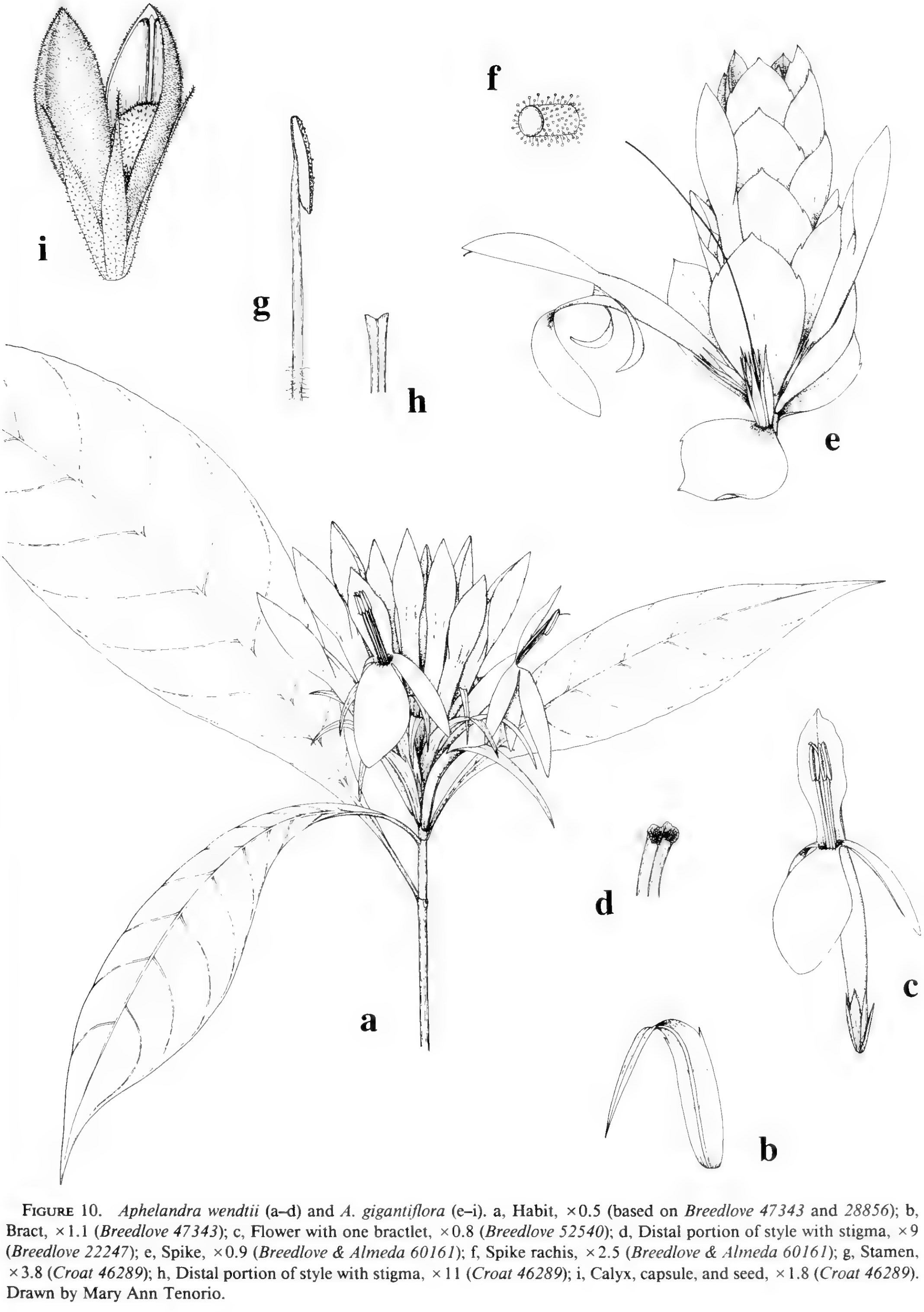

FIGURE 10. *Aphelandra wendtii* (a–d) and *A. gigantiflora* (e–i). a, Habit, ×0.5 (based on *Breedlove 47343* and *28856*); b, Bract, ×1.1 (*Breedlove 47343*); c, Flower with one bractlet, ×0.8 (*Breedlove 52540*); d, Distal portion of style with stigma, ×9 (*Breedlove 22247*); e, Spike, ×0.9 (*Breedlove & Almeda 60161*); f, Spike rachis, ×2.5 (*Breedlove & Almeda 60161*); g, Stamen, ×3.8 (*Croat 46289*); h, Distal portion of style with stigma, ×11 (*Croat 46289*); i, Calyx, capsule, and seed, ×1.8 (*Croat 46289*). Drawn by Mary Ann Tenorio.

Pedro, *D. Breedlove & F. Almeda 60706* (CAS, US); 9 mi N of Compostela, *R. McVaugh & W. Koelz 532* (MICH); 10 mi SE of Ahuacatlán on rd. to Barranca del Oro and Amatlán, *R. McVaugh & W. Koelz 758* (MICH); Mpio. Valle de Banderas, 1 km N de El Cuatante, *J. Rzedowski 17871* (MICH). **Sinaloa:** along Hwy. 40, 25.5 mi E of Concordia, *D. Breedlove 4241* (DS, DUKE, MICH); Sierra Tacuichamona, Africa, *H. Gentry 5655* (ARIZ); Mpio. Cosalá, Mineral de Nuestra Señora, *F. Hernández A. & J. Hernández V. 513* (MEXU); Sierra de Pinal, just E of El Espinal, *M. Kimnach & H. Sanchez M. 2261* (CAS, US); Sierra Madre, cañón near Santa Lucia, *Y. Mexia 421* (CAS, UC); Mpio. San Ignacio, Balboa, *J. Ortega 1161* (MEXU), *5023* (US); Sierra Madre Occidental, along Hwy, 40, 0.6 mi above El Cantil and 21 mi NE of Concordia, *A. Sanders et al. 4573* (ARIZ, CAS, UCR); Mpio. Culiacán, entre Sanalona y Los Mayos, rumbo a Tamazula, *R. Vega & F. Hernández 2260* (MEXU).

7. **Aphelandra wendtii** T. F. Daniel, sp. nov. (Fig. 10).

Type.—MEXICO. **Veracruz:** Mpio. Hidalgotitlán, Zona de Uxpanapa, along rd. to Poblado 10, NE of La Laguna and E of Río Cuevas, 15 October 1988, *T. Daniel & T. Wendt 5813* (Holotype: CAS!; isotypes: C!, CHAPA!, DUKE!, ENCB!, K!, MEXU!, MICH!, MO!, US!).

Frutex usque ad 3 m altus. Folia opposita, laminae ovatae-ellipticae vel ellipticae basi in petiolum decurrentes. Spicae plerumque subcapitatae (raro elongatae) 40–65 mm diametro ad medium. Bracteae virides lanceolatae vel ligulatae 28–58(–65) mm longae 5–12 mm latae 5–11-plo longiores quam latiores apice sensim attenuate patentes vel reflexae margine plerumque dentate, pagina abaxialis pubescens trichomatibus glandulosis et/vel eglandulosis vel fere glabrata. Corolla rubra 55–74 mm longa extus glandulosa, labium inferum lobis lateralibus obovatis vel ellipticis 17–25 mm longis 5–7.5 mm latis lobo centrali obovato vel elliptico vel subcirculari lobis lateralibus 1.1–1.4-plo longiore et 2–2.5-plo latiore. Thecae 6.5–8.1 mm longae pubescentes. Stigma infundibuliforme 0.2–0.3 mm longum. Capsula ignota.

Branched shrub to 3 m tall. Young stems terete to quadrate, sparsely pubescent with (flexuose to) antrorse to antrorse-appressed eglandular trichomes 0.4–1 mm long, soon glabrate. Leaves opposite, petiolate, petioles to 95 mm long (naked portion to 40 mm long), blades ovate-elliptic to elliptic, 120–280 mm long, 34–100 mm wide, 1.9–5.6 times longer than wide, acuminate to subfalcate at apex, gradually to somewhat abruptly attenuate-decurrent (often to node at base, surfaces sparsely pubescent with cauline type trichomes to glabrate, margin entire to sinuate-crenate. Spikes terminal, subcapitate (rarely elongate), to 70(–180) mm long (excluding flowers), 40–80 mm in diameter (excluding flowers) near midspike, rachis pubescent with antrorse eglandular trichomes to 1 mm long. Bracts green, lanceolate to strap-shaped, 28–58(–65) mm long, 5–12 mm wide, 5–11 times longer than wide, distal portion conspicuously spreading or reflexed, gradually attenuate at apex, abaxial surface pubescent with flexuose to antrorse-appressed eglandular trichomes to 1 mm long and sometimes with straight to flexuose, shorter, glandular trichomes or nearly glabrate, margin ciliate with trichomes like those of abaxial surface, dentate with 1(–2) teeth (sometimes obscure or absent) per side, teeth 0.2–3(–4.5) mm long. Bractlets subulate to lance-subulate, 9.5–16 mm long, 0.5–1.5 mm wide, apically aristate, pubescent like bracts. Calyx 11–16.5 mm long, lobes lanceolate, 2–3.5 mm wide at base, attenuate to subaristate at apex, abaxial surface pubescent with antrorse eglandular trichomes to 0.3 mm long. Corolla red, 55–74 mm long, externally pubescent with glandular and eglandular trichomes to 1.5 mm long, upper lip 20–32 mm long, entire to emarginate with rounded lobes 1–2.5 mm long to irregularly toothed with 1–2 coarse teeth along distal margin at apex, margin flared to reflexed proximally, lower lip ± perpendicular to upper lip, 17–35 mm long, lateral lobes obovate to elliptic, 17–25 mm long, 5–7.5 mm wide, lower-central lobe obovate to elliptic to subcircular, 23–34 mm long, 9–19 mm wide, 1.1–1.4 times longer and 2–2.5 times wider than lateral lobes. Stamens 45–62 mm long, posterior pair inserted ca. 1 mm distal to anterior pair, filaments pubescent proximally or throughout with filamentous eglandular trichomes, sometimes glabrous distally, thecae 6.5–8.1 mm long, pairs presented at ca. same height or posterior pair extending up to 1 mm beyond anterior pair, all 4 apically (and posterior pair dorsally) pubescent with cobwebby eglandular trichomes; staminode 0.3–18 mm long, pubescent. Style 53–65 mm long, pubescent with eglandular trichomes throughout; stigma symmetrically funnelform, 0.2–0.3 mm long. Capsule 19–20 mm long, glabrous. Seeds flattened, subcircular to subelliptic in outline, 4–4.5 mm long, 3.2–3.5 mm wide, surface covered with stiff, often apically branched or barbed trichome-like papillae.

Distribution and Habitat.—Southern Mexico (Chiapas, Tabasco, and Vercruz; Fig. 7); plants occur in lowland to montane rain forest at elevations from 140 to 1,200 m.

Phenology.—Flowering: July–January. Fruiting: December.

Two collections, the type from southeasternmost Veracruz and *Torres C. et al. 2081* from Chiapas, have bracts with entire margins. All other collections have inflorescences with at least some of the bracts dentate. Similar variation in bracteal margin is evident in other Mexican species of *Aphelandra.*

Aphelandra wendtii has been confused with, and is undoubtedly most closely related to, *A. heydeana.* Many of the collections cited below have been annotated as the latter species. For example, *Nelson 3302* was annotated by Dorothy Gibson as *A. heydeana* and was the sole basis for Wasshausen's (1975) inclusion of the species in Mexico. Although *A. heydeana* is now known from Mexico based on other collections, Nelson's collection pertains to *A. wendtii.* These two species can be distinguished by the features in the following couplet:

Inflorescence elongate, 19–35 mm in diameter (excluding flowers) near midspike; bracts lance-ovate to obovate-elliptic, 14–26 mm long, 2.2–4 times longer than wide, apex attenuate-caudate to caudate; lateral lobes of lower lip of corolla linear to oblanceolate, 5–16 mm long, 0.5–5 mm wide; lower-central lobe of corolla 1.6–4.5 times longer and 3.6–28 times wider than lateral lobes; pollen with 3-armed polar apertures .... *A. heydeana.*

Inflorescnece subcapitate (rarely elongate), 40–80 mm in diameter (excluding flowers) near midspike; bracts lanceolate to strap-shaped, 28–65 mm long, 5–11 times longer than wide, apex gradually attenuate; lateral lobes of lower lip of corolla obovate to elliptic, 17–25 mm long, 5–7.5 mm wide; lower-central lobe of corolla 1.1–1.4 times longer and 2–2.5 times wider than lateral lobes; pollen lacking polar apertures. .... *A. wendtii.*

In addition to these morphological distinctions, there appear to be ecological and geographical differences between the two taxa as well. *Aphelandra wendtii* is primarily a lowland, rain forest species restricted to the Gulf slope whereas *A. heydeana* is a highland species of pine and/or oak forests on the Pacific slope.

This species is named in honor of Dr. Tom Wendt, co-collector of the type, whose excellent series of collections from the Uxpanapa Region has significantly increased knowledge of the Mexican rain forests.

PARATYPES.—MEXICO. **Chiapas:** Mpio. Palenque, 8–9 km S of Palenque on rd. to Ocosingo, *D. Breedlove 26524* (DS, ENCB, LL), *28856* (DS), *D. Breedlove & J. Strother 46900* (CAS); Mpio. Palenque, 50 km SW of Palenque on rd. to Ocosingo near Colonia Ursulo Galvano, *D. Breedlove 47343* (CAS, DUKE, NY); Mpio. Ocosingo, 70 km SW of Palenque on rd. to Ocosingo along the Jol Uk'um, *D. Breedlove 52540* (CAS), *D. Breedlove & F. Almeda 48406* (CAS); Mpio. Chilon, along rd. to Pozo Cuevas above Agua Azul, *D. Breedlove & F. Almeda 57214* (CAS); Mpio. Ocosingo, 6–8 km N of Ocosingo along rd. to Bachajon, *D. Breedlove & A. Smith 22121* (DS, DUKE, ENCB); Mpio. Yajalon, below Yajalon, *D. Breedlove & A. Smith 22247* (DS); Mpio. Chontal, Villa Paraíso, 136 km NE of San Cristóbal de las Casas toward Palenque, 17°29'N, 92°05'W, *B. Hammel et al. 15650* (CAS, MO); 19.2 km from turn to ruins on rd. from Palenque to Ocosingo via Cascada Misolha, *M. Huft & E. Cabrera 2413* (MO); Palenque Ruins, *B. Marcks & C. Marcks 959* (LL); Mpio. Ocosingo, 2 km N de Naja camino a Palenque, *E. Martínez S. & W. Stevens 23976* (CAS); near Tumbala, *E. Nelson 3302* (US); Cascadas Mizola, W side of Palenque-Ocosingo rd., ca. 10 mi S of Palenque, *A. Reznicek & D. Gregory 297* (MICH); Mpio. del Salto, carr. Ocosingo-Palenque, 11 km N de Jerusalén (Ruíz Cortinez), *R. Torres C. et al. 2081* (MEXU); Mpio. Yajalon, 67 km S de Palenque, carr. (#199) a Ocosingo, 3.2 km S de Xanil, 17°10'N, 92°09'W, *T. Wendt et al. 2336* (CAS). **Tabasco:** Mpio. Macuspana, E end of Cerro Tortugero, 7 km S of Macuspana, *C. Gilly & E. Hernández X. 399* (GH, MICH); Parque Nacional de Agua Blanca, Macuspana, KM 64 carr. Villahermosa-Escárcega, 17°38'N, 92°30'W, *R. Cano D. 6* (CHAPA), *L. Martínez G. et al. 6* (CHAPA).

8. Aphelandra hintonii D. Wasshausen, Phytologia 25:476. 1973. TYPE.—MEXICO. **Michoacán:** Distr. Coalcomán, Naranjillo, 30 October 1941, *G. Hinton et al. 16049* (Holotype: US!; isotype: MICH!, NY!).

Shrub of unknown height. Young stems subterete to subquadrate, more or less evenly pubescent near apex with flexuose to ascendant eglandular trichomes 0.3–1 mm long, these soon becoming concentrated in 2 lines, mature stems glabrate. Leaves opposite to subopposite, petiolate, petioles to 120 mm long (naked portion to 35 mm long), blades ovate, 80–180 mm long, 45–125 mm wide, 1.6–2 times longer than wide, acute to acuminate at apex, gradually to abruptly attenuate-decurrent (often nearly to node) at base, surfaces pubescent with cauline type trichomes, margin entire to subcrenate. Spikes terminal, more or less elongate, up to 90 mm long (excluding flowers), 50–65 mm in diameter (excluding flowers) near midspike, rachis densely pubescent with flexuose to antrorsely appressed, silky glandular and eglandular trichomes 0.5–1.5 mm long (sericious). Bracts with a dark coloration distally (in dried material), ovate to obovate, 20–33(–67) mm long, 9–15(–22) mm wide, 1.8–

2.2 times longer than wide, acute to acuminate and erect at apex, surfaces and margin densely sericeous and with straight to flexuose glandular trichomes 0.3–0.7 mm long, margin entire. Bractlets lanceolate, 18–21 mm long, 2.5–4 mm wide, attenuate at apex, abaxial surface glandular-sericeous (with glands up to 1 mm long). Calyx 15–19 mm long, lobes lanceolate, 2–2.5 mm wide at base, attenuate at apex, pubescent like bractlets. Corolla red, 60–80 mm long, externally pubescent with eglandular and glandular trichomes 0.2–0.6 mm long, upper lip 17–22 mm long, entire at apex, margin flared proximally, lower lip ± perpendicular to upper lip, 19–21 mm long, lateral lobes obovate-elliptic, 14 mm long, 4.5–8 mm wide, lower-central lobe broadly elliptic, 18–21 mm long, 14–15 mm wide, 1.2 times longer and 2 times wider than lateral lobes. Stamens 45–60 mm long, posterior pair inserted ca. 1 mm distal to anterior pair, filaments proximally pubescent with filamentous eglandular trichomes, anterior pair distally pubescent with conspicuously flattened eglandular trichomes, posterior pair distally glabrous, thecae 4.5–5.1 mm long, pairs presented at ca. same height, all apically (and posterior pair dorsally) pubescent with cobwebby eglandular trichomes; staminode a triangular callous 0.5 mm long. Style 57 mm long, distally pubescent with eglandular trichomes; stigma bilobed with 1 lobe 0.1 mm long and the other 0.2 mm long. Capsule not seen.

DISTRIBUTION AND HABITAT.—West-central Mexico (Michoacán; Fig. 3); plants were collected in "woods" at an unknown elevation.

PHENOLOGY.—Flowering: October.

Aphelandra hintonii is known only from a single collection from the Nueva Galicia region of western Mexico. It has relatively large flowers, like those of species in southern Mexico, and staminal trichomes similar to the short-flowered species, *A. leariloba* and *A. madrensis,* that occur in Nueva Galicia. It appears superficially similar to *A. flava* Nees from Colombia in several features, including the large corollas and staminal pubescence. *Aphelandra flava* has yellow corollas, however, and lacks the silky trichomes on the rachis characteristic of *A. hintonii.* Additional collections of *A. hintonii* are desirable in order to more adequately delimit this species, document its overall distribution, and better understand its relationships to other species.

9. Aphelandra heydeana J. Donnell-Smith, Bot. Gaz. 18:210. 1893. TYPE.—GUATEMALA. **Santa Rosa:** Chupadero, October 1892, *E. Heyde & E. Lux 4037* (Holotype: US!; isotypes: G!, GH!, K!, M!, MO!, NY!, P!, US!).

Branched shrub to 1 m tall. Young stems subterete, with blisterlike superficial projections (lenticels), pubescent with antrorse-appressed eglandular trichomes to 0.8 mm long or glabrate. Leaves opposite, petiolate, petioles to 70 mm long (naked portion to 15 mm long), blades ovate to ovate-elliptic, 30–150 mm long, 14–76 mm wide, 1.4–4 times longer than wide, (rounded to) acuminate at apex, abruptly attenuate-decurrent (sometimes to node) at base, surfaces sparsely pubescent with antrorse to antrorse-appressed, eglandular trichomes or glabrate, margin entire to subsinuate. Spikes terminal (and sometimes in axils of distal leaves as well), more or less elongate, up to 70 mm long (excluding flowers), 19–35 mm in diameter (excluding flowers) near midspike, rachis densely pubescent with antrorse to antrorse-appressed eglandular trichomes 0.5–1.5 mm long. Bracts green (sometimes with a darker coloration distally), conduplicate, lance-ovate to obovate-elliptic, 14–26 mm long, 3.5–9 mm wide, 2.2–4 times longer than wide, distal portion widely spreading to reflexed, attenuate-caudate to caudate at apex, abaxial surface and margin pubescent with flexuose to appressed eglandular and glandular (sometimes inconspicuous) trichomes 0.1–1.5 mm long, margin dentate with 1–2 teeth (rarely obscure or absent, some always present in an inflorescence) per side, teeth 0.2–3.2 mm long. Bractlets subulate to lance-subulate, 7–11(–14) mm long, 0.8–2 mm wide, aristate at apex, abaxial surface pubescent with mostly antrorse eglandular trichomes. Calyx 9–13 mm long, lobes lanceolate, 2.5–3.5 mm wide at base, attenuate to aristate at apex, abaxial surface inconspicuously pubescent with antrorse eglandular trichomes to 0.2 mm long. Corolla orange-red (with yellow veins on lower lip) to red, 49–68 mm long, externally pubescent with glandular and eglandular trichomes to 1.5 mm long, upper lip 19–27 mm long, entire at apex, margin flared proximally or along most of the vertical sides, lower lip ± perpendicular to upper lip, 18–28 mm long, lateral lobes linear to oblanceolate, 5–16 mm long, 0.5–5 mm wide, lower-central lobe elliptic to obovate, 17–27 mm long, 8–18 mm wide, 1.6–4.5 times longer and 3.6–28 times wider than lateral lobes. Stamens 44–50 mm long, posterior pair inserted ca. 1 mm distal to anterior pair, filaments proximally pu-

FIGURE 11. *Aphelandra heydeana* from Donnell-Smith's protologue in volume 18 of the Botanical Gazette (1893). 1, Habit; 2, Corolla opened to reveal stamens; 3–4, Bract; 5, Bractlets, calyx, and gynoecium; 6, Calyx (partially removed) and gynoecium. Magnifications not provided.

bescent with filamentous eglandular trichomes, distally glabrous or pubescent with filamentous eglandular trichomes to 0.5 mm long, thecae 5–7 mm long, pairs presented at ca. same height, all apically (and posterior pair dorsally) pubescent with cobwebby eglandular trichomes; staminode absent. Style 50–60 mm long, sparsely pubescent with eglandular trichomes throughout; stigma symmetrically funnelform, 0.2–0.3 mm long. Capsule not seen. (Fig. 11).

DISTRIBUTION AND HABITATS.—Southern Mexico (Chiapas; Fig. 3), Guatemala, and El Salvador; plants occur in mixed deciduous forests with pines, pine-oak forests, and oak woodlands at elevations from 1,060 to 1,675 m.

PHENOLOGY.—Flowering: September–December.

LOCAL NAME.—"Flor de San Julián" (Gibson 1974, Guatemala).

Gibson (1974) and Wasshausen (1975) both based their report of this species in Mexico on a specimen here referred to *A. wendtii.* In fact, the species has been collected in Mexico only recently. The description above includes information from throughout the range of *A. heydeana.*

The reflexed, dentate, and apically caudate bracts of this species are similar to those of the Brazilian species, *A. chamissoniana* Nees. The closest relative of *A. heydeana* in North and Central America appears to be *A. wendtii.* These two species share numerous features including: conspicuously reflexed and usually dentate bracts, relatively large and abaxially glandular corollas, relatively long and apically pubescent thecae, and symmetrically funnelform stigmas. Distinctions between them are discussed under *A. wendtii.*

ADDITIONAL SPECIMENS EXAMINED.—EL SALVADOR. **La Libertad:** Comasagua, *S. Calderón 1402* (GH, US). GUATEMALA. **Guatemala:** KM 7 on Central American Hwy. E of Guatemala City, *C. Davidson 3249* (ENCB, F, MO); above Lake Amatitlán, 3 mi S of Villa Canales, *W. Harmon 4635* (ENCB); Amatitlán, *J. Morales R. 1175* (F). **Huehuetenango:** 35 km W of Huehuetenango, *M. Madison 1769* (GH). **Santa Rosa:** Cerro Redondo, *E. Heyde & E. Lux 6212* (G, GH, K, US); Río Chiquito, *E. Heyde & E. Lux 6213* (F, GH, K, M, MICH, MO, US); near Oratorio, *P. Standley 60671* (F, US); Río Panal, lower slopes of Volcán de Tecuamburro between Cuilapa and Chiquimulilla, *P. Standley 78561* (F, US), *78568* (F, US). **Without locality:** *I. Aguilar 303* (F), *611* (F); *E. Heyde 355* (US). MEXICO. **Chiapas:** 1.5 km SW of Ojo de Agua along rd. from El Rosario to Niquivil, *D. Breedlove 65803* (CAS, MEXU, MICH, NY, US); Mpio. Motozintla de Mendoza, 10 mi SW of Motozintla, *P. Fryxell & E. Lott 3341* (CAS, CHAPA, ENCB). COUNTRY UNDETERMINED. Without locality, *Sessé et al. 279* (F, MA).

10. Aphelandra guerrerensis Wasshausen, Phytologia 26:393. 1973. TYPE.—MEXICO. **Guerrero:** Distr. Galeana, San Andrez, 1 June 1938, *G. Hinton et al. 11199* (Holotype: US!; isotypes: G!, GH!, K!, LL!, MICH!, NY!, UC, W!).

Shrub to 2 m tall. Young stems subterete to quadrate, pubescent near apex with flexuose to ascendant-appressed or retrorse-appressed eglandular trichomes 0.2–0.8 mm long, becoming glabrate. Leaves opposite, subsessile to petiolate, petioles to 130 mm long (naked portion to 55 mm long), blades ovate-elliptic to elliptic, 40–190 mm long, 14–80 mm wide, 2.1–3.9 times longer than wide, acuminate to subfalcate at apex, ± abruptly to gradually attenuate-decurrent (often nearly to or to node) at base, surfaces and margin sparsely pubescent (especially along veins) with cauline type trichomes or becoming glabrate, margin entire to subsinuate-crenate. Spikes terminal or axillary from distal nodes, elongate, up to 180 mm long (excluding flowers), 25–50 mm in diameter (excluding flowers) near mid-spike, rachis pubescent with straight to flexuose to antrorse glandular and/or eglandular trichomes 0.05–0.8 mm long. Bracts green or distal bracts sometimes green with red coloration on distal half, often spreading with age, lanceolate to ovate to elliptic, 15–35 mm long, 4.3–22 mm wide, 1.1–4.9 times longer than wide, proximal bracts often intergrading with leaves and somewhat larger, acute to acuminate to subfalcate, erect at apex, abaxial surface pubescent with straight to curved to flexuose glandular and eglandular trichomes 0.05–0.7(–1) mm long, margin ciliate with trichomes like those of abaxial surface, entire (proximal and sometimes distal bracts) or dentate (distal bracts) with 1 tooth per side, teeth 0.2–3 mm long (teeth usually present on at least one bract per inflorescence). Bractlets subulate to lanceolate to lance-subulate, 5.5–13(–17) mm long, 0.9–1.5(–2.5) mm wide, subaristate to aristate at apex, pubescent like bracts. Calyx 8–15 mm long, lobes lance-elliptic to lanceolate to lance-subulate, 1.5–3 mm wide at base, attenuate to aristate at apex, pubescent like bracts. Corolla red, 50–85 mm long, externally pubescent with glandular and eglandular trichomes 0.1–0.6 mm long distally and with mostly eglandular trichomes 0.1–0.7 mm long proximally, upper lip 19–36 mm long, entire at apex, margin flared at base, lower lip ± per-

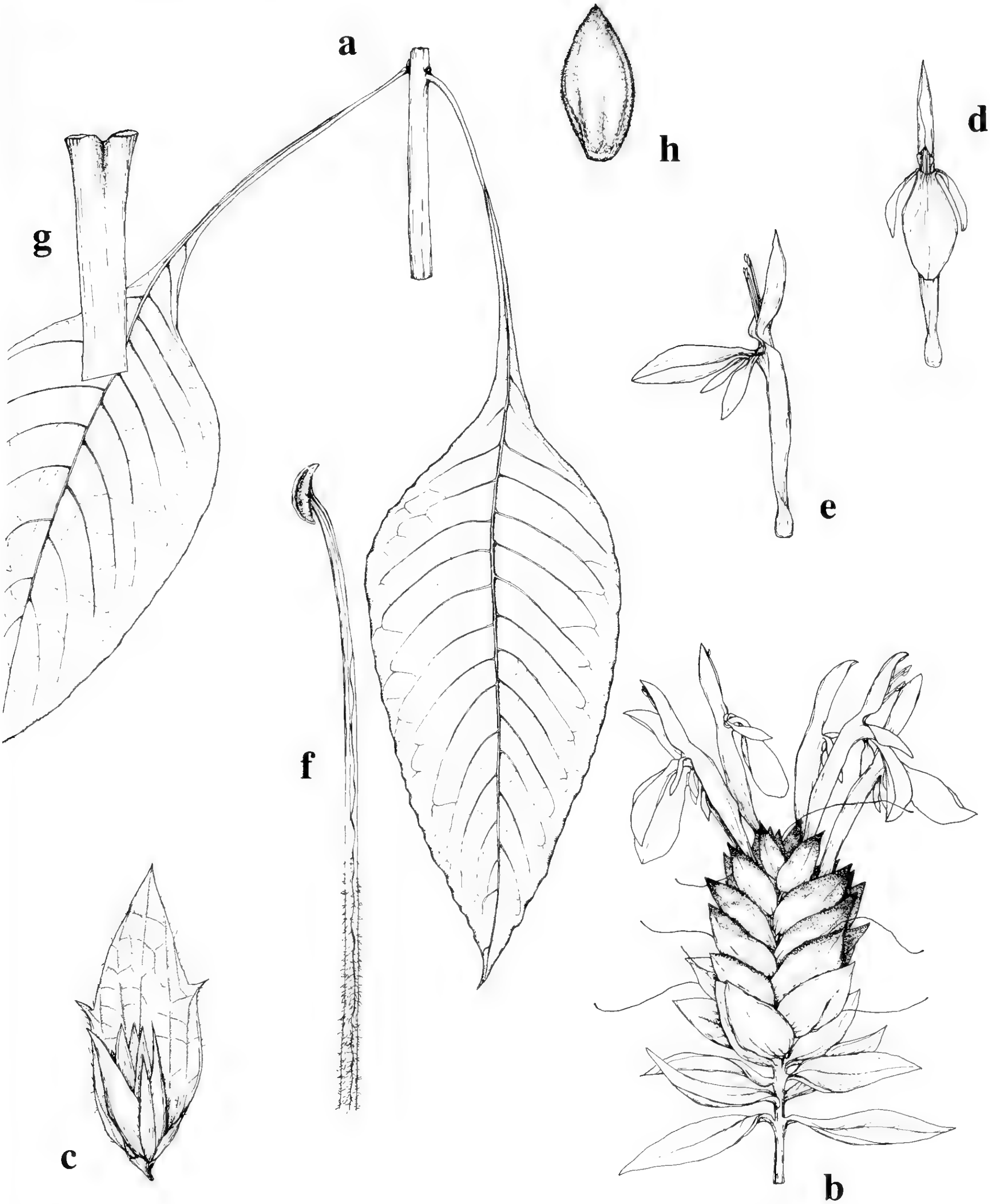

FIGURE 12. *Aphelandra guerrerensis.* a, Portion of stem with leaves, ×0.5 (*Daniel 5376*); b, Spike with flowers, ×0.5 (*Daniel 5376cv*); c, Bract, bractlets, and calyx, ×1.6 (*Daniel & Ton 6156*); d, Corolla with stamens, front view, ×0.5 (*Daniel & Ton 6156*); e, Corolla with stamens, side view with upper lip bent to reveal stamens, ×0.5 (*Daniel & Ton 6156*); f, Distal portion of stamen, ×2.1 (*Daniel 5376*); g, Distal portion of style with stigma, ×20 (*Daniel & Ton 6156*); h, Capsule, ×1.3 (*Daniel & Ton 6156*). Drawn by Nancy King.

pendicular to upper lip, 21–40 mm long, lateral lobes linear to lanceolate to oblanceolate, 7–21 mm long, 1.1–4.8 mm wide, lower-central lobe obovate to elliptic, 19–38 mm long, 5.7–19 mm wide, 1.7–3.1 times longer than and 2.7–6.7 times wider than lateral lobes. Stamens 40–60 mm long, posterior pair inserted ca. 1 mm distal to anterior pair, filaments proximally pubescent with filamentous eglandular trichomes, distally glabrous, thecae 3–4.5 mm long, posterior pair extended up to 4 mm beyond anterior pair, apically and dorsally glabrous; staminode 0.7–1 mm long, glabrous or pubescent. Style 55–75 mm long, glabrous or very sparsely pubescent with eglandular trichomes; stigma symmetrically to asymmetrically funnelform, 0.1–0.4 mm long. Capsule 14–19 mm long, pubescent with straight to retrorsely appressed (proximally) eglandular trichomes 0.1–0.3 mm long. Seeds (immature) covered with stiff, dendritic or barbed trichomelike papillae. (Fig. 12).

Distribution and Habitat.—Southern Mexico (Guerrero and Oaxaca; Fig. 7); plants occur in moist broadleaf evergreen (e.g., riparian) forests in the oak and pine zones on the Pacific slopes of the Sierra Madre Sur at elevations from 600 to 1,400 m.

Phenology.—Flowering: November–February and June; fruiting: January–February.

Prior to this study, *A. guerrerensis* was known only from the type locality in southwestern Guerrero. With some hesitation, I include several collections from southwestern Oaxaca within this species. Plants from Oaxaca resemble the type in numerous important characters including bracteal margins, corolla form, thecal pubescence, and pollen apertures. They differ from Hinton's collection only by the presence of glands among the eglandular trichomes on the rachis, bracts, bractlets, and calyx. In the latter, glandular trichomes are absent on these structures. Considering the variability in glandularity of other species (e.g., *A. madrensis* and *A. schiediana*), it does not seem overly cautious to include these collections from Oaxaca in *A. guerrerensis* until such time as the relationships between them can be better resolved.

Aphelandra guerrerensis is most similar to *A. gigantiflora* and *A. schiedeana*. Its distributional range is generally to the south and west of that of the latter taxa. In addition to the contrasting character states noted above in the key to species, *A. guerrerensis* can be further distinguished from *A. gigantiflora* by its eglandular or less conspicuously glandular inflorescence rachis and from *A. schiedeana* by its seeds covered with trichomelike papillae.

Additional Specimens Examined.—MEXICO. **Oaxaca:** along Hwy. 131 between Puerto Escondido and Sola de Vega, 63.5 km N jct. Hwy. 200, *T. Daniel 5376* (C, CAS, DUKE, MEXU, MO), cuttings from this locale grown at San Francisco Conservatory of Flowers, *T. Daniel 5376cv* (CAS); along road between Puerto Escondido and Sola de Vega, 42 km N jct. Hwy. 200 in Puerto Escondido, *T. Daniel & A. Ton 6156* (CAS, ENCB, K, MEXU, MICH, NY, US); Río Salado along Puerto Escondido-Sola de Vega road, 72 km N jct. Hwy. 200 in Puerto Escondido, *T. Daniel & A. Ton 6163* (CAS, MEXU); along Puerto Escondido-Sola de Vega road 74 km N jct. Hwy. 200 in Puerto Escondido, *T. Daniel & A. Ton 6166* (CAS); KM 182–190, Oaxaca-Puerto Escondido, *T. MacDougall s.n.* (CAS, MEXU); Río Sal, Lachao, Juquila, *T. MacDougall s.n.* (ENCB, F); Cerro del Machete, Pochutla, *B. Reko 6051* (F).

11. **Aphelandra gigantiflora** Lindau, Bull. Herb. Boiss. 3:369. 1895. Type.—"Guatemala et Costarica," *A. Warscewicz s.n.* (Lectotype: GH!, designated here, see below). *Aphelandra schiedeana* var. *gigantiflora* (Lindau) D. Gibson, Fieldiana, Bot. 34:57. 1973.

Aphelandra padillana Standley, J. Washington Acad. Sci. 14: 244. 1924. Type.—EL SALVADOR. **Ahuachapán:** mountains near Ahuachapán, 1,000 m, 9–27 January 1922, *P. Standley 19972* (Holotype: US!).

Aphelandra gigantiflora forma *lutea* Standley & Steyermark, Field Mus. Bot. 23:237. 1947. Type.—GUATEMALA. **Escuintla:** barranca of Río Gavilán, NE of Escuintla, 720 m, 16 March 1941, *P. Standley 89560* (Holotype: F).

Shrub to 2.4 m tall. Young stems subquadrate to quadrate, sparsely to densely pubescent with straight to antrorse to antrorse-appressed eglandular trichomes 0.05–0.7 mm long. Leaves opposite, petiolate, petioles to 130 mm long (naked portion to 50 mm long), blades (lance-ovate to) ovate to elliptic, 40–255 mm long, 11–117 mm wide, 1.9–4.5 times longer than wide, acuminate to subfalcate at apex, (acute to) more or less abruptly to gradually attenuate-decurrent (often nearly or to node) at base, surfaces sparsely pubescent (especially along major veins) with antrorse eglandular trichomes, margin entire to subsinuate-crenate. Spikes terminal, elongate, up to 310 mm long (excluding flowers), 28–55 mm in diameter (excluding flowers) near midspike, rachis pubescent with straight to flexuose glandular and eglandular trichomes 0.1–1.2 mm long (viscid). Bracts reddish, ovate to elliptic to obovate-elliptic, 17–33 mm long, 7.2–21 mm wide, 1.6–3 times longer than wide, sometimes spreading with age, (rounded to) acute to acuminate, erect at apex, abaxial surface and margin pubescent like rachis and with eglandular trichomes as short as 0.05 mm long as well, margin entire or dentate with 1–2 teeth per side, teeth 0.2–2.5 mm long. Bractlets subulate to lanceolate, 8–20 mm long, 0.6–1.5 mm wide, apex attenuate to aristate, pubescent like rachis. Calyx 11–17 mm long, lobes lanceolate to lance-subulate, 1.2–3.5 mm wide at base, attenuate to aristate at apex, pubescent like rachis. Corolla red, 55–74 mm long, externally pubescent like rachis, upper lip 16–29 mm long, entire to emarginate with rounded to subtriangular lobes 0.2–0.4 mm long at apex, margin not flared or proximally flared, lower lip ± perpendicular to upper lip to reflexed, 24–32 mm long, lateral lobes lance-linear to linear to linear-elliptic, 7–17 mm long, 1–5.5 mm wide, lower-central lobe obovate, 19–31 mm long, 8–17 mm wide, 1.6–3.7 times longer and 3.1–8.6 times wider than lateral lobes. Stamens 45–65 mm long, posterior pair inserted ca. 1 mm distal to anterior pair, filaments pubescent proximally and often distally with filamentous eglandular trichomes to 1 mm long, thecae 3.5–5.3 mm long, presented at ± same height or posterior pair extending up to 1 mm beyond anterior pair, posterior pair apically and dorsally pubescent with eglandular trichomes, anterior pair apically pubescent only or glabrous; staminode triangular or filamentous, 0.3–9 mm long, pubescent. Style 51–59 mm long, proximally pubescent with eglandular trichomes, distally pubescent or glabrous; stigma symmetrically funnelform to somewhat bilobed, 0.2–0.3 mm long. Capsule 17–21 mm long, pubescent with straight to flexuose eglandular trichomes 0.2–0.5 mm long. Seeds flattened, somewhat squarish, 3.7–5.5 mm long, 3–4.5 mm wide, surface covered with apically branched or dendritic trichomelike papillae to 0.2 mm long. (Fig. 10).

Distribution and Habitat.—Southern Mexico (Chiapas and Oaxaca; Fig. 3), Guatemala, and El Salvador; plants occur along streams and in mesic ravines in regions of tropical subdeciduous, moist, and pine-oak forest at elevations from 300 to 1,400 m.

Phenology.—Flowering: November–March; fruiting: January–March.

Local Name.—"Hierba del cadejo" (*Standley 19972,* El Salvador).

Some confusion exists concerning the type of this species. There are several Warscewicz collections of *A. gigantiflora* with various numbers and locality data. Photographs of a specimen that was at B, *Warscewicz 20* from "Costa Ricca et Veragua," were distributed to several herbaria by F (neg. no. 8707) under the heading "TYPES OF THE BERLIN HERBARIUM." Wasshausen (1975) cited *Warscewicz s.n.* from "Costa Rica et Veragua" as the type and noted that the specimen at B was destroyed, that there is an isotype at W, and that F photograph 8707 depicts the destroyed holotype. I was not able to locate a Warscewicz collection of this species at W. At G, there are specimens of *Warscewicz 22* and *23* from "Guatemala et Costa Ricca." The latter was annotated by Wasshausen as an isotype of *A. gigantiflora.* At GH, there is a specimen (ex B) of an unnumbered collection of Warscewicz from "Guatemala et Costarica." The collection numbers cited above are on the original labels and were written with the same pen as the locality information. Thus, they appear to be original numbers rather than later additions to the specimens. All of the specimens mentioned above were annotated by Lindau with his name. In the protologue, Lindau (1895b) provided only, "Guatemala et Costa Rica leg. v. Warscewicz." It is not known to me whether Lindau was including all of the Warscewicz collections in this statement of material examined or whether he was specifically indicating a collection with exactly this information (of which there is a duplicate at GH). The name, locality, and collector on the printed "Museum botanicum Berolinense" label at GH all appear to have been written by Lindau, who likely wrote the information on the labels of duplicates prior to distribution. Because the specimen at B (represented by F photograph 8707) has a locality at variance with that provided by Lindau in the protologue and because the number of that collection (*20*) was not cited by Lindau (who typically was attentive in citing collector's numbers in his descriptions), I do not believe that this specimen necessarily represented the holotype. If Lindau (1895b) was including all of Warscewicz's collections of *A. gigantiflora* in his statement, then all of the collections cited above (and possibly others as well) are syntypes (or possibly isosyntypes). If, instead, he was referring to a specimen at B with the information matching that of the protologue and that of the specimen at GH, then it would have been the holotype. Because it is a matter of conjecture both as to what Lindau was including in his statement of material examined and as to what collections might have been at B prior to the destruction there in 1943, I propose that the specimen at GH be chosen as the lectotype of *A. gigantiflora*. Although it is not as complete a specimen as those at G, this specimen is either an isotype, a syntype, or, at the very least, an isosyntype.

Gibson (1972, 1974) treated *A. gigantiflora* as a variety of *A. schiedeana* and noted that the former differs from the latter only by its elongated inflorescence (10–30 cm long) with more conspicuously glandular rachises and bracts. Wasshausen (1975) maintained *A. gigantiflora* as a species distinguishable from *A. schiedeana* by its longer (6.5–7.5 cm vs. ca. 6 cm) corollas. These two species are indeed similar to one another, and although there are tendencies for longer spikes (8–31 cm vs. 4–11.5 cm) and longer corollas (5.5–7.4 cm vs. 4.1–7 cm) in *A. gigantiflora,* there is sufficient overlap in the lengths of these structures to question their usefulness in delimiting the two species. Based on the data accumulated in my studies, these two species with similar ranges can be distinguished more readily by the inflorescence pubescence and seed coat characters used in the key to species above. Morphological tendencies that may further assist in distinguishing the two species include bracteal apex shape (mostly acute to acuminate in *A. gigantiflora* vs. mostly rounded to abruptly acute in *A. schiedeana*) and bracteal margin (often dentate in *A. gigantiflora* vs. entire in *A. schiedeana*).

Gibson (1972, 1974) included both *A. padillana* and *A. gigantiflora* forma *lutea* in this taxon without comment. Wasshausen (1975) also included both names as synonyms of *A. gigantiflora* and agreed with Standley and Steyermark (1947) that *A. gigantiflora* forma *lutea* differs from the typical form only by its yellow corollas. He noted that in certain other species of *Aphelandra,* corolla color varies from red to orange-red to orange-yellow. Standley (1924) noted that *A. padillana* was common in the mountains of El Salvador. The collections he cited from El Salvador are similar in all characters to Guatemalan plants resembling the type of *A. gigantiflora.*

Information from plants occurring throughout the range of *A. gigantiflora* is included in the description above. Northern Central American plants of *A. gigantiflora* differ from those occurring in southern Mexico in several minor features that are summarized in the following couplet:

Bracts often ± conspicuously dentate; bractlets 13–20 mm long, 1–1.5 mm wide; lower lip of corolla with lateral lobes 1–2.8 mm wide and central lobe 2.2–3.7 times longer than lateral lobes; thecae 3.5–4.5 mm long, posterior pair extending 1–2 mm beyond anterior pair, the anterior pair glabrous. .... Mexican plants.

Bracts entire or inconspicuously dentate; bractlets 8–14.5 mm long, 0.6–1.2 mm wide, lower lip of corolla with lateral lobes 2.5–5.5 mm wide and central lobe 1.6–2.3 times longer than lateral lobes; thecae 4.8–5.3 mm long, pairs presented at ± same height, the anterior pair apically pubescent. .... Central American plants.

The overlap in many of these characteristics and the occurrence of similar variation (e.g., bracteal teeth can vary from present and conspicuous to absent on the same plant) in other species of *Aphelandra* precludes formal taxonomic recognition of the Mexican variants at this time. Additional collections and studies of *A. gigantiflora* are needed in order to understand better the variation among plants in southern Mexico and their relationship to those in Central America.

The differences noted among plants from these two regions permit some speculation about the Sessé and Mociño collections cited below. These collections (which probably represent only a single collection with duplicates distributed from Pavon's herbarium) resemble plants from Central America. Thus, they were likely collected by Mociño during his travels in 1769–98 through the region that is now Guatemala and El Salvador (McVaugh 1977).

Another collection from southern Mexico with similarities to *A. gigantiflora* has pollen that is apparently unique in the genus. *Delgado S. et al. 655* (Oaxaca: Mpio. Juquila, 16 km SO de San Pedro Juchatenango, sea 8 km E de Juquila, pine-oak forest at 1,600 m, CAS, CHAPA, ENCB, MEXU, NY) differs from *A. gigantiflora* primarily by its lance-ovate bracts. Unlike that described for any other species of *Aphelandra,* however, pollen from this collection has pseudocolpal (or colpoid) rings in each mesocolpium. Pollen from this collection (Fig. 2h, i) also lacks the three-armed polar apertures characteristic of *A. gigantiflora.* Because further collections and studies will be necessary in order to determine its status, information from *Delgado S. et al. 655* is not included in the description above.

Additional Specimens Examined.—EL SALVADOR. **Ahuachapán:** without locality, *S. Padilla 418* (US); vicinity of Ahuachapán, *P. Standley 19771* (GH, US). **La Libertad:** Comasagua, *S. Calderón 1364* (US); Santa Tecla, *S. Calderón 1422* (US); Finca Paraíso on N slope of a mountain ¼ mi S of Santa Tecla, *M. Carlson 89* (UC); Puerta de la Laguna, *F. Weberling 2155* (M). **San Vicente:** Volcán de San Vicente, *P. Standley 21512* (GH, US); vicinity of San Vicente, *P. Standley 21680* (US). **Sonsonate:** Finca Chilata, *P. Standley 19315* (US). GUATEMALA. **Escuintla:** Río Guacalate, *P. Standley 60209* (US). **Guatemala:** Amatitlán, Barranca de Eminencia, *J. Donnell-Smith 2696* (US). **Sacatepéquez:** near Las Lajas, *P. Standley 58132* (US); below Barranco Hondo, *P. Standley 88992* (US). MEXICO. **Chiapas:** Mpio. Arriaga, La Mina Microwave Station, *D. Breedlove 56298* (CAS), *D. Breedlove & F. Almeda 60161* (CAS); Mpio. Cintalapa, near La Mina Microwave Station, *D. Breedlove & T. Daniel 70900* (CAS, DUKE, ENCB, F, GH, K, LL, MEXU, MICH, MO, NY, US); near La Sepulcura, 10 km N of Arriaga, *D. Breedlove & T. Daniel 70938* (CAS); Mpio. Arriaga, 13 km N of Arriaga along Hwy. 195, *D. Breedlove & E. McClintock 23739* (DS), *D. Breedlove & R. Thorne 30561* (DS); along Hwy. 190 ca. 2 mi E of Oaxaca border, *T. Croat 46289* (MO); Rizo de Oro, Cintalapa, *T. MacDougall s.n.* (F, MEXU); 40 km W of Tuxtla Gutiérrez on Hwy. 190, *M. Sørensen 18* (C). **Oaxaca:** Distr. Tehuantepec, 8.9 km N de Lachiguiri, *R. Torres C. et al. 4307* (CAS). COUNTRY UNDETERMINED. "Guatemala et Costa Rica," *A. Warscewicz 22* (G); without locality, *M. Sessé et al. 278* (F, MA); "Nouvelle Espagan," *M. Sessé et al. s.n.* ex hb. Pavon (G, OXF).

12. Aphelandra schiedeana Schlecht. & Cham. Linnaea 5:95. 1830. Type.—MEXICO. **Veracruz:** Hacienda de la Laguna, Barranca de Tioselo, October 1828, *C. Schiede 118* (Holotype: B, destroyed, photos F, G, GH, MICH, MO, US; lectotype: M!, designated here; isotypes: BM!, OXF!, W!). *Lagochilium schiedeanum* (Schlecht. & Cham.) Nees in Martius, Fl. Bras. 9:87. 1847.

Shrub to 2.3 m tall. Young stems subterete to quadrate, pubescent with antrorse-appressed eglandular trichomes 0.2–0.6 mm long, becoming glabrate, mature stems often with blisterlike projections. Leaves opposite, petiolate, petioles to 100 mm long (naked portion to 45 mm long), blades lance-elliptic to elliptic, 43–220 mm long, 9–60 mm wide, 2.7–5.8 times longer than wide, acuminate to subfalcate at apex, gradually to abruptly attenuate-decurrent (sometimes nearly to node) at base, surfaces sparsely pubescent with cauline type trichomes, becoming glabrate, margin entire to subcrenate. Spikes terminal, elongate, up to 115 mm long (excluding flowers), 20–40 mm in diameter (excluding flowers) near midspike, rachis pubescent with straight to flexuose to antrorse eglandular trichomes 0.2–0.4 mm long. Bracts reddish, green tinged with red, or entirely green, sometimes spreading with age, ovate to elliptic to obovate-elliptic, 11–30 mm long, 3.5–18 mm wide, 1.6–2.4 times longer than wide, rounded (and often slightly emarginate) to acute (to acuminate at base of spike), erect at apex, abaxial surface puberulent with eglandular and glandular (often absent) trichomes less than 0.05–0.2 mm long and often with some longer antrorse eglandular trichomes mostly along midvein, margin entire, ciliate with eglandular trichomes to 0.5 mm long. Bractlets subulate to lance-subulate, 6–14.5 mm long, 1–2 mm wide, subaristate to aristate at apex, abaxial surface pubescent with straight to antrorse (or flexuose along margin) eglandular trichomes (rarely with a few inconspicuous glandular trichomes as well) to 0.6 mm long. Calyx 9–15 mm long, lobes lanceolate, 2–3.2 mm wide at base, attenuate to aristate at apex, pubescent like bractlets. Corolla reddish, 41–70 mm long, externally pubescent with glandular and eglandular trichomes 0.2–0.9 mm long, upper lip 16–26 mm long, entire to emarginate with lobes subtriangular, 0.2–1 mm long at apex, margin not flared or proximally flared, lower lip ± perpendicular to upper lip, 18–28 mm long, lateral lobes linear to linear-lanceolate, 7.5–15 mm long, 1–3.7 mm wide, lower-central lobe obovate, 17–28 mm long, 6–14.5 mm wide, 1.8–2.4 times longer and 2–6.1 times wider than lateral lobes. Stamens 37–53 mm long, posterior pair inserted ca. 1 mm distal to anterior pair, filaments nearly glabrous to pubescent throughout with filamentous eglandular trichomes, thecae 3–5.5 mm long, posterior pair extending up to 2.5 mm beyond anterior pair, posterior pair dorsally and often apically pubescent with cobwebby hairs, anterior pair glabrous; staminode not evident or triangular and 0.2 mm long. Style 38–58 mm long, glabrous or pubescent with eglandular trichomes; stigma symmetrically funnelform, 0.2–0.4 mm long. Capsule 13–22 mm long, densely pubescent with straight to retrorse eglandular trichomes 0.1–0.3 mm long. Seeds flattened, somewhat squarish, 4–6 mm long, 3.5–4.5 mm wide, nearly smooth or irregularly covered with low, rounded encrustations.

Distribution and Habitat.—Southern Mexico (Chiapas, Oaxaca, and Veracruz; Fig. 9), Guatemala, and El Salvador; plants occur in regions of montane rain forest, pine-oak forest, and cloud forest at elevations from 900 to 2,460 m; sometimes cultivated for ornament.

PHENOLOGY.—Flowering: July–March; fruiting: December–April.

Wasshausen (1975) noted that *A. schiedeana* was known only from Mexico and Guatemala whereas Gibson (1974) included El Salvador within the distributional range of the species but did not cite any collections from the latter country. The occurrence of *A. schiedeana* in El Salvador is documented by the specimen cited below.

In addition to the characters noted in the key above, this species is usually recognizable by its elliptic, apically rounded or abruptly acute, marginally entire, and eglandular puberulent (i.e., with trichomes up to 0.2 mm long) bracts. Plants from Veracruz and Oaxaca all have bracts of this types. Some plants from Chiapas (e.g., *Breedlove 49662, Laughlin 419, Matuda 5211,* and *Ton 2087*), Guatemala (e.g., *Metzler 39, Skutch 1724,* and *Williams et al. 26112*), and El Salvador (e.g., *Williams et al. 15159*) have bracts with somewhat longer (i.e., up to 0.5 mm) eglandular trichomes either on the proximal portion, along the midvein, or near the apex of the bracts and inconspicuous glandular trichomes (up to 0.2 mm long) on the distal portion of the bracts. Such bracts show similarities to some of those in *A. gigantiflora* and *A. guerrerensis. Aphelandra schiedeana* can always be distinguished from the latter two species by its seeds that lack trichome-like papillae. Unfortunately, seeds are not often present on flowering collections of *Aphelandra. Aphelandra schiedeana* can be distinguished further from *A. guerrerensis* by the presence of three-armed polar apertures on its pollen grains and from *A. gigantiflora* by its eglandular inflorescence rachis and inconspicuously glandular (if at all) bracts. Bracteal margin (entire vs. often dentate) is a character tendency that can also be useful for distinguishing *A. schiedeana* from these species. Further distinctions are discussed under *A. guerrerensis* and *A. gigantiflora.*

ADDITIONAL SPECIMENS EXAMINED.—EL SALVADOR. **Santa Ana:** Finca Pilón, Cerro de Los Naranjos, Volcán Santa Ana, *L. Williams et al. 15159* (MO). GUATEMALA. **El Quiché:** waterfalls 4 km N of Nebaj, *M. Metzler 39* (MO). **San Marcos:** S of San Marcos toward Castalia, *L. Williams et al. 26112* (UC, W). MEXICO. **Chiapas:** Mpio. Tenejapa, Yochib, paraje of Kotol Te', *D. Breedlove 7367* (DS, F, MICH, US); Mpio. Tenejapa, near paraje Yashanal, *D. Breedlove 49662* (CAS, LL, NY); Mpio. Tenejapa, near Yochib, Paraje Koltolte', *D. Breedlove 53401* (CAS); Mpio. Motozintla de Mendoza, SW side of Cerro Mozotal, 11 km NW of jct. of rd. to Motozintla along rd. to El Porvenir and Siltepec, *D. Breedlove & B. Bartholomew 55761* (CAS); Cerro Briyo, between Rancho Concepción and Obispo (between Ocozocoautla and Villaflores), *I. Langman 3876* (US); Mpio. Zinacantan, paraje Vo'bits, *R. Laughlin 419* (DS, F, US); Mt. Ovando, *E. Matuda 126* (GH, LL, MEXU, MICH, MO, US), *3955* (GH, MEXU, MICH, MO), *6100* (F, LL, MEXU, MO, US); Fraylesca, near Siltepec, *E. Matuda 5211* (F, LL, MEXU, MO, US); Estacado, Mapastepec, *E. Matuda 18219* (MEXU); Jalapa, Triunfo, Escuintla, *E. Matuda 18454* (DS, F); Sn. Juan P., Escuintla, *E. Matuda 18470* (F, MEXU); Rancho Concepción y Cerro Brujo, *F. Miranda 5158* (MEXU); Sierra Soconusco, from Escuipulas to Cañada Honda, *E. Xolocotzi & A. Sharp X-302* (DS); Mpio. Tenejapa, paraje of Yash'anal, *A. Ton 2087* (DS, ENCB, F, LL, MICH, US). **Oaxaca:** Hwy. 125 between Tlaxiaco and Pinotepa Nacional, 1.53 mi N of Putla de Guerrero, *T. Croat 45912* (MO); Distr. Putla, La Cascada, 5 km NE de Hacienda sobre el camino San Vicente-San Isidro, *A. García M. et al. 3146* (CAS); Mpio. Tuxtepec, Isla de Málsaga, en la presa Miguel Alemán, *L. González Q. 1786a* (DS, F, MICH, MO); Distr. del Centro, *Herrgo & C. Conzatti H* (US); Río Chicahuastla, S. Vicente Putla, *T. MacDougall H151* (NY, US); Distr. Teotitlán, 5.1 km NW de Huautla de Jiménez hacia Teotitlán del Camino, *R. Torres C. & M. Antonio M. 6547* (CAS). **Veracruz:** Orizaba, *D. Bilimek 314* (P), *341* (GH, K, P), *M. Botteri 156* (P), *249* (GH), *800* (BM, G, K, P); Cerro de San Cristóbal, Orizaba, *R. Bonilla B. F-4334* (CHAPA); Vallee de Cordova, *E. Bourgeau 1998* (G, P); Région d'Orizaba, Río Blanco, *E. Bourgeau 3099* (BR, C, G, GH, K, M, MICH, MO, P, S, US); Teocelo, Cascada de Texolo, 5 km de Teocelo, *J. Calzada 2069* (F); El Marzo, 1 km adelante de Santa Ana Atzacan, 18°55'N, 97°05'W, *G. Castillo C. et al. 133* (CHAPA, F); Teocelo, Barranca de Teocelo, *M. Chazaro B. 1210* (F), *M. Chazaro B. et al. 1064* (F), *M. Zola B. 125* (F); Río Jamapa, ca. 4 mi NE of Coscomatepec, *T. Croat 43965* (MO); Cascada de Texolo a 5 km de Teocelo, *J. Ismael C. 2069* (ENCB); Cerro San Cristóbal, W of Orizaba, *I. Langman 3592* (US); Cerro San Cristóbal frente a Orizaba, *A. Lot 1104* (CHAPA, F, GH, LL); near Orizaba, *C. Pringle 5910* (US), *5912* (GH, MEXU, US); Cerro de San Cristóbal, 5 km SW de Orizaba, *J. Rzedowski 12180* (ENCB); Tuxpango, *A. Sharp 441705* (MO); près la Vera Cruz, *A. Sumichrast 806* (G); Mpio. Teocelo, Teocelo, *F. Ventura A. 11915* (MEXU), *12241* (MEXU); Mpio. Teocelo, La Barranca, *F. Ventura A. 14836* (MEXU); Mpio. Chocamán, Río de Chocamán, *F. Ventura A. 17847* (MEXU). **State undetermined:** without locality, *C. Schiede & F. Deppe s.n.* 28 Aug. (OXF), *A. Sumichrast 800* (G).

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RESUMEN

Se encuentran 12 especies del genero *Aphelandra* en México: *A. aurantiaca, A. gigantiflora, A. guerrerensis, A. heydeana, A. hintonii, A.leariloba, A. madrensis, A. scabra, A. schiedeana, A. speciosa, A. verticillata,* y *A. wendtii.* Seis (*A. guerrerensis, A. hintonii, A. leariloba, A. madrensis, A. verticillata,* y *A. wendtii*) son endémicas al país. Se describe *A. wendtii* como especie nueva de las selvas cálido-húmedas de Veracruz, Tabasco, y Chiapas. Se designa un neotipo para *Hemisandra aurantiaca* y se designan lectotipos para *A. acutifolia, A. aurantiaca* var. *roezlii, A. gigantiflora, A. haenkeana, A. madrensis,* y *A. schiedeana.* El polen de todas las 12 especies es tricolpado. Seis especies tienen un número de cromosomas de $n = 14$. Claves a los géneros mexicanos de Aphelandreae y las 12 especies de *Aphelandra* en México son presentadas.

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Appendix A

Specimens of *Aphelandra* from which Pollen was Examined

A. aurantiaca: *D. Breedlove & T. Daniel 71287, G. Shapiro 262*; *A. gigantiflora*: *D. Breedlove & T. Daniel 70900, P. Standley 19771*; *A. guerrerensis*: *T. Daniel 5376gh, G. Hinton et al. 11199, B. Reko 6051*; *A. heydeana*: *D. Breedlove 65803*; *A. hintonii*: *Hinton et al. 16049*; *A. leariloba*: *T. Daniel 2138cv*; *A. madrensis*: *T. Daniel 5276, E. Langlassé 806, E. Lott 865*; *A. scabra*: *T. Daniel 5328*; *A. schiedeana*: *D. Breedlove 53401, F. Ventura A. 12241*; *A. speciosa*: *T. Croat 40837*; *A. verticillata*: *T. Daniel et al. 3295, G. Hinton 13486, H. Moore 5503, J. Rzedowski 27991*; *A. wendtii*: *D. Breedlove & A. Smith 22121, T. Daniel & T. Wendt 5813*; *A. sp.*: *A. Delgado S. 655.*

Appendix B

Index to Collections Examined

The numbers in parentheses refer to the corresponding species in the text.

Abbott, R. 506 (1).
Acosta, M. & J. Dorantes 613 (2).
Acosta P., R. et al. 32 (2).
Aguilar, I. 303 (9), 611 (9).
Alva, R. & S. Cook 1677 (6).
Alvarez G., A. 23 (5).
Anderson, W. & C. Laskowski 4224 (2).
Andrieux, G. 131 (2).
Andrle, R. 87 (3).
Angel R., O. s.n. (6).
Arcos V., R. 151 (2).
Armor, A. V30 (2).
Avila B., C. 5 (12).
Barclay, G. 1973 (2).
Barr, R. & Dennis 65-373A (3).
Beaman, J. 5195 (3).
Bilimek, D. 314 (12), 341 (12).
Boege, W. 374 (2), 497 (2).
Bonilla B., R. F-4334 (12).
Botteri, M. 156 (12), 249 (12), 800 (12).
Bourgeau, E. 1998 (3), 1998 (12), 3099 (12).
Bradburn, A. & S. Darwin 1176 (2), 1185 (2).
Breedlove, D. 4241 (6), 6463 (2), 7367 (12), 7609 (2), 13879 (2), 20154 (2), 26116 (3), 26460 (3), 26524 (7), 27476 (2), 27890 (2), 28299 (2), 28856 (7), 28950 (2), 29011 (2), 31250 (3), 33349 (2), 36727 (2), 37621 (2), 38236 (2), 42842 (2), 47219 (2), 47311 (3), 47327 (2), 47343 (7), 47345 (3), 47363 (3), 49151 (3), 49152 (2), 49662 (12), 52486 (2), 52540 (7), 52785 (2), 53401 (12), 53638 (2), 56298 (11), 56376 (2), 65534 (2), 65803 (9), 66976 (2), 70400 (2), 70668 (2).
Breedlove, D. & F. Almeda 48406 (7), 48438 (3), 57212 (3), 57214 (7), 57242 (2), 57256 (3), 57522 (3), 60161 (11), 60706 (6).
Breedlove, D. & B. Bartholomew 55761 (12).
Breedlove, D. & T. Daniel 70900 (11), 70909 (2), 70938 (11), 71274 (3), 71287 (3), 71320 (2).
Breedlove, D. & G. Davidse 55322 (2).
Breedlove, D. & R. Dressler 29788 (3).
Breedlove, D. & B. Keller 49550 (3).
Breedlove, D. & E. McClintock 23729 (11), 23772 (2).
Breedlove, D. & P. Raven 13351 (2).
Breedlove, D. & A. Smith 21959 (2), 22121 (7), 22247 (7), 22544 (2).
Breedlove, D. & J. Strother 46596 (2), 46841 (2), 46900 (7).
Breedlove, D. & R. Thorne 20667 (2), 30561 (11), 30734 (2).
Butterwick, M. 184 (2).
Cabrera, E. & G. Durán 750 (2).
Cabrera, E. & H. de Cabrera 3301 (2), 6199 (2), 9474 (2), 9562 (2), 9673 (2), 10786 (2), 10986 (2).
Cabrera, E. & L. Cortez 191 (2), 269 (2), 339 (2).
Cabrera, E. & R. Torres 1073 (2).
Calderón, S. 1364 (11), 1402 (9), 1422 (11).
Calzada, J. 59 (3), 1052 (2), 1537 (3), 1626-B (2), 2069 (12).
Calzada, J. & A. Gómez-Pompa 2304 (2).
Calzada, J. et al. 3788 (2), 6461 (2).
Cano D., R. 6 (7).
Carlson, M. 89 (11), 3066 (2).
Castillo C., G. et al. 133 (12).
Cedillo T., R. & R. Torres 1044 (2).
Cedillo T., R. et al. 1649 (2).
Chan, C. & E. Ucan 871 (2).
Chavelas P., J. et al. ES2391 (2), ES-4281 (2).
Chazaro B., M. 1210 (12).
Chazaro B., M. et al. 1064 (12).
Chiang, F. 334 (2).
Chiang, F. et al. 949 (2).
Cochrane, T. et al. 11722 (5).
Conzatti, C. 3735 (2).
Cortés, L. & R. Torres C. 36 (2).
Cowan, C. 5025 (2).
Croat, T. 5777 (2), 40837 (4), 43885 (2), 43965 (12), 45704 (2), 45415 (6), 45912 (12), 46289 (11), 47496 (2), 47519 (2).
Croat, T. & D. Hannon 63133 (3).
Crockett, R. 150 (2).
Cruz, C. de la, V. s.n. (6).
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Nee, M. & G. Schatz 19980 (3).

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NEW AND INTERESTING *GOMPHONEMA* (BACILLARIOPHYCEAE) SPECIES FROM EAST AFRICA

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ABSTRACT: The taxonomy and ultrastructure of five *Gomphonema* Ehrenb. species from East Africa, including two described as new, are presented. Ultrastructure of East African species is compared with congeners and shown to differ in several aspects. *Gomphonema africanum* West, *G. aequatoriale* Hust., *G. kilhamii* sp. nov., and *G. paddockii* sp. nov. are endemic to the region and appear to be closely related by virtue of the unusual structure of their stigmata and lack of puncta occlusions. These species of *Gomphonema* may also be closely allied to *Gomphocymbella beccari* (Grun.) Forti, which has a similar, elongate stigma. *Gomphonema clevei* Fricke, which also appears to be endemic to East Africa, resembles *Reimeria sinuata* (Greg.) Kociolek & Stoermer with regard to stigma morphology. The systematic position of this putative group is unclear.

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INTRODUCTION

A large body of information on diatoms from East Africa has accumulated over the last century, including the works of Fricke (1902), Müller (1905), West (1907), Hustedt (1949), Cholnoky (1954), Kufferath (1956), Monteira (1963), and Gasse (1986). These important floristic works, and others (see Ross 1983; Gasse 1986 for extensive bibliographies) indicate *Gomphonema* Ehrenb. species are an important component of the region's diatom flora. Ross (1983) has noted *Gomphonema* species of the region are unique and has listed five species he considers endemics.

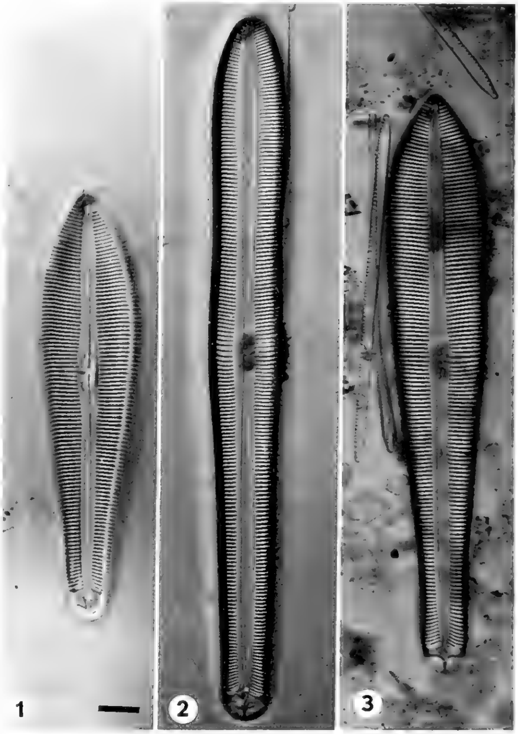
Despite the attention East African *Gomphonema* species have received, questions remain regarding circumscription of taxa. Reports on the morphology and distribution of *G. clevei* Fricke, for example, vary greatly (compare Fricke 1902 with Krammer and Lange-Bertalot 1986). Valve ultrastructure of most East African *Gomphonema* species is unknown; the only published observations are those of Gasse (1980) for a diatom identified as *G. africanum* West. Additionally, core material we have inspected from Lake Tanganyika contains specimens that appear to be new to science.

In this report we consider the taxonomy and ultrastructure of five *Gomphonema* species from East Africa.

MATERIALS AND METHODS

Observations were made on material from several sources. Cleaned material from cores taken from Lake Tanganyika was supplied to us by John Kingston (Queen's University). The original source of this material was Tom Johnson (Duke University). Samples from Lake Rudolf were taken by Robert Ross (The Natural History Museum, London), and material utilized in this study includes BM 1367, 1368, 1370, 1371, 1396, 1397, and 1398. This material, as well as the holotype slide for *G. africanum* from Lake Tanganyika, was kindly provided by David Williams of The Natural History Museum, London.

Material from these sources was boiled in nitric acid and alternately rinsed and settled in distilled water to remove oxidation by-products. Cleaned material was air-dried onto cover glasses and mounted onto microscope slides with Hyrax®. Light microscopic observations were made with Reichart Polyvar, Olympus OH-2, and Leitz Ortholux microscopes. For scanning electron microscopy (SEM), cover glasses containing air-dried material were mounted onto aluminum stubs and coated with approximately 20 nm of gold-palladium. Material was viewed on JEOL T-100 and Hitachi H-520 SEMs.



FIGURES 1–3. *Gomphonema africanum,* "clavate" type. FIGURE 1. Specimen from holotype slide, BM 78079, "Tanganyika 26-viii-'04, Cunnington 79." FIGURES 2, 3. Specimens from Lake Tanganyika, core, station 10, 100 cm. Scale bar = 10 μm.

RESULTS

Gomphonema Ehrenberg 1832

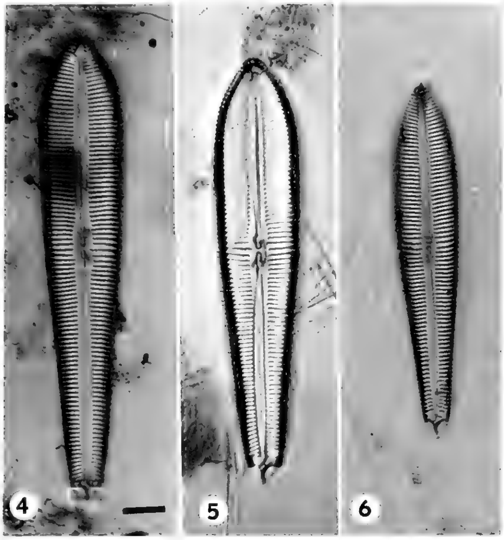
Gomphonema africanum West

(Figs. 1–21, 26)

Valves 70–230 μm long, 14–25 μm wide, and highly variable in outline. A number of distinct morphologies can be identified. One group, which includes specimens from the holotype slide (BM 78079), is strongly clavate, broadest near the headpole, and has "turris"-like/apiculate headpoles (Figs. 1–6). A second group (Figs. 7–9) is lanceolate-clavate and broadest at the center of the valve, while a third group is linear-lanceolate (Figs. 10–13). A prominent apical pore field (APF) positioned at footpole and one large spine visible at headpole (Fig. 11). Raphe lateral and straight. One to several stigmata have external openings near puncta, making them somewhat difficult to observe. Axial area narrow, becoming slightly wider around central area. Striae distinctly punctate and uniseriate. Striae radiate along most of length of valve, strongly radiate at footpole. Striae 8–12/10 μm and consistently finer at footpole. Small septum and pseudoseptum present at each pole.

In the SEM, external stigmal openings oblong relative to rounded puncta (Figs. 14, 15). Puncta unoccluded, but this may be caused by preservation problems on the subfossil specimens, which show other signs of valve degredation/dissolution (Fig. 16). External proximal raphe ends terminate close to one another (Fig. 15). Internally, central nodule bears recurved proximal raphe ends (Figs. 17, 18). Central nodule eccentric to raphe slit and stigmata project obliquely from near puncta onto it (Figs. 20, 21, 26). Pseudosepta visible at poles (Figs. 17, 19), and marginal lamina runs length of valve (Figs. 18, 26).

COMMENTS.—These observations on general



FIGURES 4–6. *Gomphonema africanum,* "clavate" type, specimens from Lake Tanganyika, core, station 10, 100 cm. Scale bar = 10 μm.

valve morphology agree well with the original description of West (1907) and Hustedt's (1949) detailed treatment. The size range reported here is wider than previously recognized. Formal taxonomic recognition of the different morphologies described here awaits additional observations on shape variability, particularly of larger specimens.

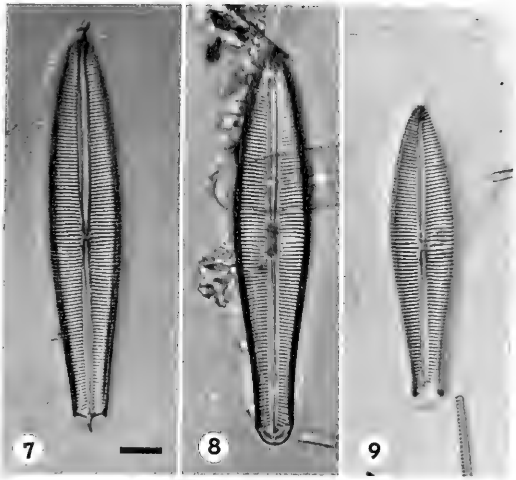
Foged's (1966) illustrations of this species from Ghana are more reminiscent of *G. gracilis* var. *turris* Hust. than *G. africanum.*

Gomphonema kilhamii, Kociolek & Stoermer, sp. nov.
(Figs. 22–25, 27–31)

DESCRIPTION.—Valves trullate in outline, 70–180 μm long, 12–21 μm broad, headpole acute, footpole rounded and broader than headpole. Striae parallel-radiate, distinctly punctate, 9–10/10 μm at mid-valve, 11–13/10 μm at poles. Axial area straight, narrow, and contains laterally expanded raphe. Isolated stigma conspicuous, located close to striae. Internal proximal raphe ends distinct. Small pseudoseptum present at each pole.

HOLOTYPE.—Light microscopic preparation 216039, CAS (Fig. 23).

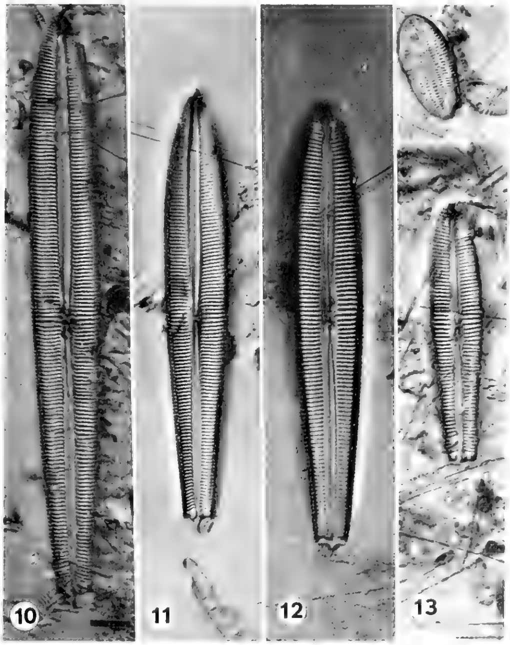
ISOTYPES.—Light microscopic preparations, ANSP and BM.



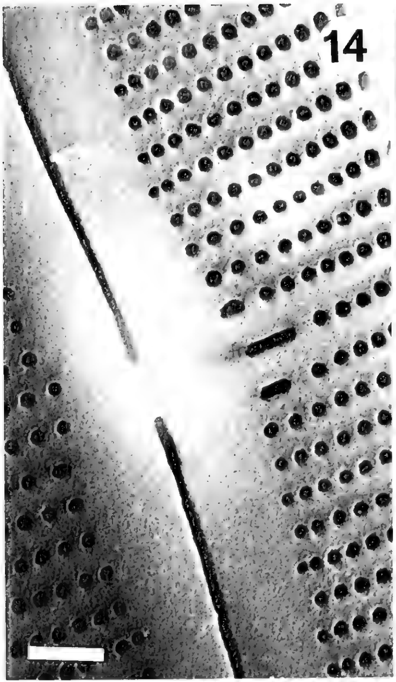
FIGURES 7–9. *Gomphonema africanum,* "lanceolate" type, specimens from Lake Tanganyika, core, station 10, 100 cm. Scale bar = 10 μm.

TYPE LOCALITY.—Lake Tanganyika, core, station 10, 100 cm.

In the SEM, puncta appear dash-like or narrowly tear-drop shaped (Figs. 27, 29, 30). External proximal raphe ends dilated and stigmal



FIGURES 10–13. *Gomphonema africanum,* "linear" type, specimens from Lake Tanganyika, core, station 10, 100 cm. Scale bar = 10 μm.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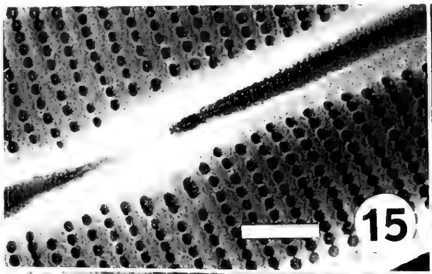
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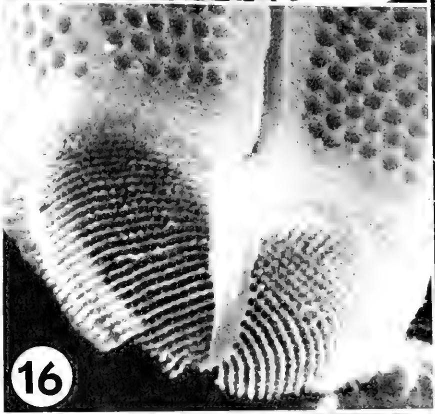
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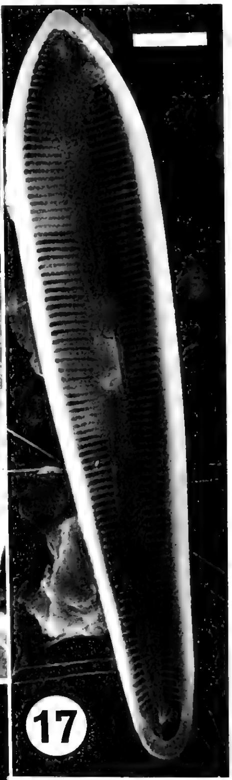
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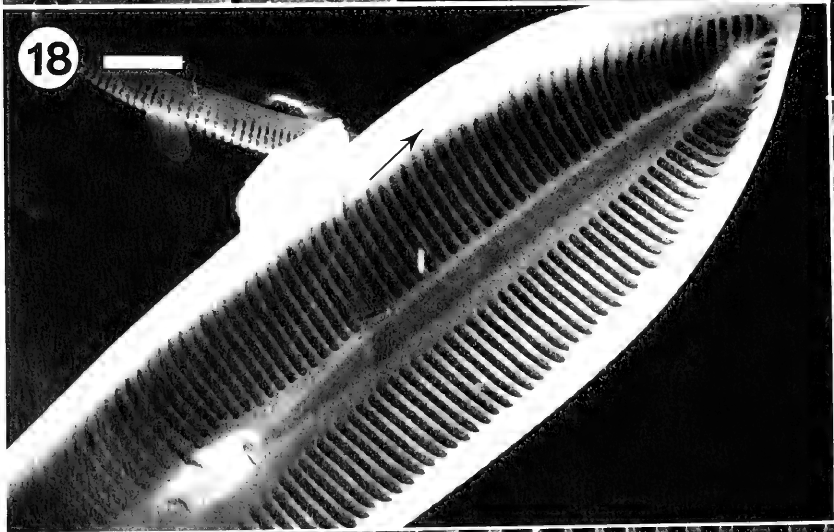
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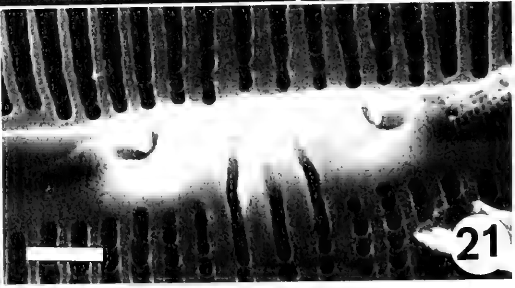
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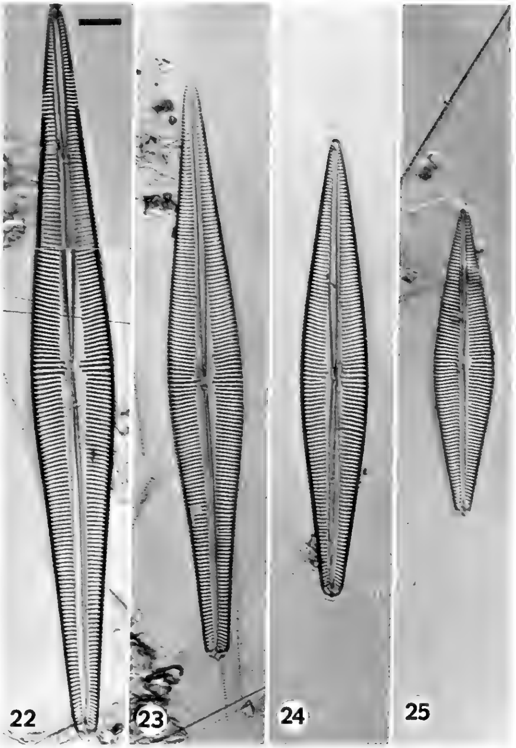
opening irregular and larger than puncta (Fig. 30). APF bisected by distal raphe end, producing different-sized lobes of APF. Porelli round and extend around raphe end along mantle (Fig. 29). At headpole, puncta slit-like and raphe curves onto mantle before reaching valve terminus (Fig. 27). Deflection of distal raphe end prior to valve terminus is unique among gomphonemoid diatoms studied thus far. Small projection occurs at headpole (Fig. 28). Internally, stigmal opening is an elongate slit, terminating on central nodule. Proximal raphe ends recurved. Pseudoseptum prominent and helictoglossa visible at headpole (Fig. 31).

COMMENTS.—This presumably extinct member of the Lake Tanganyika flora is distinguished by the angled, trullate shape of the valve. Although not abundant in the core material, specimens are easily recognized by the size and shape of the valves. Gasse's illustration identified as *G. africanum* (1980: pl. 50, Figs. 25, 26) resembles *G. kilhamii.* This species is dedicated to the late Peter Kilham, in honor of his work on African lakes.



FIGURES 22–25. *Gomphonema kilhamii,* specimens from Lake Tanganyika, core, station 10, 100 cm. Scale bar = 10 μm.

Gomphonema paddockii, Kociolek & Stoermer, sp. nov.
(Figs. 32, 33; 41, 42)

DESCRIPTION.—Valves broadly lanceolate-clavate, 94–103 μm long, 20–21 μm broad. Wide axial area, extending beneath striae, contains expanded, straight raphe. Striae radiate, strongly radiate at the footpole, 10/10 μm at mid-valve, 13–14/10 μm at poles. Stigma prominent, elongate, runs from central nodule towards striae.

HOLOTYPE.—Light microscopic preparation #216040, CAS.

ISOTYPES.—Light microscopic preparations, ANSP and BM.

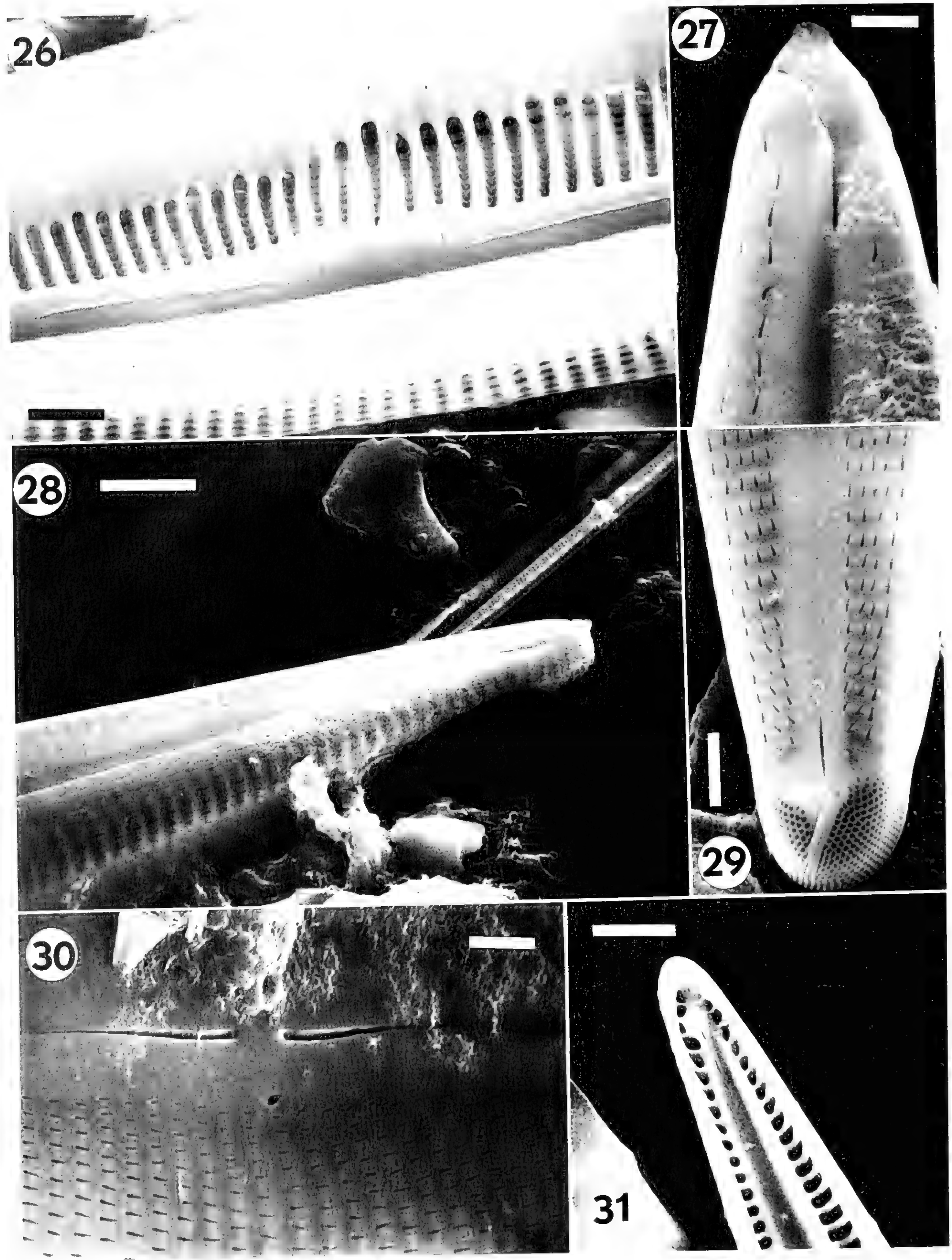
TYPE LOCALITY.—Lake Tanganyika, core, station 10, 100 cm.

In the SEM, recurved internal proximal raphe ends terminate on the edges of central nodule. Internal stigmal opening elongate and ends on central nodule (Figs. 41, 42).

COMMENTS.—This taxon is, like *G. kilhamii,* presumed extinct, since it is conspicuous but not previously reported in the many studies of Recent diatoms from Lake Tanganyika. This species is named in honor of T.B.B. Paddock, former Curator of Diatoms at the British Museum, for his excellent work on diatom taxonomy, ultrastructure, and systematics.

←

FIGURES 14–21. *Gomphonema africanum,* SEM, specimens from Lake Tanganyika, core, station 10, 100 cm. FIGURES 14, 15. External view of linear central area with elongated stigmal openings and round, unoccluded puncta. Scale bars = 2 μm and 2.8 μm, respectively. FIGURE 16. External view of footpole showing raphe bisecting apical pore field. Scale bar = 2.8 μm. FIGURE 17. Internal view of valve showing central nodule and poles with pseudosepta. Scale bar = 10 μm. FIGURE 18. Internal view of central nodule to headpole showing marginal lamina (arrow) and large helictoglossa. Pseudoseptum is visible near headpole. Scale bar = 5 μm. FIGURE 19. Internal view of footpole showing pseudoseptum and large helictoglossa. Scale bar = 2 μm. FIGURES 20, 21. Internal views of central nodule with recurved proximal raphe ends and elongate internal stigmal openings. Scale bars = 2 μm.



FIGURES 26–31. *Gomphonema* spp., SEM, specimens from Lake Tanganyika, core, station 10, 100 cm. FIGURE 26. *G. africanum*, internal view showing central nodule with recurved proximal raphe ends. Marginal lamina is visible. Scale bar = 3.5 μm. FIGURE 27. *G. kilhamii*, external view of headpole showing raphe curving onto mantle before terminus of valve. Scale bar = 1 μm. FIGURE 28. External view of headpole showing slit-like puncta and small protrusion at valve end. Scale bar = 3.5

Gomphonema aequatoriale Hustedt
(Figs. 34–40, 43–47)

Valves lanceolate-clavate 25–60 μm long, 8–10 μm broad, with headpoles squared-off and footpoles rounded. Striae punctate, parallel at headpole, becoming radiate towards central nodule. Striae radiate near footpole. Striae 8–10/10 μm near mid-valve, 10–13/10 μm at poles. External opening of single stigma positioned close to end of a median stria. Raphe lateral, slightly undulate. Prominent septa and pseudosepta present at poles.

In the SEM, puncta oblong, nearly circular or tear-drop shaped and usually uniseriate, although they may occur in rows of two. Occlusions lacking in puncta. External proximal raphe ends dilated and stigmal opening round (Figs. 43, 44). At headpole distal raphe end curves and terminates on mantle (Fig. 44). APF bisected by distal raphe end. Two lobes of APF porelli of different sizes (Fig. 45). Porelli round, similar in shape to puncta but much smaller in size. Pseudosepta present at poles and helictoglossae offset from raphe slit internally (Fig. 46). Recurved internal proximal raphe ends and an elongate stigmal opening present on central nodule (Figs. 46, 47).

COMMENTS.—Hustedt (1949) described *G. aequatoriale* as being 50–100 μm long and 12–16 μm wide. Hustedt's measurements are almost exactly twice the values recorded for the populations from Lake Rudolf examined in this study. Simonsen's (1987: pl. 527, Figs. 16–20) illustrations of Hustedt's specimens range from 30–57.5 μm in length. Hustedt apparently erred in his illustrations and description of this species. Otherwise, populations described here are in accordance with Hustedt's (1949) observations.

Gomphonema clevei Fricke
(Figs. 48–59)

Valves lanceolate-clavate with broadly rounded or protracted headpole and rounded footpole, 15–39 μm long, 4–8 μm broad. Radiate striae 12–14/10 μm. Raphe lateral and undulate. Axial area narrow at poles, becoming broader towards center of valve. Single stigma present.

In the SEM, puncta have external flaps and puncta openings appear slit-like or c-shaped (Figs. 55–57). External proximal raphe ends dilated and stigmal opening round, positioned near proximal raphe ends (Fig. 55). Distal raphe ends deflected onto valve mantle (Figs. 55, 57). Porelli of APF round, unoccluded, and physically separated from puncta by unornamented area. In girdle view, each valve has two open, punctate girdle bands (Fig. 56). One band closed at headpole, other closed at footpole. Each cingulum has small septum. Pseudosepta and helictoglossae present at poles (Fig. 58). Raised central nodule bears recurved proximal raphe ends and round stigmal opening (Fig. 59).

COMMENTS.—The taxonomy of *G. clevei* is poorly understood and this appears to have led to confusion regarding its distribution. Krammer and Lange-Bertalot (1986) suggest that *G. clevei* is cosmopolitan. Fricke (1902) illustrated a small group of East African specimens, 14.5–27 μm long and 4.5–6.5 μm broad, with 9–13 striae per 10 μm, and recent figures by Gasse (1986) are similar to Fricke's original illustrations. Müller (1905) described *G. brachyneura,* a linear-lanceolate species also from East Africa, as 16–34 μm long, 4–5 μm wide, and having 13–15 striae in 10 μm; and Cholnoky (1954) considered *G. clevei* and *G. brachyneura* conspecific. Hustedt's (1938) concept of *G. clevei* from Java, Bali, and Sumatra appears to be different from Fricke's (Krammer and Lange-Bertalot 1986), in that Hustedt's figures have a more linear valve outline and broader axial area (Hustedt 1938; see also Krammer and Lange-Bertalot 1986). Hustedt also described *G. clevei* var. *javanica* Hust., which differs markedly from the nominate variety in shape of the valve and striae pattern (Hustedt 1938; Simonsen 1987). Subsequent reports of *G. clevei* made from Europe (Foged 1977, 1979), America (Patrick *in* Patrick and Reimer 1975; Camburn et al. 1978) and Australia (Foged 1978) appear to follow Hustedt's concept of this species. A reconsideration of the material of Hus-

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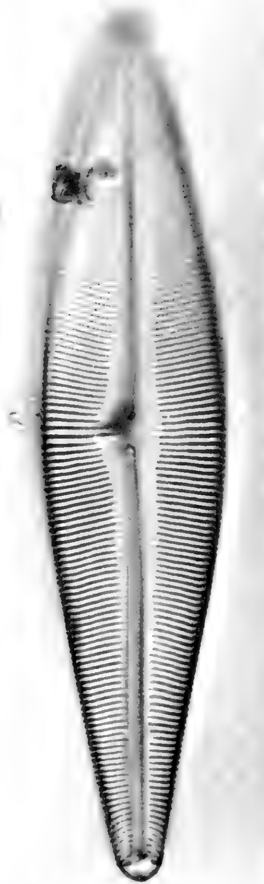
μm. FIGURE 29. External view of footpole showing bilobed apical pore field, with lobes being of different sizes. Porelli are round and extend around distal raphe end on valve mantle. Scale bar = 2 μm. FIGURE 30. External view of central area showing tear drop shaped puncta, rounded stigmal opening, and dilated proximal raphe ends. Scale bar = 2 μm. FIGURE 31. Internal view of headpole showing prominent pseudoseptum. Scale bar = 3.5 μm.



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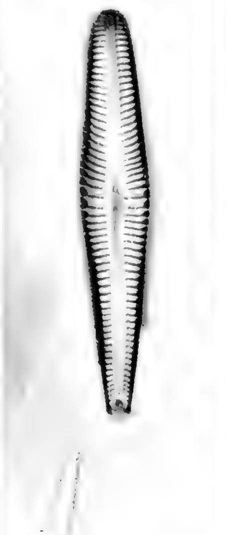

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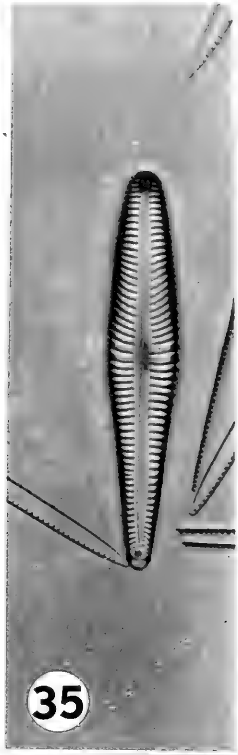

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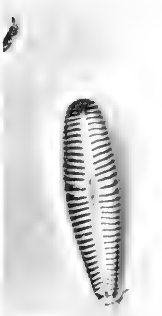

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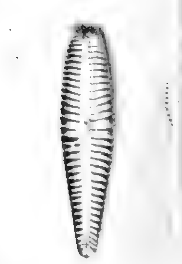

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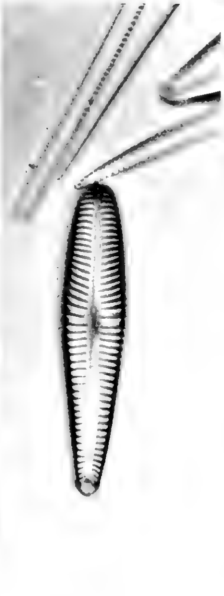

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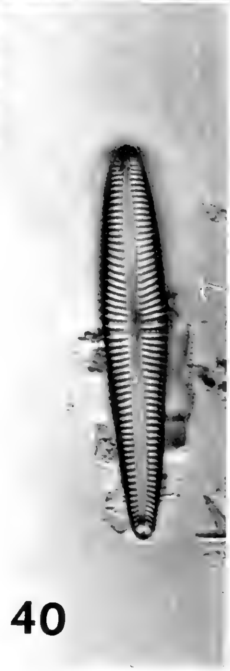

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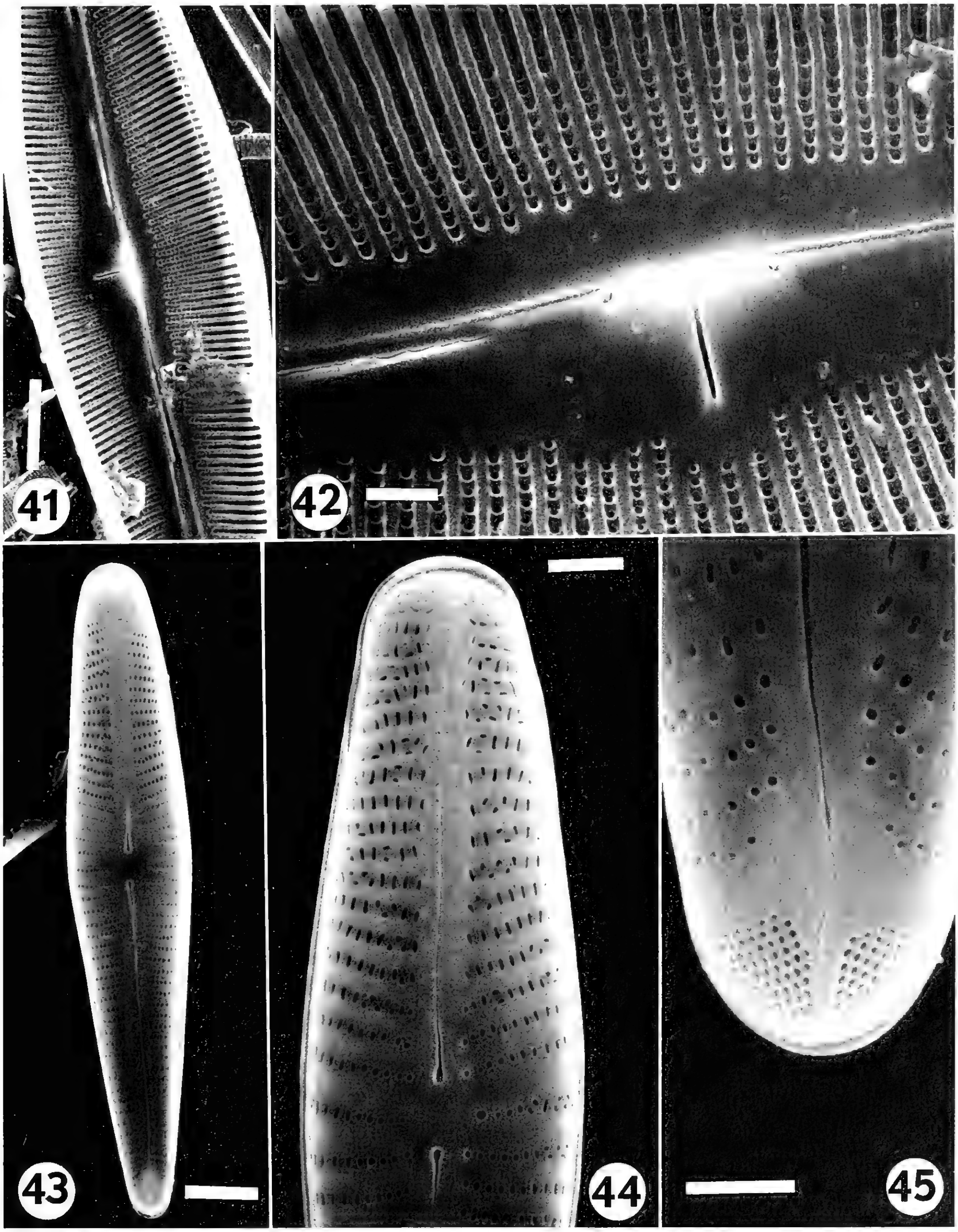
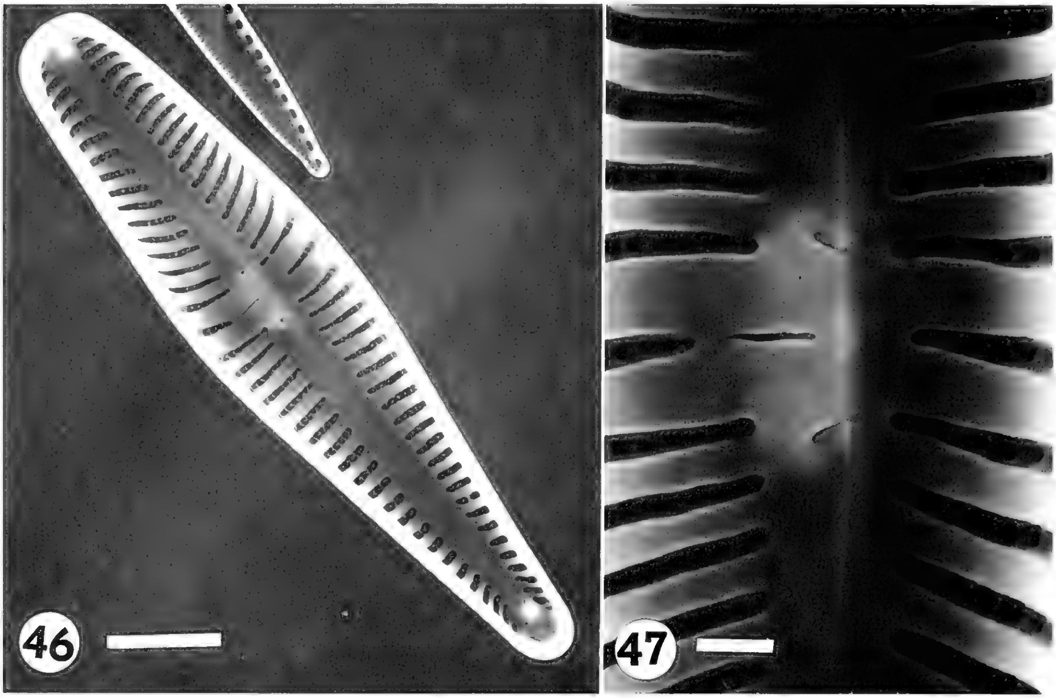
FIGURES 32–40. *Gomphonema* spp. FIGURES 32, 33. *G. paddockii*, specimen from Lake Tanganyika, core, station 10, 100 cm. FIGURES 34–40. *G. aequatoriale*, specimens from Lake Rudolf. Scale bar = 10 μm.



FIGURES 41–45. *Gomphonema* spp., SEM. FIGURES 41, 42. *G. paddockii,* specimens from Lake Tanganyika, core, station 10, 100 cm, internal views of central nodule showing recurved proximal raphe ends and elongate stigmal opening. Scale bars = 10 μm and 2 μm, respectively. FIGURES 43–45. *G. aequatoriale,* specimens from Lake Rudolf, external views. FIGURE 43. Valve view showing outline, narrow axial area and dilated proximal raphe ends. Scale bar = 5.5 μm. FIGURE 44. Central nodule to headpole, with slit-like striae, round stigmal opening, and distal raphe end extending onto valve mantle. Scale bar = 2 μm. FIGURE 45. Footpole with bilobed apical pore field. Porelli are round and smaller than puncta. Scale bar = 1.3 μm.



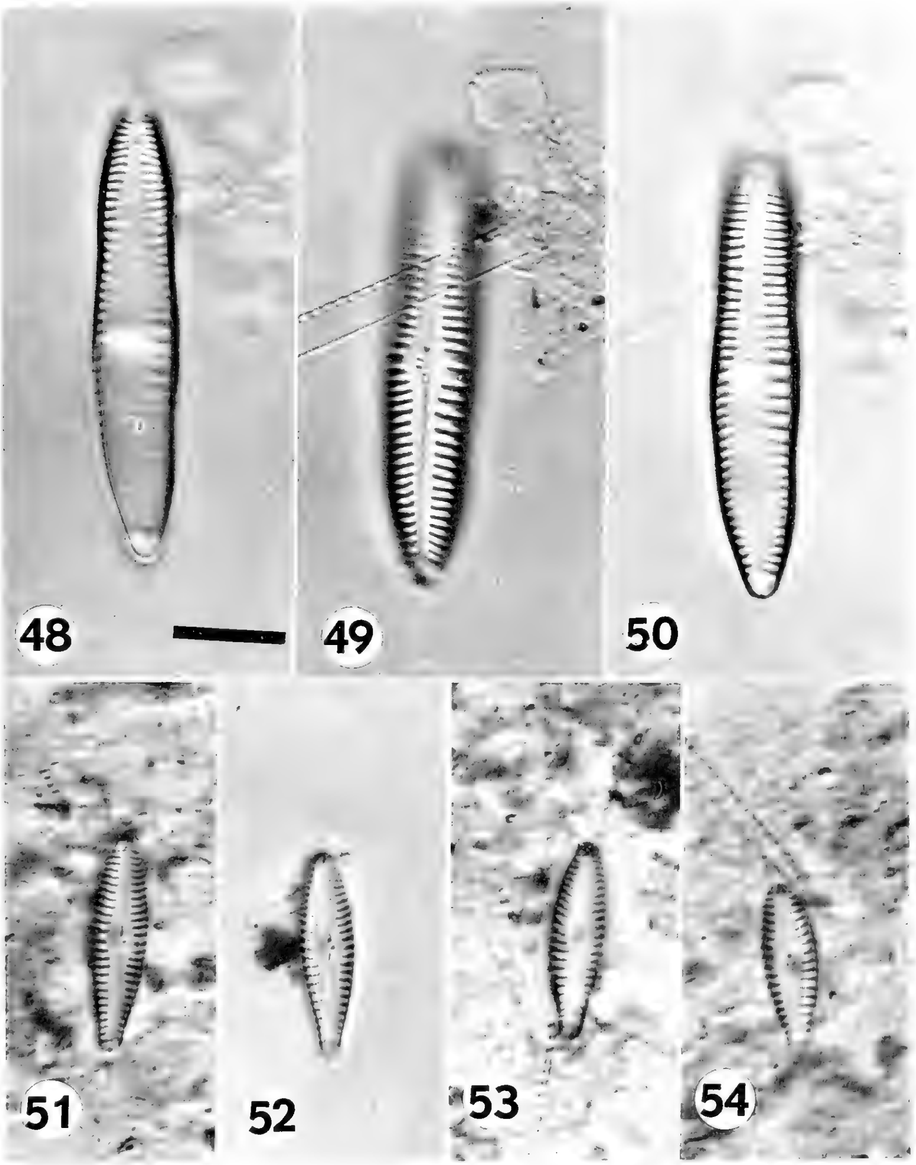
FIGURES 46–47. *Gomphonema aequatoriale*, SEM, specimens from Lake Rudolf, internal views. FIGURE 46. Valve view showing pseudosepta and helictoglossae at poles and internally raised central nodule. Scale bar = 5 μm. FIGURE 47. Central nodule with broadly recurved proximal raphe ends and elongate stigmal opening. Scale bar = 1 μm.

tedt, Foged, and others is necessary to determine if *G. clevei* is indeed cosmopolitan or just a complex of superficially similar taxa. Such a reconsideration may also determine if Fricke's species is limited to East Africa.

Krammer and Lange-Bertalot (1986: pl. 164, Figs. 17–19) suggest intermediate morphologies exist between *G. angustatum* Agardh (=*G. intricatum* Kützing, Kociolek and Stoermer in press c), *G. rhombicum* Fricke, and *G. clevei*. The specimens illustrated by Krammer and Lange-Bertalot do not appear to us to resemble one another except in outline of the valves. The individuals are small (all about 20 μm), although it has been well-documented that small specimens of different taxa tend to converge on similar shapes during size diminution (Geitler 1932). With reference to groups of *Surirella* Turpin species, Krammer and Lange-Bertalot (1987) have stated, ". . . if the smaller stages are examined . . . the general uniformity in valve outline and valve surface hardly allows the two groups to be separated." Krammer and Lange-Bertalot's reference to the need to look at "entire populations" (1987) to make "correct identifications" of *Surirella* species is equally applicable to *Gomphonema* species.

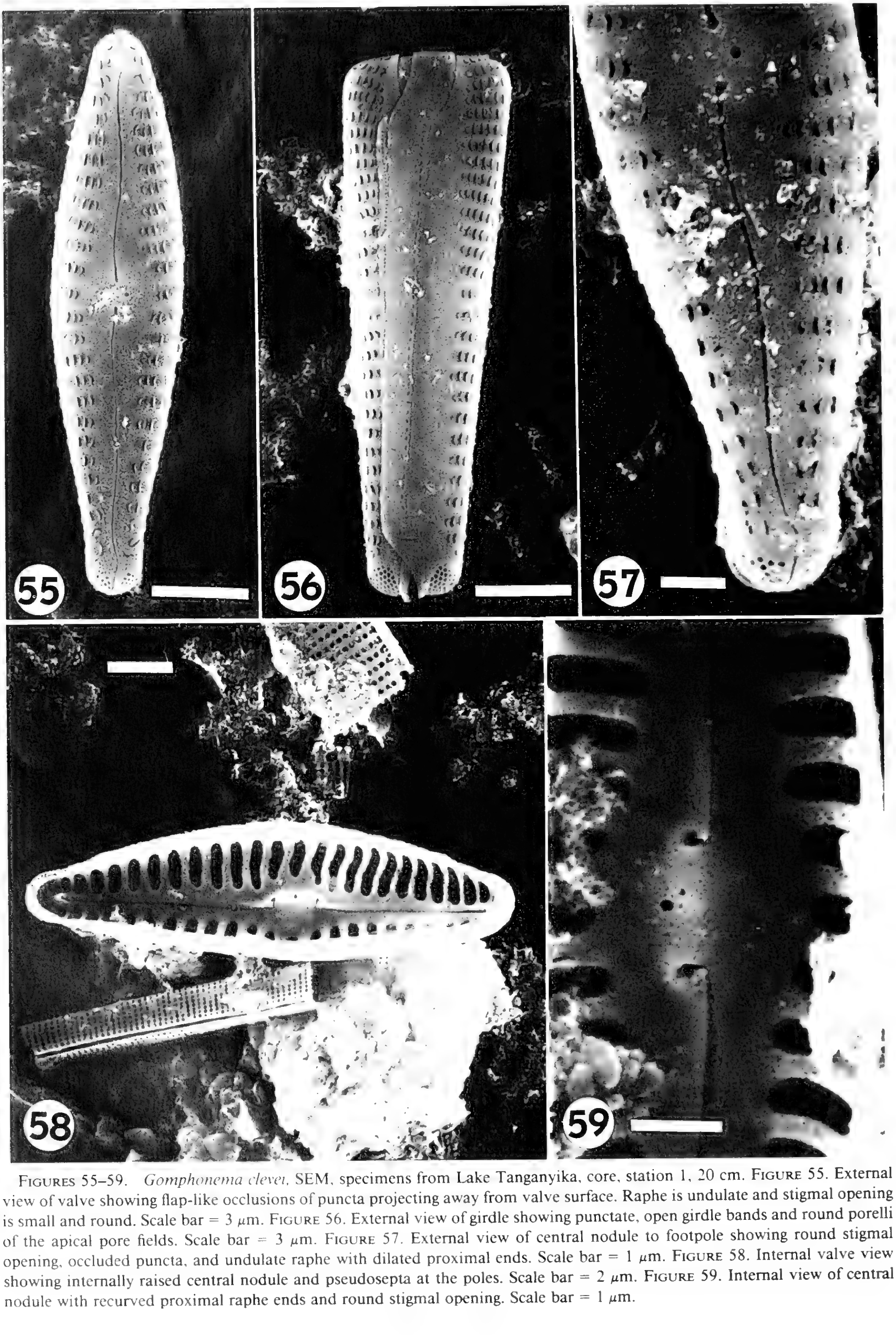
DISCUSSION

Four of the five *Gomphonema* species considered here appear unique relative to other previously investigated members of the genus on the basis of valve morphology. *Gomphonema africanum, G. aequatoriale, G. kilhamii,* and *G. paddockii* all have elongated internal stigmal openings and lack siliceous occlusions in the puncta. Most "typical" *Gomphonema* species have short, slit-like internal stigmal openings that reside mainly on the central nodule (e.g., Dawson 1972, 1973) and have siliceous occlusions on the exterior or interior of the puncta (Kociolek and Stoermer 1990a, in press). These East African species are apparently endemic to the region and, considering their morphological similarities, may represent a distinct clade. These East African



FIGURES 48–54. *Gomphonema clevei*, specimens from Lake Tanganyika, core, station 1, 20 cm. FIGURES 48–50 are of an auxospore valve (?) at different levels of focus. Scale bar = 10 μm.

species may also represent the sister group to *Gomphocymbella beccari* (Grun.) Forti, an East African endemic which also has a similar stigma structure (Round et al. 1990; pers. obs.). The observation of a group of closely related *Gomphonema* species in East African Rift Valley lakes is similar to the report by Kociolek and Stoermer (1988b) of sister taxa of the *Gomphoneis quadripunctata* species complex from Lake Baikal. These reports of evolutionary lineages of gomphonemoid diatoms from specific geographic areas suggest that other regions with endemic species are worthy of examination (e.g., Indo–Malaysian Archipelago, Hustedt 1942), and this may ultimately lead to a new understanding of freshwater diatom biogeography.



FIGURES 55–59. *Gomphonema clevei*, SEM, specimens from Lake Tanganyika, core, station 1, 20 cm. FIGURE 55. External view of valve showing flap-like occlusions of puncta projecting away from valve surface. Raphe is undulate and stigmal opening is small and round. Scale bar = 3 μm. FIGURE 56. External view of girdle showing punctate, open girdle bands and round porelli of the apical pore fields. Scale bar = 3 μm. FIGURE 57. External view of central nodule to footpole showing round stigmal opening, occluded puncta, and undulate raphe with dilated proximal ends. Scale bar = 1 μm. FIGURE 58. Internal valve view showing internally raised central nodule and pseudosepta at the poles. Scale bar = 2 μm. FIGURE 59. Internal view of central nodule with recurved proximal raphe ends and round stigmal opening. Scale bar = 1 μm.

The other species considered here, *G. clevei,* also appears distinct from most other "typical" members of the genus. Although *G. clevei* has puncta occluded by flaps as well as other attributes in common with *Gomphonema* species (e.g., a single, bilobed APF and asymmetry about the transapical axis), it possesses a simple, round, internal stigmal opening. The structure of the internal stigmal opening of *G. clevei* resembles that of *Reimeria sinuata* (Greg.) Kociolek & Stoermer (Schoeman and Archibald 1978; Kociolek and Stoermer 1987) and *Cymbella diluviana* (Krasske) Florin (Kociolek and Stoermer 1990b). A number of authors have suggested a close relationship between *Reimeria* Kociolek & Stoermer and gomphonemoid diatoms (e.g., Krammer 1982; Round et al. 1990), while Kociolek and Stoermer (1988a) have suggested *Reimeria* is more closely related to cymbelloid diatoms. If the type of stigmal opening found in *G. clevei* and *Reimeria* is a derived condition, it may support the view of a close relationship between these two taxa. How this relationship is considered in the context of cymbelloid-gomphonemoid diatom phylogeny is, at present, unclear.

The five East African *Gomphonema* species treated here appear to be endemic to the region (pending taxonomic review of *G. clevei*), and this expands Ross's (1983) list of endemics for the East African flora. Additional studies appear warranted to determine if the level of endemism exhibited by Recent diatoms in East Africa mirrors the high levels found for other organisms. The apparent extinction of *G. kilhamii* and *G. paddockii* suggests that levels of endemic diatom species in East Africa may have been higher in the recent past. Other apparently endemic *Gomphonema* species are known from local diatomites (e.g., *G. swatmanii* Reinhold). Further studies are needed to document species and their distributions through time to determine if levels of endemism and diversity have changed in the region.

ACKNOWLEDGMENTS

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A REVISION OF THE WASP GENUS *KOHLIELLA* (HYMENOPTERA: SPHECIDAE)

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Abstract: The revision includes a redescription of the genus, a key to the species, a phylogenetic analysis, a summary of the known life history, distribution records, and maps. The two known species of *Kohliella* from southern Africa (*K. alaris* and *K. stevensoni*) are redescribed; the previously unknown female of *K. stevensoni* and a new species (*K. anula*) from Sri Lanka are described. Previously unnoticed characters are used in descriptions and cladistic analysis.

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Introduction

General.—Brauns (1910) established *Kohliella* for his new species *K. alaris* from South Africa. Arnold (1924) described a second species, *K. stevensoni,* from Zimbabwe, and K. V. Krombein recently collected representatives of a third, undescribed species in Sri Lanka. A revision of these species, integrating all available information, is presented here. Finding previously unnoticed characters and reconstructing the phylogeny of the species were among the primary goals.

Technical Terms.—Generally the terminology of Bohart and Menke (1976) has been adopted, except I have followed Michener and Fraser (1978) for mandibular terms. The following terms are redefined here for clarification or for convenience:

Disk: central part of a sclerite, e.g., scutal disk.
Mandible:
  acetabular groove—see Fig. 2;
  adductor ridge—extends distad from the mandibular base at its inner (concave) face and gradually becomes visible from the outside; the visible portion is part of the mandibular posterior margin (in *Kohliella,* this portion is markedly, roundly expanded);
  condylar ridge—arises from the condyle, extends distad, and constitutes the basal portion of the posterior mandibular margin; it is conspicuously angulate distally in *Kohliella*;
  condyle—mandibular articulation on the occipital side of the head capsule;
  posterior margin—extends between condyle and mandibular apex; externoventral margin of Bohart and Menke (1976), lower margin of Michener and Fraser (1978); (the term posterior is preferred because the head is hypognathous and this edge is thus oriented posterad);
  trimmal carina—cutting edge (or inner margin) of the mandible.
Sternum, tergum: abbreviations for gastral sternum, gastral tergum.
Vertex:
  length—the distance between a hindocellar

scar's hindmargin and an imaginary line connecting the eye hindcorners (i.e., the point where the inner and posterior portions of the orbit meet); width—the shortest interocular distance.

Sources of Material.—Institutions that sent material for study are abbreviated in the text as follows: AMG: Albany Museum, Grahamstown, South Africa (Friedrich W. Gess); BMNH: British Museum (Natural History), London, England (Colin R. Vardy); CAS: California Academy of Sciences, San Francisco, California; SAM: South African Museum, Cape Town, South Africa (Vincent B. Whitehead); SMWN: State Museum, Windhoek, Namibia (John Irish, Eugene Marais); also via Ole Lomholdt, ZMK; TMP: Transvaal Museum, Pretoria, South Africa (Robert B. Toms); USNM: United States National Museum (Smithsonian Institution), Washington, D.C. (Karl V. Krombein, Arnold S. Menke); ZMK: Zoological Museum, Copenhagen, Denmark (Ole Lomholdt).

Genus **Kohliella**

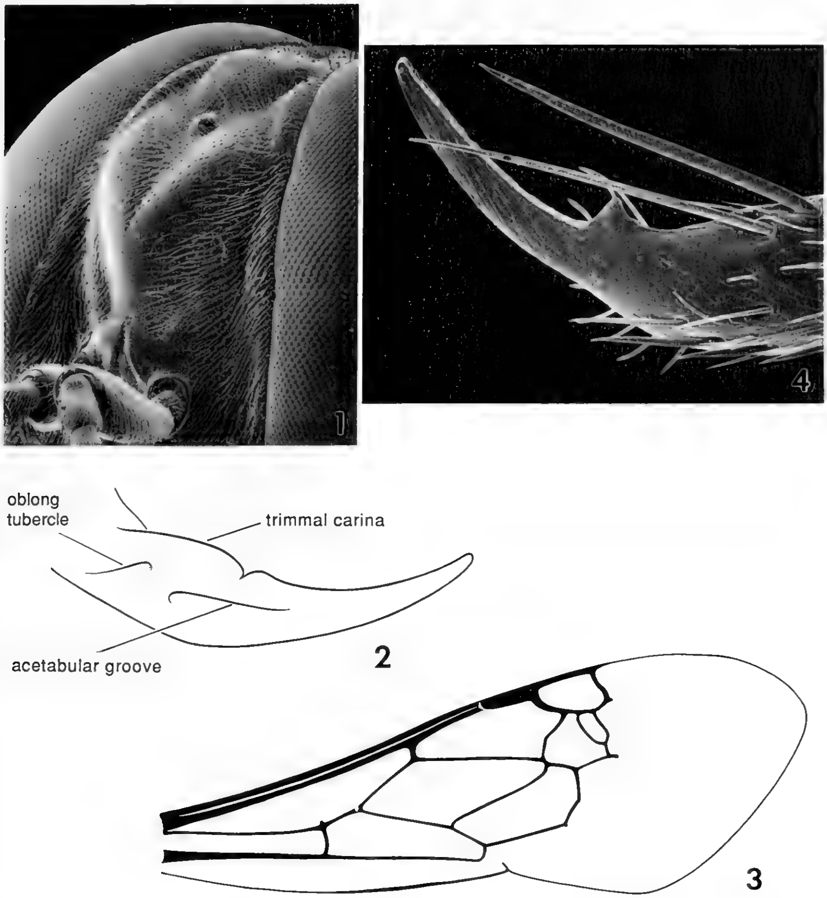
Kohliella Brauns, 1910:668. Type species: *Kohliella alaris* Brauns, 1910:669, by monotypy.

Diagnosis.—Like other members of Larrini, subtribe Tachytina, *Kohliella* has flat, elongate ocelli (Bohart and Menke 1976). Within the tribe, the genus is characterized by the following five autapomorphies: (1) frons with a V-shaped swelling (Fig. 1); (2) mandible with oblong tubercle near proximal end of acetabular groove (Figs. 2, 20); (3) third submarginal cell petiolate posteriorly (Fig. 3); (4) lateral carina of tergum I evanescent behind spiracle and absent posteriorly; and (5) sternum I largely glabrous (setose only basally). In addition, the female claws have a subbasal tooth (Fig. 4), a condition that in Larrinae is shared only with some *Liris*. Bohart and Menke (1976) thought that the strongly compressed mouthparts were also diagnostic, but actually this character has little diagnostic value. First, the prementum is sharply compressed in *K. alaris* and *K. stevensoni* but not in *K. anula* (where it is strongly convex, as it is in some *Prosopigastra*), and, second, the stipites are inclined toward each other at an angle that varies from less than 90° to about 150°. (The inclination, in most other Larrinae, is about 120–150°.)

Description.—*Kohliella* was described in detail by Bohart and Menke (1976), but it is redescribed below to take into account the new species from Sri Lanka, the unknown female of *K. stevensoni*, and some structures not considered previously. The major structural characters of the genus other than the autapomorphies follow:

Posterior mandibular margin notched; notch delimited proximally by angulate apex of condylar ridge, and distally by markedly, roundly expanded distal portion of adductor ridge. Frons with glabrous swelling above each antennal socket (swellings oriented obliquely and nearly joining mesally). Hindocellar scars widely diverging anterolaterad (their long axes forming an angle of about 130°), moderately elongate (scar shorter than distance that separates it from midocellus). Occipital carina joining hypostomal carina. Propodeum short, distance between metanotum and spiracle less than spiracle's length; dorsum setose throughout (*K. anula*) or glabrous mesally. No additional sclerites between metasternal apex and propodeum. Third submarginal cell petiolate posteriorly (Fig. 3). Forecoxal apex not expanded into process. Foretarsomere I with five ventral spines in female and three in male (length of spines about 2.0× apical width of tarsomere in female and 1.8–2.1× in male); female foretarsus with rake that consists of long, flexible setae. Hindtarsomere II long (0.5–0.7× hindtarsomere I). Female claws with subbasal tooth (Fig. 4). Tergum I without short, oblique carina extending from anterolateral corner. Tergum II not carinate laterally. Female tergum VI fairly convex: angle between lateral margin of tergum and lateral margin of pygidial plate, in side view, about 30–40°, pygidial plate with anteriorly evanescent lateral margin, without preapical row of punctures. Sting, including sheaths, slightly flattened, almost circular in cross section. Male sterna without velvety patches; tergum VII not depressed apically; gonostyle ventrally with a few setae.

Additional characters that vary in related genera but which are universal in *Kohliella* include: labrum flat, not emarginate; stipes flat; mouthparts not elongate; clypeus produced into a lobe mesally; anterior portion of lateral clypeal section concave, concavity delimited from above by transverse ridge; inner orbits convergent above; paramandibular process broadly separated from back side of clypeus (mandibular socket open); hindtibia not ridged; marginal cell short (foremargin 1.2–1.8× maximum width); foretibia spinose on outer side; inner hindtibial spur with stout, spaced rays in distal half; female:



FIGURES 1–4. Generic characters of *Kohliella* exemplified by *K. alaris*: 1—female face, 2—female mandible, 3—forewing, 4—claw of female hindtarsus.

trimmal carina with cleft and subbasal tooth that is modified into long, rounded lobe (Fig. 2), dorsal length of flagellomere I 2.9–3.3 × apical width, spines of foretarsal rake compressed laterally near base and compressed dorsoventrally near apex (three to five basal spines of foretarsomere I not compressed apically), forebasitarsus I with eight or nine rake spines, foretarsomere II and III with two rake spines each, forefemoral venter shiny, with few, sparse punctures, venter of tarsomere V with straight apical margin (i.e., margin not expanded into a lobe); male: tergum VII without lateral pygidial carinae, sternum VIII not emarginate apically, foretarsus with well-developed rake.

LIFE HISTORY.—Life history is known for only one species, *K. alaris* (Gess and Gess, 1980). Wasps become active after noon, "when the heat of the day is past its peak," sometimes as late as 16:15 hr. Nests are dug in flat, sandy areas with sparse vegetation. Nest construction precedes hunting. The female uses her forelegs for digging but carries away larger particles in her mandibles. The burrow enters the soil at a flat angle and has one or several secondary branches, some of which end in a cell. The entrance is temporarily closed during the provisioning period when the wasp is away. Nymphal tree crickets *Oecanthus filiger* Walker, 1871 (=*O. capensis* de Saussure, 1878), 6.0–15.8 mm long, are used as prey; all have their antennae partly amputated (amputation presumably takes place shortly after capture). They are carried in flight beneath the wasp's body, head forward. The female lands close to the nest entrance, drops the prey, opens the nest by raking the sand away, enters, turns around within, and draws the prey in headfirst. Several prey are stored in a cell, venter up and head inward. The wasp's egg, attached to the prey by its cephalic end, is placed behind the right or left prothoracic coxa and oriented transversely across the venter. In the six cases observed, the egg was deposited on prey that was brought in first, second, or fourth, suggesting that oviposition may be postponed until a prey of suitable size is obtained.

GEOGRAPHIC DISTRIBUTION.—*Kohliella* occurs in two widely separated areas: Sri Lanka and southern Africa (from Zimbabwe and Namibia to the Cape of Good Hope area).

RELATIONSHIPS TO OTHER LARRINI.—Bohart and Menke (1976) produced a dendrogram of the larrin genera, which was presumably based on the 50 characters listed on page 224 (the dendrogram was intuitive, since branches were not supported by character distribution and plesiomorphies may have been used as well). Bohart and Menke's dendrogram indicated that *Kohliella* was most closely related to *Holotachysphex, Parapiagetia, Prosopigastra,* and *Tachysphex.* Pulawski (1979) recognized additional apomorphies and analyzed phylogenetic relationships of the latter four genera. My current analysis indicates that *Kohliella* is a member of a holophyletic lineage that includes *Holotachysphex, Parapiagetia,* and *Tachysphex.* This clade is characterized by an oblong, glabrous swelling above each antennal socket. Another synapomorphy, the loss of a basal oblique carina on tergum I, is also found in *Gastrosericus,* many *Tachytes,* and *Larropsis chilopsidis* Cockerell and W. Fox, 1897. This carina is present in the other Larrinae, including *Prosopigastra,* and in most other Sphecidae, although species with petiolate gaster such as Sphecinae and most Pemphredoninae are obvious exceptions.

CHARACTER ANALYSIS.—The three closest relatives of *Kohliella* (i.e., *Holotachysphex, Parapiagetia,* and *Tachysphex*) were used as the outgroup in establishing character transformations and polarities, although other Larrini were considered. I regard as plesiomorphic those states that are shared by *Kohliella* and the outgroup, and as apomorphic those states that are found only in some *Kohliella* but not in the outgroup. Character states that occur in some *Kohliella* and some members of the outgroup were not polarized unless additional evidence indicated that they have developed independently. Fourteen characters were considered, but unequivocal polarities were established only for the first seven. Several unpolarized characters were subsequently polarized during the analysis (see PHYLOGENETIC ANALYSIS). The polarized characters are (0: plesiomorphic, 1 and 2: apomorphic):

(1) Prementum: 0. evenly convex, 1. knife-like. The generalized prementum of the Sphecidae is evenly convex, but it is knife-like, compressed (at least apically) in two species of *Kohliella* (*K. alaris* and *K. stevensoni*) and in *Aha,* a member of the Miscophini. The knife-like prementum is clearly an apomorphy, independently acquired in the two genera.

(2) Shape of thorax: 0. not flattened, 1. flattened.

The thorax of most Larrinae is essentially circular in cross section, but strongly flattened dorsoventrally in *K. stevensoni,* in some Australian *Tachysphex* (*T. depressiventris* R. Turner, 1916, *T. foliaceus* Pulawski, 1977, and *T. persistans* R. Turner, 1916), and to a lesser degree in some *Liris* (e.g., an unidentified species from Sri Lanka). A flat thorax is clearly derived and also independently acquired in all three genera: *Liris* is only distantly related to *Kohliella* as evidenced by many characters (Bohart and Menke 1976, placed these genera in different subtribes), and *Tachysphex* with a depressed thorax are all members of a specialized lineage (Pulawski 1977, 1988). The flattened thorax is correlated with the depressed forecoxa in *K. stevensoni* and the *Tachysphex* listed above.

(3) Propodeal dorsum: 0. ridged, 1. sparsely punctate.

The propodeal dorsum is rugose in *Holotachysphex,* rugose or variously ridged in *Tachysphex,* and mostly ridged in *Parapiagetia.* It is, however, partly punctate with ridges evanescent in some *Parapiagetia* such as *P. subpetiolata* (Brèthes, 1909), and the sculpture varies individually in others, e.g., *P. genicularis* (F. Morawitz, 1890). In the latter, the dorsal ridges are either well defined or evanescent; when so, the integument is shiny, punctate. In *Kohliella,* the dorsum is either ridged (*K. anula, K. alaris*) or punctate (*K. stevensoni*). I regard the latter condition as a specialization independently acquired by *Parapiagetia* and *Kohliella.*

(4) Propodeal vestiture: 0. dorsum setose throughout, 1. narrowly asetose medially, 2. broadly asetose.

The propodeal dorsum is setose throughout in *Holotachysphex,* most *Parapiagetia,* and most *Tachysphex,* but glabrous posteriorly in some *Parapiagetia,* glabrous in *Tachysphex sinaiticus* Pulawski, 1964, and many *T. tenuis* R. Turner, 1908, and largely glabrous in many *T. walkeri* R. Turner, 1908 (the latter three species are members of specialized lineages, and in neither is the glabrous area sharply delimited). The dorsum is setose in most other Larrini, but with a glabrous, well defined area mesally in *Ancistromma, Larropsis, Prosopigastra,* and also in *Tachytes dichrous* F. Smith, 1856, and *T. pygmaeus* Kohl, 1888. In *Kohliella,* the dorsum is setose throughout in *K. stevensoni,* narrowly glabrous mesally in *K. anula,* and broadly glabrous in *K. alaris.*

(5) Sternal setae of male: 0. sterna setose throughout, 1. sterna asetose.

Male sterna are setose throughout in most Larrinae, including *Holotachysphex* and *Parapiagetia,* although the setae may be variously modified. The sterna are asetose in *Kohliella anula,* and sterna III–VI are largely asetose in several *Tachysphex.* The absence of setae is a convergence, because in *Tachysphex* this condition occurs only in derived species groups, e.g., *T. julliani* and *T. albocinctus* groups, and in *Tachysphex menkei* Pulawski, 1982 of the *T. brullii* group (Pulawski 1971, 1988).

(6) Gastral apex and genitalia of male: 0. generalized, as in *K. alaris* and *K. stevensoni,* 1. complex, as in *K. anula* (see these species for details).

The gastral apex and genitalia in the male of *K. anula* are unique in Larrinae and clearly autapomorphic.

(7) Tibial dorsum: 0. setose throughout, 1. glabrous.

The tibiae are evenly setose throughout in most Larrinae (including *Kohliella anula*), but the tibial dorsum is glabrous in some species that live in open areas with high sun activity such as deserts (e.g., *Holotachysphex turneri* Arnold, 1923, *K. alaris,* and *K. stevensoni*). Apparently, the glabrous tibial dorsum is a specialization independently acquired in these two genera. Possibly, the glabrous integument may reflect solar rays.

I was unable to polarize the following characters:

(8) Clypeal lobe of male: a. angulate laterally, b. rounded.

The clypeal lobe in male Larrini is either angulate laterally (the lobe is thus clearly delimited) or evenly arcuate (the free margin of the lobe forms a single curved line with the rest of the clypeal margin). Both types are found in most genera, although the lobe is only angulate in *Ancistromma* and only arcuate in *Larropsis.* The absence of the lobe corners is usually (as in *K. stevensoni*) correlated with absence of the tooth on the inner mandibular margin.

(9) Episternal sulcus: a. complete, b. incomplete.

The episternal sulcus in Larrini extends to the anteroventral margin of the mesopleuron (sulcus complete) or ends before reaching the margin (sulcus incomplete). Bohart and Menke (1976: 224) listed the complete sulcus among the ancestral characters of Larrinae, but an incomplete one (ending near margin) is predominant in my outgroup. The sulcus is incomplete in *Holotachysphex,* most *Parapiagetia* including *P. genicularis* (F. Morawitz, 1890), one of the most primitive members of the genus, the vast majority of *Tachysphex,* and also in *K. anula.* It is complete in some *Parapiagetia* (e.g., *P. tridentata* Tsuneki, 1972), some *Tachysphex* (such as *T. nigricolor* Dalla Torre, 1897), and in *K. alaris* and *K. stevensoni.*

(10) Punctation of mesothoracic venter: a. dense, b. sparse.

Punctures are almost contiguous on the mesothoracic venter in *Holotachysphex,* most *Parapiagetia,* and most *Tachysphex,* but several to many diameters apart in some *Parapiagetia* (e.g., *P. genicularis* and *P. tridentata*) and several unrelated *Tachysphex* such as *T. iridipennis* (F. Smith, 1873) and *T. nitidissimus* de Beaumont, 1952. Punctures are almost contiguous in *K. anula,* but sparse, many diameters apart in *K. alaris* and *K. stevensoni* (interspaces shiny).

(11) Male forefemur: a. entire, b. emarginate basally.

The male forefemur is entire in most Larrinae (including *Parapiagetia*) and is emarginate basally in *Holotachysphex,* most *Tachysphex,* and some *Tachytes*; the basal emargination of *Ancistromma* and *Larropsis,* situated in a different plane, may not be homologous. The emarginate femur of the above genera is clearly specialized (Bohart and Menke 1976), but reversals appar-

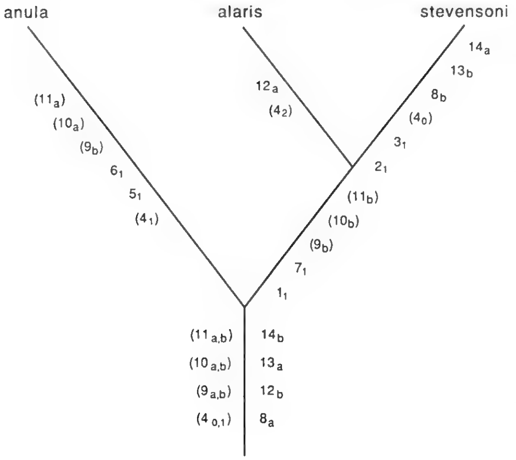


FIGURE 5. Phylogenetic relationship among species of *Kohliella.* Numbers refer to the characters discussed in the text. Numerical subscripts indicate the originally polarized characters and alphabetical subscripts the originally unpolarized characters. Numbers in parentheses represent characters that remain unpolarized (they were superimposed on the cladogram branches to show their distribution).

ently have occurred. For example, the *T. geniculatus* group of *Tachysphex* has an entire forefemur, but the elongate mouthparts and an unusually broad vertex suggest that these species descended from less specialized forms in which the femora were emarginate (Pulawski 1971). In *Kohliella,* the forefemur is entire in *K. anula,* and emarginate basally in the other two species. It is not clear if the condition of *K. anula* is plesiomorphic or a reversal.

(12) Shape of setae: a. straight, b. sinuate.

The setae of Sphecidae (including the outgroup) are either straight or sinuate. In *Kohliella,* the setae are straight in *K. alaris* (some setae bent apically), straight on vertex but sinuate on other body parts in *K. anula,* and all sinuate in *K. stevensoni.* I recognize only two states: thoracic setae straight, and thoracic setae sinuous.

(13) Vertex setae: a. short, b. long.

Vertex setae vary in length in the outgroup and other Larrinae. They are short in *K. alaris* and *K. anula,* but long in *K. stevensoni.* Species with long setae occur in three habitat types: in deserts, mountains, and humid tropical or subtropical areas.

(14) Forefemoral setae: a. venter setose, b. glabrous.

The forefemoral venter is evenly setose in most Larrinae (including *K. stevensoni*), but glabrous or nearly so in many lineages (glabrous in *K. alaris* and *K. anula*).

PHYLOGENETIC ANALYSIS.—Of the 14 characters analyzed, only the first seven are polarized and only two (1 and 7) are synapomorphies, significant in reconstructing relationships. The remaining characters are either autapomorphies (2, 3, 5, 6) or multistate (4). The most parsimonious cladogram for the three species (Fig. 5) was generated manually, using the two polarized characters only. The nonpolarized character states were subsequently mapped on the tree in the most parsimonious way. The cladogram was verified using Henning86 version 1.5, a parsimony computer package by James F. Farris. The number of steps is 16 and the consistency index (excluding the autapomorphies, i.e., characters 2, 3, 4, and 5) is 100. The cladogram suggests that:

(1) The two African *Kohliella* are sister species, thus more closely related to each other than to *K. anula.*

(2) Contrary to my initial interpretation, the states of character 4 (entirely setose and glabrous propodeal dorsum) cannot be polarized (i.e., it is equally parsimonious to regard each of them as either ancestral or derived).

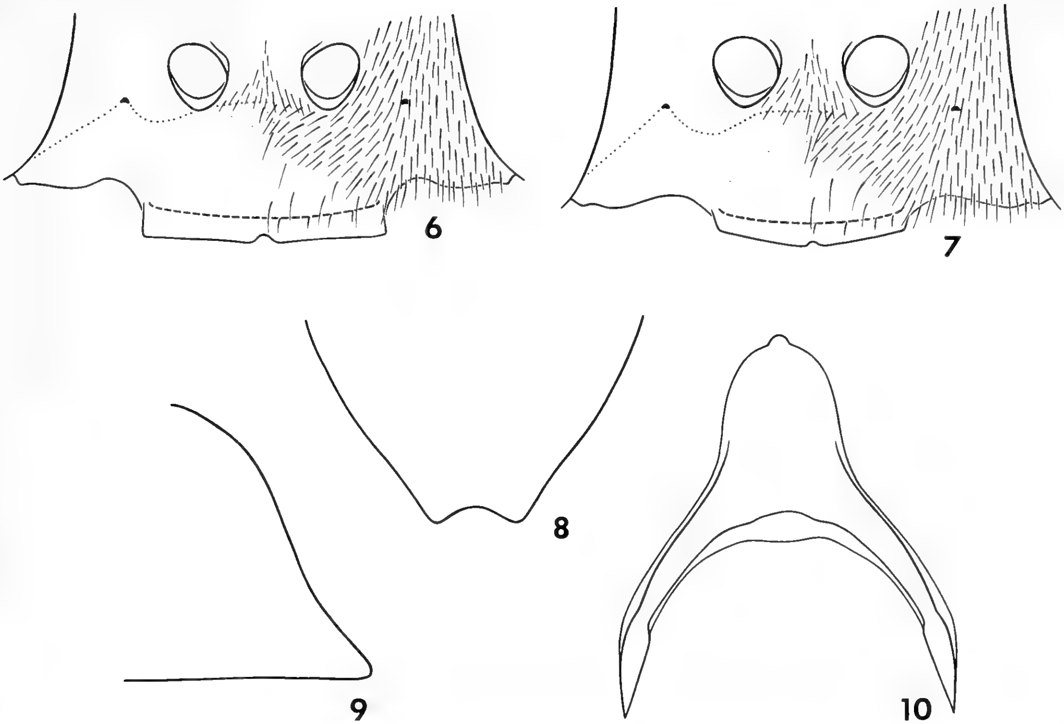
(3) The following initially unpolarized character states of *Kohliella* are derived: clypeal lobe of male not angulate laterally (8b), thoracic setae straight (12a), vertex setae long (13b), and forefemoral venter setose (14a).

(4) Three characters cannot be polarized: length of episternal sulcus (9), punctation of mesothoracic venter (10), and presence or absence of forefemoral notch (11). It is equally parsimonious to regard each of the two states as either plesiomorphic or apomorphic.

A better knowledge of the cladistic relationships in the outgroup may either corroborate or invalidate the above conclusions.

KEY TO THE SPECIES

1. Vertex setae sinuous, about 0.8× basal mandibular width; propodeum: dorsum setose throughout, dorsum and side sparsely punctate; forecoxal venter flat; tibiae red; female: thorax strongly flattened; male: clypeal lobe rounded, not angulate laterally (Fig. 30), inner mandibular margin not



FIGURES 6–10. *Kohliella anula*: 6—female clypeus, 7—male clypeus, 8—male tergum VII dorsally, 9—male tergum VII laterally, 10—male sternum VIII.

dentate (Fig. 31); Zimbabwe, Namibia .... 3. *K. stevensoni* Arnold

- Vertex setae straight, about 0.3× basal mandibular width; propodeum (Fig. 17): dorsum glabrous mesally, dorsum transversely ridged, side ridged or with almost uniform, dull microsculpture; forecoxal venter convex; tibiae black; female thorax of usual shape; male: clypeal lobe angulate laterally (Figs. 7, 19), inner mandibular margin with tooth 2

2. Gaster black; distance between corners of clypeal lobe 1.6 (female) and 1.4–1.5 (male)× clypeal length (Figs. 18, 19); punctures many diameters apart on scutal disk and mesothoracic venter; male: tergum VII convex, straight apically, sterna III–VI densely punctate apically, sternum VIII rounded apically (Fig. 23), forefemur emarginate basoventrally (Figs. 21, 22); South Africa, Zimbabwe. .... 2. *K. alaris* Brauns

- Gaster red; distance between corners of clypeal lobe 2.8 (female) and 2.3 (male)× clypeal length (Figs. 6, 7); punctures less than one diameter apart on scutum and mesothoracic venter; male: tergum VII saddle-shaped (Fig. 9), emarginate apically (Fig. 8), sterna sparsely punctate, sternum VIII pointed apically (Fig. 10), forefemur entire; Sri Lanka .... 1. *K. anula* sp. n.

DESCRIPTIONS OF SPECIES

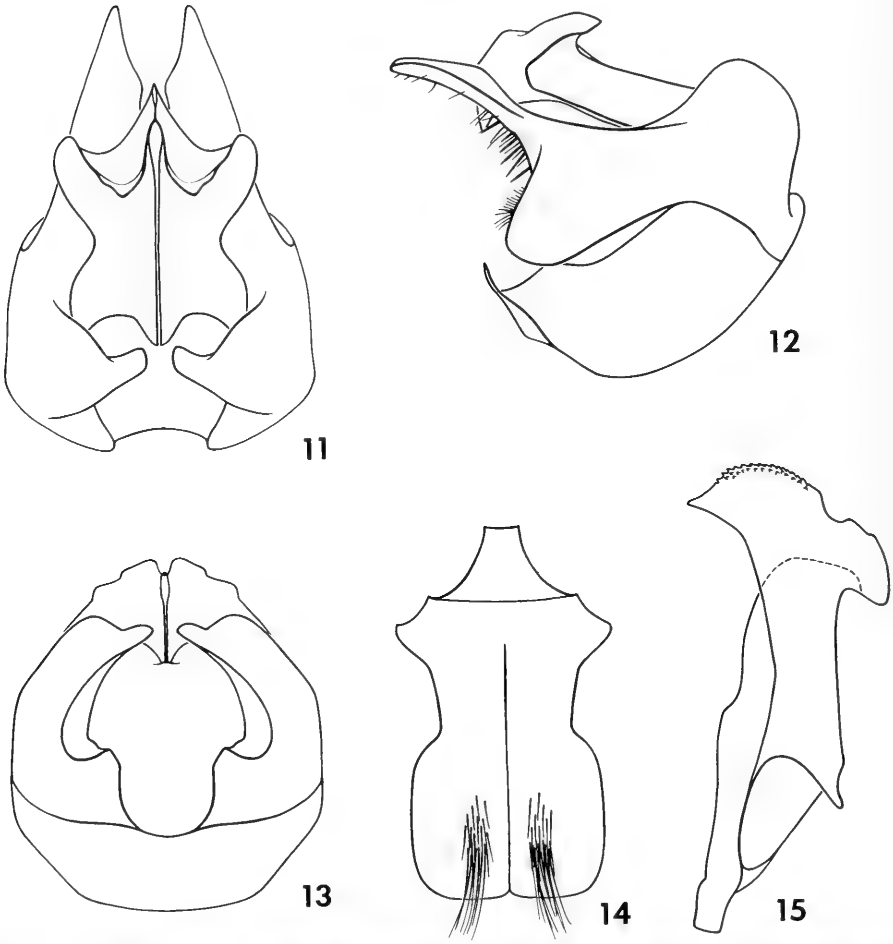
Diagnostic characters for each species are given in the key and are not repeated in the descriptions.

Kohliella anula sp. n.

(Figures 6–15)

DERIVATION OF NAME.—Queen Anula, King Devanampiya Tissa's sister-in-law, was the first in Sri Lanka to be ordained a Buddhist nun; noun in apposition.

DESCRIPTION.—Clypeal lobe angulate laterally (Figs. 6, 7). Mouthparts moderately compressed laterally, prementum convex but not blade-like.



FIGURES 11–15. *Kohliella anula*: 11—male genitalia dorsally, 12—male genitalia laterally, 13—male genitalia dorsobasally, 14—volsella, 15—penis valve.

Vertex width 0.9× length. Punctures less than one diameter apart on scutum and mesothoracic venter. Episternal sulcus ending well before reaching anteroventral mesopleural margin. Propodeum: dorsum transversely ridged, with glabrous area that is not broadened anterad, side with well defined ridges. Forecoxal venter convex. Forefemoral venter glabrous. Tibiae densely setose throughout. Setae straight on vertex, sinuous adjacent to hypostomal carina, mesopleuron, and propodeum. Setal length (expressed as fraction of basal width of mandible): 0.3 on vertex, about 0.6 between mandibular condyle and occipital carina, about 1.0 between propodeal side and hindface.

Gaster red, legs black.

♀.—Distance between corners of clypeal lobe 2.8× clypeal length. Most spines of foretarsal rake spatulate. Length 10.0 mm.

♂.—Distance between corners of clypeal lobe 2.3× clypeal length. Inner mandibular margin with tooth. Dorsal length of flagellomere I 2.2× apical width. Foretrochanteral and forefemoral venters flattened but not notched. Tergum VII saddle-like, apical margin emarginate (Figs. 8, 9). Sterna sparsely punctate, glabrous (with only a few, sparse setae). Sternum VIII bent down apically, hindmargin pointed (Fig. 10). Length 6.0–7.3 mm. Genitalia (Figs. 11–15): Volsellae fused into flat, oblong, weakly sclerotized plate (Fig. 14); plate small, about 0.6 length of penis valve.

COLLECTING PERIOD.—15–16 February 1979.

HABITAT.—The specimens were collected in Dry Zone thorn scrub jungle on damanas, open areas of sandy loam soil with sparse tufts of grass and a few small shrubs. The elevation is about 30 m and the average annual rainfall about 1,200 mm.

GEOGRAPHIC DISTRIBUTION.—Sri Lanka (Fig. 16).

RECORDS.—Holotype: ♀, Sri Lanka: Mannar District: 0.8 km NE Kokmotte in Wilpattu National Park, about 8°32′N, 80°02′E, on the north side of the Moderagam Aru (=River), one of the boundaries with Puttalam District, K.V. Krombein, T. Wijesinhe, S. Siriwardane, T. Gunawardane (USNM).

Paratypes: same data (2 ♂, CAS, USNM).

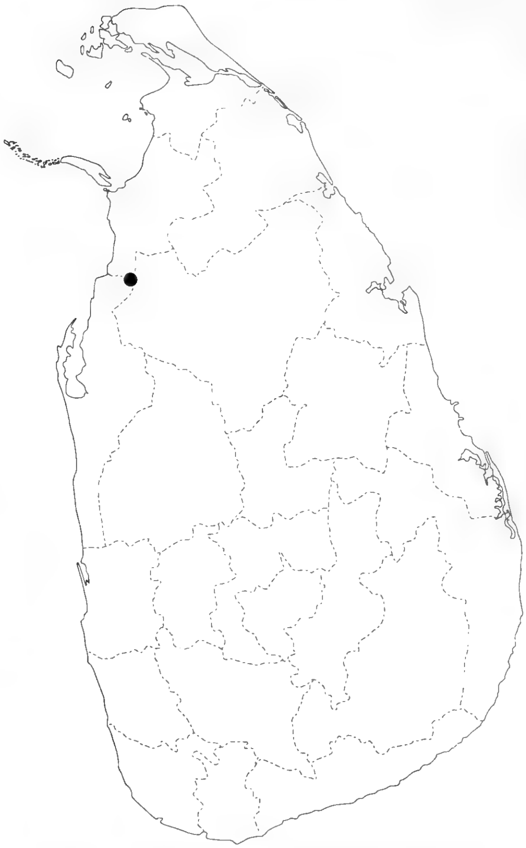


FIGURE 16. Map of Sri Lanka indicating type locality of *Kohliella anula*.

Kohliella alaris Brauns

(Figures 17–27)

Kohliella alaris Brauns, 1910:669, ♂. Holotype: South Africa: Cape Province: Willowmore (TMP), examined.—Arnold, 1922:135 (revision), 1924:43 (♀; South Africa and Zimbabwe); de Beaumont, 1967:510 (South Africa: Table Mountain); Bohart and Menke, 1976:286 (listed); Gess and Gess 1980:45 (life history); Gess, 1981:20 (South Africa; nesting in friable soils), 40 (digging nest), 47 (prey).

DESCRIPTION.—Clypeal lobe angulate laterally (Figs. 18, 19). Mouthparts strongly compressed laterally, prementum blade-like apically. Vertex width 0.9× length. Punctures many diameters apart on mesothoracic venter and also on female scutal disk, one to two diameters apart on male scutum. Episternal sulcus extending to anteroventral mesopleural margin. Propodeum: dorsum transversely ridged, with glabrous area that is broadened anterad (ridges in glabrous area extremely fine); side dull, densely ridged (ridges dense, ill defined or reduced in many specimens). Forecoxal venter convex. Forefemoral venter glabrous. Midtibia glabrous dorsally (also female hindtibia). Setae straight on vertex, curved apically on gena and propodeum. Setal length (expressed as fraction of basal width of mandible): 0.3 on vertex, 0.4 between mandibular condyle and occipital carina, 0.6 between propodeal side and hindface.

Gaster and legs black, apical tarsomeres ferrugineous.

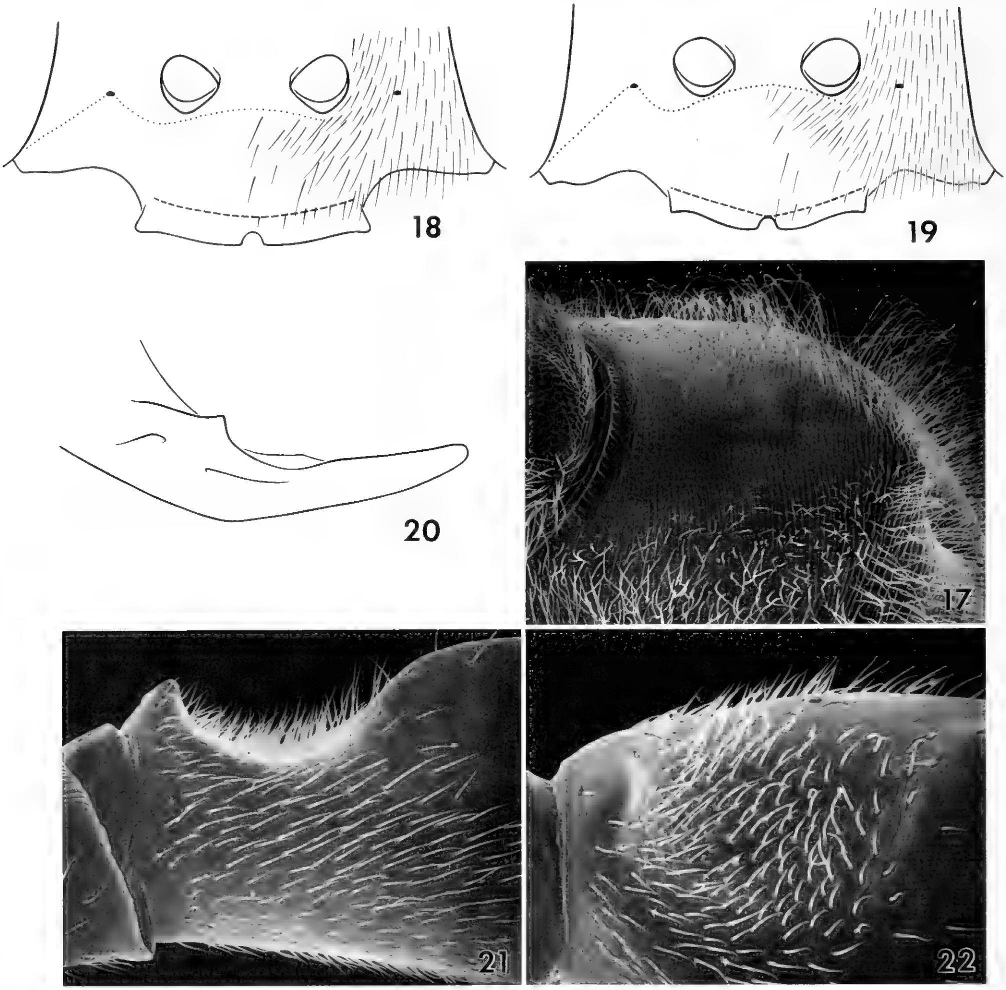
♀.—Distance between corners of clypeal lobe 1.6× clypeal length. Foretarsal rake consisting of simple spines. Length 7.6–9.8 mm.

♂.—Distance between corners of clypeal lobe 1.4–1.5× clypeal length. Inner mandibular margin with tooth (Fig. 21). Dorsal length of flagellomere I 2.1× apical width. Foretrochanteral venter notched basally. Forefemur notched basoventrally, notch lined with setae. Tergum VII convex dorsally, apical margin straight. Sterna III–VI apically setose and densely punctate. Sternum VIII straight, its apical margin rounded (Fig. 23). Genitalia (Figs. 24–27): Length 6.5–8.4 mm.

COLLECTING PERIOD.—November (Brauns 1910), early December to early March (Gess and Gess 1980), early February to mid-April (specimens from Zimbabwe).

GEOGRAPHIC DISTRIBUTION.—South Africa, Zimbabwe (Fig. 28).

RECORDS.—SOUTH AFRICA. **Cape Province:** Alicedale (Gess and Gess 1980), Augrabies Falls National Park (F. W. Gess, pers. comm.), Ceres (7 ♀, 13 ♂, BMNH; 1 ♀, 1 ♂, USNM), Hex River (1 ♀, SAM), Hilton 18 km WNW Grahamstown (3 ♀, 3 ♂, CAS), Hout Bay on Cape Peninsula (de Beaumont 1967), Huguenot, 33°43′S, 18°58′E (1 ♂, BMNH), Jonkershoek,



FIGURES 17–22. *Kohliella alaris*: 17—propodeal dorsum, 18—female clypeus, 19—male clypeus, 20—male mandible, 21—male forefemoral notch in profile, 22—bottom of male forefemoral notch.

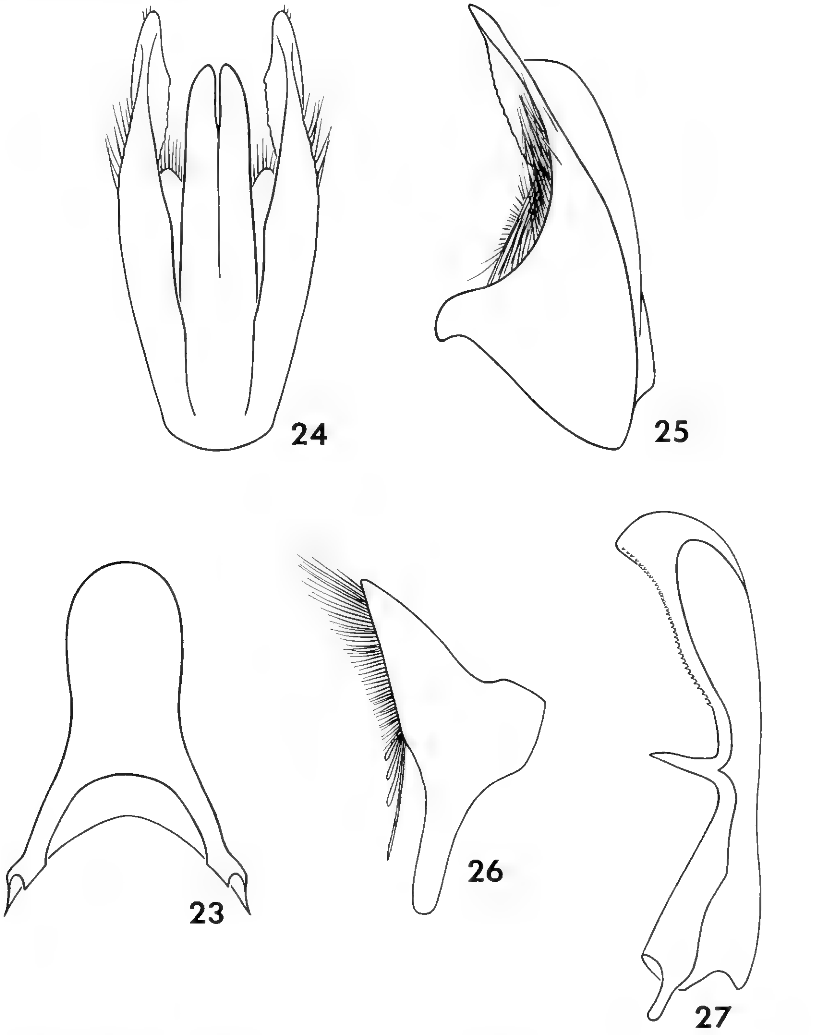
33°58′S, 18°58′E (1 ♀, BMNH), Mitchell Pass, 32°33′S, 26°53′E (1 ♂, BMNH), Silvermine Nature Reserve on Cape Peninsula (8 ♀, 2 ♂, BMNH), Table Mountain in Cape Town (1 ♀, SAM), Tierberg, 33°07′42″S, 22°16′24″E (F. W. Gess, pers. comm.), Wellington (2 ♀, 4 ♂, CAS), Willowmore (1 ♂, TMP, holotype of *K. alaris*). **Transvaal:** Modderfontein (1 ♂, SAM), 5 mi N Warmbad (1 ♀, 3 ♂, USNM). ZIMBABWE: Bulawayo (2 ♀, 1 ♂, SAM), Nyamandhlovu (1 ♀, 1 ♂, SAM).

Kohliella stevensoni Arnold

(Figures 29–33)

Kohliella Stevensoni Arnold, 1924:42, ♂, incorrect original capitalization. Lectotype: ♂, Zimbabwe: Sawmills (SAM), **present designation**, examined.—Bohart and Menke, 1976:286 (listed).

DESCRIPTION.—Clypeal lobe and thoracic punctation sexually dimorphic. Mouthparts strongly compressed laterally, prementum bladelike apically. Vertex width 1.0–1.2× length. Episternal sulcus extending to anteroventral mesopleural margin. Propodeum: dorsum sparsely punctate, setose throughout, side unsculptured except sparsely punctate posteriorly. Forecoxal venter flat. Forefemoral venter setose. Mid- and hindtibiae glabrous dorsally. Setae sinuous on vertex, gena, and thorax; setal length (expressed as fraction of basal width of mandible): about



FIGURES 23–27. *Kohliella alaris*: 23—male sternum VIII, 24—male genitalia dorsally, 25—male genitalia laterally, 26—volsella, inner side, 27—penis valve.

0.8× on vertex and tergum I basally, about 1.0 adjacent to hypostomal carina and between propodeal side and hindface.

Gastral segments I–III red, remainder black. Femora red in female; male fore- and midfemora all black or black basally and red apically, hindfemur all red or black basally. Tibiae and tarsi red.

♀.—Clypeal lobe angulate laterally (Fig. 29), distance between corners 1.5× clypeal length. Thorax strongly flattened. Punctures two to four diameters apart on scutum, many diameters apart on mesothoracic venter. Spines of foretarsal rake spatulate. Length 13.0 mm.

♂.—Clypeal lobe not angulate laterally, its free margin forming single curved line with rest of clypeal margin (Fig. 30). Inner mandibular margin not dentate (Fig. 31). Dorsal length of flagellomere I 2.6–2.8× apical width. Punctures one to two diameters apart on scutal disk, up to two or three diameters apart on mesothoracic venter. Foretrochanteral venter shallowly notched basally. Forefemur notched basoventrally, notch covered with dense, erect setae. Tergum VII convex dorsally, apical margin straight. Sterna III–VI apically setose and densely punctate. Sternum VIII straight, its apical margin rounded. Genitalia: general shape as in *K. alaris* (see Figs. 24, 25); volsella (Fig. 26); penis valve (Fig. 27). Length 8.4–10.0 mm.

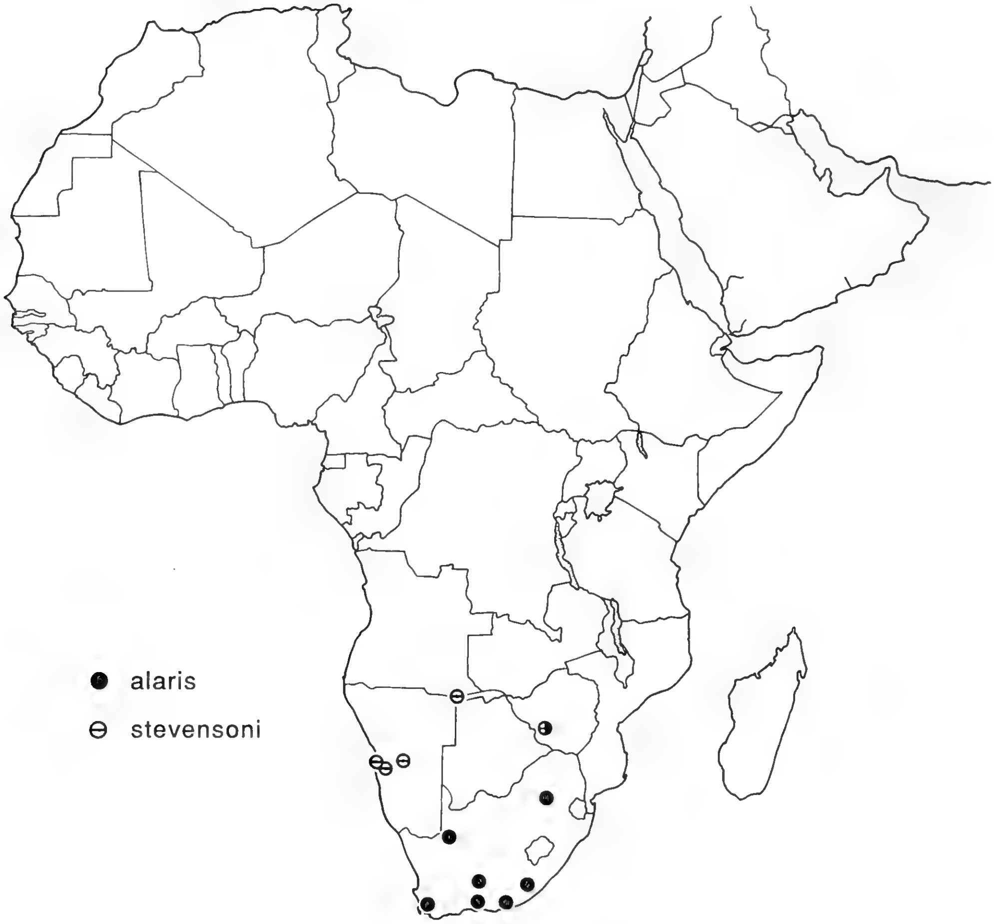


FIGURE 28. Geographic distribution of *Kohliella alaris* and *K. stevensoni* (the combined symbol indicates that both species occur in one locality).

COLLECTING PERIOD.—February, August, October (specimens from Namibia), July (specimens from Zimbabwe).

GEOGRAPHIC DISTRIBUTION.—Zimbabwe, Namibia (Fig. 28).

RECORDS.—NAMIBIA: **Kaokoland:** Ondorusu Falls, SE 1713 Bd [=between 17°15′ and 17°30′S and 13°45′ and 14°00′E] (1 ♀, SMWN). **Kavango District:** Andara (1 ♀, 1 ♂, SMWN; 1 ♀, ZMK), Popa Falls, 18°07′S, 21°33′E (1 ♀, CAS; 1 ♀, 1 ♂, SMWN). **Maltahöhe District:** Blässkranz, 24°06′S, 16°14.5′E (1 ♀, SMWN). **Swakopmund District:** Gobabeb, Kuiseb River bed (1 ♂, ZMK). **Windhoek District:** Windhoek (2 ♀, SMWN). ZIMBABWE: Sawmills (2 ♂, SAM, lectotype and paralectotype of *K. stevensoni*).

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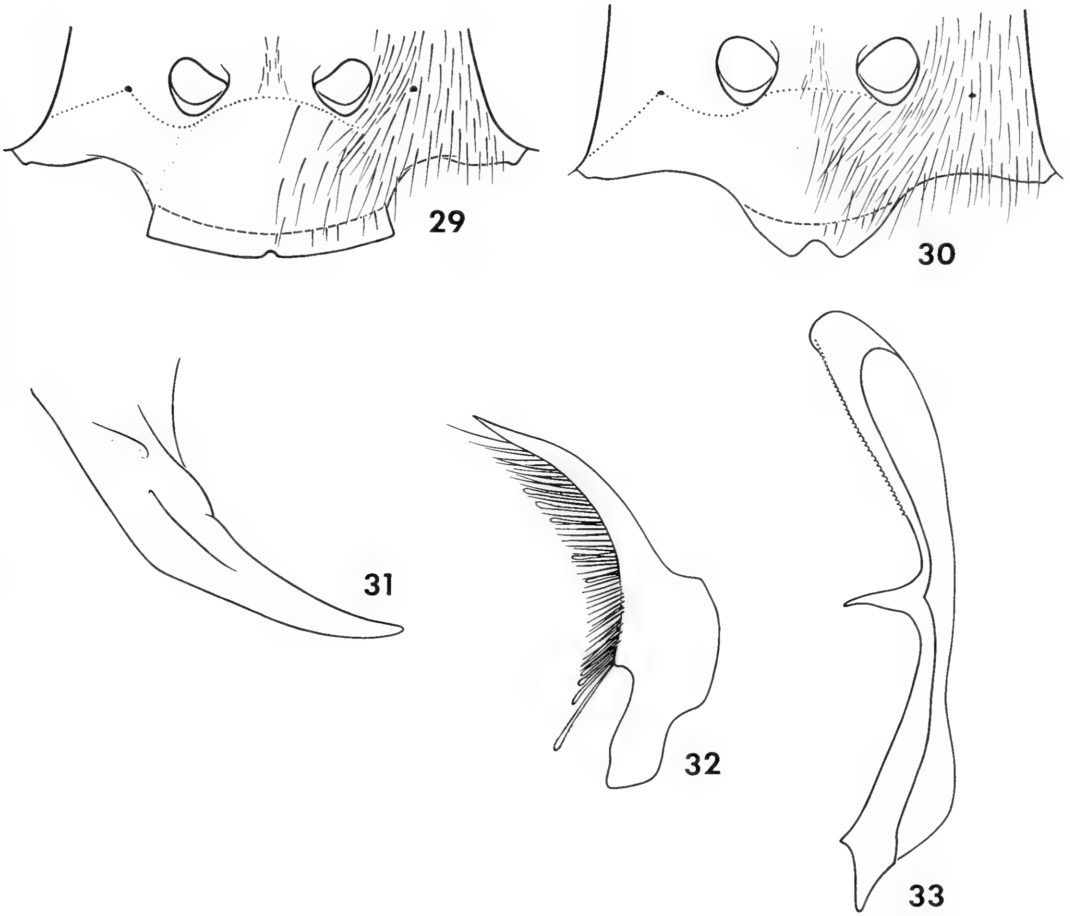

FIGURES 29–33. *Kohliella stevensoni*: 29—female clypeus, 30—male clypeus, 31—male mandible, 32—volsella, inner side, 33—penis valve.

formation on the habitat of *Kohliella anula*; to John Irish for information on Namibian localities; and to Friedrich W. Gess for donating specimens of *K. alaris*. Mary Ann Tenorio took the scanning electron micrographs and prepared the illustrations and the map of Africa, and George L. Venable generated the map of Sri Lanka.

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ONISCIDEA (ISOPODA) OF THE SAN FRANCISCO BAY AREA

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Abstract: From June 1975 to May 1991 we collected samples of Isopoda, Oniscidea from 176 sites in the area surrounding San Francisco Bay, California, including the outer coast from Bolinas Lagoon, Marin County to Half Moon Bay, San Mateo County. Seventeen species of isopods were represented in these collections. Nine of these species were entirely restricted to littoral habitats, and the remaining eight were found in a variety of habitats. Eleven of the species are native to western North America, and the remaining six species are introductions from the Old World. Two of the species collected have not been previously reported from San Francisco Bay. All 19 species known or expected in the San Francisco Bay Area are discussed and figured, and a key and information concerning their distributions both within the Bay Area and throughout North America are provided. The results of this survey are discussed in relation to previous reports, and several errors in the literature concerning the oniscid isopods of the San Francisco Bay Area are corrected.

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INTRODUCTION

Even though the San Francisco Bay Area (referred to in this report as the Bay Area) has been the subject of a long history of zoologic study, information concerning Isopoda, Oniscidea of this region has been sparse. The more significant reports dealing with this area that concern this group have been those of Stuxberg (1875), Arcangeli (1932), and Miller (1938). Miller's work comprised the only comprehensive survey of this group in the Bay Area, and little has been done on the oniscids of this area in the 53 years since its publication. In summarizing existing reports and his own collections, Miller (1938) listed a total of 19 oniscid isopods from the Bay Area. However, in the course of our studies on San Francisco Bay oniscids, we have found Miller's list outdated and inaccurate in several respects. As the literature stands, it would be difficult for anyone not intimately familiar with this group to accurately identify to species the oniscid isopods from this area.

These observations led us to conduct an extensive survey of the oniscid isopods of the San Francisco Bay Area. In this paper we report the results of this survey. An updated list of species, figures, and a key to the Bay Area oniscids are presented. Our results are discussed in relation to previous reports on the oniscids of this area.

MATERIALS AND METHODS

From June 1975 to May 1991 samples of oniscid isopods were collected from 176 sites in the Bay Area (see Fig. 1 for sampling locations and Table 1 for details of collection sites). A variety of habitats are represented by these collection sites. However, littoral habitats were emphasized and riparian habitats were infrequently sampled. Most of the collections included in this survey were made from January 1989 to May 1991, but these were supplemented with a number of samples from our collections made as early as 1975.

Isopods were collected by hand from an area of usually less than two square meters, preserved in the field in 70% ethanol, and transported to the laboratory where they were identified using the following references: Arcangeli (1932), Hatch (1947), Menzies (1950), Miller (1975), Mulaik and Mulaik (1942), Richardson (1905), Schultz (1984), Schultz et al. (1982), and Van Name (1936, 1940). Representative specimens have been deposited in the Department of Invertebrate Zoology and Geology at the California Academy of Sciences (catalog nos. CASIZ 075314–075578) and the Department of Invertebrate Zoology, Santa Barbara Museum of Natural History (catalog Nos. SBMNH 35353–35450).

RESULTS

With this survey the number of species of oniscid isopods known or expected from the San Francisco Bay Area is 19. A list of these species and the sites at which they were collected is given in Table 2.

Nine of the species collected were entirely restricted to littoral habitats: *Ligia occidentalis* Dana, 1853; *Ligia pallasii* Brandt, 1833; *Littorophiloscia richardsonae* (Holmes and Gay, 1909); *Mauritaniscus littorinus* (Miller, 1936); *Detonella papillicornis* (Richardson, 1904); *Armadilloniscus coronacapitalis* Menzies, 1950; *Armadilloniscus lindahli* (Richardson, 1905); *Armadilloniscus holmesi* Arcangeli, 1933; and *Alloniscus perconvexus* Dana, 1856. Two species were riparian: *Ligidium latum* Jackson, 1923 and *Ligidium gracile* (Dana, 1856). The remaining six species were found in a variety of terrestrial habitats: *Protrichoniscus heroldi* Arcangeli, 1932; *Porcellio scaber* Latreille, 1804; *Porcellio dilatatus* Brandt and Ratzeburg, 1833; *Porcellio laevis* Latreille, 1804; *Porcellionides floria* Garthwaite and Sassaman, 1985; and *Armadillidium vulgare* (Latreille, 1804). Eleven of the species collected are Pacific Coast endemics (*L. occidentalis, L. pallasii, L. latum, L. gracile, P. heroldi, L. richardsonae, D. papillicornis, A. coronacapitalis, A. lindahli, A. holmesi,* and *A. perconvexus*), and the remainder are introductions from Europe (*P. scaber, P. dilatatus, P. laevis, P. floria,* and *A. vulgare*) and possibly Africa (*M. littorinus*).

Key to the Oniscid Isopods of the San Francisco Bay Area

1a. Flagellum of antenna two composed of more than 10 articles. Antenna one small but conspicuous 2

1b. Flagellum of antenna two composed of 6 or fewer articles. Antenna one usually minute and inconspicuous 5

2a. Both rami of uropod inserted distally on peduncle 3

2b. Exopod of uropod inserted proximal to endopod on peduncle 4

3a. Distance between eyes equal to length of one eye. Basal article of uropod several times longer than broad (Fig. 2) .... 1. *Ligia occidentalis*

3b. Distance between eyes equal to twice length of one eye. Basal article of uropod about as broad as long (Fig. 3) .... 2. *Ligia pallasii*

4a. Surface of body smooth and shiny, lacking conspicuous scales .... 4. *Ligidium gracile*

4b. Surface of body rough, with sparse scales. .... 3. *Ligidium latum*

5a. Eyes absent. Pereopod seven with conspicuous tuft of setae on upper margin of distal article (Fig. 6) .... 5. *Protrichoniscus heroldi*

5b. Eyes present. Pereopod seven without tuft of setae on upper margin of distal article 6

6a. Flagellum of antenna two composed of 3–5 articles 7

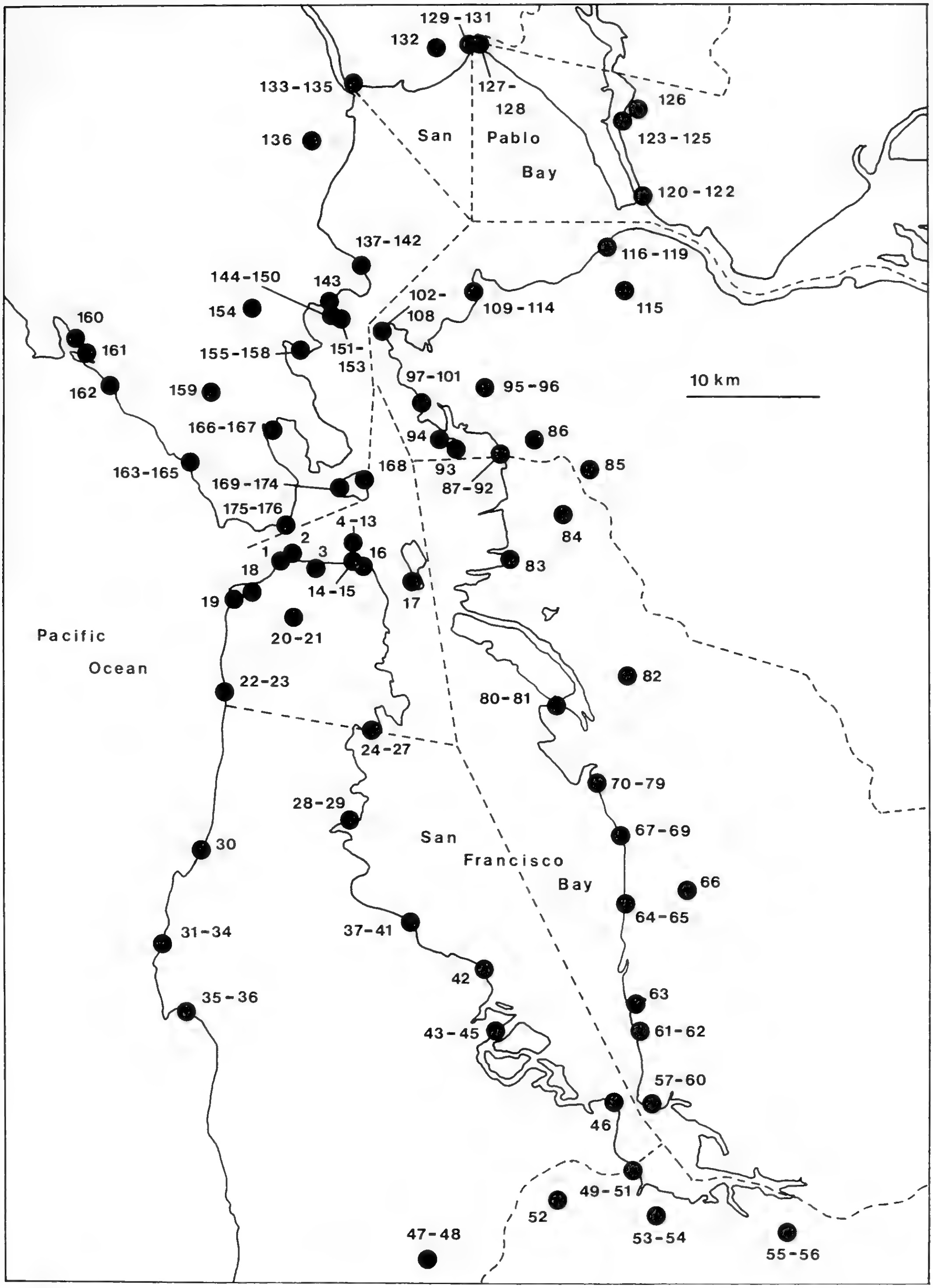

FIGURE 1. Map of the San Francisco Bay Area showing the location of all 176 collection sites referred to in this study. Dashed lines represent county boundaries.

TABLE 1. COLLECTION SITES.

Collection site	Date	Locality
San Francisco County:		
1	6 Apr 1989	San Francisco, ocean side of Fort Point
2	6 Apr 1989	San Francisco, Fort Point National Historic Site
3	13 Feb 1980	San Francisco, Palace of Fine Arts
4–13	10 Jun 1989	San Francisco, Alcatraz Island
14	6 Apr 1989	San Francisco, Fort Mason
15	6 Apr 1989	San Francisco, Aquatic Park
16	7 Dec 1979	San Francisco, corner of Levenworth and Beach
17	26 May 1988	San Francisco, Yerba Buena Island
18	5 Dec 1979	San Francisco, Palace of the Legion of Honor
19	26 Dec 1979	San Francisco, Sutro Heights Park
20	6 Dec 1979	San Francisco, Golden Gate Park, Temple of Music
21	30 May 1989	San Francisco, Golden Gate Park, Strybing Arboretum
22–23	Aug 1989	San Francisco, Fort Funston
24–27	6 Apr 1989	San Francisco, corner of Harney and Jamestown
San Mateo County:		
28–29	6 Apr 1989	South San Francisco, corner of Utah and Littlefield
30	Aug 1989	Pacifica, Rockaway Beach
31	26 Dec 1979	Montara
32–34	Aug 1989	Montara State Beach
35–36	Aug 1989	El Granada, Pillar Point Harbor
37–40	6 Apr 1989	Burlingame, corner of Airport and Lang
41	6 Apr 1989	San Mateo, Coyote Point Municipal Park
42	26 Feb 1989	Foster City
43–45	20 May 1989	San Carlos, Steinberger Slough
46	8 Apr 1989	Ravenswood Bird Observatory
47–48	30 Jul 1989	Portola Valley, corner of Alpine and Portola
Santa Clara County:		
49	12 Feb 1989	Palo Alto, mouth of San Francisquito Creek
50	12 Feb 1989	Palo Alto, Palo Alto Airport
51	12 Feb 1989	Palo Alto, yacht harbor
52	21 Jun 1975	Palo Alto, Stanford University
52	3 May 1991	Palo Alto, Stanford University
53–54	12 Feb 1989	Mountain View, Mountain View Tidal marsh
55–56	12 Feb 1989	Alviso, Alviso Marina County Park
Alameda County:		
57–60	14 May 1989	Fremont, one mile south of Dumbarton Bridge
61–63	8 Apr 1989	Fremont, Coyote Hills Regional Park
64–65	21 Apr 1989	Hayward, end of Breakwater Avenue
66	15 Nov 1979	Hayward, Western Blvd.
67–69	14 May 1989	San Lorenzo, Hayward Regional Shoreline
70–72	21 Apr 1989	San Leandro, San Leandro Marina
73–79	6 May 1989	San Leandro, San Leandro Marina
80–81	29 Nov 1980	Alameda, Bay Farm Island
82	21 Dec 1978	Oakland, corner of Maxwell and Brookdale
83	10 Jun 1989	Emeryville, corner of I-80 and Powell
84	11 Apr 1989	Berkeley, University of California
Contra Costa County:		
85	22 Dec 1978	Tilden Regional Park, Lake Anza
86	27 Dec 1978	El Cerrito, Clayton Street
87–92	22 Apr 1989	Richmond, Point Isabel Regional Park
93–94	9 Jun 1988	Richmond, Brooks Island
95	11 Nov 1978	Richmond, corner of 39th and Barrett
96	4 Dec 1979	Richmond, corner of 39th and Barrett
97–100	27 Mar 1989	Richmond, Point Richmond

TABLE 1. CONTINUED.

Collection site	Date	Locality
101	14 Nov 1979	Richmond, Point Richmond
102–103	10 Apr 1988	East Brothers Island
104–108	19 Mar 1990	East Brothers Island
109–114	26 Mar 1989	Point Pinole Regional Shoreline
115	13 Feb 1980	Rodeo, Seascape Circle
116–119	7 Apr 1989	Rodeo, San Pablo Avenue
Solano County:		
120–122	5 Nov 1989	Vallejo, near corner of Lemon and Alden
123–125	5 Nov 1989	Vallejo, Hwy. 37 at east shore of Mare Island Strait
126	7 Apr 1989	Vallejo, corner of Hwy. 37 and Sacramento St.
127–128	5 Nov 1989	mouth of Sonoma Creek, east shore
Sonoma County:		
129–131	5 Nov 1989	mouth of Sonoma Creek, west shore
132	5 Nov 1989	Hwy. 37 at Tolay Creek
133–135	5 Nov 1989	Port Sonoma Marina
Marin County:		
136	5 Nov 1989	Hwy. 37 at Novato Creek
137–139	28 May 1989	China Camp State Park
140–142	10 Jun 1989	China Camp State Park
143	28 May 1989	San Rafael, Loch Lomond Marina
144–150	17 Feb 1990	West Marin Island
151–153	14 Jan 1989	East Marin Island
154	20 Feb 1982	San Rafael, Latham Street
155–158	6 Apr 1989	San Quentin State Prison
159	27 Sep 1986	Muir Woods National Monument
160	30 May 1986	Bolinas Lagoon
161	27 Sep 1986	Bolinas Lagoon
162	30 May 1986	Stinson Beach
163–165	30 May 1989	Muir Beach
166–167	11 Mar 1989	Marin City, end of Pohono Street
168	6 Jun 1990	Angel Island State Park
169–174	2 Apr 1989	Angel Island State Park
175–176	11 Mar 1989	Lime Point, north end of Golden Gate Bridge

6b. Flagellum of antenna two composed of 2 articles 13

7a. Flagellum of antenna two composed of 3 articles 8

7b. Flagellum of antenna two composed of 4–5 articles 10

8a. Body flattened. No cone-shaped process below eye (Fig. 7) .... 6. *Littorophiloscia richardsonae*

8b. Body somewhat convex dorsally. With cone-shaped processes below eyes 9

9a. Endopod of pleopod one of male expanded near tip. Posterolateral margin of basal segment of uropod not greatly produced (Fig. 13) .... 12. *Alloniscus perconvexus*

9b. Endopod of pleopod one of male not expanded near tip. Posterolateral margin of uropod usually produced (Fig. 14) .... 13. *Alloniscus mirabilis*

10a. Uropods extending well beyond posterior body margin. Peduncle of antenna two with numerous tubercle-like papillae surmounted with tufts of setae (Fig. 9) .... 8. *Detonella papillicornis*

10b. Uropods not extending much beyond posterior body margin. Peduncle of antenna two without tubercle-like papillae or tufts of setae 11

11a. Capable of conglobation. Rostrum truncate (Fig. 11) .... 10. *Armadilloniscus lindahli*

TABLE 2. DISTRIBUTION OF ONISCID ISOPOD SPECIES AMONG COLLECTION SITES. SEE FIGURE 1, TABLE 1 FOR THE LOCATIONS OF THE COLLECTION SITES.

Species	Collection sites
Ligiidae	
[a]*Ligia occidentalis*	12, 14, 24, 29, 30, 39, 68, 70, 72, 78, 88, 98, 102, 113, 118, 120, 139, 143, 144, 152, 156, 161, 164, 166, 171, 172, 176
[a]*Ligia pallasii*	1, 33
[a]*Ligidium latum*	162, 163
[a]*Ligidium gracile*	163
Trichoniscidae	
[a]*Protrichoniscus heroldi*	110, 114, 159
Halophilosciidae	
[a]*Littorophiloscia richardsonae*	24, 30, 35, 49, 54, 59, 63, 70, 89, 111, 113, 117, 127, 131, 137, 138, 140, 141, 161, 173
Bathythropidae	
[a]*Mauritaniscus littorinus*	22, 25, 26, 27, 29, 38, 40, 42, 46, 50, 56, 61, 62, 65, 67, 68, 73, 75, 80, 143, 160, 165
Scyphacidae	
Detonella papillicornis	25, 42, 89, 97, 99, 100, 122, 143, 144, 150, 151, 155, 158, 160, 173
Armadilloniscus coronacapitalis	25, 29, 42, 43, 45, 49, 54, 59, 60, 63, 70, 83, 92, 111, 117, 119, 124, 128, 134, 137, 138, 140, 160, 161, 170
[a]*Armadilloniscus lindahli*	25, 51, 54, 60, 67, 73, 79, 81, 99, 160, 161
[a]*Armadilloniscus holmesi*	15, 25, 37, 40, 42, 68, 70, 73, 76, 79, 87, 92, 97, 99, 150, 151, 161, 166, 173
Oniscidae	
[a]*Alloniscus perconvexus*	22, 23, 113
[b]*Alloniscus mirabilis*	
Porcellionidae	
[a]*Porcellio scaber*	2, 6, 8, 9, 10, 11, 12, 13, 16, 18, 19, 20, 21, 22, 30, 31, 34, 47, 48, 52, 84, 85, 93, 94, 95, 96, 97, 101, 105, 108, 123, 124, 126, 127, 128, 130, 134, 135, 136, 138, 141, 142, 145, 146, 147, 149, 153, 160, 163, 165, 168, 169, 174, 175
[a]*Porcellio dilatatus*	3, 4, 5, 6, 7, 10, 11, 17, 20, 21, 31, 32, 36, 47, 48, 50, 52, 66, 82, 104, 105, 108, 109, 110, 112, 115, 136, 141, 147, 153, 168, 175
[a]*Porcellio laevis*	28, 41, 42, 44, 50, 52, 53, 55, 58, 66, 69, 74, 80, 90, 91, 101, 112, 113, 114, 115, 143, 157
[a]*Porcellionides floria*	52, 107, 115, 154
Armadillidiidae	
[a]*Armadillidium vulgare*	8, 9, 11, 16, 17, 21, 26, 30, 31, 41, 42, 50, 52, 53, 55, 57, 61, 64, 66, 68, 71, 77, 80, 82, 85, 86, 90, 93, 94, 95, 96, 97, 101, 103, 106, 110, 112, 114, 115, 116, 121, 125, 126, 129, 132, 133, 135, 136, 137, 138, 142, 143, 148, 153, 154, 158, 160, 165, 167, 169, 175
Armadillidae	
[a]*Venezillo microphthalmus*	

[a] Reported from the San Francisco Bay Area by Miller (1938).

[b] Not yet reported from the Bay Area but occurrence there likely.

11b. Not capable of conglobation. Rostrum acute 12

12a. Penultimate article of peduncle of second antenna with hooked flange on lateral border. Surface of body of mature female covered with conspicuous tubercles (Fig. 10) .... 9. *Armadilloniscus coronacapitalis*

12b. Penultimate article of peduncle of second antenna without hooked flange. Surface of body relatively smooth, with low rounded tubercles (Fig. 12) .... 11. *Armadilloniscus holmesi*

13a. Surface of body covered with fine scales. Exopod of pleopod one of male with knob-like process on inner margin (Fig. 8) .... 7. *Mauritaniscus littorinus*

13b. Surface of body smooth or not, but not

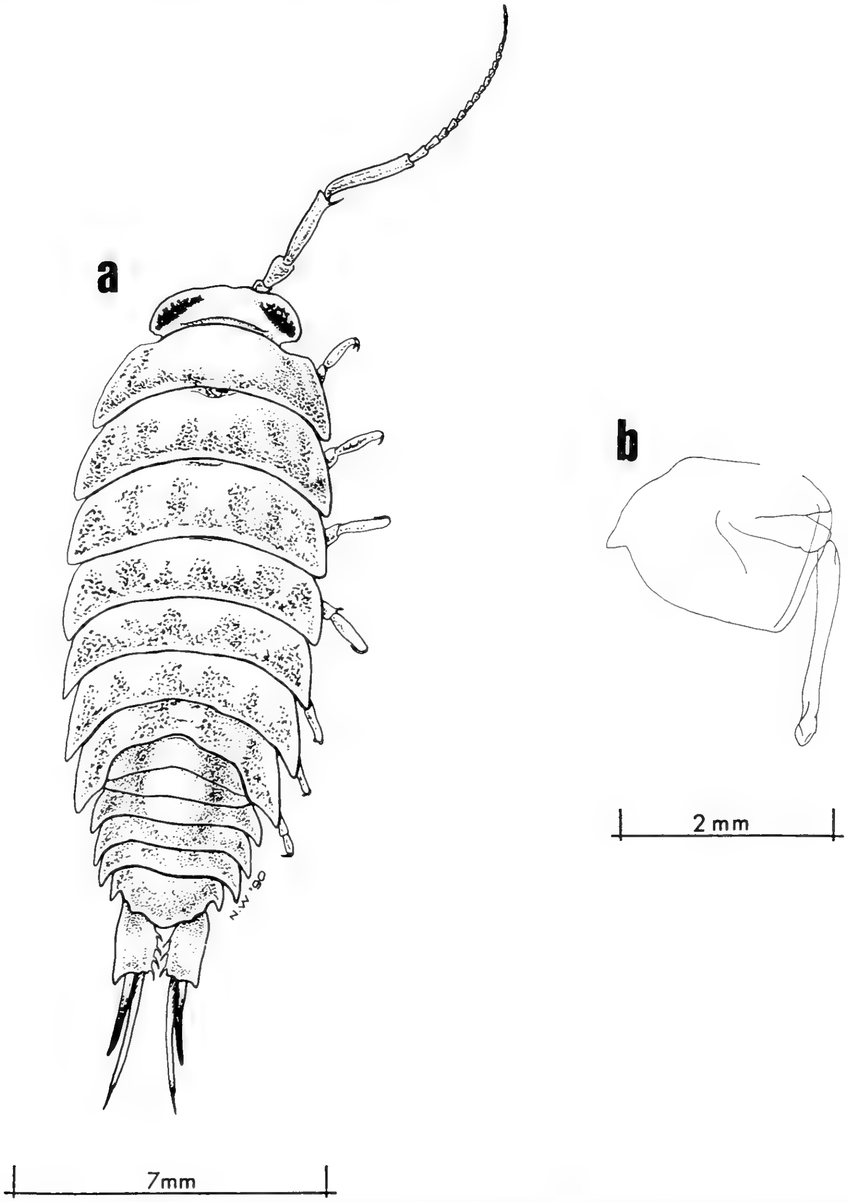

FIGURE 2. *Ligia occidentalis*: a, dorsal view; b, right male pleopod 2. Original drawings by Nancy Walker from CASIZ 075510.

adorned with scales. No knob-like process on exopod of pleopod one 14

14a. Not capable of conglobating. Uropods extending well beyond posterior body margin 15

14b. Capable of conglobating. Uropods not extending beyond posterior body margin 18

15a. Usually with a waxy bloom or frosted appearance in life. No frontal or marginal lobes on cephalon. Pleon abruptly narrower than pereon (Fig. 18) .... 17. *Porcellionides floria*

15b. Without a bloom or frost. Distinct frontal and/or marginal lobes on cephalon. Pleon continuous with pereon 16

16a. Surface of body smooth. Posterolateral margin of pereonite one barely produced posteriorly (Fig. 17) .... 16. *Porcellio laevis*

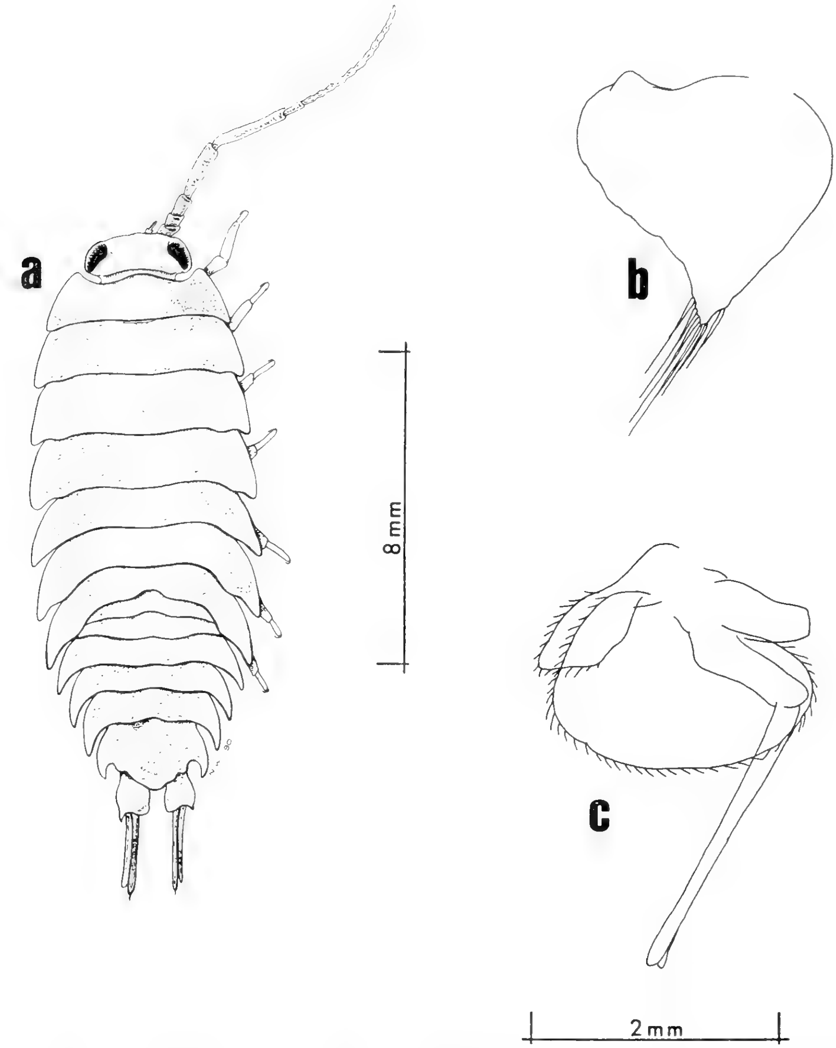

FIGURE 3. *Ligia pallasii*: male specimen, a, dorsal view; b, exopod, right male pleopod 1; c, right male pleopod 2. Original drawings by Nancy Walker from CASIZ 075488.

16b. Surface of body tuberculate. Posterolateral margin of pereonite one manifestly produced posteriorly 17

17a. Telson spatulate, rounded (Fig. 16) .... 15. *Porcellio dilatatus*

17b. Telson pointed (Fig. 15) .... 14. *Porcellio scaber*

18a. Eyes with many more than 4 ommatidia. Telson trapezoidal. Exopods of uropods large (Fig. 19) 18. *Armadillidium vulgare*

18b. Eyes composed of about 4 ommatidia. Telson hourglass shaped. Exopods of uropods minute and inserted near inner margin of basal article (Fig. 20) .... 19. *Venezillo microphthalmus*

SPECIES ACCOUNTS

1. **Ligia occidentalis** Dana, 1853

(Fig. 2)

Ligia occidentalis is commonly encountered in rocky littoral habitats in sheltered and open coast environments along the California coast from Sonoma County to the Gulf of California (Ricketts and Calvin 1968; Garthwaite et al. 1985).

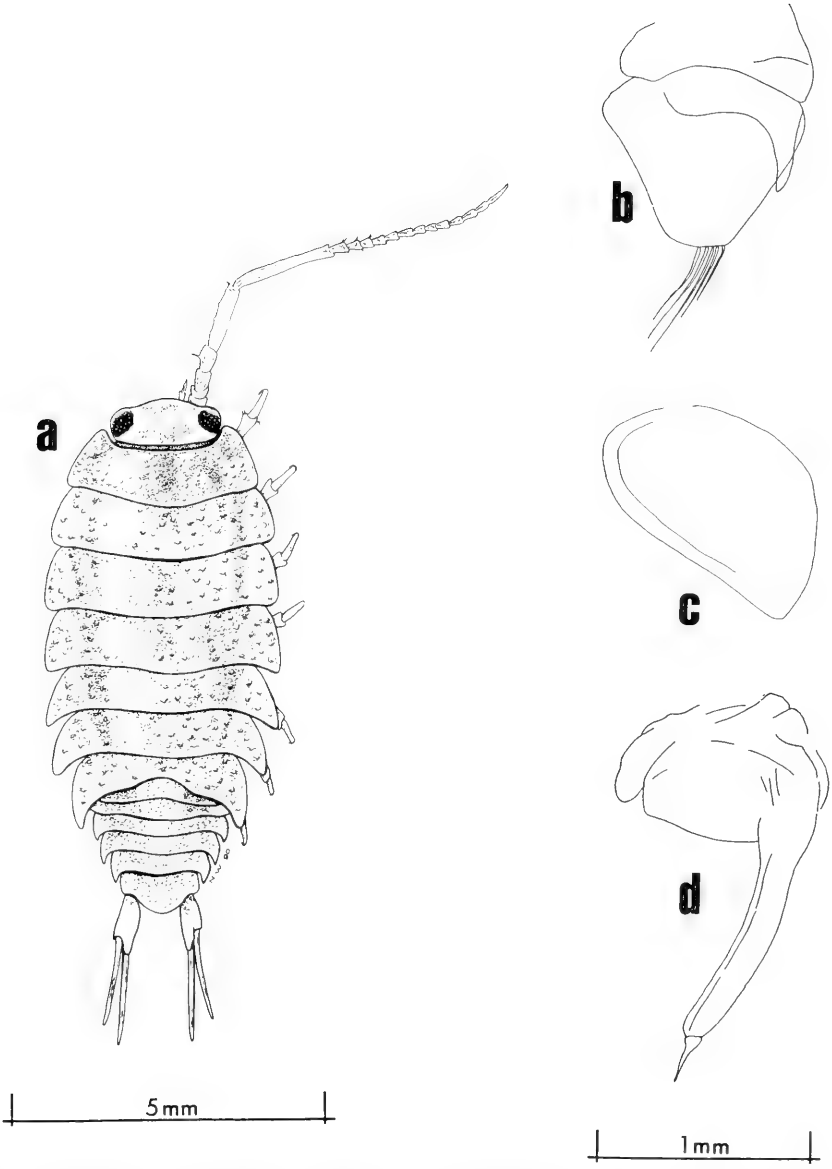

FIGURE 4. *Ligidium latum*: a, dorsal view; b, exopod, right male pleopod 1; c, exopod, right male pleopod 2; d, endopod, right male pleopod 2. Original drawings by Nancy Walker from CASIZ 075498.

This species was originally described from the San Francisco Bay Area on the basis of specimens taken from the Sacramento River (Dana 1853). Although the area covered in our survey stopped at the Verazano Straights, Ricketts and Calvin (1968) stated that *L. occidentalis* occurs on the shores of the Sacramento River. In the Bay Area, Richardson (1904) reported this species from Sausalito (Marin County), and Miller (1938) collected it at Moss Beach and Montara (San Mateo County) and stated that it was widely distributed throughout the San Francisco Bay region. We found *L. occidentalis* to be very common and widely distributed in the Bay Area, predominantly along rocky shores both within the bay and along the open coast.

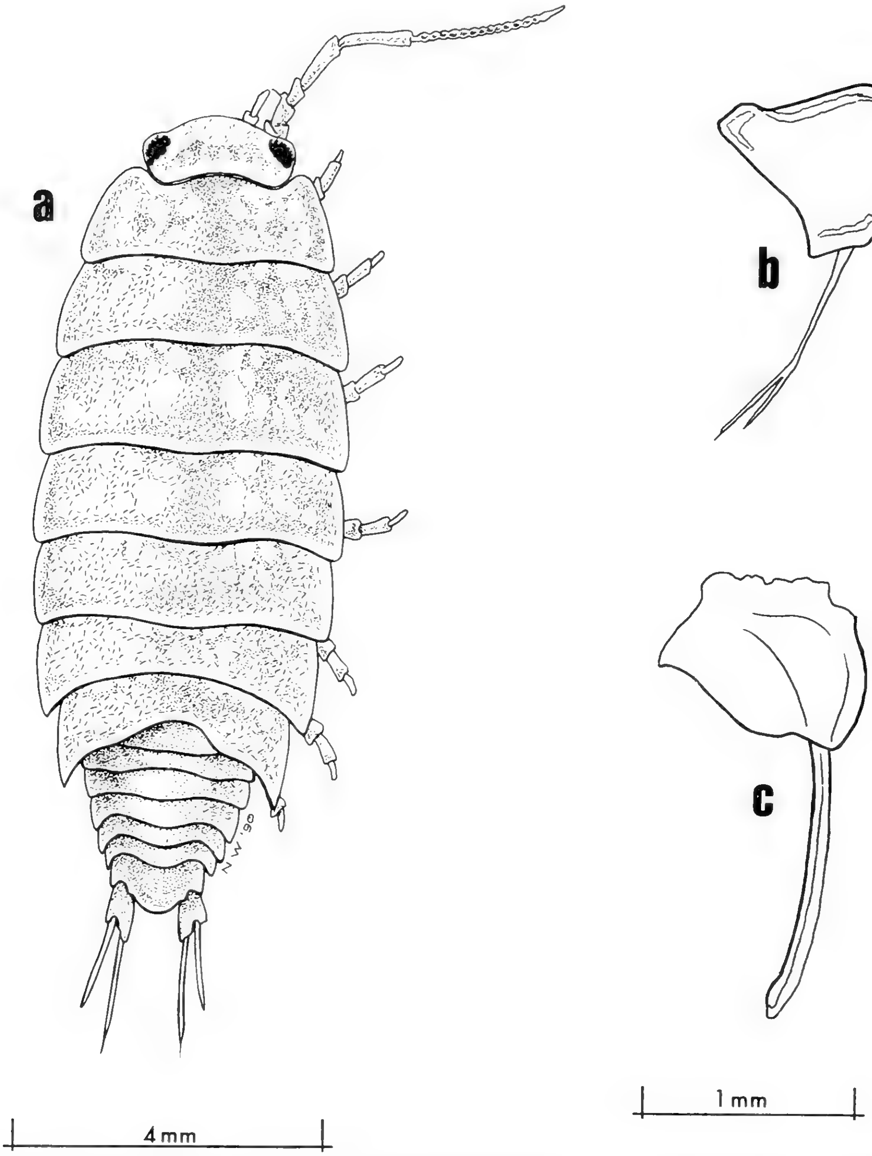

FIGURE 5. *Ligidium gracile*: a, dorsal view; b, exopod, right male pleopod 1; c, right male pleopod 2. Original drawings by Nancy Walker from CASIZ 075490.

2. **Ligia pallasii** Brandt, 1833

(Fig. 3)

Another littoral species found in rocky habitats, *L. pallasii* occurs from Santa Cruz, Santa Cruz County, California to Alaska (Ricketts and Calvin 1968; Garthwaite, unpubl.), but appears to be restricted to open coast environments. In the Bay Area, Miller (1938) collected this species on the outer coast at Montara, San Mateo County. In this survey, we collected *L. pallasii* from rocky habitats at two localities (sites 1 and 33, Fig. 1) on the outer coast.

3. **Ligidium latum** Jackson, 1923

(Fig. 4)

Ligidium latum, a riparian species originally described from San Francisco (Jackson 1923), is

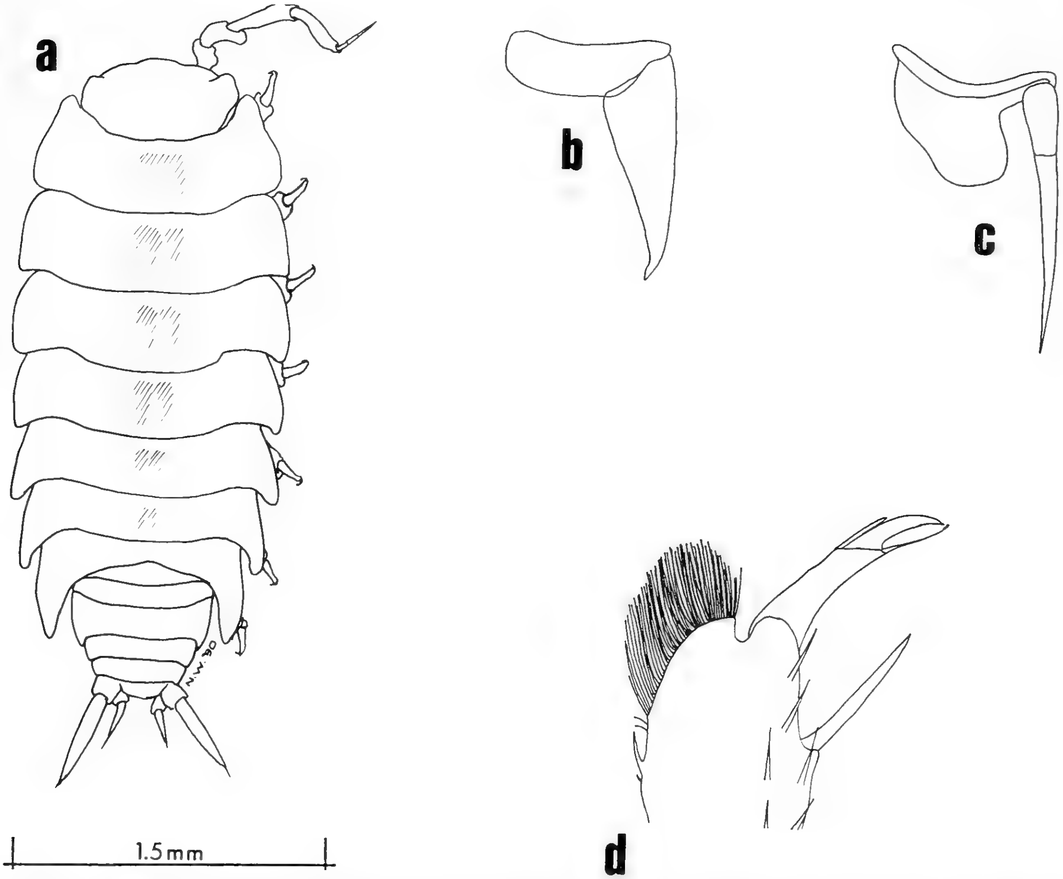

FIGURE 6. *Protrichoniscus heroldi*: a, dorsal view (original drawing by Nancy Walker from CASIZ 075423); b, right male pleopod 1; c, right male pleopod 2; d, distal segment of male pereopod 7 (b–d adapted from Arcangeli 1932, magnifications not provided).

widely distributed in California but infrequently collected. Outside the San Francisco Bay Area, we have collected it at Refugio Creek, Santa Barbara County (Garthwaite et al. 1985) and at three sites in Santa Cruz County (Swanton, 10 May 1986; Bonny Doon, 29 May 1986; and Henry Cowell Redwoods State Park, 10 May 1986). Within the Bay Area, *L. latum* has been collected from Mission Peak, Alameda County (Van Name 1940). In this survey, we collected *L. latum* at sites 162 and 163 only.

4. **Ligidium gracile** (Dana, 1856)

(Fig. 5)

Ligidium gracile, another riparian species, is widely distributed in California. The Santa Barbara Museum of Natural History has specimens of this species collected on Tranquillon Mountain, Vandenberg Air Force Base, Santa Barbara County, and it has been reported from Eureka and Richardson Grove State Park, Humboldt County (as *Ligidium gracilis*; Miller 1938). Outside of the San Francisco Bay Area, we have collected this species at several sites in Santa Cruz County (Swanton, 10 May 1986; Bonny Doon, 29 May 1986; Henry Cowell Redwoods State Park, 10 May 1986; and Forest of Nisene Marks State Park, 10 May 1986) and two sites in Sonoma County (Shell Beach at Sea Ranch, 1 June 1986; Stump Beach, 1 June 1986). In the Bay Area, this species has been reported from San Francisco, San Francisco County (as *Ligidium hypnorum* (Cuvier, 1792), a European species; Stuxberg 1875); Santa Clara, Santa Clara County (Jackson 1923); Angel Island, Marin County (Van Name 1936); Berkeley, Alameda County (as *L. gracilis*; Miller 1938); and Moss

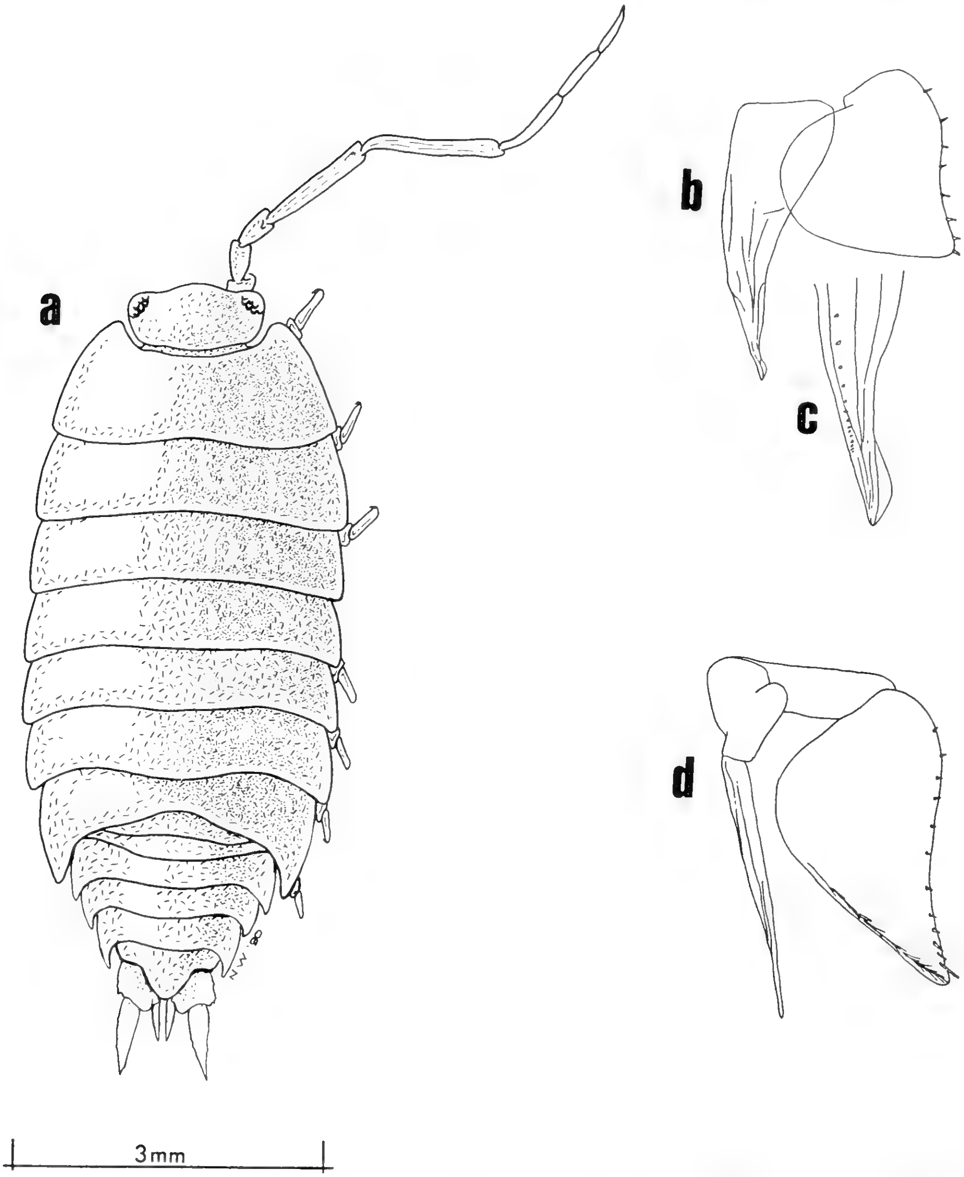

FIGURE 7. *Littorophiloscia richardsonae*: a, dorsal view (original drawing by Nancy Walker from CASIZ 075421); b, left male pleopod 1; c, enlargement of tip of endopod of male pleopod 1; d, left male pleopod 2 (b–d adapted from Taiti and Ferrara 1986, magnifications not provided).

Beach, San Mateo County (as *L. gracilis*; Miller 1938). We collected *L. gracile* only at Muir Beach (site 163; Table 2, Fig. 1).

5. **Protrichoniscus heroldi** Arcangeli, 1932
(Fig. 6)

Protrichoniscus heroldi was originally described from specimens collected at San Mateo, San Mateo County, and Muir Woods, Marin County (Arcangeli 1932). Although uncommon, this species is widely distributed in California, having been collected in Calaveras, Tulare, and Santa Cruz counties (Mulaik and Mulaik 1943) and in Riverside and San Bernadino counties (Garthwaite et al. 1985). One of us (RLG) has collected this species from Cave Gulch, near Santa Cruz, Santa Cruz County (1 August 1986) and at Drytown, Amador County (2 November 1986).

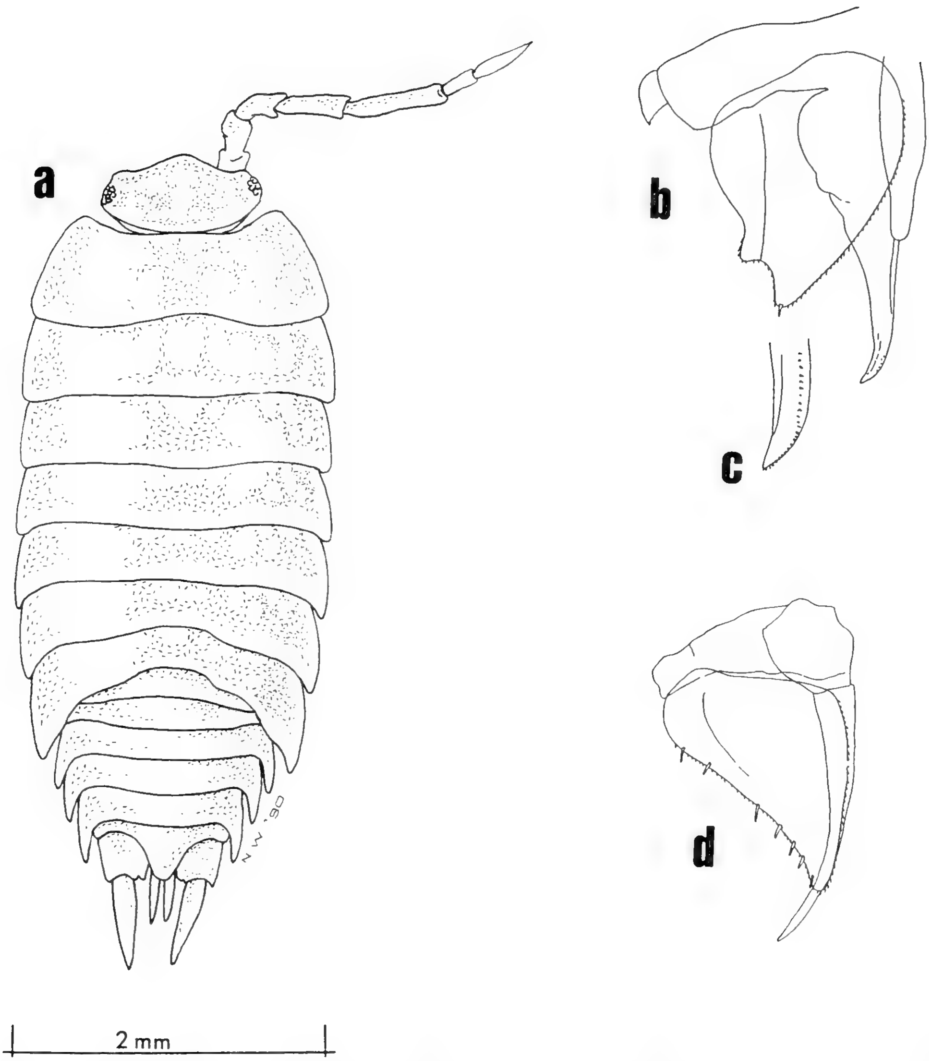

FIGURE 8. *Mauritaniscus littorinus*: a, dorsal view (original drawing by Nancy Walker from CASIZ 075327); b, right male pleopod 1; c, enlargement of tip of endopod of male pleopod 1; d, right male pleopod 2 (b–d adapted from Schultz et al. 1982, magnifications not provided).

We collected *P. heroldi* at Muir Woods (site 159) and Point Pinole (sites 110 and 114; Table 2, Fig. 1).

6. **Littorophiloscia richardsonae** (Holmes and Gay, 1909)

(Fig. 7)

Littorophiloscia richardsonae is a common Pacific Coast littoral species, found in marshes, along bays and estuaries, and on the outer coast from Baja California, Mexico to Washington (Garthwaite et al. 1985). In the San Francisco Bay Area, Miller (1938) collected this species (which he refered to as *Philoscia richardsonae*) at Alameda, Alameda County. In this survey, we found *L. richardsonae* to be a common species throughout the Bay Area.

7. **Mauritaniscus littorinus** (Miller, 1936)

(Fig. 8)

Mauritaniscus littorinus has had a complex taxonomic history, and the true identity of this taxon remains in doubt. Miller described it as a

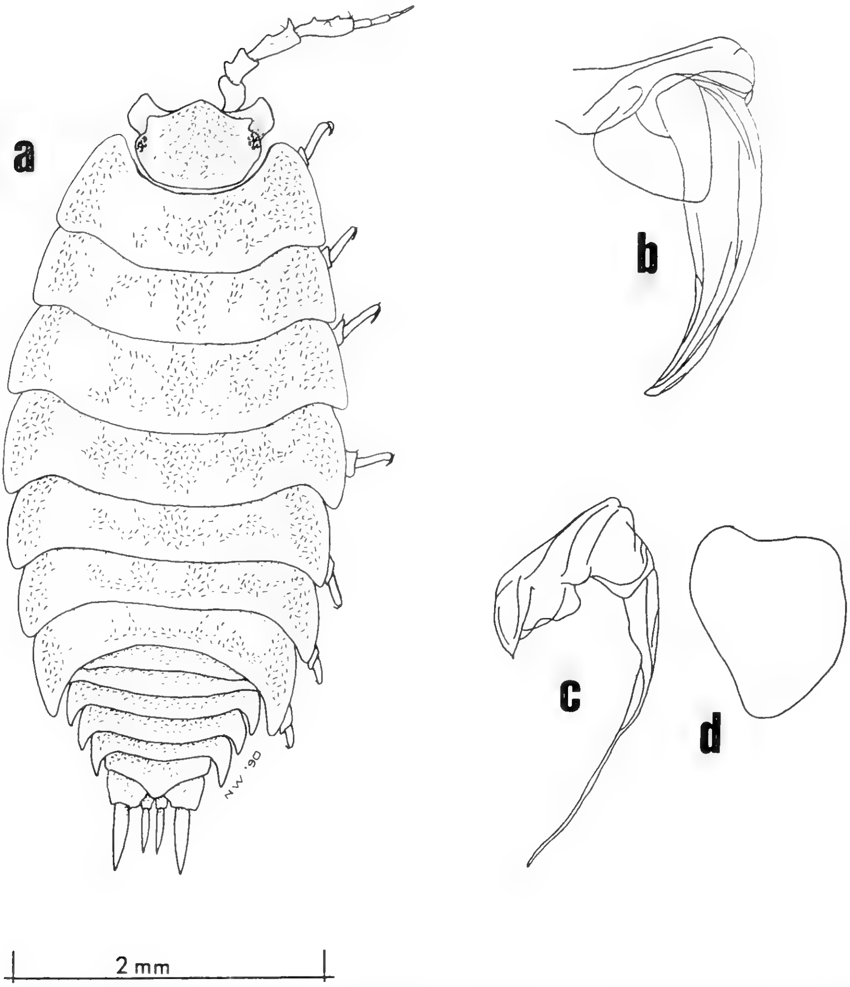

FIGURE 9. *Detonella papillicornis*: a, dorsal view (original drawing by Nancy Walker from CASIZ 075449); b, right male pleopod 1; c, endopod of right male pleopod 2; d, exopod of right male pleopod 2 (b–d adapted from Lohmander 1927, magnifications not provided).

new species, *Porcellio littorina* Miller, 1936, on the basis of specimens he collected in the San Francisco Bay Area on Bay Farm Island, Alameda County. Schultz et al. (1982) later transferred this species to the genus *Mauritaniscus.* Ferrara and Taiti (1989), however, assert without supporting data that this species is synonymous with *Niambia capensis,* an African oniscid first described from South Africa as *Metoponorthus capensis* (Dollfus, 1895). Until a more complete comparison of *M. littorinus* and *N. capensis* is published, we retain the name *M. littorinus* for this species. *Mauritaniscus littorinus* has been found along the California coast from San Francisco Bay to San Diego, San Diego County (Schultz et al. 1982). The specimen of *M. littorinus* reported from Bay Center, Pacific County, Washington by Hatch (1939) as *P. littorina* was actually an immature specimen of *P. scaber* (see Hatch 1947). We found *M. littorinus* to be common and widely distributed in littoral sites throughout the Bay Area.

8. **Detonella papillicornis** (Richardson, 1904)

(Fig. 9)

This littoral species was originally described from Alaska (Richardson 1904) and has only recently been reported from California (Garthwaite 1988). In the area included in this survey, we collected *D. papillicornis* at Bolinas Lagoon,

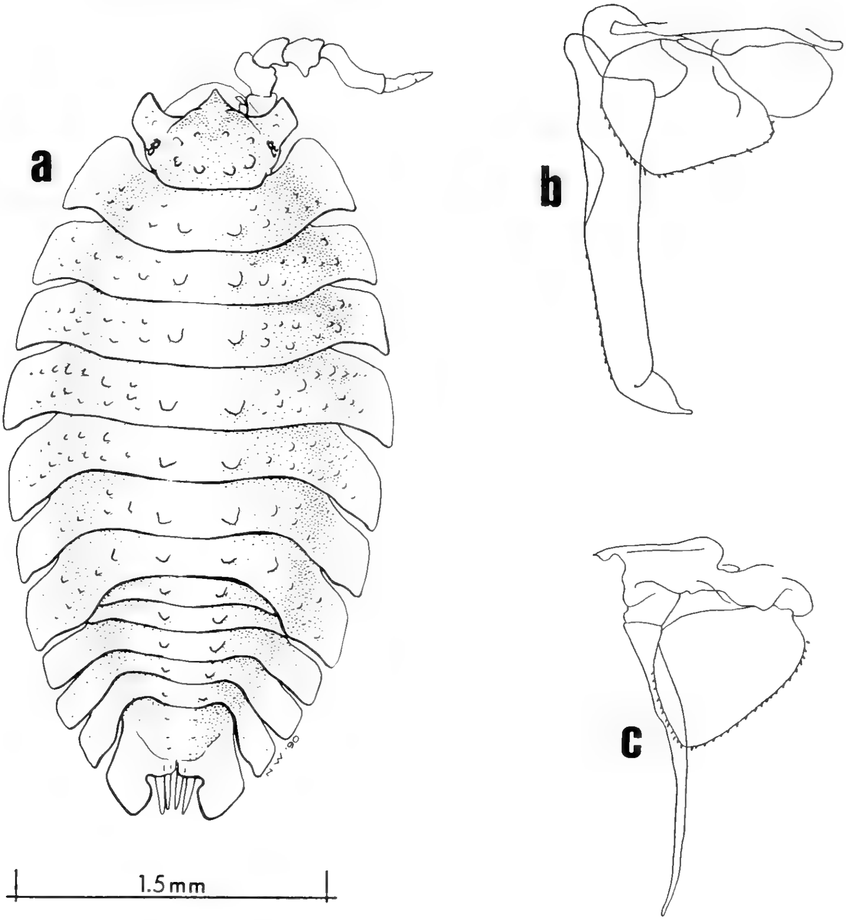

FIGURE 10. *Armadilloniscus coronacapitalis*: female specimen, a, dorsal view (original drawing by Nancy Walker from CASIZ 075392); b, left male pleopod 1; c, left male pleopod 2 (b, c adapted from Menzies 1950, magnifications not provided).

Marin County, and in littoral sites throughout San Francisco Bay, where it is rather common.

9. **Armadilloniscus coronacapitalis** Menzies, 1950

(Fig. 10)

Armadilloniscus coronacapitalis was originally described from Tomales Bay, Marin County, California (Menzies 1950) and was recently reported from San Miguel and Anacapa islands, California (Garthwaite et al. 1985). In the San Francisco Bay Area, this littoral species has previously been reported from Bolinas Lagoon, Marin County (Garthwaite 1988). We found it to be common and widespread in littoral habitats throughout San Francisco Bay.

10. **Armadilloniscus lindahli** (Richardson, 1905)

(Fig. 11)

This species has been collected from littoral habitats from Baja California, Mexico to Marin County, California (Garthwaite et al. 1985; Garthwaite 1988). In the San Francisco Bay Area, Richardson (1905) reported it from Oakland, Alameda County (as *Actoniscus lindahli*) and Miller (1938) reported it from Bay Farm Island, Alameda County (as *Actoniscus lindahli*). In this survey we found *Armadilloniscus lindahli* in large numbers at Bolinas Lagoon, Marin County, and in littoral sites throughout San Francisco Bay, although in the Bay it is nowhere very common.

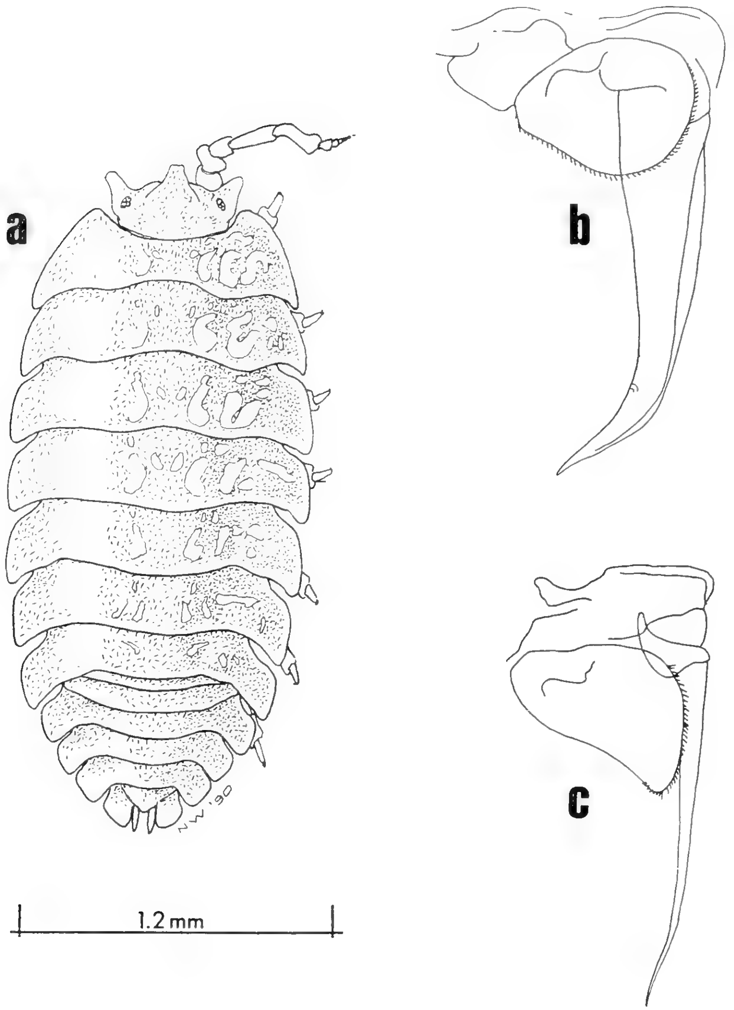

FIGURE 11. *Armadilloniscus lindahli*: a, dorsal view (original drawing by Nancy Walker from CASIZ 075317); b, right male pleopod 1; c, right male pleopod 2 (b, c adapted from Menzies 1950, magnifications not provided).

11. **Armadilloniscus holmesi** Arcangeli, 1933

(Fig. 12)

Armadilloniscus holmesi is common along the Pacific Coast and can be found in marshes, bays, and estuaries from Washington to Baja California, Mexico (Garthwaite et al. 1985). In the San Francisco Bay Area Miller (1938) reported it from Bay Farm Island, Alameda County (as *Actoniscus tuberculatus* [Holmes and Gay, 1909]). We found *A. holmesi* to be very common and widely distributed throughout San Francisco Bay and present but less common at Bolinas Lagoon.

12. **Alloniscus perconvexus** Dana, 1856

(Fig. 13)

This species occurs from southern California to Washington on sandy beaches where it burrows into the sand under detritus at approximately the high tide line (Garthwaite et al. 1985). In the San Francisco Bay Area, Arcangeli (1932) reported it from San Mateo, San Mateo County, and Miller (1938) collected it at Moss Beach, San Mateo County. In this survey, we found *A. perconvexus* at Fort Funston (sites 22 and 23) along the open coast and at Point Pinol (site 113) within the bay (Table 2, Fig. 1).

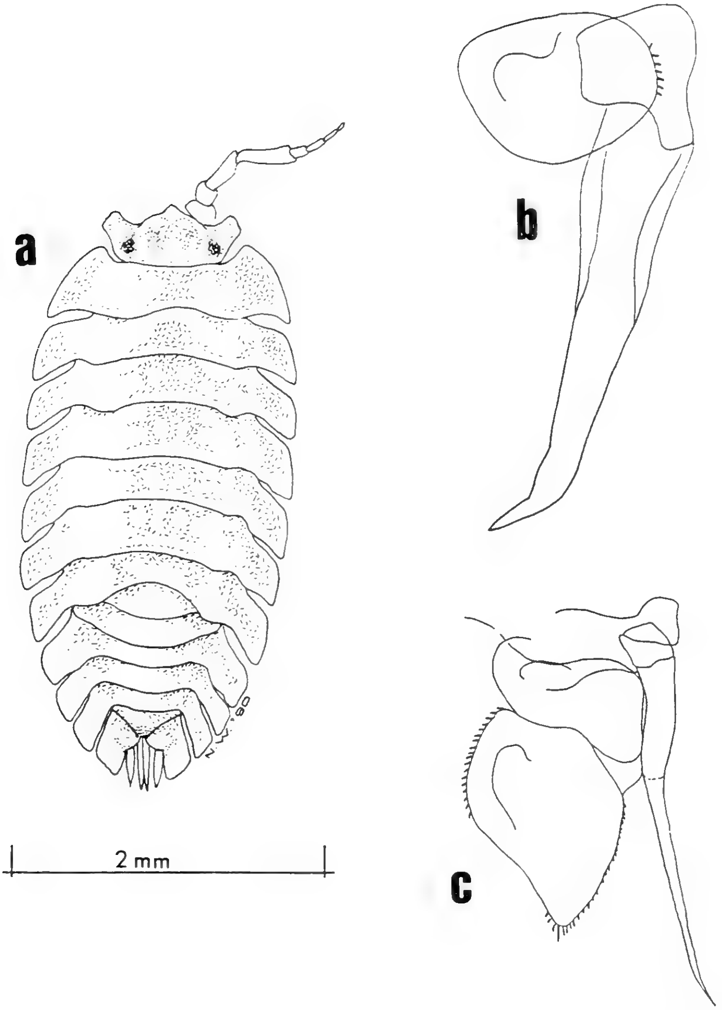

FIGURE 12. *Armadilloniscus holmesi*: a, dorsal view (original drawing by Nancy Walker from CASIZ 075412); b, right male pleopod 1; c, right male pleopod 2 (b, c adapted from Menzies 1950, magnifications not provided).

13. **Alloniscus mirabilis** (Stuxberg, 1875)

(Fig. 14)

Alloniscus mirabilis has rarely been collected but is widely distributed in California, having been found in San Diego County, Orange County, San Luis Obispo County, San Mateo County, and on the California Channel Islands (Garthwaite et al. 1985). Although we have not found this species in the area included in this survey, we have included it here because it has been found at localities nearby (Pebble Beach, San Mateo County; Garthwaite et al. 1985), and there is no reason why it should not be present in the Bay Area.

14. **Porcellio scaber** Latreille, 1804

(Fig. 15)

Although this species is of European origin, it is common throughout most of the United States and is one of the most common oniscids of the Pacific Coast (Garthwaite, unpubl.). In the San Francisco Bay Area it was reported by Stuxberg (1875) from San Francisco, San Francisco County and Sausalito, Marin County; and by Arcangeli (1932) from San Mateo, San Mateo County.

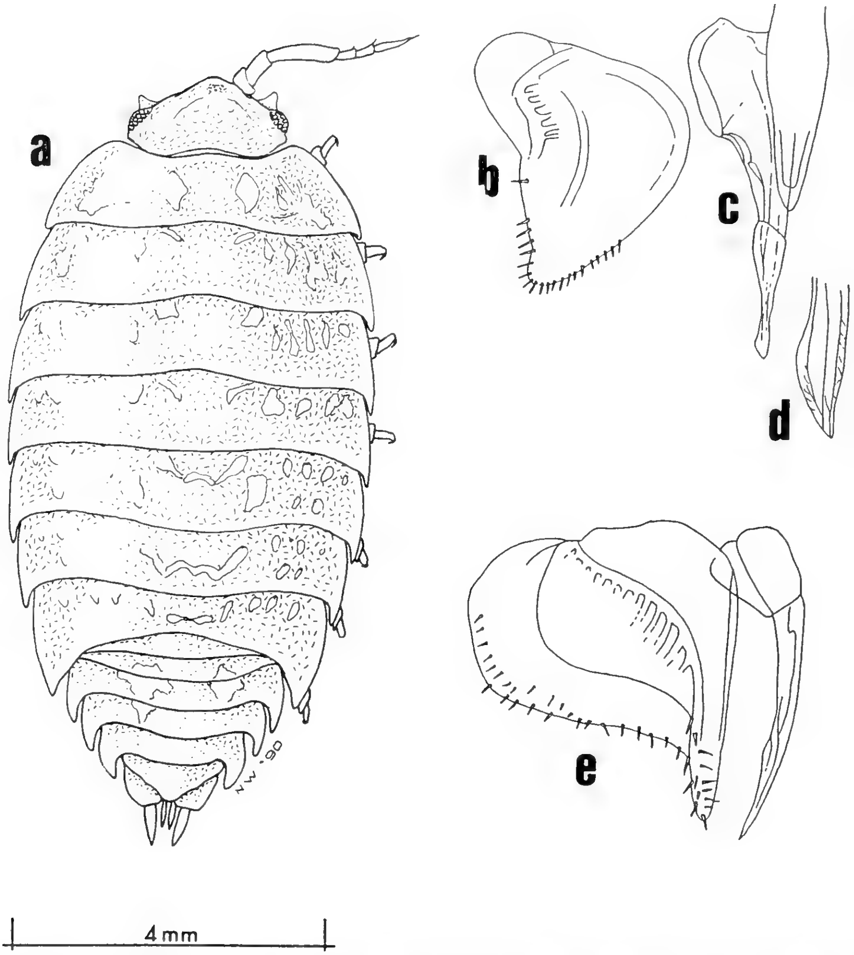

FIGURE 13. *Alloniscus perconvexus*: a, dorsal view (original drawing by Nancy Walker from CASIZ 075425); b, exopod of right male pleopod 1; c, endopod of right male pleopod 1; d, enlargement of tip of endopod of right male pleopod 1; e, right male pleopod 2 (b–e adapted from Schultz 1984, magnifications not provided).

Miller (1938), who collected it at Oakland and Berkeley, Alameda County and Moss Beach, San Mateo County, reported it as widely distributed in the San Francisco Bay Area (Miller 1936). We have found this species to be the only truly terrestrial isopod established in the Farallon Islands where it is common on South Farallon. We found *P. scaber* common throughout the Bay Area.

15. **Porcellio dilatatus** Brandt and Ratzeburg, 1833

(Fig. 16)

Like *Porcellio scaber, P. dilatatus* is a European introduction that has become widely distributed throughout the Pacific states. Miller (1936), who listed it as *Porcellio spinicornis* Say, 1818, reported it as widely distributed in the San Francisco Bay Area and collected it at Berkeley, Alameda County, and Moss Beach, San Mateo County (Miller 1938). We found *P. dilatatus* widely distributed and moderately common throughout the Bay Area.

16. **Porcellio laevis** Latreille, 1804

(Fig. 17)

Another widely distributed European species, *P. laevis* was first reported from the San Francisco Bay Area by Stuxberg (1875) who mistakenly described it as a new species, *Porcellio formosus,* from San Francisco, San Francisco County. Arcangeli (1932) redescribed *P. for-*

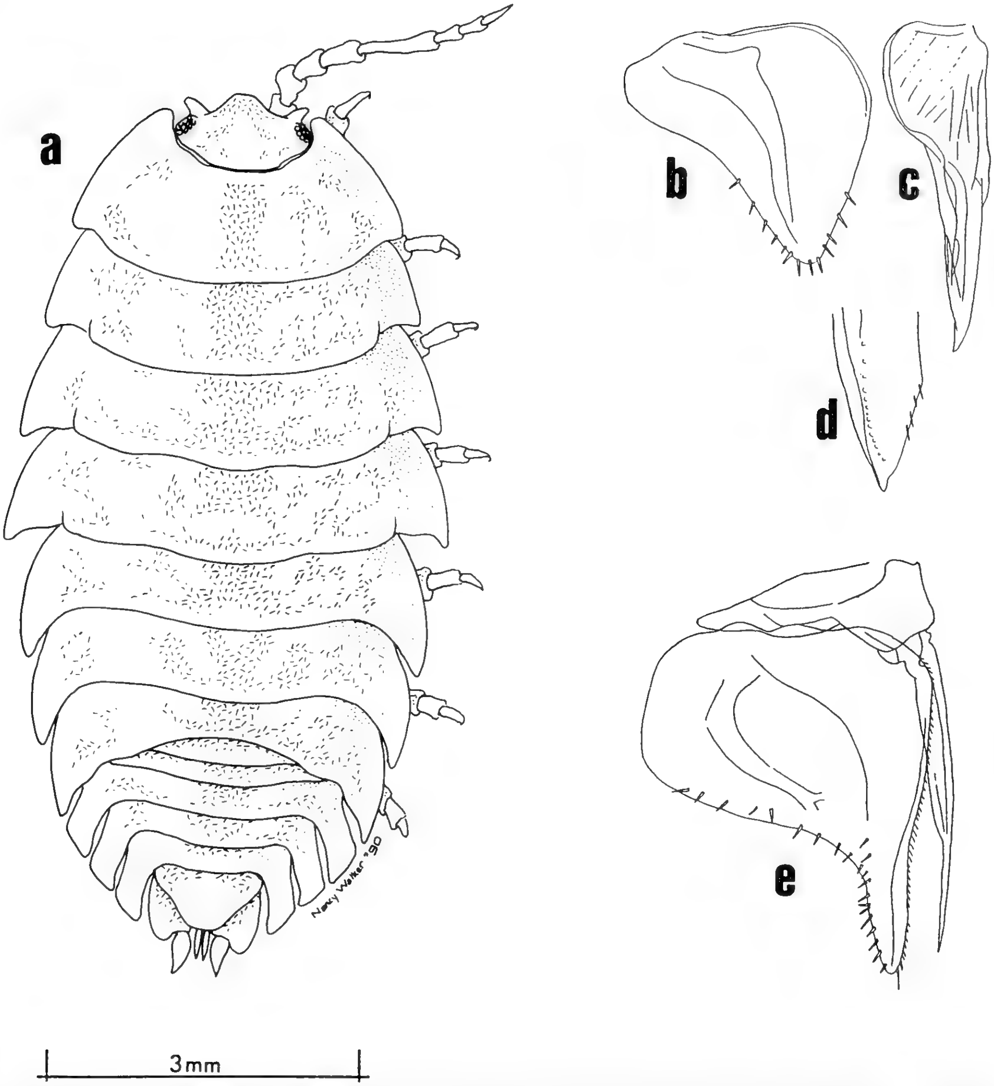

FIGURE 14. *Alloniscus mirabilis*: a, dorsal view (original drawing by Nancy Walker from CASIZ 075422); b, exopod of right male pleopod 1; c, endopod of right male pleopod 1; d, enlargement of tip of endopod of right male pleopod 1; e, right male pleopod 2 (b–e adapted from Schultz 1984, magnifications not provided).

mosus (on the basis of specimens from Louisiana and Texas). Thus, Miller (1936) thought the species valid. However, Van Name (1940) states that the specimens described by Arcangeli were apparently *Porcellionides virgatus* (Budde-Lund, 1885). Miller (1936) found *P. laevis* to be widely distributed throughout the San Francisco Bay Area and collected it at Berkeley and Oakland (Alameda County), and Moss Beach (San Mateo County). We also found *P. laevis* common and widely distributed throughout the Bay Area.

17. **Porcellionides floria** Garthwaite and Sassaman, 1985

(Fig. 18)

In North America, this European introduction is morphologically very similar to *Porcellionides pruinosus* (Brandt, 1833) which is also from Europe (Garthwaite and Sassaman 1985). Although it is impossible to assign individuals of these two taxa definitively to species without fresh specimens (see Garthwaite and Sassaman 1985), all

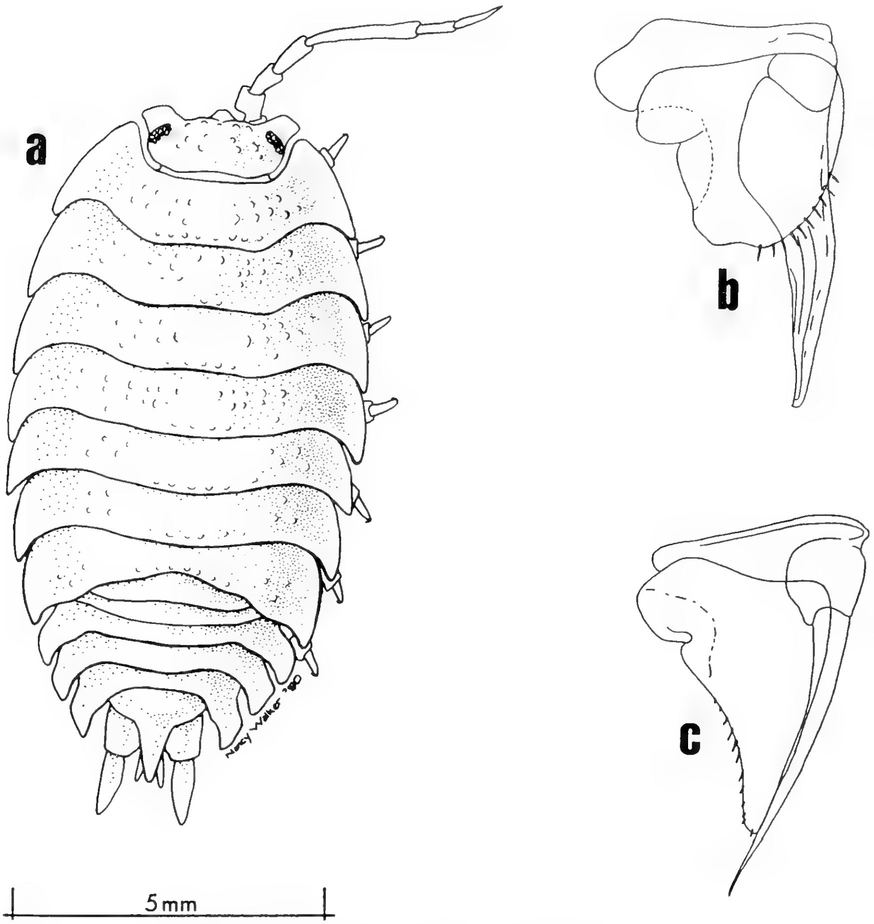

FIGURE 15. *Porcellio scaber*: a, dorsal view (original drawing by Nancy Walker from CASIZ 075527); b, right male pleopod 1; c, right male pleopod 2 (b, c adapted from Wachtler 1937, magnifications not provided).

recent collections of *Porcellionides* from California have been *P. floria* with the exception of a single collection of *P. pruinosus* from Death Valley, Inyo County (Garthwaite and Sassaman 1985). On this basis we assume all previous reports of *P. pruinosus* from the San Francisco Bay Area to be *P. floria*. In the Bay Area, *P. floria* was reported by Stuxberg (1875) (as *Porcellio maculicornis* Koch, 1835–44) from San Francisco, San Francisco County. Miller (1938), who listed it as *Metaponorthus pruinosus* (Brandt, 1833) collected this species at Berkeley and Oakland (Alameda County), and Mount Diablo (Contra Costa County). We collected *P. floria* at only four localities: Rodeo (site 115), San Rafael (site 154), East Brothers Island (site 107) and on Stanford University campus (site 52, Table 2, Fig. 1).

18. **Armadillidium vulgare** (Latreille, 1804)

(Fig. 19)

Armadillidium vulgare is another European introduction that is widely distributed and very common throughout California and most of North America. In the San Francisco Bay Area, it has been reported by Essig (1926) from "the San Francisco Region," by Arcangeli (1932) from San Mateo, San Mateo County (as *Armadillidium cinereum* [Zenker, 1793]), and by Miller (1938), who collected it in Berkeley, Oakland, and Alameda (Alameda County), and Moss Beach (San Mateo County). We found *A. vulgare* very common and widely distributed throughout the Bay Area.

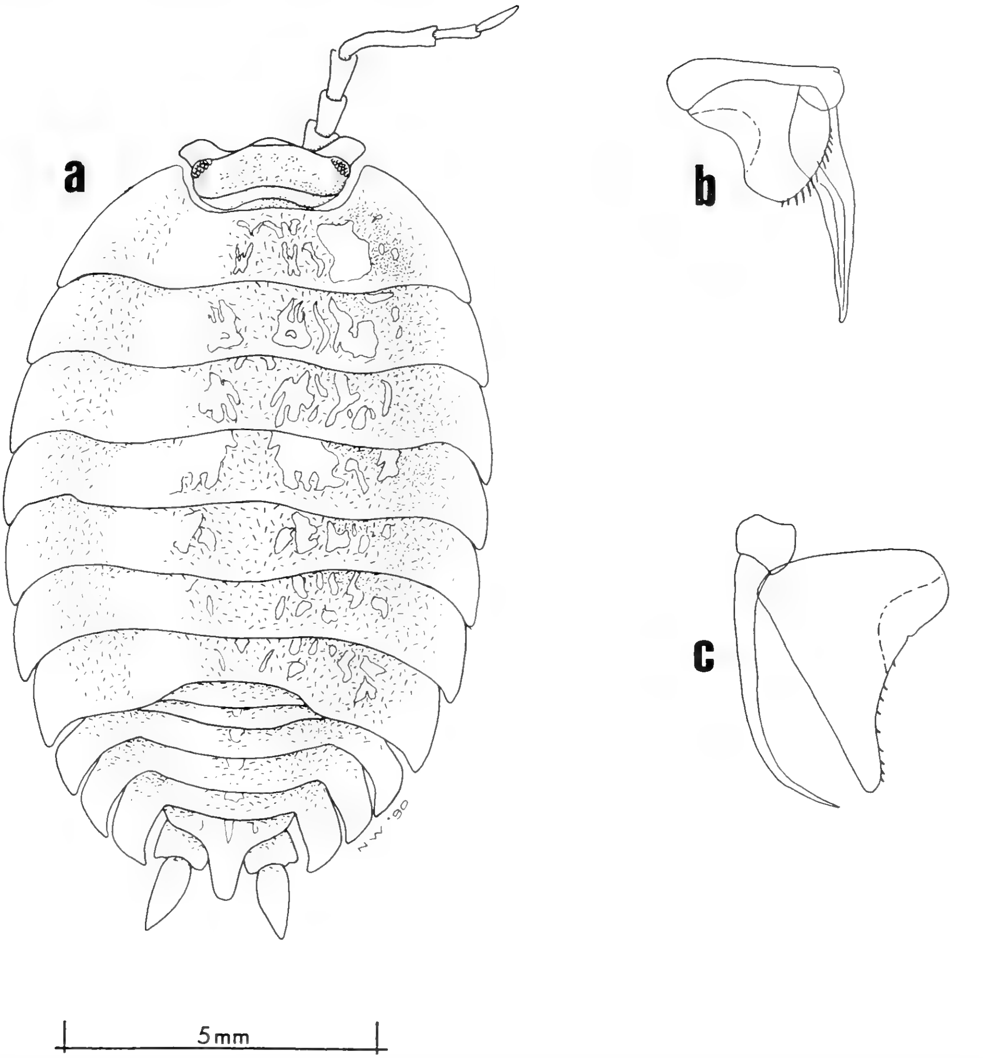

FIGURE 16. *Porcellio dilatatus*: a, dorsal view (original drawing by Nancy Walker from CASIZ 075509); b, right male pleopod 1; c, right male pleopod 2 (b adapted from Wachtler, 1937, magnifications not provided; c adapted from Edney 1953, magnifications not provided).

19. **Venezillo microphthalmus** (Arcangeli, 1932) (Fig. 20)

This species was first described (as *Armadillo microphthalmus*) on the basis of specimens collected in the San Francisco Bay Area at Saratoga, Santa Clara County (Arcangeli 1932). Although it was later collected at several localities in Tulare and Calaveras counties in California (Mulaik and Mulaik 1942), it has never again been collected in the Bay Area, and the only recent collections made of this species have been from the Channel Islands of southern California (Garthwaite et al. 1985). We did not encounter *V. microphthalmus* in our survey, but we have deposited specimens of this species from Santa Barbara Island (collected 24 January 1984) in the California Academy of Sciences for reference (catalog No. CASIZ 075538).

DISCUSSION

Although there have been several significant changes in the known distribution of oniscid isopods in the San Francisco Bay Area since Miller's (1938) summary, the distribution and relative

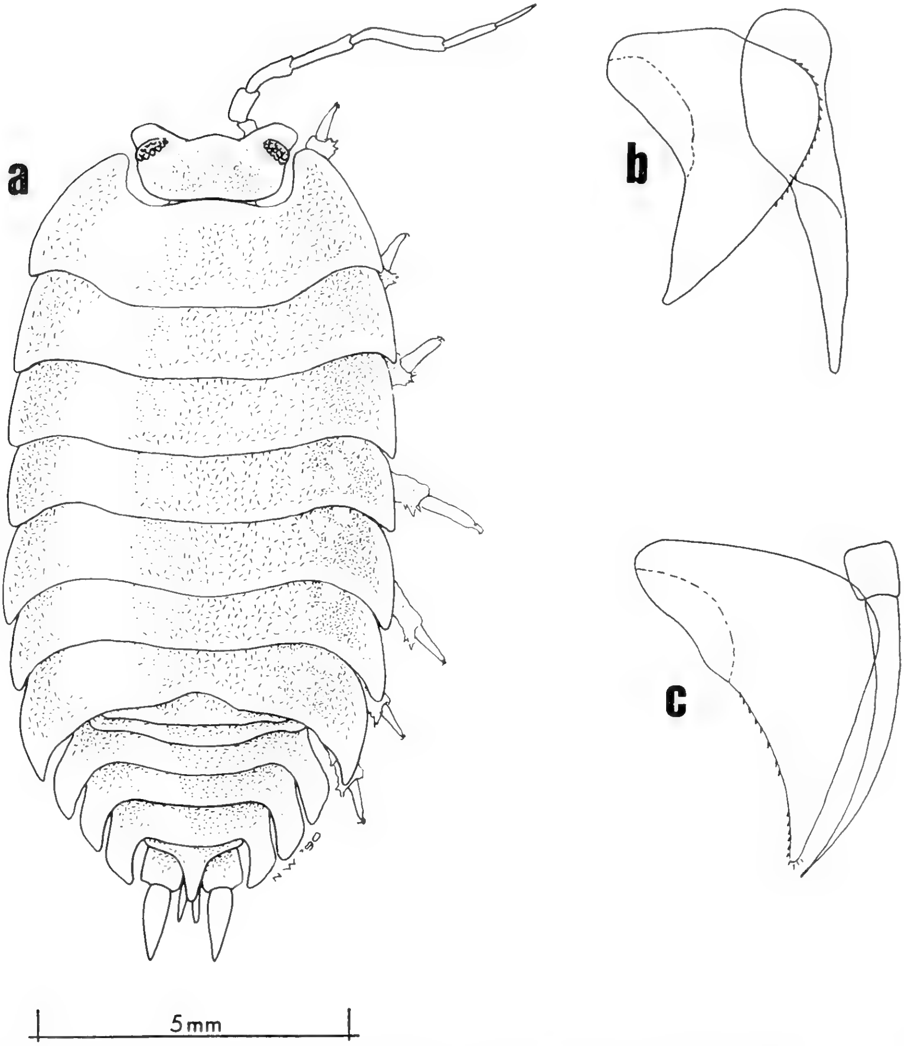

FIGURE 17. *Porcellio laevis*: a, dorsal view (original drawing by Nancy Walker from CASIZ 075336); b, right male pleopod 1; c, right male pleopod 2 (b, c adapted from Edney 1953, magnifications not provided).

abundance of most species appear to have remained about the same. Taking into account nomenclatural changes and mistaken identifications, and disregarding *Cubaris californica* (Budde-Lund, 1885) (which was so poorly described that it could not be recognized again if found and for which no types appear to exist), Table 2 lists the oniscid isopods collected in the present survey and those previously reported from the Bay Area.

In this survey, we found the non-littoral oniscid fauna of the San Francisco Bay Area to be dominated, in general, by four introduced species of European origin. *Armadillidium vulgare* was by far the most common non-littoral species encountered, found at 61 of the 176 sites surveyed (Table 2). Next in abundance were *Porcellio scaber* (found at 54 sites), *P. dilatatus* (34 sites), and *P. laevis* (22 sites) (Table 2). The native California non-littoral oniscids were much rarer. We found *Protrichoniscus heroldi* at only three sites, *Ligidium latum* at two sites, *L. gracile* at one site, and *Venezillo microphthalmus* was not encountered at all. The introduced species *Porcellionides floria* was also found to be rare in the Bay Area (found at only four sites). Our results for non-littoral isopods are similar to those of Miller (1936, 1938) who also found *A. vulgare*,

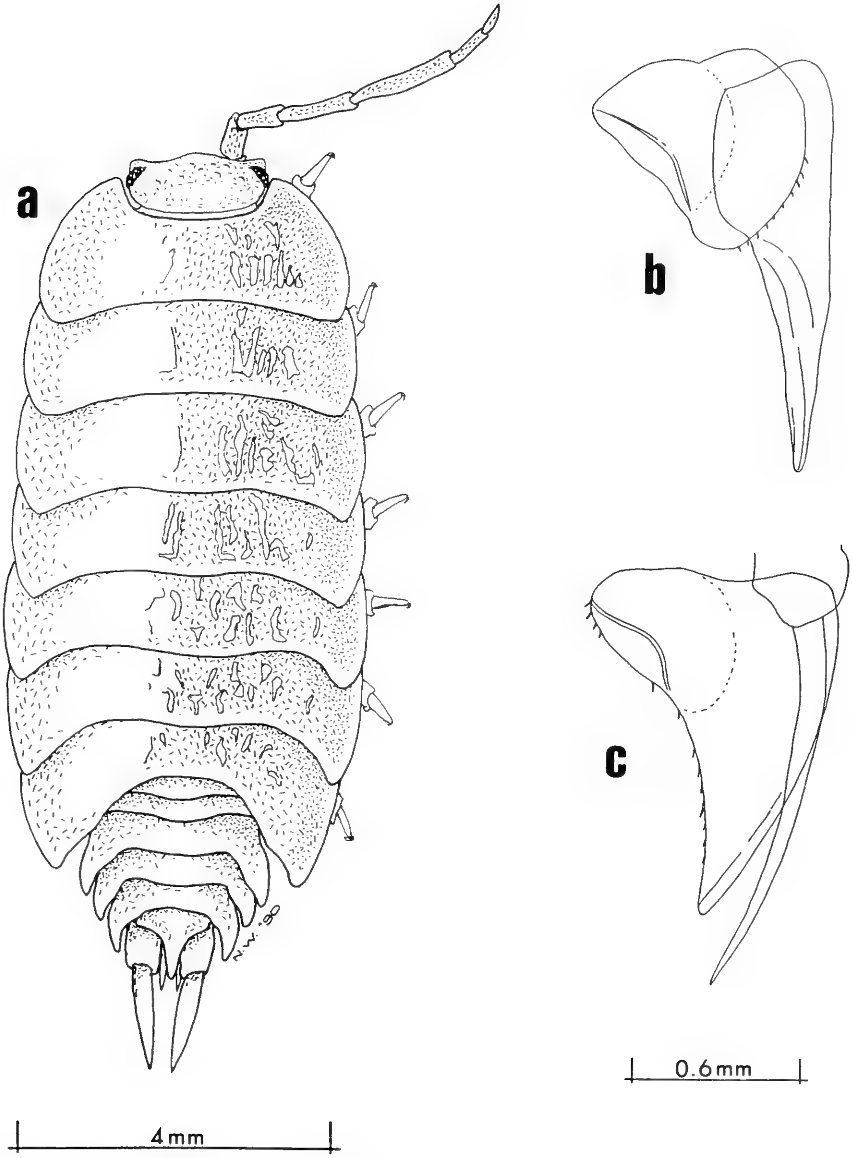

FIGURE 18. *Porcellionides floria*: a, dorsal view (original drawing by Nancy Walker from CASIZ 075424); b, right male pleopod 1; c, right male pleopod 2 (b, c adapted from Gruner 1966, as *Metoponorthus pruinosus*).

Porcellio scaber, Porcellio dilatatus, and *Porcellio laevis* to all be widely distributed in the Bay Area (whereas he did not collect *Protrichoniscus heroldi, Ligidium latum,* or *Venezillo microphthalmus*). Miller (1938) collected *Ligidium gracile* and *Porcellionides floria* from three sites each in the Bay Area.

Of the littoral oniscids, *Ligia occidentalis* was the most commonly encountered (found at 27 sites). However, this species was closely followed in abundance by a number of other littoral species including *Armadilloniscus coronacapitalis* (25 sites), *Mauritaniscus littorinus* (22 sites), *Littorophiloscia richardsonae* (20 sites), and *Armadilloniscus holmesi* (19 sites), while *Detonella papillicornis, Armadilloniscus lindahli, Alloniscus perconvexus,* and *Ligia pallasii* were found at 15 sites, 11 sites, three sites, and two sites respectively (Table 2). Miller (1938) also found *Ligia occidentalis* to be the most common littoral

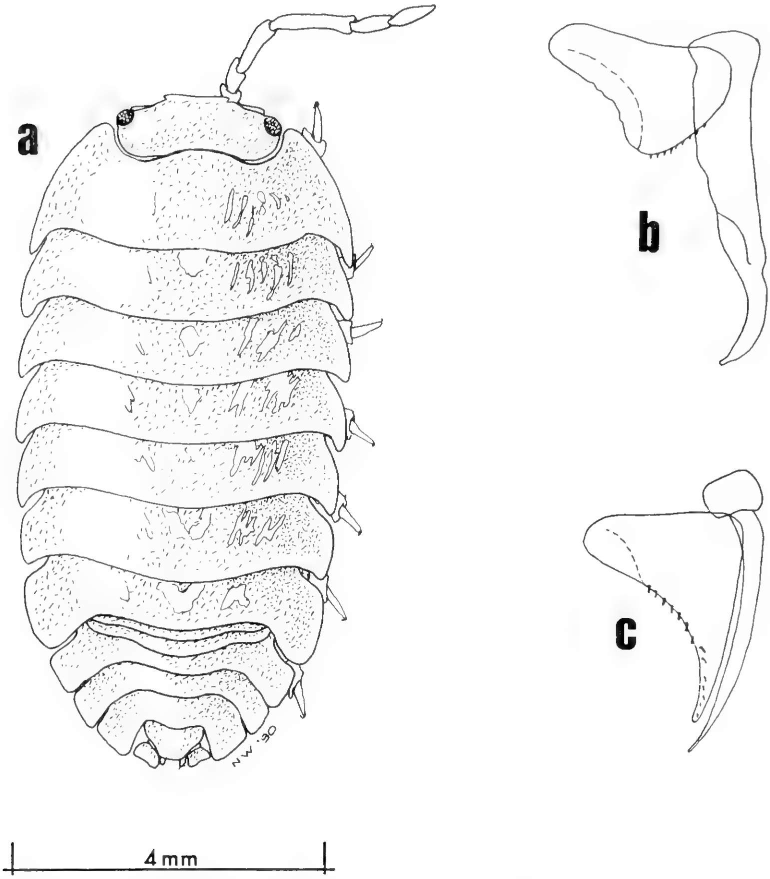

FIGURE 19. *Armadillidium vulgare*: a, dorsal view (original drawing by Nancy Walker from CASIZ 075526); b, right male pleopod 1; c, right male pleopod 2 (b, c adapted from Edney 1953, magnifications not provided).

species in the Bay Area, whereas the other littoral species that he encountered he collected from only a single locality each.

Conspicuously absent from Miller's list are *Armadilloniscus coronacapitalis* and *Detonella papillicornis. A. coronacapitalis* was first reported from Tomales Bay, Marin County, California by Menzies (1950). Since this description it has been found in Bolinas Lagoon, Marin County (Garthwaite 1988) and on the Channel Islands of southern California (Garthwaite et al. 1985). We found it to be widely distributed throughout San Francisco Bay, where it was the second most commonly encountered littoral species (found at 25 sites). Although *A. coronacapitalis* has apparently not been reported from elsewhere in the world, its late discovery and apparent rapid expansion into new areas are characteristic of introduced species. If Miller's (1938) list is an accurate indication of the oniscids of San Francisco Bay at that time, then the possibility exists that *A. coronacapitalis* is not native to California. However, in the absence of more direct evidence and because it is present on the California Channel Islands we consider it to be native.

Similarly, if previous reports on San Francisco Bay oniscids have been accurate, then *Detonella papillicornis* appears to have been recently established in the Bay Area as well. Although this species was present in the first collections of oniscids from Alaska (Richardson 1904), it has only recently been reported from sites in California. Taiti (personal communication) collected it from Tomales Bay, Marin County, and Garthwaite (1988) reported it from Bolinas Lagoon, Marin County. In this survey, we found *D. papillicornis*

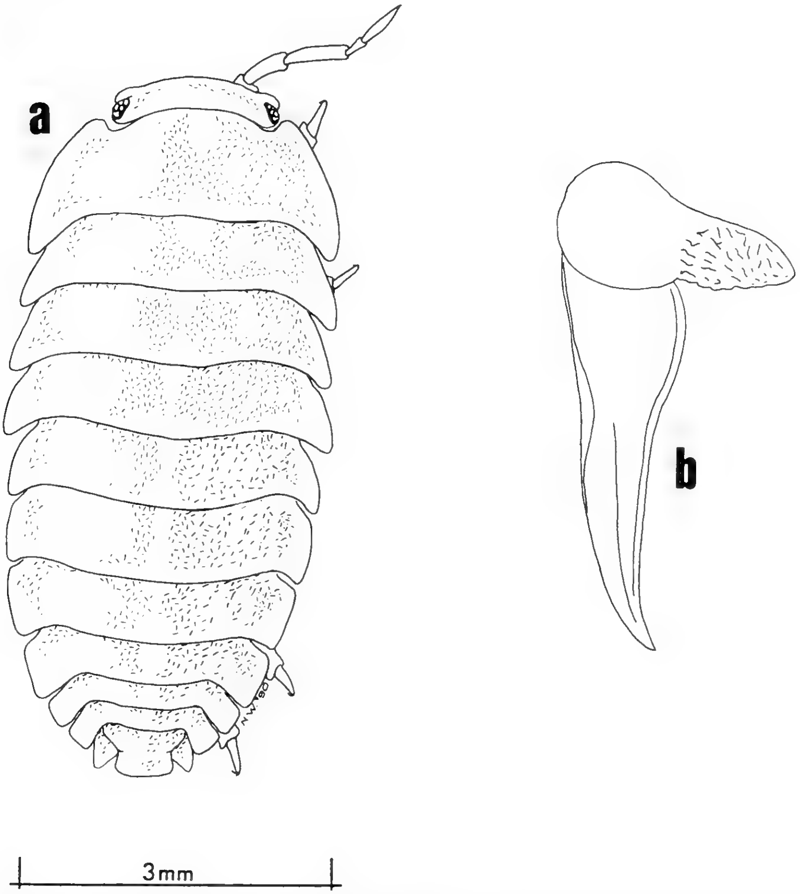

FIGURE 20. *Venezillo microphthalmus*: a, dorsal view (original drawing by Nancy Walker from CASIZ 075538); b, left male pleopod 1 (adapted from Arcangeli 1932, magnifications not provided).

to be widely distributed and moderately common in San Francisco Bay (found at 15 sites).

Although Miller (1936) was the first to report *Mauritaniscus littorinus* from California, he found it at only a single locality in San Francisco Bay (Bay Farm Island, Alameda County). If Miller's report is an accurate indication of oniscid distributions at the time then this species has undergone a remarkable range expansion in the intervening years. *Mauritaniscus littorinus* is now widely distributed throughout the Bay Area, where it was the third most frequently encountered littoral species (found at 22 sites), and is also commonly found along the California coast from San Francisco Bay to San Diego County (Schultz et al. 1982).

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TWO NEW DAMSELFISHES OF THE GENUS *CHROMIS* (PERCIFORMES: POMACENTRIDAE) FROM THE SOUTH PACIFIC

By

John E. Randall

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Abstract: Two new pomacentrid fishes of the genus *Chromis* are described from the South Pacific. *Chromis pamae,* collected at the Pitcairn group, southern Tuamotus, and the Austral Islands, is distinctive in having XV, 10-11 (usually 10) dorsal rays, II, 10-12 anal rays, 18-21 tubed lateral-line scales, a slender body (depth 2.7-3.1 in SL), and blue-green color (scales edged in brown dorsally), the median fins black (except posteriorly), and the pectorals with a large black spot at the base and axil; it is closely allied to *C. randalli* Greenfield and Hensley from Easter Island. *Chromis bami,* from the Pitcairn group, Austral Islands, and Tonga (based on a photograph), has XII, 13-14 (usually 13) dorsal rays, II, 12-14 anal rays, 16-18 pectoral rays, 14-16 tubed lateral-line scales, body depth 2.1-2.2 in SL, free margin of suborbital extending to below rear edge of pupil, and coloration dark brown, becoming brownish yellow on chest and abruptly white a short distance posterior to rear base of dorsal fin; its closest relative appears to be *C. alleni* Randall, Ida, and Moyer, from southern Japan and Taiwan.

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Introduction

Commencing in December 1970, the senior author, with support from the National Geographic Society, had the opportunity to collect fishes in French Polynesia, the Pitcairn group, and the Cook Islands from the 30 m schooner *Westward.* Two specimens of a slender damselfish of the genus *Chromis* that were unknown to him were speared outside the reef at Temoe Atoll in the Gambier group of the Tuamotu Archipelago, and detailed color notes were taken. Two days later a series of 26 specimens of the same species were obtained in a large rotenone station at uninhabited Oeno Atoll in the Pitcairn group. Among the 55 other species of fishes taken were five specimens of a dark brown, white-tailed *Chromis* believed at the time to be *C. margaritifer* Fowler. Additional specimens of both species of *Chromis* were collected later at Pitcairn Island and the Austral Islands. A color photograph was taken of the slender *Chromis,* but no photograph or color notes were made of the dark brown

FIGURE 1. *Chromis pamae* n. sp., holotype, 103.8 mm SL, Pitcairn Island, BPBM 16905.

Chromis with the white tail. Had the senior author been aware, as he is today, that there are at least 14 Indo-Pacific species of *Chromis* that are dark brown with white or whitish tails, the Pitcairn specimens might have received more attention.

Later, when curating fishes of the *Westward* collections at the Bishop Museum, Gerard R. Allen noted that the brown, white-tailed *Chromis* was not *C. margaritifer* but probably an undescribed species. In his *Damselfishes of the South Seas,* Allen (1975) discussed it as *Chromis* sp. "E," provided a diagnosis, and published a photograph of a preserved specimen. He treated the slender *Chromis* similarly as sp. "H," but utilized a color photograph provided by the senior author of a specimen from Pitcairn (not Mangareva as labeled by Allen).

In March 1983, the senior author observed a single individual of a dark brown *Chromis* with a pure white caudal peduncle and fin in 17 m at Vava'u, Tonga, which he did not recognize; it had a distinct yellow cast on the chest, whitish lips, and a large black spot covering the pectoral-fin base. An underwater photograph was taken (unfortunately slightly out of focus). The fish was speared but escaped and was not seen again. The sharp vertical demarcation from the brown body to the white tail on the photograph is slightly posterior to the rear base of the dorsal and anal fins. This is the same location for the color demarcation of the Pitcairn and Austral Islands specimens. The latter specimens also have the same black spot at the pectoral-fin base.

When the junior author visited Pitcairn in 1988, he collected more specimens of the brown, white-tailed *Chromis* and recorded its life color. He and resident Steven Christian (who at age 15 had been among the collectors of the two species of *Chromis* at Pitcairn in early 1971) obtained eight additional specimens of the species. His color notes match that of the photograph of the Tonga *Chromis.* There is little doubt that the Tonga fish is the same species as the one in Pitcairn. During that visit, the junior author was able to collect additional specimens of species of *Chromis* previously unknown from Pitcairn.

With the description of these two new species of *Chromis,* we now recognize 56 valid Indo-Pacific species of the genus, not including seven with which the senior author is familiar but that remain unpublished (two of these represented only by small juveniles and one only from a photograph taken from a submersible). In addition to Allen (1975), other publications that regionally review the Indo-Pacific species of *Chromis* are Randall and Swerdloff (1973); Allen and Randall (1980); Randall, Ida, and Moyer (1981); Allen (1985); Allen *in* Smith and Heemstra (1986); and Randall, Allen, and Steene (1990).

MATERIALS AND METHODS

Type specimens of new species of *Chromis* have been deposited in the Australian Museum, Sydney (AMS); British Museum (Natural History), London (BMNH); Bernice P. Bishop Museum, Honolulu (BPBM); California Academy of Sciences, San Francisco (CAS); National Science Museum of Tokyo (NSMT); and the U.S. National Museum of Natural History, Washington, D.C. (USNM).

Lengths given for type specimens are standard length (SL), which is the straight-line distance from the front of the upper lip or median upper teeth (whichever is most anterior) to the base of the caudal fin (distal end of the hypural plate). Head length is measured from the same anterior point to the end of the opercular membrane, and snout length from the same point to the fleshy edge of the orbit. Body depth is the maximum depth from the base of the dorsal fin. Body width is the greatest width just posterior to the gill opening. Orbit diameter is the greatest fleshy diameter, and interorbital width the least fleshy width. Caudal peduncle depth is the least depth, and caudal peduncle length is measured horizontally from the rear base of the anal fin to the caudal fin base. The length of the base of the spinous portion of the dorsal fin is measured from the front of the base of the first dorsal spine to just behind the base of the last dorsal spine. Caudal concavity is the horizontal distance from vertical at the tips of the shortest and longest caudal rays.

The last two dorsal and anal rays are counted as one when there is no space between their bases. Pectoral-ray counts include the slender, short, uppermost ray. Lateral-line scale counts are made only of those scales with external tubes; usually there is at least one pored scale posterior to the last tubed scale. Gill-raker counts include rudiments; the upper limb count is given first, and the raker at the angle is included in the count of the lower limb.

Proportions in the text are step-in measurements rounded to the nearest 0.05. Data in parentheses in the descriptions below refer to paratypes.

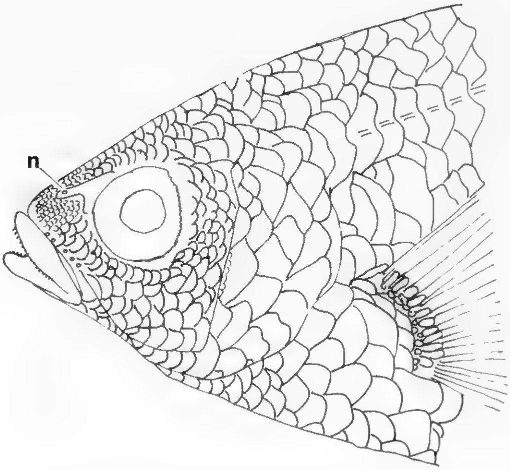

FIGURE 2. Head of *Chromis pamae* n. sp., paratype, 72.5 mm SL, Oeno Atoll, CAS 76003. Nasal opening indicated by "n."

Chromis pamae n. sp.

(Figs. 1, 2; Tables 1–3)

Chromis sp. "H" Allen, 1975:98, figure at bottom of p. 101.
Chromis sp. Randall, Smith, and Feinberg, 1990:24.
Chromis sp. 5 Allen, 1991:89.

HOLOTYPE.—BPBM 16905, male, 103.8 mm SL, Pitcairn Island (25°04′S, 130°06′W), off Christian's Point, reef in 7.5 m, spear, J. Randall, 3 Jan 1971.

PARATYPES.—BPBM 13501, 4 (78.0–87.8 mm), Tuamotu Archipelago, Gambier group, Temoe Atoll, outside reef on north side, 4.5–9 m, spear, J. Randall, 16 Dec 1970. AMS I.31222-001, 3 (67.5–75.7 mm), BMNH 1991.5.20.4-6, 3 (73.2–75.5 mm), BPBM 16457, 10 (41.0–86.9 mm), CAS 76003, 4 (43.7–72.5 mm), NSMT-P.34681, 3 (49.4–75.0 mm), and USNM 316516, 4 (48.0–76.5 mm), Pitcairn group, Oeno Atoll, north side, outside reef off small boat passage, reef and adjacent sand, 12–18.5 m, rotenone, J. Randall and crew of *Westward*. BPBM 16922, 5 (48.6–101.7 mm), Pitcairn Island, off The Rope, reef in 28–30.5 m, rotenone, J. Randall and party, 23 Dec 1970. BPBM 16887, 9 (28.3–55.8 mm), Pitcairn Island, reef on north side of Gannet Ridge, 40–44.5 m, rotenone, J. Randall and party, 6 Jan 1971. BPBM 12958, 93.8 mm, Rapa, off Hiri Bay, reef in 18 m, spear, J. Randall, 10 Feb 1971. BPBM 13681, 60.2 mm, Austral Islands, Tubuai, ca. 2 km SW of anchorage off pass, reef in 15 m, spear, J. Randall, 26 Feb 1971.

Table 1. Fin-ray counts of holotypes and paratypes of *Chromis pamae* and *C. bami.*

	Dorsal soft rays					Anal soft rays					Pectoral rays					
	10	11	12	13	14	10	11	12	13	14	16	17	18	19	20	21
C. pamae	23	4				1	23	3							2	25
C. bami				26	1			2	21	4	2	22	3			

Diagnosis.—Dorsal rays XV,10 (10–11); anal rays II,10–12; pectoral rays 20–21 (usually 20); procurrent upper and lower caudal spines 2; tubed lateral-line scales 18–21; scales on head extremely small; body elongate for genus, depth 2.7–3.1 in SL; caudal fin deeply forked, caudal concavity, 3.8–4.7 in SL; body metallic blue to blue-green, scale edges brown dorsally; median fins black except clear posteriorly; a large black spot at base and axil of pectoral fins.

Description.—Dorsal rays XV,10 (10–11), first soft ray simple, remaining rays branched; anal rays II,11 (10–12), all soft rays branched; pectoral rays 21 (20–21), upper and lower two simple; pelvic rays I,5, all soft rays branched; principal caudal rays 15, median 13 branched; upper and lower procurrent caudal rays 4, anterior 2 spiniform; tubed lateral-line scales 19 (18–21); posterior midlateral pored or weakly tubed scales in continuous series 7 (7–12); longitudinal scale series from upper end of gill opening to base of caudal fin 29 (29–31); scales above lateral line to origin of dorsal fin 3; scales below lateral line to origin of anal fin 8; circumpeduncular scales 16; gill rakers 9 + 26 (9–10 + 24–27; total gill rakers 33–37); branchiostegal rays 6; supraneural (predorsal) bones 3; vertebrae 11 + 15 (5 specimens).

Body elongate, depth 2.75 (2.7–3.1) in SL, and compressed, width 2.15 (2.0–2.2) in depth; head length 3.45 (3.1–3.5) in SL; dorsal profile of head only slightly convex; snout length 3.65 (3.7–4.1) in head; orbit diameter 3.7 (2.8–3.65) in head; venteroposterior edge of orbit rimmed with small fleshy papillae; interorbital space convex, the least width 3.2 (2.85–3.3) in head; caudal peduncle longer than deep, the least depth 2.35 (2.35–2.6) in head.

Mouth terminal to slightly inferior, strongly oblique, forming an angle of about 45° to longitudinal axis of body; mouth small, upper jaw length 3.1 (2.9–3.2) in head, maxilla extending slightly posterior to a vertical at front edge of orbit; an outer row of conical teeth in jaws, 30 on side of upper jaw and 25 on side of lower of holotype, progressively larger anteriorly, stoutest at front of lower jaw; an inner band of small villiform teeth in jaws in 3–4 irregular rows anteriorly in upper jaw and 2–3 in lower, narrowing to a single row on sides of jaws; tongue triangular with rounded apex; longest gill raker on lower arch near angle, as long as longest gill filaments, 1.95 in orbit diameter of holotype; nostril prominent, with a low fleshy rim, anterior to upper edge of pupil nearly half the distance to front of snout at base of upper lip; pores of lateralis system on head very small and difficult to detect.

A small, flat, acute spine on opercle in line with upper end of preopercular margin and lower edge of pupil; margin of preopercle smooth to slightly irregular, the corner rounded and not projecting; anterior end of preopercular margin slightly anterior to a vertical at front of pupil; lower edge of suborbital scaled.

Scales finely ctenoid; anterior lateral line ending below onset of soft portion of dorsal fin; scales on head extremely small, progressively smaller anteriorly; head fully scaled except for lips, a narrow zone at front of snout at base of upper lip, front of chin, edge of orbit, and a narrow diagonal zone from orbit to anterior nostril; a low scaly sheath at base of dorsal and anal fins with a narrow pointed band of small scales extending out on each interradial membrane, one edge of this band adjacent to the posterior spine; very small scales extending nearly to posterior border of caudal fin; small scales basally on paired fins; a narrow, pointed, scaly process about three-fourths length of pelvic spine midventrally between bases of pelvic fins; a slender axillary scale

Table 2. Counts of tubed lateral-line scales of type specimens of *Chromis pamae* and *C. bami.*

	14	15	16	17	18	19	20	21
C. pamae					1	12	13	1
C. bami	2	22	3					

TABLE 3. Gill-raker counts of type specimens of *Chromis pamae* and *C. bami.*

	Upper rakers			Lower rakers								Total rakers									
	8	9	10	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
C. pamae		21	6					1	10	11	5						1	7	14	3	2
C. bami	8	19		2	9	9	6	1				2	4	6	9	6					

above each pelvic fin about half length of pelvic spine.

Origin of dorsal fin above third to fourth lateral-line scales; its interspinous membranes only slightly incised except for first two; dorsal spines slender; the first 3.3 (3.15–3.65) in head, the second 2.3 (2.15–2.55); fifth usually longest, 1.75 (1.8–2.1) in head; last dorsal spine about half length of longest spine; third dorsal soft ray usually longest, 1.55 (1.6–1.75) in head; origin of anal fin below base of twelfth dorsal spine; anal spines notably stouter than dorsal; first anal spine short, 5.0 (4.4–5.1) in head, second 1.75 (1.7–1.85); first anal soft ray longest, 1.65 (1.6–1.85) in head; caudal fin long and deeply forked with attenuate tips, fin length 2.95 (2.55–3.0) in head, caudal concavity 4.55 (4.0–4.7) in head; third or fourth pectoral ray longest, 3.6 (3.6–3.8) in SL; origin of pelvic fins below lower pectoral-fin base, first soft ray longest, just reaching or extending slightly beyond anus, 3.95 (3.5–4.45) in SL.

Color of holotype in alcohol brown, paler ventrally and on head; lips notably pale; fins pale except scaled base of dorsal and anal fins and lobes of caudal fin; a dark brown spot at base of pectoral fins; axil of pectoral fins dark brown. The holotype has faded more than the paratypes; dorsal and anal fins of paratypes are dark brown and paler posteriorly.

Color of holotype when fresh (from 120 mm color transparency) light metallic blue (dusky blue dorsally), with scale edges brown (brown scale edges broader and darker dorsally), shading to silvery-lavender ventrally on body and head; dorsal and anal fins black except posteriorly where membranes are bluish white, rays brown to dark brown; a narrow bluish silver band at base of anal fin; caudal fin black, shading to bluish white on posterior margin, rays in this zone partly brown; pectoral fins with clear membranes, rays narrowly edged in brown; a large black spot at base and axil of pectoral fin; pelvic fins yellowish; iris yellow, inwardly blackish yellow.

The following color notes were made from four specimens, 78–87.8 mm SL, from Temoe Atoll in the Tuamotus immediately after capture: body blue-green, scale edges brown; centers of scales dorsally on caudal peduncle just behind rear base of dorsal fin light greenish yellow (seen as a faint yellow spot in life); dorsal and anal fins black except second anal spine, which is bluish, and membranes of outer two-thirds of soft portion of dorsal fin and outer part of membranes of last four anal rays, which are clear; pectoral fins slightly dusky with a large black spot at base and axil; pelvic fins light yellow.

ETYMOLOGY.—Named *pamae* in honor of Pamela J. McCosker, a slender specimen of comparable beauty.

REMARKS.—This species is known from two islands of the Pitcairn group, one atoll in the Gambier group of the Tuamotu Archipelago, and Tubuai in the Austral Islands; these islands lie between latitudes 23° and 25°S. The fish is common in the Pitcairn Islands; it has been collected from depths of 4.5–44.5 m.

Its closest relative, known only from Easter Island, is *Chromis randalli* Greenfield and Hensley, which also has a fusiform body, a dorsal ray count of XV,10 (these are the only two *Chromis* with XV dorsal spines), and very small scales on the head. Also unique within the genus is the presence in both species of fleshy papillae at the posterior and ventral edge of the orbit. These orbital papillae are also seen on the damselfish *Lepidozygous tapeinosoma* and certain species of the serranid genus *Pseudanthias.* All of these fishes are slender-bodied; they feed on zooplankton well above the substratum but must swim swiftly to cover with the approach of predaceous fishes. We believe the papillae may function to ensure a smooth flow of water over the eye when swimming rapidly.

Chromis pamae differs from *C. randalli* in its more slender form (average body depth 2.83 in SL, compared to 2.58 for *C. randalli*); modally 11 instead of 10 anal soft rays; 18–21 instead of 21–22 tubed lateral-line scales; smaller size (the

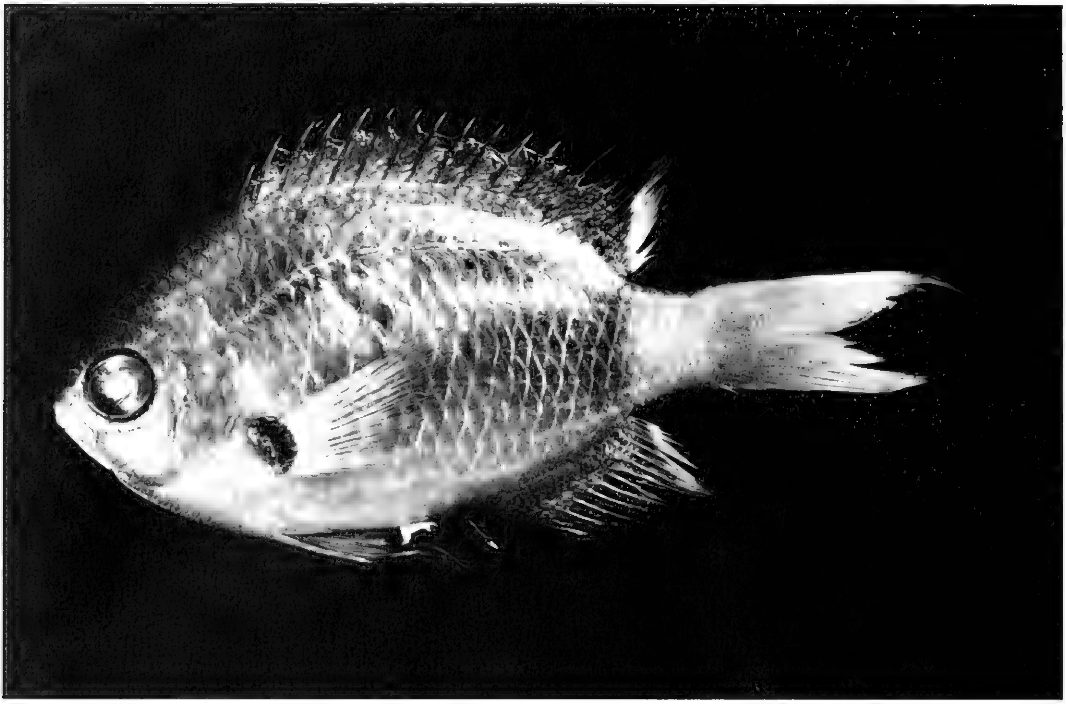

FIGURE 3. *Chromis bami* n. sp., holotype, 49.2 mm SL, Pitcairn Island, CAS 75992.

holotype, largest of 47 specimens, was 103.8 mm SL, as compared to 18 specimens of *C. randalli* reported by Greenfield and Hensley (1970), five of which were 124–128 mm SL); and in its color. *Chromis randalli* lacks the large black spot at the pectoral base (although it has a small diffuse dark spot at the upper edge of the base).

Chromis bami n. sp.

(Figs. 3–4, Tables 1–3)

Chromis sp. "E" Allen, 1975:95, lower figure of p. 100.
Chromis sp. 2 Allen, 1991:88.

HOLOTYPE.—CAS 75992, 49.2 mm SL, male, Pitcairn Island, Bounty Bay, about 1 km north of Duddie's Cocknuts, reef with live coral, 30.5–36.5 m, quinaldine, J. McCosker and S. Christian, 13 May 1988.

PARATYPES.—CAS 63215, 7 (23.2–46.0 mm), collected with the holotype. BPBM 16524, 5 (37.6–55.0 mm), Pitcairn group, Oeno Atoll, north side, outside reef off small boat passage, reef and adjacent sand, 12–18.5 m, rotenone, J. Randall and crew of *Westward*, 18 Dec 1970. AMS I.31223-001, 2 (38.0–47.5 mm), BMNH 1991.5.20.2-3, 2 (33.2–52.0 mm), NSMT-P.34680, 3 (34.7–58.5 mm), and USNM 316515, 3 (30.2–58.3 mm), Pitcairn Island, off Bounty Bay, reef at edge of sand with live coral, 30.5–40 m, rotenone, J. Randall, D. Cannoy and D. Bryant, 26 Dec 1970. BPBM 16687, 8 (28.3–55.8 mm), Pitcairn Island, reef on north side off Gannet Ridge, 40–44.5 m, rotenone, J. Randall and party, 6 Jan 1971. BPBM 12782, 2 (34.3–55.5 mm), Austral Islands, Raivavae, outside barrier reef south of Motu Haa, reef in 33 m, spear and quinaldine, J. Randall, 25 Feb 1971. BPBM 13683, 47.3 mm, Austral Islands, Tubuai, outside barrier reef 1 mile SW of anchorage off pass, reef in 15 m, powerhead blast, J. Randall and R. McNair, 26 Feb 1971. BPBM 13695, 2 (20.7–56.8 mm), Austral Islands, Rurutu, northeast side off Moerai, 27.5 m, quinaldine, J. Randall and D. Cannoy, 27 Feb 1971.

DIAGNOSIS.—Dorsal rays XII,13–14 (usually 13); anal rays II,12–14; pectoral rays 16–18; upper and lower procurrent spiniform caudal rays 2; tubed lateral-line scales 14–16; gill rakers 8–9 + 20–24; body depth 2.1–2.2 in SL; orbit diameter 2.25–2.7 in head; free margin of subor-

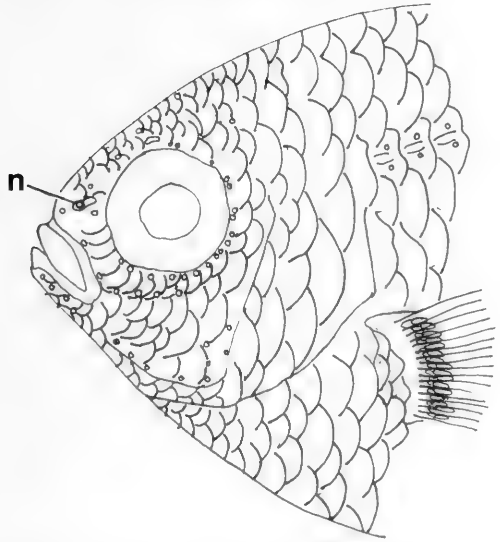

FIGURE 4. Head of *Chromis bami* n. sp., holotype, 49.2 mm SL, Pitcairn Island, CAS 75992. Nasal opening indicated by "n."

bital extending posterior to or nearly to a vertical at rear edge of pupil; caudal fin deeply forked, second and thirteenth branched ray filamentous, caudal concavity 1.95–4.45 in SL; body coloration dark brown with a yellow cast over chest, abruptly white posterior to a demarcation on caudal peduncle a short distance behind rear base of dorsal and anal fins; lips whitish; a large black spot at pectoral-fin base; triangular distal end of each dorsal interspinous membrane black.

DESCRIPTION.—Dorsal rays XII,13 (13–14); anal rays II,13 (12–14), all soft rays of dorsal and anal fins branched in adults (first rays of these fins may be simple in juveniles); pectoral rays 15 (14–16), upper two and lower two rays simple; pelvic rays I,5, all soft rays branched; principal caudal rays 15, median 13 branched, second and thirteenth produced to long filaments; upper and lower procurrent caudal rays 4, anterior two spiniform; tubed lateral-line scales 15 (14–16); pored scales in continuous series midlaterally on caudal peduncle 8 (7–11); longitudinal scale series from upper end of gill opening to caudal-fin base 28 (27–28); scales above lateral line to origin of dorsal fin 3; scales below lateral line to origin of anal fin 8; circumpeduncular scales 16; gill rakers 9 + 23 (8–9 + 20–24); branchiostegal rays 6; supraneural (predorsal) bones 3; vertebrae 11 + 15 (4 specimens).

Body moderately deep, depth 2.05 (2.1–2.2) in SL, and compressed, width 2.7 (2.6–2.9) in depth; head length 3.3 (3.05–3.4) in SL; dorsal profile of head slightly convex; snout length 3.5 (3.5–3.9) in head; orbit diameter 2.6 (2.25–2.7) in head; interorbital space convex, the least width 2.7 (2.6–2.9) in head; caudal peduncle depth about equal to its length, the least depth 2.0 (1.95–2.35).

Mouth terminal and strongly oblique, forming an angle of about 45° to longitudinal axis of body; mouth small, upper jaw length 3.0 (2.9–3.1) in head, maxilla just reaching or extending slightly posterior to a vertical at front edge of orbit; an outer row of conical teeth in jaws, largest anteriorly, particularly three pairs of upper and two of lower teeth; 25 upper and 23 lower teeth on each side of jaw of holotype; a narrow band of villiform teeth lingual to outer row, in two to three irregular rows anteriorly in jaws, narrowing to a single row on side of jaws; tongue triangular, the tip rounded; longest gill raker on first gill arch (on lower limb near angle) as long as longest gill filaments, about one-third orbit diameter of holotype; nostril large with a fleshy rim, located at level of upper edge of pupil, more than one-third distance to front of snout at base of upper lip; pores of lateralis system on head prominent (see Fig. 4).

Opercle ending posteriorly in a small flat spine varying from slightly acute to slightly obtuse and covered by a scale; edge of preopercle smooth to slightly irregular, the corner broadly rounded (some specimens with a slight concavity in margin above corner); upper end of preopercular margin covered by scales; ventroanterior end of margin nearly reaching a vertical at front edge of orbit; free edge of suborbital nearly or just reaching a vertical at rear edge of pupil.

Scales finely ctenoid; anterior lateral line ending beneath front of soft portion of dorsal fin; scales on head not very small; head fully scaled except for lips, a narrow zone at front of snout at base of upper lip, and a narrow diagonal band containing nostrils that passes from orbit to front of snout; a low scaly sheath at base of dorsal and anal fins; a narrow pointed band of scales on each interspinous membrane of dorsal and anal fins, reaching about three-fourths distance to spine tips; small scales on soft portions of dorsal and anal fins extending a maximum of about one-third distance to fin margin; small scales on caudal fin extending more than three-fourths distance to posterior margin (ignoring length of filamentous rays); small scales present only basally on pectoral fins; pelvic fins with a slender scaly process midventrally between bases that extends about half distance to pelvic spine tips; a slender pointed axillary scale above and adjacent to each pelvic fin, about two-thirds length of pelvic spine.

Origin of dorsal fin above third lateral-line scale; interspinous membranes of dorsal fin moderately incised; dorsal spines slender; first dorsal spine 3.2 (3.2–3.75) in head; second dorsal spine 2.2 (2.0–2.5) in head; fifth to twelfth dorsal spines subequal, the longest 1.8 (1.75–2.0) in head; sixth dorsal soft ray longest, 1.1 (1.05–1.25) in head; origin of anal fin below base of tenth dorsal spine; first anal spine slender, 3.05 (2.9–3.4) in head; second anal spine twice as stout as dorsal spines, its length 1.5 (1.55–1.7) in head; seventh or eighth anal soft ray longest, 1.15 (1.15–1.35) in head; caudal fin deeply forked, the second and thirteenth principal rays filamentous (being branched, each has two long filaments), fin length (including filaments when intact) 1.8 (1.35–2.35) in SL, caudal concavity 3.5 (1.95–4.45) in SL; third or fourth pectoral ray longest, 3.1 (2.8–3.2) in SL; origin of pelvic fins below lower pectoral-fin base; first pelvic soft ray filamentous, reaching beyond origin of anal fin, its length 2.75 (2.4–3.0) in SL.

Color of holotype in alcohol dark brown to a vertical demarcation about a pupil distance posterior to rear base of dorsal fin; caudal peduncle and fin posterior to demarcation whitish; spinous portion of dorsal fin dark brown, the outer triangular part of each interspinous membrane, including cirrus at tip, black; soft portion of dorsal fin dark brown anteriorly to margin at fourth ray, the rest of fin whitish distally, the brown progressively more restricted to base until last ray where only the short basal scaled part brown; anal fin dark brown to eighth soft ray tip, then abruptly whitish like dorsal fin, the brown progressively less to end of fin where only basal part of last ray pigmented; pectoral fins pale except brown at edges of rays and a large oblong black spot at base and axil of fin; pelvic fins dark brown.

Color of head and body of holotype in life dark brown, shading to brownish yellow on chest and abruptly white on anterior caudal peduncle; caudal fin white; dorsal and anal fins dark brown like body, except black at edge of membrane between spine tips and transparent posteriorly in a vertical demarcation; pectoral fins transparent with a large black spot at base and in axil; pelvic fins dark brown; lips pale.

ETYMOLOGY.—Named *bami* in honor of Foster Bam, friend, photographer, and diving companion.

REMARKS.—*Chromis bami* has been collected or observed on reefs in the depth range of 12–44.5 m. We have specimens of this small *Chromis* from only two islands of the Pitcairn group and three of the Austral Islands. It was observed at Ducie Island in the Pitcairn group, the easternmost atoll in Oceania. Also, as indicated above, an underwater color photograph taken at Vava'u, Tonga, revealed its presence at that archipelago. Vava'u lies 1,350 km to the west of Rurutu in the Austral Islands; therefore this damselfish could be expected at the southern Cook Islands, which lie intermediate to Vava'u and the Australs. It might also extend to the west of Tonga in the same southern subtropical latitude. Several insular shore fishes are broadly distributed across the South Pacific in the southern subtropical zone but are not reported from tropical waters. Examples are the muraenid *Enchelycore ramosus* (Griffin), the serranid *Trachypoma macracanthus* Günther, the labrid *Anampses femininus* Randall, and the soleid *Aseraggodes bahamondei* Randall and Meléndez, all of which range from Easter Island to at least Lord Howe Island (the last-mentioned species is known thus far only from these two islands). Other species of *Chromis* collected in the Pitcairn group include *C. acares* Randall, *C. agilis* Smith, *C. xanthura* (Bleeker), and *C. vanderbilti* (Fowler), all of which occur in tropical as well as subtropical seas.

Chromis bami seems most closely related to *C. alleni* Randall, Ida, and Moyer (1981) from southern Japan and Taiwan, sharing with it a similar color pattern with the abrupt transition from dark anterior body to white tail at exactly the same place on the anterior caudal peduncle, similar body proportions and meristic data, the free margin of the suborbital extending the same distance posteriorly, and the same caudal fin morphology. *Chromis alleni* differs in its overall dark head and body coloration being a deep yellow-brown or orange-brown; also it lacks the distal black pigmentation on the interspinous membranes of the dorsal fin. There are slight meristic differences: the dorsal rays of *C. alleni* are XII-XIII, 12–13, and *C. bami* is XII,12–14; tubed lateral-line scales of *C. alleni* are 15–17, and *C. bami* are 16–18; gill rakers of *C. alleni* are 7–9 + 18–22, and *C. bami* has 9–10 + 20–24. In addition, *C. alleni* has a smaller eye (10.6–12% SL, compared to 11–14.5% SL for *C. bami*), and the membranes of the spinous portion of the dorsal fin of *C. alleni* are more deeply incised. It is likely that *C. alleni* and *C. bami,* now restricted to subtropical northern and southern localities, respectively, are descendants of an ancestral population that was continuously distributed when seas were cooler.

RÉSUMÉ

Deux Pomacentridés nouvelles du genre *Chromis* sont édités de l'Océanie. *Chromis pamae* n. sp., récoltés au groupe des Pitcairn, Tuamotus sud, et les Isles Australes, est la plus voisine de *C. randalli* de l'Isle de Pâques. *Chromis bami* n. sp., du groupe des Pitcairn, les Isles Australes, et Tonga (elle a été photographié, mais non récoltée), est la plus voisine de *C. alleni* du sud de Japon et de Taiwan. Les deux espèces nouvelles sont distingués par leur couleurs et caractères méristiques et morphométriques.

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